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DISSERTATION

TROPHIC STRUCTURE AND FUNCTION OF STREAM FOOD WEBS ALONG A GRADIENT OF METAL CONTAMINATION

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2001

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DAREN M. CARLISLE ENTITLED TROPHIC STRUCTURE AND FUNCTION OF STREAM FOOD WEBS ALONG A GRADIENT OF METAL CONTAMINATION BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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ABSTRACT OF DISSERTATION

TROPHIC STRUCTURE AND FUNCTION OF STREAM FOOD WEBS ALONG A GRADIENT OF METAL CONTAMINATION

Bioenergetics and food webs have long been central themes in ecology and have greatly expanded our understanding of nature. Within a food web framework, estimates of consumption and energy flow through populations facilitate linking population-level contaminant effects to ecosystem-level effects. For this purpose, we used estimates of population production, diet composition, and bioenergetic principles of aquatic insects to quantify food web linkages in five Rocky Mountain headwater streams that varied in metal contamination. Our overall goals were to 1) link the effects of contaminants on individuals and populations to effects on species assemblages, functional guilds, and ecosystem process; 2) determine the influence of food web and assemblage structure on ecosystem functions; and 3) determine the role of species in ecosystem processes. Quantitative sampling of benthic macroinvertebrates, chemistry, and habitat occurred monthly from May-November. We explicitly quantified uncertainty in our analyses by bootstrapping samples of population density, biomass, diet composition, and energetic efficiencies. Relative to reference streams, population production of metal-sensitive mayflies was lower in light and moderately polluted streams, and absent in the stream with highest Zn levels. Although periphyton food quality and quantity were lower in polluted streams than in reference streams, individual growth of herbivorous mayflies was similar among streams. We therefore concluded that among-stream variation in population production resulted from differences in population abundances caused by metal sensitivity. Low production and consumption of heptageniids had a large impact on ecosystem functions because these taxa dominate energetic fluxes from primary producers to the remaining food web. Slight reductions in heptageniid production were associated with lower total energy flow in a stream with metal levels considered safe for aquatic life. A similar pattern was observed for leaf-shredding insects and leaf litter decomposition. Collectively, our results indicate that some (e.g., energetic fluxes from from herbivory and leaf litter decomposition) ecosystem processes in Rocky Mountain streams are controlled by a small number of species, many of which are sensitive to anthropogenic stressors. Consequently, even relatively small reductions in population abundances and species composition may have far-reaching effects on ecosystem functions.

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CHAPTER 1:

BIOENERGETIC FOOD WEBS AS A MEANS OF LINKING TOXICOLOGICAL EFFECTS ACROSS SCALES OF ECOLOGICAL ORGANIZATION

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ABSTRACT

Although significant progress has been made in our ability to predict population-level consequences of toxic effects on individuals, extending this predictive ability to communities, functional guilds, and ecosystems will require more integration of ecological theory into environmental science. Bioenergetics and food webs have long been central themes in ecology and greatly expanded our understanding of nature. Although numerous energetic-based toxicological endpoints have been developed, few have extended this framework beyond the individual level. Most energetic endpoints include individual growth, and only occasionally is this integrated with population dynamics. However, population-level energetic analyses (e.g., secondary production) integrate individual and population processes, and provide two key parameters: consumption and energy flow. Within a food web framework, estimates of consumption and energy flow through populations facilitate linking population-level contaminant effects to ecosystem-level effects. Several examples are given to illustrate the utility of this approach.

INTRODUCTION

The ultimate goal of environmental stewardship is the restoration and maintenance of ecosystems (Levin et al. 1984, Cairns and Bidwell 1996). However, our ability to accomplish this goal has been limited largely because our understanding of ecosystems is based on simplified models of nature's complexity (Levin et al. 1984, Pimm 1991). For example, ecologists often study populations or assemblages at spatio-temporal scales smaller than those at which many ecological processes occur (Pimm 1991, Levin 1992). Similarly, environmental toxicologists have traditionally studied the effects of contaminants on individual organisms or species assemblages at temporal scales of a few days (Cairns and Pratt 1989). We should not be surprised, therefore, when predictions from oversimplified models do not withstand the test of reality (Cairns 1983, 1986). The limitations of bioassays, microcosms, mesocosms and short-term experiments are well documented (Kimball and Levin 1985, Yodzis 1988, Sarnelle 1997). Schindler (1987, 1998) demonstrated that bioassays and mesocosm experiments did not accurately mimic whole lakes because the limited scales of these experimental systems did not include several physical and biological phenomena that occur at large spatio-temporal scales. Similarly, Fairchild et al. (1992) observed effects on planktonic communities using mesocosms that would not have been predicted using single species bioassays.

Because most research is conducted at small scales (Schindler 1998), it is necessary to extrapolate experimental results to larger, more realistic scales (e.g., the ecosystem). A major reason we face this challenge is that experimental control and causation are strong at small spatio-temporal scales and sub-organismal levels, but ecological relevance is low (Clements 1997). Conversely, although whole-ecosystem experiments have high ecological relevance (Schindler 1998), experimental control and replication are low. Because there is little evidence that more ecosystem-level experiments are possible in the future, research approaches that integrate experiments and observation at multiple scales are required (Culp et al. this volume). The failure to integrate has left us with numerous toxicological endpoints (e.g. biomarkers, tissue concentrations, community indices) that have unknown ecological relevance. Ecologists have begun to recognize the importance of linking the sub-disciplines of population biology, community ecology, and ecosystem science (Jones and Lawton 1995). Ecotoxicologists have also recently called attention to this issue (Clements and Kiffney 1994, Sibley et al. this volume). Despite this increase in attention however, few integrative studies have emerged, perhaps due to the lack of an accepted methodology to link biological processes across scales (Jones and Lawton 1995).

The accompanying papers in this volume represent state-of-the-art approaches to linking contaminant effects from the molecular to the population level. The objective of this paper is to suggest an approach by which we can extend population-level effects to communities and ecosystems. The method I propose is based on bioenergetics and food webs. Although these principles are not new, seemingly few environmental toxicologists recognize that when used together, they provide a framework for linking populations and ecosystems. This paper is not intended to be a thorough review of bioenergetics or food web literature. Partial reviews are provided in Pimm (1982), Pimm et al. (1991), Hall and

Raffaelli (1993), and Polis and Winemiller (1996). Instead, I have selected a few studies that were both notable in the ecological discipline and have great potential in ecotoxicology. Where possible, data from my own work and selected research of others will be used to illustrate ideas and support my assertions.

FOOD WEBS: A UNIFYING CONCEPT

The study of food webs has been a dominant theme in ecology (Fretwell 1987). Efforts to understand the structure and dynamics of ecosystems have focused on the interrelationships among populations (MacArthur 1955) and trophic levels (Hairston et al. 1960). Food webs have provided the conceptual framework for these theoretical efforts, and have also proved invaluable in ecological applications (e.g., Carpenter et al. 1985). Recent research also shows the ability of food web analyses to link processes across scales of time, space, and ecological organization (Cuffney et al. 1990, Parmelee 1995, Abrams et al. 1996, Menge et al. 1996, Wheeler 1996, Tavares-Cromar and Williams 1996, Benke and Wallace 1997).

Food webs are conceptualized in three ways; these include topological or descriptive, interaction, and energetics-based webs (Figure 1.1). Descriptive or topological webs depict trophic linkages among populations as present or absent (Figure 1.1a). Linkages are generally identified by observations, gut analyses, or the literature. Topological webs for many systems have been published, and are the basis for a large literature known as "food web theory" (Winemiller and Polis 1996). Interaction webs, in contrast, are much less common and require experimental manipulation of constituent populations. This approach yields an interaction web that identifies dynamic linkages among populations based on both trophic and non-trophic relationships (Figure 1.1b). Interaction webs have been the means of identifying keystone species in many ecosystems (Paine 1992, Power et al. 1996). Energetic-based approaches quantify the relative importance of food web linkages in terms of energy flow. For a given consumer, the amount of each food (e.g., in biomass or calories) ingested is estimated over a specific time period (Figure 1.1c). Energetic-based approaches to studying trophic structure have a long history. The pioneering work of Lindeman (1942), Odum (1957), and Hutchinson 1959) emphasized relationships between energy flow and the trophic structure of ecosystems.

ECOLOGICAL ENERGETICS

Key to linking processes across scales is an understanding of how variation at one level influences variation at adjacent levels, and what "information" is transferred among levels (Levin 1992). Because the information passing through ecosystems includes trophic, structural, and biogeochemical (Grimm 1995), measuring among-scale variation in these processes could be useful for linking contaminant effects across scales. For aquatic ecosystems, energetic analyses have a large foundation in the literature (Lindeman 1942, Strayer and Likens 1986, Benke et al. 1988, Eggleton, et al. 1996) and may therefore be a fruitful approach.

Energetics-based approaches in ecology have at least two major strengths. First, energy flow must obey thermodynamic laws, and is therefore a tractable quantity in ecosystems. Second, energy is a common unit of measurement that is relevant at multiple scales of time, space, and ecological organization. For example, energetic budgets can be logically constructed for individuals (Kitchell 1983), populations (Benke 1993), and entire ecosystems (Webster and Meyer 1997). Although energetic linkages among scales can be obscure, there is evidence that individual energetics can influence ecosystem patterns and processes (Parmelee 1995, DeAngelis 1995).

CURRENT USAGE IN ECOTOXICOLOGY

Although food webs have long been a central theme in ecology, the integration of food web research into ecotoxicology has been slow. Moriarty (1988) recognized the slow integration of ecological principles into toxicology and devoted more than one third of his monograph to ecological issues, almost half of which discussed food web dynamics. In contrast, more recent ecotoxicology texts address food webs much less. Hoffman et al. (1995) and Newman (1993) give limited coverage of food webs in their respective volumes. Trophic structure has been used to predict variation in contaminant concentrations among trophic levels (Thomann 1989, Fjellheim and Raddum 1996, Vander Zanden and Rasmussen 1996) and trophic pathways have been used to model contaminant dynamics (Kucklick et al. 1996). However, the ability to predict contaminant concentrations in a given ecological compartment is insufficient unless those concentrations are linked to ecological effects (Clements 1997). This requires an understanding of both energetic (and hence contaminant) flows and contaminant-related effects on trophic structure.

In contrast to food webs, energetic-based approaches have seen considerable use in ecotoxicology. Most approaches focus on the energetics of individuals, then attempt to relate individual-level endpoints (e.g., growth) to population abundance or structure. For example, numerous studies have used individual growth as an endpoint in chronic toxicity tests (Sibley et al. 1997). Other researchers have found that physiological energetics and the integrative endpoint "scope for growth" were sensitive to toxicological effects (Sobral and Widdows 1997, Cranford et al. 1999). Weis et al. (this volume) linked alterations in neurotransmitter functioning to reduced growth and fecundity of a *Fundulus* population.

A comprehensive integration of toxicant effects and individual energetics was recently performed by Beyers et al. (1999a;1999b). They established concentration-response relationships for physiological parameters in a well-established fish bioenergetics model (Kitchell 1983) then used these relationships to predict growth rates of smallmouth bass exposed to sub-lethal levels of dieldrin. The strength of their approach is the ability to isolate the multitude of factors that potentially influence individual energetics. For example, they found that relative to variation in food quantity and temperature, the effects of chronic dieldrin exposure on bass growth were biologically insignificant. Although from a toxicological standpoint these results seem uninteresting, from a management and ecological perspective they are significant. In using this energetic approach, they were able to simultaneously do what most other energetic methods have not; this includes: 1) establishing direct relationships between stressors and physiological parameters, 2) isolating direct and indirect effects, and 3) isolating the effects of natural versus anthropogenic stressors.

In addition to energetics-based analyses, other approaches have linked molecular and individual effects to population-level consequences. Sibley et al. (1996) used life-table analyses to test the chronic effects of metals on aquatic organisms. Linke-Gamanick et al. (1999) measured responses of several life-history parameters to toxicants. Theodorakis et al. (this volume) and Sibely et al. (this volume) linked molecular-level endpoints to population structure. Although these studies convincingly integrate among levels of ecological organization, generalizations beyond the population level are difficult.

THE PROPOSED NEXT STEP

I assert that extending toxicological effects beyond populations requires "scaling-up" energetic analyses to the population level, then linking populations with food web analyses. Population level energetics provides two related pieces of information that facilitate linking populations to ecosystems. First, by combining individual and population energetics, we can calculate consumption for a given population. Time-specific estimates of consumption among populations are the basis of energetic food webs (Figure 1c), and provide a direct link to other populations in an ecosystem. This combination of energetics and food web analysis has great potential in providing insight into ecological processes (Hairston and Hairston 1993, Hall and Raffaelli 1993), as well as ecotoxicological effects (see examples below). The second piece of information gained from population energetics is an estimate of energy flow through the population. Over a given time interval, the combined growth of individuals represents population productivity, and is expressed as a rate of mass or energy flow per unit time (Benke 1993). This measure also provides a basis for linking populations to ecosystems via food web and trophic flow analyses (Mageau et al. 1998).

Population Energetics

In a classic review of bioenergetic concepts in streams, Benke et al. (1988) proposed a model of population dynamics from a bioenergetics perspective (Figure 1.2). This model integrates individual and population energetics. Just as growth integrates many processes within individuals, production (accrual of biomass through time) integrates many population processes. These include biomass, abundance, mean individual growth rates, and fecundity (Benke 1993). Primary production (autotrophy) and secondary production (heterotrophy) are therefore useful endpoints in toxicological applications because they integrate lethal and sub-lethal contaminant effects across individuals within populations. Although primary production has often been used for this purpose (Schindler et al. 1985, Fairchild et al. 1992), far fewer studies have examined the effects of contaminants on secondary production (Benke 1993).

The factors likely to control secondary production of a consumer are also illustrated in Figure 1.2. Various habitat characteristics may influence population biomass by controlling either population abundance or individual biomass. The accumulation of biomass is dependent on the availability and consumption of resources and the efficiency with which this energy is converted to new biomass within individuals. The assimilation efficiency (AE) represents the proportion of energy that is not egested or excreted, and the net production efficiency (NPE) represents the remaining fraction of energy that is not needed for metabolism and therefore becomes new biomass. Losses to population abundance/biomass include consumption by consumers and other forms of death. Note that consumption by and of the consumer link the population to lower and higher trophic levels, respectively. Quantification of these processes is possible within a bioenergetic framework.

The potential effects of contaminants on population production are illustrated in figure 1.3. Contaminants may influence production directly, by altering assimilation efficiency (c), net production efficiency (d, Herrmann and Anderson 1986, Gorham and Vodopich 1992), and mortality (e, Fiancé 1978, Coyle et al. 1993). In addition, indirect effects on production may be initiated through alterations to consumable resource quality or quantity (a, Goodyear 1972, Wallace et al. 1987), feeding behavior (b, Woltering et al. 1978, Sandheinrich and Atchison 1989, Pennuto and deNoyelles 1993), and mortality due to predation (f, Hatfield and Anderson 1972, Sullivan et al. 1978, Camargo and Ward 1992). Although researchers have studied these effects for decades, few have explicitly integrated these endpoints to determine the mechanisms behind contaminant effects on population production.

An Example with Insect Populations in Metal-polluted Streams: I estimated annual production of aquatic insect populations in five Rocky Mountain streams subjected to varying levels of chronic metal contamination. Quantitative benthic samples were collected monthly during the ice-free season (May-October). All non-chironomid insect taxa were identified to genus or species under a 40X dissecting microscope, and body lengths were measured to the 0.1 mm with an ocular micrometer. Length-mass equations from the literature (Smock 1980) were used to estimate individual mass. Most taxa exhibited distinct cohorts, so population production was estimated using the increment-summation method (Benke 1996).

For illustrative purposes I present results from two streams, and for two species representing distinct trophic levels. *Cinygmula* is a common primary consumer in headwater Rocky Mountain streams (Ward and Kondratieff 1992), and was present in all but the most polluted study site. Because *Cinygmula* is present in chronically polluted streams, it may be capable of developing physiological tolerance to metal exposure (Luoma and Carter 1991). However, annual production of *Cinygmula* was much lower (97.80 vs. 442.98 mg/m^2) in a chronically polluted stream (Mosquito) than in a nearby reference stream (East Fork). The significance of this difference in production will be discussed shortly, but I first turn to the possible individual-and population-level mechanisms behind this observation.

As illustrated in Figure 3, several alternative (although not mutually exclusive) hypotheses can explain variation in population production. Since production is the product of individual growth and population abundance, I primarily consider these two possibilities. Mean individual growth rates of *Cinygmula* were similar ($t=-0.732$, $df=6$, $P=0.492$)) among these two streams (0.015 vs. 0.020 mg/d for East Fork and Mosquito, respectively). Conversely, springtime population densities of *Cinygmula* were nearly

30X higher (t=13.597, df=5, P<0.000) in East Fork than Mosquito (397 vs. 14 /m^2, respectively). It is therefore likely that the observed differences in production are attributable to population densities. *Cinygmula* and other heptageniid mayflies are among the most sensitive taxa to acute metal exposure (Kiffney and Clements 1994). The presence of *Cinygmula* in Mosquito Creek is therefore due to the ability of a few tolerant individuals to survive and reproduce. Because mayfly populations can be maintained with a very small number of ovipositing females (Schmidt et al. 1995), it is not surprising that *Cinygmula* is able to persist in this chronically polluted environment even though its abundance is low.

The predominant predator of *Cinygmula* is the stonefly *Megarcys signata*. Like *Cinygmula* , production of *M. signata* was higher in East Fork than in Mosquito Creek (629 vs 299 mg/m2, respectively). In the autumn (September-October), mean individual growth rates in Mosquito Creek were higher (t=-7.079, df=2, P=0.019) than those in East Fork (0.19 vs. 0.05 mg/d, respectively). During the spring however (May-July), growth rates in East Fork were higher (t=-9.614, df=2, P=0.011) than in Mosquito (1.83 vs. 0.34 mg/d, respectively). Throughout the nymphal period, mean individual mass of *M. signata* in East Fork (30.35 mg) was larger (t=4.461, df=221, P<0.000) than individuals in Mosquito Creek (17.44 mg). Densities of *M. signata* were similar in East Fork and Mosquito Creeks in the autumn (40 vs. 34 indiv./m^2, respectively; t=0.326, df=4, P=0.761) and higher in East Fork in the spring (24 vs. 6 indiv./m2, respectively; t=2.60, df=4, P=0.06). These results suggest that most of the difference in population production of *M. signata* is attributable to individual-level energetics.

Energetic Food Webs

With estimates of consumption and energy flow for a collection of populations, it is possible to link these populations using an energetic-based food web. Population consumption is generally quantified indirectly using the principle of energy mass balance. For example, if growth, AE, and NPE are known for a population, we can estimate total consumption by subtraction. Recent advances in radiotracer studies provide a way of directly measuring consumption in the field (Rowan and Rasmussen 1996) and may prove invaluable in future food web energetics studies. Total consumption may then be used to represent community-level trophic interactions (Figure 1.4), or summed across functional guilds as in trophic flow analyses (Ulanowicz 1996). For example, Benke and Wallace (1997) quantified the energy flow through a guild of omnivorous caddisfly larvae. They showed that energetic pathways were dominated by detritus and animal material, and that three taxa consumed >99% of the energy passing through the guild. From such analyses, it is clear which populations contribute most to ecosystem processes and serve as energy sources for higher trophic levels.

An Example with Food Webs in Metal-polluted Streams: Alterations in the production of the primary consumer *Cinygmula* were associated with changes in food web structure and ecosystem function in Mosquito Creek. Quantitative gut analyses were performed on collections of nymphs taken every two weeks during the ice-free period.

Gut contents of predators were counted and identified to family or genus, then converted to mass using length-mass equations. Gut contents of non-predators were mounted on microscope slides and categorized under 200X magnification as either animal material, course detritus, fine detritus, algae, diatoms, or fungus. The trophic basis for population production was computed using the methods of Benke and Wallace (1980). The contribution to population production of each item in the diet was estimated by using values of AE and NPE from the literature (Benke and Wallace 1980, Huryn 1996), then dividing the population production by the product of these parameters. Stable isotopes of C and N were used to describe food web structure (Fry 1991, Hershey and Peterson 1996).

Bioenergetic food webs for *M. signata* indicate how contaminant-induced reductions in primary consumer populations could influence secondary consumers (Figure 1.4). The period of greatest growth of *M. signata* in East Fork occurs during spring, when feeding upon *Cinygmula* and other metal-sensitive mayflies provides 35% of its production. Conversely, the period of greatest growth in Mosquito Creek is autumn, when metal-tolerant Orthocladiinae contributes 86% of its production. Springtime production of *Cinygmula* and other metal-sensitive mayflies in Mosquito Creek is very low, and the diet of *M. signata* is again dominated by small Orthocladiinae. The low production of *Cinygmula* (and other mayflies) in the chronically-polluted stream may be due to *M. signata* shifting its spring diet to include smaller prey types. Small-bodied prey may not be energetically adequate given the large body size of *M. signata* during the spring or the cost of foraging in a prey-depauperate environment. In addition, NPE and AE may be lower in the polluted stream due to an energetic costs of tolerance (Wilson 1988). The possible mechanisms behind lower growth rates of Mosquito *M. signata* are currently under study. Paradoxically, the dominance of small prey in the polluted stream in autumn may be energetically better for young *M. signata*, resulting in better growth rates during the early nymphal period.

Isotopic analysis of food web structure revealed ecosystem-level consequences of reduced herbivore productivity in Mosquito Creek (Figure 1.5). Relative to the population in East Fork, the C source of *Cinygmula* in Mosquito Creek contained more FBOM (fine benthic organic matter≈detritus). Similarly, *M signata* in Mosquito Creek contained more C from detritivores than populations in East Fork. These patterns were corroborated by the energetic food web analysis which showed that most of the production of *M. signata* was attributed to Orthocladiinae (detritivores) in Mosquito and mayflies (herbivore-detritivores) in East Fork. Although the trophic position (scaled on $\delta^{15}N$ axis) of *M. signata* was similar in both streams, the energy reaching upper trophic levels is predominately from detrital sources in the chronically-polluted site. This is indicative of stressed ecosystems (Odum 1985).

Interaction Webs

With predictions about population abundances, consumption, and behavior, it is also possible to link populations to ecosystem processes using interaction webs. Experimental manipulation is admittedly difficult in many ecosystems. For example, experimental removal of only mayfly taxa from a stream is currently not possible. However, when such experimentation is feasible, strong inferences can be made about the ecosystem-level consequences of contaminant-caused changes in populations. I have not found an example of this approach with toxicological applications. Clearly, more attention should be given to this approach.

Ecosystem-level Analyses and Comparisons

Energetic analyses are an under-used method for assessing the effects of stress on ecosystems. By further scaling-up energetic analyses to functional guilds, we can test hypotheses about the effects of contamination on ecosystems using comparative approaches. The fact that energy is a universal entity facilitates cross-ecosystem comparisons (Ulanowicz and Wulff 1991). Ulanowicz (1996) used a trophic flow network analysis of two tidal marshes to evaluate the effects of thermal effluent on these ecosystems. He posited three specific hypotheses that formally represented the potential effects of anthropogenic stress on 1) trophic efficiencies, 2) the structure of recycle pathways, and 3) system size and organization (Odum 1985). By estimating trophic interactions among 20 functional groups, carbon flows through each system were quantified. Results showed that relative to the unstressed system 1) smaller proportions of energy reached the highest trophic level, 2) food chains were shorter, and 3) efficiencies were diminished at all trophic levels, especially at the highest level, in the stressed ecosystem. The lengths and number of recycle pathways were also diminished in the stressed ecosystem. The major contribution of Ulanowicz's study is that it rigorously tests Odum's theories and demonstrates that ecosystems are capable of coherent responses to anthropogenic stressors. This paradigm is not predicated on the dictum that ecosystems are superorganisms (Mageau et al. 1998). Rather, it assumes that ecosystems exhibit some degree of organized dynamics. This study also demonstrates the capability of extending an energetic approach beyond single individuals and populations to include functional groups and ecosystems.

SUMMARY AND CONCLUSIONS

This paper was intended to present an approach that facilitates generalizing contaminant effects above the population level. A secondary goal was to implore those practicing ecotoxicology to consider the "eco-", wherein dominant ecological paradigms are more fully integrated into the concepts of environmental toxicology (Cairns 1989). Towards that end, I reiterate two important points. First, Fretwell (1983) argued that the study of food webs is the central theory of ecology. Regardless of the statement's validity, one cannot dispute that food web studies have produced tremendous insights into the functioning of natural systems, and there needs to be more application of these approaches in ecotoxicology. Finally, the need to integrate populations and ecosystems is an emerging theme in ecology (Jones and Lawton 1995). A successful way to accomplish this task is by scaling-up energetic analyses to populations and trophic guilds, then combining these entities into food webs and trophic flow networks. Although the evidence is still emerging, the approach holds great promise in our efforts to understand and predict human imprints on earth's ecosystems.

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LITERATURE CITED

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371-395 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Benke, A. C. 1993. Concepts and patterns of invertebrate production in running waters. Edgardo Baldi Memorial Lecture. Verhandlungen Der Internationalen Vereinigung Fur Theoretische Und Angewandte Limnologie **25**:15-38.

Benke, A. C. 1996. Secondary production of macroinvertebrates. Pages 557-578 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology. Academic Press, San Diego, California, USA.

Benke, A. C., C. A. S. Hall, C. P. Hawkins, R. H. Lowe-McConnel, J. A. Stanford, K. Suberkopp, and J. V. Ward. 1988. Bioenergetic considerations in the analysis of stream ecosystems. Journal of the North American Benthological Society **7**:480-502.

Benke, A. C. and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology **6**:108-118.

Benke, A. C. and J. B. Wallace. 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. Ecology **78**:1132-1145.

Beyers, D. W., J. A. Rice, and W. H. Clements. 1999a. Evaluating biological significance of chemical exposure to fish using a bioenergetics-based stressor-response model. Canadian Journal of Fisheries and Aquatic Sciences **56**:823-829.

Beyers, D. W., J. A. Rice, W. H. Clements, and C. J. Henry. 1999b. Estimating physiological cost of chemical exposure: integrating energetics and stress to quantify toxic effects in fish. Canadian Journal of Fisheries and Aquatic Sciences. **56**:814-822.

Cairns, J. Jr., 1983. Are single species toxicity tests alone adequate for estimating environmental hazard? Hydrobiologia **100**:47-57.

Cairns, J. Jr. 1986. The myth of the most sensitive species. BioScience **36**:670-672.

Cairns, J. Jr. 1989. Will the real ecotoxicologist please stand up? Environmental Toxicology and Chemistry **8**:843-844.

Cairns, J. Jr. and J. R. Bidwell. 1996. The modification of human society by natural systems: discontinuities caused by the exploitation of endemic species and the introduction of exotics. Environmental Health Perspectives **104**:1142-1145.

Cairns, J. Jr. and J. R. Pratt. 1989. The scientific basis of bioassays. Hydrobiologia **188/189**:5-20.

Camargo, J. A. and J. V. Ward. 1992. Differential sensitivity of *Dugesia dorotocephala* and *Cheumatopsyche pettiti* to water acidification: ecological implication for predator-prey interactions. Archives of Environmental Contamination and Toxicology **23**:59-63.

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

Clements, W. H. 1997. Effects of contaminants at higher levels of biological organization in aquatic ecosystems. Reviews in Toxicology **1**:107-146.

Clements, W. H., and P. M. Kiffney. 1994. Assessing contaminant effects at higher levels of biological organization. Environmental Toxicology and Chemistry **13**:357-359.

Coyle, J. J., D. R. Buckler, C. G. Ingersoll, J. F. Fairchild, and T. W. May. 1993. Effect of dietary selenium on the reproductive success on bluegills (*Lepomis macrochirus*). Environmental Toxicology and Chemistry **12**:551-565.

Cranford, P. J., D. C. Gordon, K. Lee, S. L. Armsworthy, and G. H. Tremblay. 1999. Chronic toxicity and physical disturbance effects of water- and oil-based drilling fluids and some major constituents on adult sea scallops *(Placopecten magellanicus)*. Marine Environmental Research **48**:225-256.

Cuffney, T. F., J. B. Wallace, and G. J. Lugthart. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. Freshwater Biology **23**:281-299.

DeAngelis, D. L. 1995. Relationships between the energetics of species and large-scale species richness. Pages 263-272 *in* C.G. Jones and J.H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Eggleton, M. A., E. L. Morgan, and W. L. Pennington. 1996. Effects of liming on an acid-sensitive southern Appalachian stream. Restoration Ecology **4**:247-263.

Fairchild, J.F., T.W. La Point, J.L. Zajicek, M.K. Nelson, F.J. Dwyer, and P.A. Lovely. 1992. Population-, community- and ecosystem-level responses of aquatic mesocosms to pulsed doses of a pyrethroid insecticide. Environmental Toxicology and Chemistry **11**:115-129.

Fiancé, S. B. 1978. Effects of pH on the biology and distribution of *Ephemerella funeralis* (Ephemeroptera). Oikos **31**:332-339.

Fjellheim, A., and G. G. Raddum. 1996. Weir building in a regulated west Norwegian river: Long term dynamics of invertebrates and fish. Regulated Rivers Research and Management **12**:501-508.

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

Fry, B. 1991. Stable isotope diagrams of freshwater food webs. Ecology **72**:2293-2297.

Goodyear, C. P. 1972. A simple technique for detecting effects of toxicants or other stresses on a predator-prey interaction. Transactions of the American Fisheries Society **2**:367-370.

Gorham, C. T., and D. S. Vodopich. 1992. Effects of acidic pH on predation rates and survivorship of damselfly nymphs. Hydrobiologia **242**:51-62.

Grimm, N.B. 1995. Why link species and ecosystems? A perspective from ecosystem ecology. Pages 5-15 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

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

Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. American Naturalist **142**:379-411.

Hall, S. J., and D. G. Raffaelli. 1993. Food webs: Theory and reality. Advances in Ecological Research **24**:187-239.

Hatfield, C. T., and J. M. Anderson. 1972. Effects of two insecticides on the vulnerability of Atlantic salmon (*Salmo salar*) parr to brook trout (*Salvelinus fontinalis*) predation. Journal of the Fisheries Research Board of Canada **29**:27-29.

Herrmann, J., and K. G. Anderson. 1986. Aluminum impact on respiration of lotic mayflies at low pH. Water, Air, and Soil Pollution **30**:703-709.

Hershey, A. E., and B. J. Peterson. 1996. Stream food webs. Pages 511-532 *in* F.R. Hauer and G.A. Lamberti, editors. Methods in Stream Ecology. Academic Press, San Diego, California, USA.

Hoffman, D. J., B. A. Rattner, G. A. Burton, and J. Cairns, Jr. 1995. Handbook of Ecotoxicology. Lewis Publishers, Boca Raton, Florida, USA.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnology and Oceanography **41**:243-252.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist **93**:145-159.

Jones, C. G., and J. H. Lawton. 1995. L inking species and ecosystems. Chapman and Hall, New York, New York, USA.

Kiffney, P. F., and W. H. Clements. 1994. Effects of heavy metals on a macroinvertebrate assemblage from a Rocky Mountain stream in experimental microcosms. Journal of the North American Benthological Society **13**:511-523.

Kimball, K. D., and S. A. Levin. 1985. Limitations of laboratory bioassays: The need for ecosystem-level testing. BioScience **35**:165-171.

Kitchell, J.F. 1983. Energetics. Pages 312-338 *in* P. W. Webb and D. Weihs, editors. Fish biomechanics. Praeger, New York, New York, USA.

Kucklick, J. R., H. R. Harvey, P. H. Ostrom, N. E. Ostrom, and J. E. Baker. 1996. Organochlorine dynamics in the pelagic food web of Lake Baikal. Environmental Toxicology and Chemistry **15**:1388-1400.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1967.

Levin, S. A., K. D. Kimball, W. H. McDowell, and S. F. Kimbal. 1984. New perspectives in ecotoxicology. Environmental Management **8**:375-442.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-418.

Linke-Gamenick, I., V. E. Forbes, and R. M. Sibly. 1999. Density-dependent effects of a toxicant on life-history traits and population dynamics of a capitellid polychaete. Marine Ecology- Progress Series **184**:139-148.

Luoma, S.N., and J.L. Carter. 1991. Effects of trace metals on aquatic benthos. Pages 261-300 *in* M. C. Newman and A. McIntosh, editors. Metal ecotoxicology: Concepts and applications. Lewis Publishers, Chelsea, Michigan, USA.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology **36**:533-536.

Mageau, M. T., R. Costanza, and R. E. Ulanowicz. 1998. Quantifying the trends expected in stressed ecosystems. Ecological Modeling **112**:1-22.

Menge, B.A., B. Daley, and P. A. Wheeler. 1996. Control of interaction strength in marine benthic communities. Pages 258-274 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Moriarty, F. 1988. Ecotoxicology: The study of pollutants in ecosystems. Academic Press, London, England.

Newman, M.C. 1993. Quantitative methods in aquatic ecotoxicology. Lewis Publishers, Boca Raton, Florida, USA.

Odum, E.P. 1985. Trends expected in stressed ecosystems. BioScience **35**:419-422.

Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs **27**:55-112.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature **355**:73-75.

Parmelee, R.W. 1995. Soil fauna: Linking different levels of the ecological hierarchy. Pages 107-117 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York. USA.

Pennuto, C. M., and F. deNoyelles, Jr. 1993. Behavioral responses of *Drunella coloradensis* (Ephemeroptera) nymphs to short-term pH reductions. Canadian Journal of Fisheries and Aquatic Sciences **50**:2692-2697.

Pimm, S.L. 1982. Food webs. Chapman and Hall, London, England.

Pimm, S.L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois, USA.

Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature **350**:669-674.

Polis, G.A., and K.O. Winemiller. 1996. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

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

Rowan, D. J., and J. B. Rasmussen. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}C). Canadian Journal of Fisheries and Aquatic Sciences **53**:734-745.

Sandheinrich, M. B., and G. J. Atchison. 1989. Sublethal copper effects on bluegill, *Lepomis macrochirus*, foraging behavior. Canadian Journal of Fisheries and Aquatic Sciences **46**:1977-1985.

Sarnelle, O. 1997. Daphnia effects on microzooplankton: Comparisons of enclosure and whole-lake responses. Ecology **78**:913-928.

Schindler, D. W. 1987. Detecting ecosystem responses to anthropogenic stress. Canadian Journal of Fisheries and Aquatic Sciences **44**:6-25.

Schindler, D. W. 1998. Replication versus realism: The need for ecosystem-scale experiments. Ecosystems **1**:323-334.

Schindler, D. W., K. H. Mills, D. F. Malley, D. L. Findlay, J. A. Shearer, I. J. Davies, M. A. Turner, G. A. Linsey, and D. R. Cruikshank.. 1985. Long-term ecosystem stress: The effects of years of acidification on a small lake. Science **228**:1395-1401.

Schmidt, S. K., J. M. Hughs, and S. E. Bunn. 1995. Gene flow among conspecifc populations of *Baetis* spp. (Ephemeroptera) - Adult fight and larval drift. Journal of the North American Benthological Society **14**:147-157.

Sibley, P. K., G.T. Ankley, A.M. Cotter, and E.N. Leonard. 1996. Predicting chronic toxicity of sediments spiked with Zinc: An evaluation of the acid-volatile sulfide model using a life- cycle test with the midge *Chironomus tentans*. Environmental Toxicology and Chemistry **15**:2102-2112.

Sibley, P.K., D.A. Benoit, and G.T. Ankley. 1997. The significance of growth in *Chironomus tentans* sediment toxicity tests: Relationship to reproduction and demographic endpoints. Environmental Toxicology and Chemistry **16**:336-345.

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

Sobral, P., and J. Widdows. 1997. Effects of Copper exposure on the scope for growth of the clam *Ruditapes decussatus* from southern Portugal. Marine Pollution Bulletin **34**:992-1000.

Strayer, D. L., and G. E. Likens. 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology **67**:303-313.

Sullivan, J. F., G. J. Atchison, D. J. Kolar, and A. W. McIntosh. 1978. Changes in predator-prey behavior of fathead minnows (*Pimephales promelas*) and largemouth bass (*Micropterus salmoides*) caused by cadmium. Journal of the Fisheries Research Board of Canada **35**:446-451.

Tavares-Cromar, A.F., and D.D. Williams. 1996. The importance of temporal resolution in food web analysis: Evidence from a detritus-based stream. Ecological Monographs **66**:91-113.

Thomann, R.V. 1989. Bioaccumulation model of organic chemical distribution in aquatic food chains. Environmental Science and Technology **23**:699.

Ulanowicz, R.E. 1996. Trophic flow networks as indicators of ecosystem stress. Pages 358-368 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Ulanowicz, R. E., and F. Wulff. 1991. Comparing ecosystem structures: The Chesapeake Bay and the Baltic Sea. Pages 140-166 *in* J. G. Cole, G. Lovett, and S. Findlay, editors. Comparative analysis of ecosystems: Patterns, mechanisms, and theories. Springer-Verlag, New York, New York, USA.

Vander Zanden, M. J., and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: Impact on contaminant bioaccumulation in lake trout. Ecological Monographs **66**:451-477.

Wallace, J. B., T. F. Cuffney, C. C. Lay, and D. Vogel. 1987. The influence of an ecosystem-level manipulation on prey consumption by a lotic dragonfly. Canadian Journal of Zoology **65**:35-40.

Ward, J.V., and B. C. Kondratieff. 1992. An illustrated guide to the mountain stream insects of Colorado. University Press of Colorado, Niwot, Colorado, USA.

Webster, J. R., and J. L. Meyer. 1997. Organic matter budgets for streams: A synthesis. Pages 141-161 *in* J. R. Webster and J. L. Meyer, editors. Stream organic matter budgets. Journal of the North American Benthological Society **16**:3-161.

Wilson, J. B. 1988. The cost of heavy-metal tolerance: An example. Evolution **42**:408-413.

Winemiller, K. O., and G.A. Polis. 1996. Food webs: What can they tell us about the world? Pages 1-22 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Woltering, D. M., J. L. Hedtke, and L. J. Weber. 1978. Predator-prey interactions of fishes under the influence of ammonia. Transactions of the American Fisheries Society **107**:500-504.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508-515.

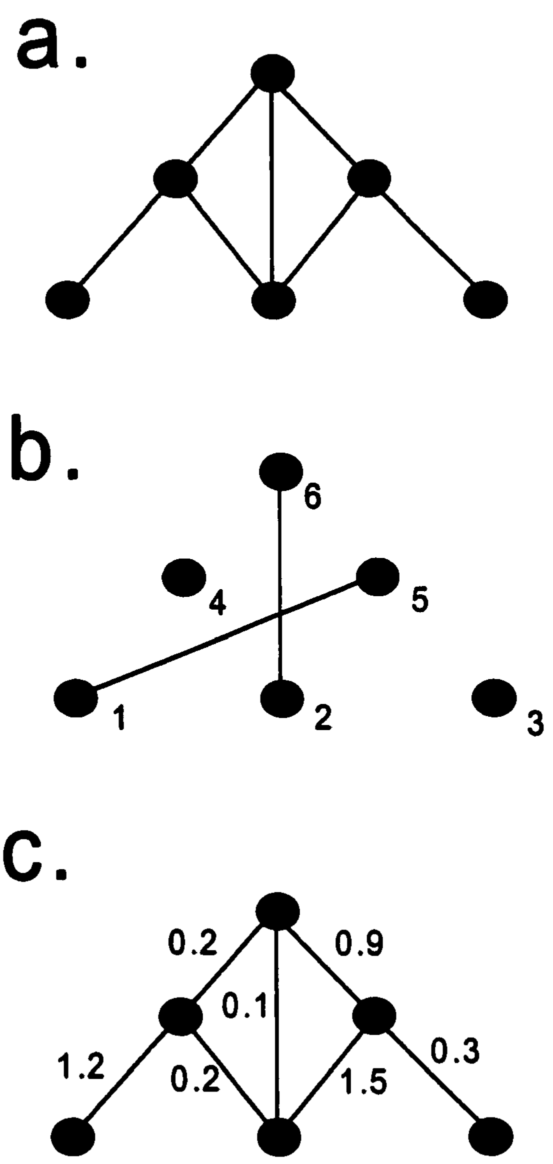

Figure 1.1. Diagrammatic representation of three approaches to study food webs. Topological webs (a) depict all known trophic relationships as either present or absent. Interaction webs (b) depict dynamic relationships between populations. In this example, populations 1 and 5, and 2 and 6 are dynamically linked. Variations in all other populations have no effect on food web structure and dynamics. Energetic webs (c) depict linkages among populations in terms of energy flow (e.g., mg C year^{-1}).

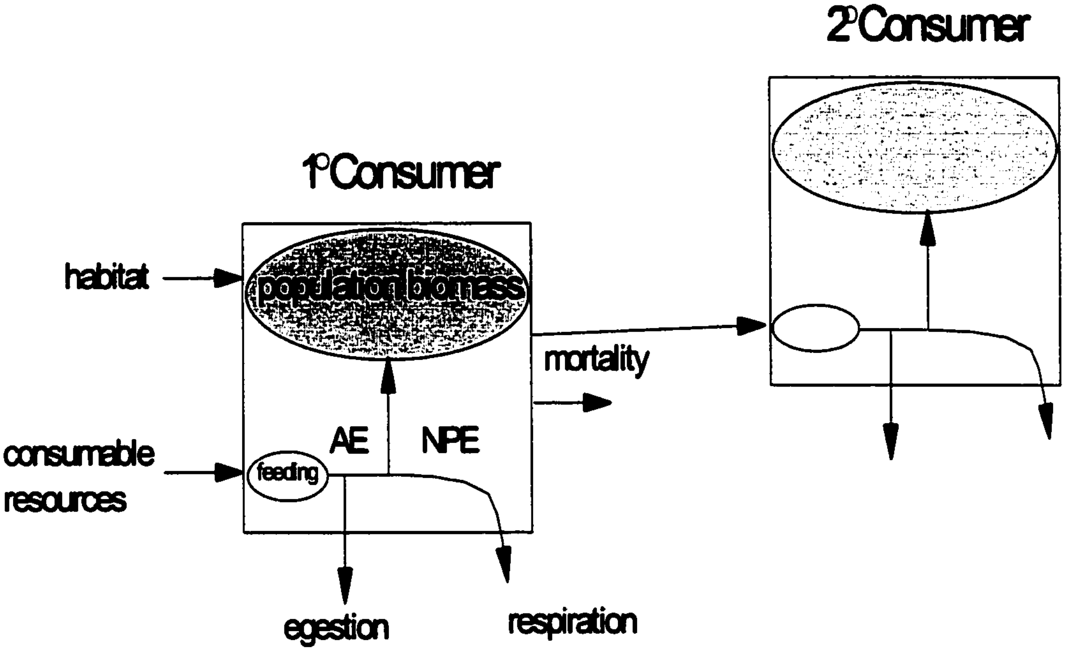

Figure 1.2. Model of population dynamics from a bioenergetics perspective, modified from Benke et al. 1988. See text for explanation.

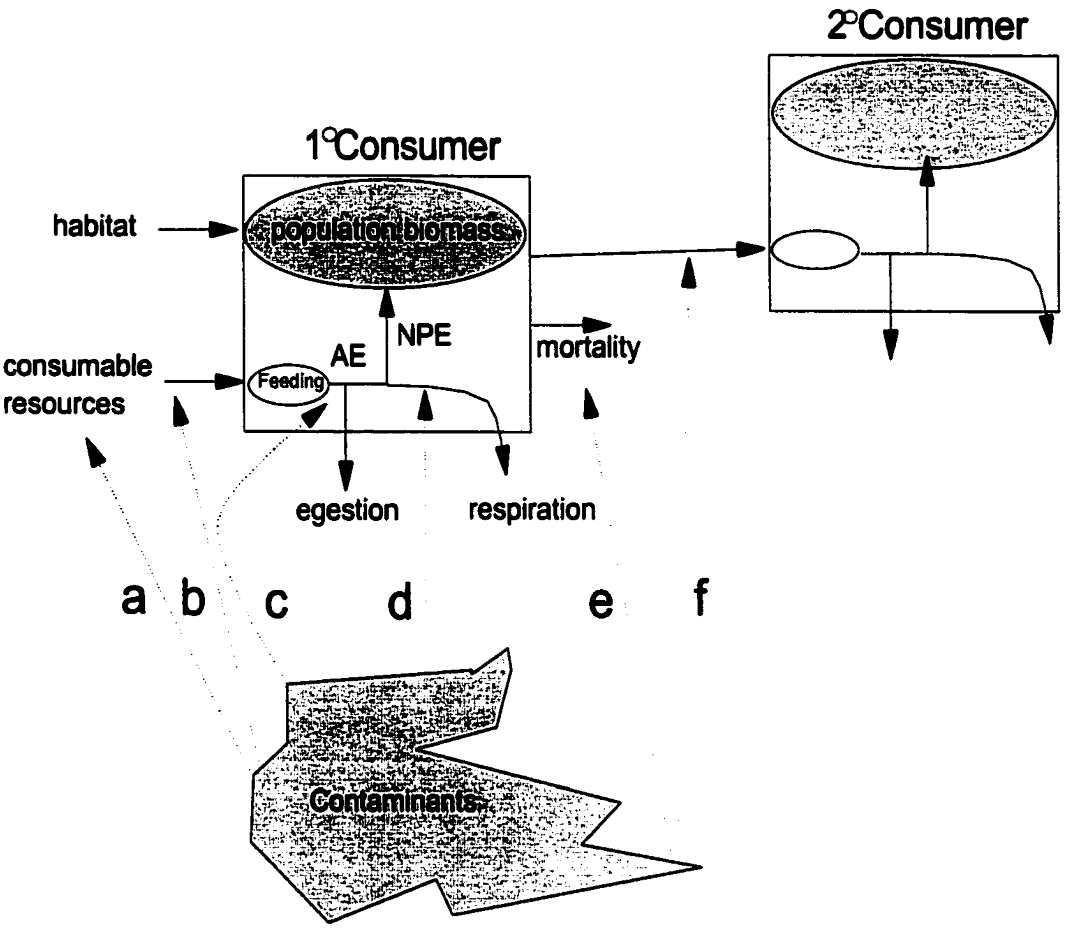

Figure 1.3. Hypothetical effects of chronic contaminant exposure on population energetics. See text for explanation.

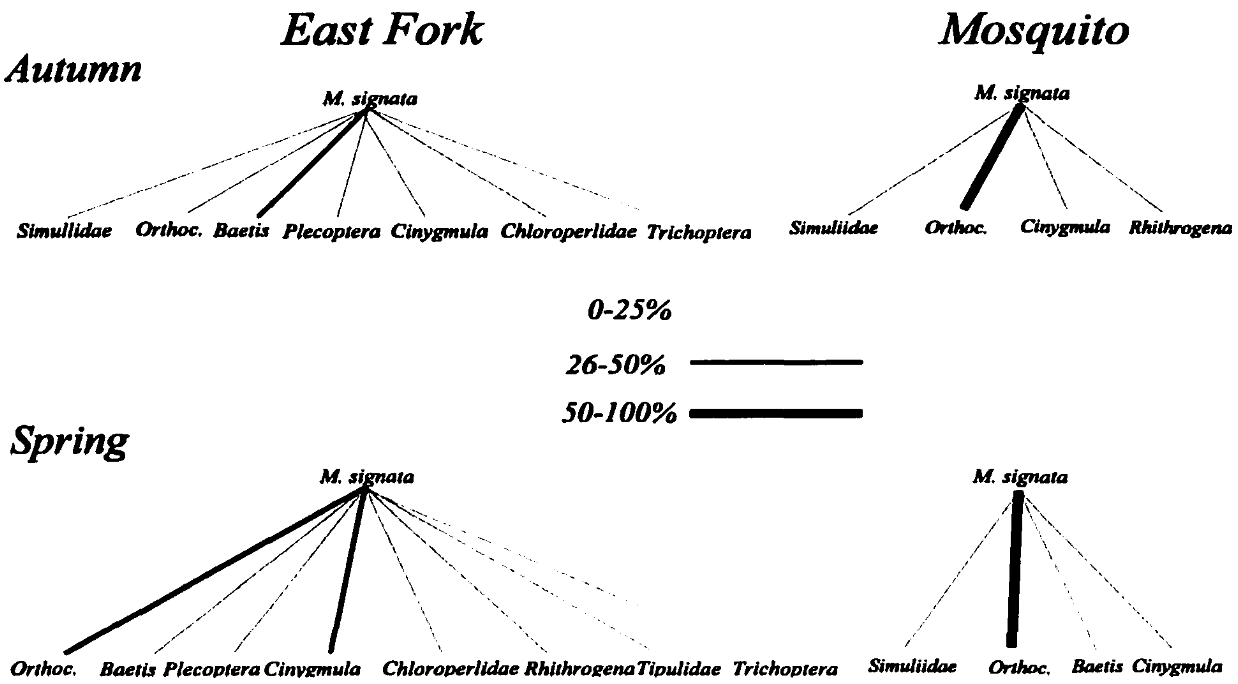

Figure 1.4. Energetic food webs of M. signata in East Fork and Mosquito Creeks during autumn 1998 and spring 1999. Percentages represent the relative contribution of each diet item to the production of *M. signata*. Orthoc. = Orthocladiinae.

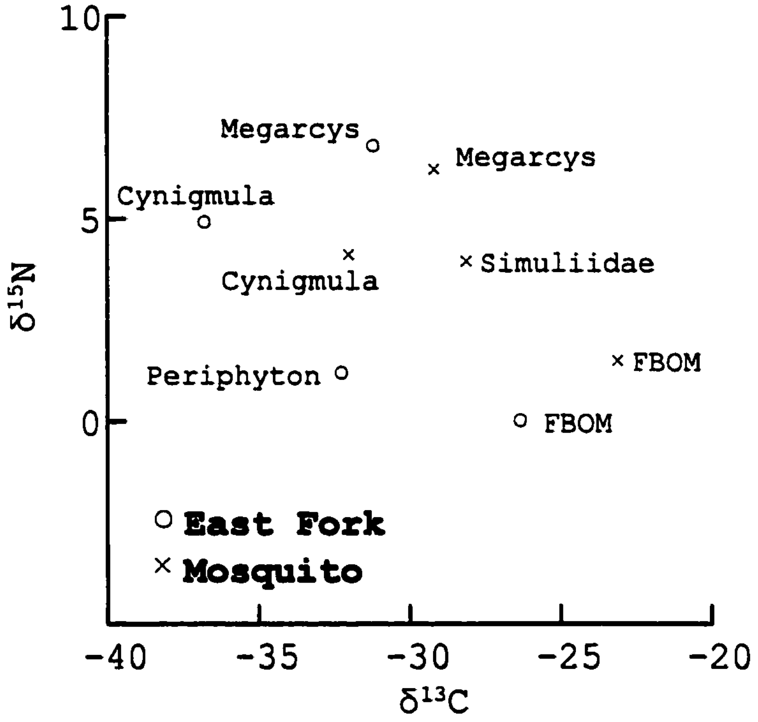

Figure 1.5. Trophic structure in East Fork and Mosquito Creeks as depicted by stable isotope analyses. FBOM = fine benthic organic matter (primarily detritus).

CHAPTER 2:

GROWTH AND SECONDARY PRODUCTION OF AQUATIC INSECTS ALONG A POLLUTION GRADIENT IN ROCKY MOUNTAIN STREAMS

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ABSTRACT

Secondary production integrates processes that occur at individual and population levels of ecological organization. Secondary production of functional groups of aquatic insects influences ecosystem processes. We used estimates of secondary production and production:biomass ratios (P/B) to test several hypotheses about the effects of chronic metal contamination on insect populations and functional groups of Rocky Mountain headwater streams. Quantitative samples of benthic insects, chemistry, and habitat were collected monthly during the ice-free period (May-November) from five 2nd to 3rd-order streams that varied primarily in metal contamination. Secondary production was estimated for the 19 dominant taxa using increment-summation, size-frequency, and P/B methods. Uncertainty was estimated by bootstrapping estimates of mean abundance, biomass, and cohort production intervals. Secondary production of metal-sensitive Heptageniidae (*Rhithrogena robusta*, *Cinygmula* spp., and *Epeorus longimanus*) was disproportionately lower in light to moderately contaminated streams. Growth estimates and experiments to estimate food quality and quantity revealed that lower production was mostly due to reduced population abundances in contaminated streams. Heptageniid mayfly populations that persisted in contaminated streams had different P/B ratios and life histories than organisms in nearby reference streams. Scraper production was disproportionately lower in contaminated streams relative to other functional groups, which implied that relatively low metal contamination may have ecosystem-wide, energetic consequences.

INTRODUCTION

Secondary production is an integrative measure of population dynamics that provides insights into individual-, population-, and ecosystem-level processes. Individual bioenergetic processes are manifested as growth rates, which equate to production when summed across an entire population (Benke et al. 1988). Production measures the ultimate somatic and reproductive output of populations. Production is also a measure of energy flow through a population and, if combined with trophically interacting populations, also represents energy flow through a food web (Benke and Wallace 1997, Huryn and Wallace, 2000).

Although studies on secondary production of stream insects are numerous, several knowledge gaps remain (see reviews by Waters 1977, Benke 1993). Benke (1993) reviewed most of the secondary production literature and observed that studies were biased towards small, temperate streams in North America. Furthermore, studies in cold (e.g., mean annual temperature < 5.0° C), high latitude (or elevation) streams are rare. Benke (1993) also reported that < 25% of the 159 studies to date had measured production of the entire macroinvertebrate assemblage. As a result, our understanding of community secondary production is limited to about 40 streams world-wide. Few studies have tested specific hypotheses about the factors that regulate production across environmental gradients (but see Krueger and Waters 1983, Koetsier et al. 1996). Nevertheless, across-gradient comparisons of production dynamics within and among species are necessary to improve our understanding of the abiotic and biotic controls of stream energetics (Benke et al. 1988).

Metals from abandoned mines are a dominant environmental stressor in western stream ecosystems (Caruso and Ward 1998). Most research has examined the influence of metals on community structure, and has supported one or more of the following generalizations. First, heptageniid mayflies are usually the most sensitive insect taxa to metal contamination (Clements et al., 2000), and are therefore much less abundant in polluted streams. Second, stoneflies are generally tolerant to metals with the possible exception of some predatory species (Kiffney and Clements 1994, Clements et al., 2000). Third, insect assemblages in polluted sites are dominated by a few tolerant species that rapidly colonize disturbed habitats (Leland et al. 1989). Fourth, periphyton communities are sensitive to metals and revert to early-successional stages, with tolerant species dominating contaminated environments (Medley and Clements 1998). These patterns are consistent in metal- (and other contaminants) polluted systems and offer a useful tool for identifying metal-affected streams. However, changes in community composition do not always reflect ecosystem-level processes (Lawton 1994, Frost et al. 1995, Grime 1997). For example, these generalizations do not indicate whether productivity or element cycling are affected by the contaminant. Few studies have examined how contaminants affect population and ecosystem energetics in streams. As a result, our understanding of how metals and other contaminants influence stream ecosystem function is incomplete.

The purpose of our study was to determine how secondary production, a functional measure of individuals and populations, may be influenced by metal contamination. Specifically, we compared assemblage composition, individual growth, annual production, and population turnover (annual P/B) among streams differing in metal contamination. Our high elevation study sites (3100-3300 m) also gave us the opportunity to assess how invertebrate production in these streams compares with more thoroughly studied, low-elevation systems. An additional goal was to relate our knowledge of expected changes in community structure to ecosystem processes that are influenced by the production of insect functional feeding groups (Wallace and Webster 1996).

METHODS

Hypothesis Formulation

Based on predictable alterations of benthic community structure in metal-polluted streams, we proposed several hypotheses about individual-, and population-level processes. Disproportionate reductions of some species in polluted streams may result from direct toxicity and/or a combination of cumulative indirect and sub-lethal effects. Although the acute sensitivity of heptageniids and other taxa to metals is well documented (Clements and Kiffney 1995, Clements et al., 2000), populations that persist in chronically-polluted environments may suffer from reductions in food quality (Medley and Clements 1999), sub-lethal effects of chemical detoxification on metabolism and growth (e.g., "cost" of tolerance sensu Wilson 1988, Mulvey and Diamond 1991), and alterations in life history (Lehmkuhl 1979, Hatakeyama et al. 1997). Our first hypothesis, therefore, was that reductions in individual growth and population biomass of sensitive species contributed to reduced production in metal-polluted streams. Further, individual biomass may be minimized and growth rate maximized in environments where risk of mortality is high (Huryn and Wallace 2000). The annual P/B ratio (Waters 1969, Benke 1993) summarizes the relationship between biomass and growth. We hypothesized that annual P/B would be higher for populations in metal-polluted streams than those in non-polluted streams.

Patterns of insect productivity along a contaminant gradient may also reflect ecosystem processes. Reductions in predator productivity imply alterations in trophic structure that may have ecosystem-wide consequences (Power 1995). Similarly, reductions in productivity of other functional groups may indicate alterations of additional ecosystem processes. Because heptageniid mayflies are grazers of periphyton, we predicted that population reductions of heptageniids in metal-polluted streams leads to reduced herbivory.

Study Sites

We selected five study streams that varied strongly in metal contamination but were similar in elevation, discharge, and other habitat characteristics. East Fork Creek is at the headwaters of the Arkansas River and drains the Mosquito Range in central Colorado. Fourmile, Mosquito, and Buckskin Creeks drain the east side of the Mosquito Range and are tributaries to the South Platte River. Snake River is a tributary of the Colorado River. These high gradient watersheds are U-shaped glacial valleys with sparse soil development and vegetative cover. About 25% of the land cover is bare rock confined to the highest elevations (up to 4300 m). The dominant vegetative cover is sub-alpine tundra and alpine willow (*Salix* spp.). Scattered evergreens occur in valley bottoms at lower (<3300 m) elevations. Loamy, skeletal soils thinly cover bedrocks, which are mostly composed of metamorphic gneisses or felsic composites. Streams remain frozen and snow-covered for 7-8 months each year, followed by a characteristic snowmelt-driven hydrograph throughout the rest of the year. Willow is the dominant riparian vegetation and provides sparse canopy cover (D. Carlisle, pers. obs.). The streams are dominated by riffle habitats with small-large cobble. We selected a 500 m study reach on each stream that was similar in elevation and valley form.

Water Chemistry

Water chemistry was measured bi-monthly from May 1 -October 1, then monthly thereafter for an entire year. On each sampling occasion, pH and conductivity were measured with hand-held probes (Quickchek® models 106, 116, Orion Research, Inc., Beverly, MA). A 15 ml grab sample was taken for total metals, and a second 15 ml sample was filtered (0.45 μm) for dissolved metal analysis. Both samples were immediately acidified to pH < 2.0 with concentrated nitric acid. A 1-l grab sample was taken from a riffle area, stored on ice, and returned to the laboratory for analysis of alkalinity and total hardness using standard methods (Clescari et al. 1998). Analyses for Cd, Cu, and Zn were performed on an atomic absorption spectrophotometer. Because metal toxicity varies with water hardness, among stream comparisons of metal concentrations must be standardized. We standardized metal concentrations using the hardness-adjusted chronic criterion value set by U.S. EPA (CDPHE 1999). Total hardness measured on each sample date was used to compute the chronic criterion value for each metal. We then calculated the ratio of measured dissolved metal concentration to the chronic criterion value for each sample date. Consequently, we expect ratios <1 to be protective of aquatic biota whereas ratios >1 indicate potential toxic effects.

Habitat

Discharge was estimated bi-monthly from May1-October 1, then monthly during the remaining ice-free period. A section of the channel with a minimum of turbulent flow and eddies was selected, and water velocities (cm/s) measured with a flow meter (Marsh-McBirney model 200, Fredrick, MD) at 20 cm intervals. Depth to the nearest cm was also measured at each point. Discharge (m^3/s) was calculated using the continuity equation. Because ice and snow prevented discharge measurements during November-April, we assumed that average winter discharge was equal to the mean of the November and April estimates.

Temperature was continuously monitored with data loggers (Optic StowAway ®, Onset Computer Corp., Pocasset, MA). Stream channel width was measured during low flow as the width of the wetted channel. Basin size, stream slope, and elevation were estimated with digital elevation models for each basin obtained from U.S. Geological Survey.

Benthic Invertebrates

Quantitative samples of benthic macroinvertebrates were collected monthly from May-November. Five 0.1-m^2 samples were collected in riffle areas with a Hess sampler (150 μm Nitex net) and preserved in 5% Formalin. In the laboratory, each sample was placed in a white enamel pan and animals >1 mm were removed from the debris. Sub-samples were taken with randomly placed cores (2 cm dia.) that each removed 8% of the total volume. Initially, three sub-samples were taken and animals removed and counted under 40X magnification. Additional sub-samples were taken until ≈300 individual insects had been removed (Elliott 1971). Animals were identified to species (subfamily for small midges) and body lengths of at least 50 individuals were measured to the nearest 0.1 mm using an ocular micrometer. Length-mass relationships of Benke et al. (1999) were used to convert body length measurements to dry mass.

Secondary production was estimated using three methods, with some modifications due to our inability to sample during winter. We used the increment summation method (Benke 1996) for taxa that exhibited distinct cohorts based on length-frequency analyses. With the exception of chironomids, we used the size-frequency method (Benke 1996) for all other insects. Estimates of the cohort production interval for these taxa were obtained from our own length-frequency analyses or from the literature. Because our study streams were frozen and inaccessible from November-May, sampling was impossible during this period. We therefore used the average of the last (usually November) sample in the fall and the first (usually mid-May) sample in the spring to estimate biomass (increment summation method) or length frequencies (size frequency method) for winter months. Production for functional feeding groups (based on Merritt and Cummins 1996) was estimated by summing production and associated variances across constituent populations.

Literature estimates of temperature- and mass-specific growth rates for Chironomidae (e.g., Huryn 1990, Hauer and Benke 1991) are not applicable to our study streams. Minimum temperatures encompassed by these relationships are much greater than mean annual temperatures in high elevation streams. We observed temperatures near 0 °C for almost 6 months in several 2-3rd order Colorado streams (D. Carlisle, unpublished data). Consequently, applying temperature-growth equations established elsewhere to midges in the Rocky Mountains would likely underestimate production. We therefore calculated chironomid production using estimates of annual P/B ratios from the literature (Tokeshi 1995). Based on an extensive review, Tokeshi (1995) reported that several genera of Orthocladiinae common at high latitudes exhibited P/B ratios from 1.4-2.3. Because at least two orthoclad genera were found in our study sites, we used this range of P/B ratio to calculate production for Orthocladiinae. Frequency distributions of reported P/B ratios for Chironominae revealed a mode from 1-3 (Tokeshi 1995), particularly for taxa known to be merovoltine. We selected this range of P/B values to calculate production for Chironominae.

Uncertainty associated with production estimates was quantified with a bootstrapping procedure (e.g, Brey 1990, Huryn 1996). Bootstrapping is a non-parametric re-sampling procedure used to estimate sampling variance of variables with complex or unknown frequency distributions and in situations where adequate replication is logistically difficult (Efron 1982). All data used to estimate production were randomly re-sampled 1000 times with replacement (Wilkinson and Engelman 1996). These data were then used to calculate 1000 estimates of biomass, production, and P/B. For the size frequency method, CPI was also re-sampled assuming a normal distribution of estimates obtained from the literature (e.g., Huryn 1996). Vectors of 1000 estimates were then used to calculate approximate 95% confidence intervals for production and P/B ratios using the bias-corrected percentile method (Meyer et al. 1986).

We limited growth rate comparisons to mayflies because these taxa vary in metal sensitivity and often have defined cohorts. Cohort growth rates were estimated by fitting exponential growth models to relationships between mean mass and time (Hawkins 1986). Specific growth (G) (Waters 1977) was calculated using regression analysis with the equation: $W_t = W_0e^{kt}$, where W_0 = mean mass at time zero, W_t = mean mass at time t, and k = instantaneous coefficient of growth. Among-stream growth rates were compared for each species using analysis of covariance (ANCOVA), where P=0.05. All statistical analyses were performed using SYSTAT (Wilkinson 1996).

Growth Experiment

To determine the influence of metal-polluted periphyton on grazer growth, we measured growth of *Baetis tricaudatus* (Dodds) after feeding on periphyton from polluted and unpolluted sites for eight days. We placed non-glazed ceramic tiles in shallow (<0.5 m) riffles of Fourmile, Mosquito, and Snake River in mid-June, 1998. After a 30-day colonization period, tiles were removed, placed in aerated insulated coolers, and returned to the Stream Research Laboratory at Colorado State University. Four tiles were placed in each of five chambers (350 μm mesh) and placed in circulating stream microcosms (see full description in Kiffney and Clements 1994). Five *B. tricaudatus* from the Cache la Poudre River, a nearby unpolluted river, were placed in each growth chamber. The experiment employed five chambers as replicates from each stream. Initial and final body lengths were measured after anesthetizing with CO_2. Specific growth (G) was calculated using the mean initial and final weights across individuals within each replicate chamber. Growth among treatments was compared with ANOVA.

Periphyton food quantity and quality from each site was determined by measuring chlorophyl a and ash-free dry mass (AFDM) on control tiles at the end of the experiment. Periphyton was scraped from all control tiles with a hard bristle brush. A random aliquot was removed from the slurry, from which chlorophyl a was measured (Clescari et al. 1998). The remaining sample was dried to constant weight at 60°C then combusted at 500° C for 1 hr. Samples were re-weighed after cooling in a desiccator for 1 hr, and AFDM was calculated as the difference between dry weight and ashed-weight. Mean AFDM and chlorophyl a among streams was compared with ANOVA.

RESULTS

Chemical and Physical Conditions

Watershed area and slope, stream gradient, mean pH, channel width, annual degree days, and elevation varied less than 1.5-fold among streams (Table 2.1). Median discharge and conductivity varied 2-fold. In contrast, alkalinity and Zn levels varied 28- and 12-fold, respectively. Mean daily temperature ranged from 0° (November-April) to 11° C (August), but varied little among streams (Figure 2.1). East Fork and Fourmile Creeks were on average the warmest and coldest streams, respectively (Table 2.1, Figure 2.1).

We report metals data only for Zn because Cd and Cu often occurred at concentrations near or below analytical detection limits (5 μg/l). Seasonal variation in Zn levels was substantial (Figure 2.2). Zn levels in Fourmile and East Fork were generally below the chronic criterion. These streams were therefore considered reference. Zinc levels in Buckskin Creek (hereafter "low-metals" stream) were consistently ≈2X the chronic criterion, and peaked during spring runoff. Zn levels in Mosquito Creek (hereafter "moderate-metals" stream) varied from 2-4X the chronic criterion and were highest during the fall. Zn levels in Snake River (hereafter "high-metals" stream) showed a similar temporal pattern, but were up to 9X the chronic criterion value.

Macroinvertebrate Assemblage Composition

A total of 39 taxa were collected during the course of this study. Of these, 14 were too rare to calculate production, and six species of *Rhyacophila* were lumped due to uncertainty associated with identification of early instars. We calculated production for the remaining 19 taxa, which represented 85-95% of the total abundance and biomass collected at all sites.

Abundance and biomass of major taxonomic groups varied considerably among streams (Figure 2.3, Table 2.2). Total biomass (mg DM / 0.1 m^2) ranged from ≈65-200 in the reference streams , 25-95 in the low-metals stream, 10-75 in the moderate-metals stream, and 0.5-5 in the high-metals stream. In general, metal-sensitive Heptageniidae were much less abundant in streams of moderate-high metals than in reference and low-metals streams. Fifteen of 19 major taxa were more abundant in the reference and low-metals streams than in the moderate to high-metals streams. In contrast, *Prosimulium* spp., *Arctopsyche grandis*, and *Drunella doddsi* were most abundant in the moderate-metals stream.

The relative dominance of major taxa varied seasonally (Figure 2.3). Chironomidae was the numerically dominant taxon in all streams, with densities > 1,256 / 0.1 m^2 in Fourmile Creek. Chironominae (mostly *Tanytarsini* spp.) dominated reference and low-metals streams in the spring and/or fall. Heptageniidae dominated assemblages in reference and low-metals streams during the summer. In contrast, *B. tricaudatus* dominated the assemblage in the moderate-metals stream during summer and fall. With the exception of the moderate and high-metals streams, total assemblage biomass was lower in summer than in spring and fall.

Mayfly Growth Rates

Although growth rates varied significantly among streams for heptageniids (*Cinygmula* spp., *E. longimanus*, and *R. robusta*), growth rates of other mayflies (*B. bicaudatus*, *B. tricaudatus*, and *D. doddsi*) were similar among streams (Table 2.3).

Growth of *E. longimanus* was slightly lower in the low-metals stream (Buckskin) than the remaining streams, but these results were only marginally significant (P = 0.1). *Cinygmula* spp. growth was 8X higher in the moderate-metals stream (Mosquito) than all other streams, where growth was similar. Growth of *R. robusta* was lower in the low and moderate-metals streams than in the reference streams.

Growth Experiment

Periphyton food quantity and quality differed significantly along the metals gradient (Figure 2.4a). Periphyton from a reference stream (Fourmile) contained 2X more organic matter than that from moderate and high-metals streams. Periphyton from the reference stream also contained 2X more chlorophyl a than periphyton from the moderate-metals stream, and >50X more than periphyton from the high-metals stream. Growth of *B. tricaudatus* also differed significantly among treatments (Figure 2.4b). Specific growth rates of *B. tricaudatus* that fed on periphyton from a reference stream were 30-50% higher than those that fed on periphyton from contaminated streams.

Annual Production of Major Taxa

Annual production of heptageniid mayflies varied substantially along the metals gradient (Table 2.4, Figure 2.5a), and was absent in the high-metals stream. *Epeorus longimanus* production varied 2X between reference streams, and was 5X higher than in low- and moderate-metals streams. Production of *Cinygmula* spp. also varied 2X between reference streams, and was 6-7X higher than in low- and moderate-metals streams. Production of *R. robusta* varied ≈2X between reference and low-metals streams, and was 6X higher than in the moderate-metals stream.

Production of three other mayfly species varied less strongly than heptageniids along the metal gradient (Table 2.4, Figure 2.5a), although all species were absent from the high-metals stream. Production of *B. bicaudatus* varied ≈2X along the metal gradient. Production of *B. tricaudatus* was highest in the moderate-metals and one reference stream, and similar among the remaining streams. Production of *D. doddsi* varied ≈2X along the metals gradient.

Production of several plecopteran taxa varied along the metal gradient (Table 2.4, Figure 2.5b). Production of *M. signata* was similar in the reference streams and ≈2X lower in the low and moderate-metals streams. *Suwallia* spp. and *Sweltsa* spp. were probably represented by several species (B. Kondratieff, pers. comm.) with varying life-history patterns. Production of *Suwallia* spp. was similar in the reference streams, 5X lower in the low and moderate-metals streams, and ≈30X lower in the high-metals stream. *Sweltsa spp.* production was similar in a reference and low-metals stream, and zero in all other streams. *Zapada* spp. was one of only three taxa that were present consistently in the high-metals stream, and it also occurred in all other streams. Production of *Zapada* spp. varied <2X among all but the high-metals stream, where it was ≈5X less than in the remaining streams. Production for *Paraleuctra* spp. was measurable in one reference and the low-metals stream, where production was 6X higher than in the former. *Taenionema pallidum* and *Doddsia occidentalis* co-occurred in all but the moderate and high-metals stream. Production was similar in the reference streams and slightly less in the low-metals stream.

Production of several trichopteran and dipteran taxa also varied among streams (Table 2.4, Figure2.5c). We encountered at least six species of *Rhyacophila*, but their individual life histories are unknown. Production for the genus was highly variable and highest in the reference streams, ≈2X lower in the low-metals stream, and ≈5X lower in the moderate-metals stream. *Arctopsyche grandis* production was present in one reference stream and the moderate-metals stream, and was similar in both. *Prosimulium* sp. production was highest in the moderate-metals stream and one reference stream, 2X lower in the low-metals stream, 3X lower in the other reference stream, ≈10X lower in the high-metals stream. Tanytarsini was the dominant Chironominae taxon. Production was highest in the reference streams, ≈2X lower in the low-metals stream, and 18X lower in the moderate and high-metals streams. Orthocladiinae production was similar among reference, low-, and moderate-metals streams, and 5X lower in the high-metals stream.

Total assemblage production varied >120X along the metal gradient (Table 2.4). Total production in low-, moderate-, and high-metals streams was 2X, 3X, and 121X lower, respectively, than the reference streams.

Annual P/B of Major Taxa and Assemblages

Annual P/B ratios varied considerably among taxa and streams (Table 2.5, Figure 2.6). *Baetis tricaudatus* P/Bs varied < 2X among reference and low-metals streams, and was 3X lower in the moderate-metals stream. *Cinygmula* spp. P/B ratios were highly variable and 2X higher in the moderate-metals stream than the remaining streams. Uncertainty was also high for *E. longimanus* in the moderate-metals stream, but P/B was 3X higher there than in the remaining streams–which were all similar. Annual P/B ratios for *M. signata* were higher in one reference stream than the remaining streams (Table 2.5, Figure 2.6). Annual P/B ratios for *Suwallia* spp., *Sweltsa* spp., *bicaudatus, D. doddsi*, and *T. pallidum* did not vary appreciably among streams. *Zapada* spp. annual P/B was higher in one reference stream than the remaining streams, which were all similar. *Prosimulium* sp. annual P/B ratios varied considerably, but were not significantly different among streams. *Rhyacophila* spp. P/B ratios were consistent among streams. *A. grandis* P/B ratio was higher in the moderate-metals stream than in the reference stream.

Total insect assemblage annual P/B ratios did not always vary as expected (Table 2.5). Assemblage P/B ratios varied <2X among the reference and low-metals streams, but was 2X higher than reference in the moderate-metals stream and ≈2X lower than reference in the high-metals stream.

Functional Group Production

The relative contribution of functional groups to total assemblage production varied along the metal gradient as predicted (Figure 2.7). Predators and scrapers dominated production in the reference and low-metals streams. In contrast, collector-gatherers and predators dominated production in the moderate- and high-metals streams. The relative contribution of scrapers to total production declined from about 30-50% in the reference and low-metals streams to <5% in the high-metals stream. The relative contribution of shredders declined in similar fashion, from about 15% to less than 5% in the moderate- and high-metals streams.

Total production of functional groups also varied strongly among streams (Figure 2.7). Scraper production was similar in the reference streams, ≈50% lower in the low-metals stream, 85% lower in the moderate-metals stream, and absent in the high-metals stream. Shredder production was similar between the reference and low-metals streams, and ≈70% -95% lower in the moderate- and high-metals streams, respectively. Total production of collector-gatherers and predators was highly variable, but exhibited a declining trend along the metal gradient. Collector-filterer production was about 3X higher in one reference and the moderate-metals stream than in the remaining streams.

DISCUSSION

Comparative analyses of secondary production are useful for relating variation in individual and population energetics to ecosystem level processes. By estimating secondary production of several species along a pollution gradient, we were able to link patterns in population abundances associated with metal contamination to population energetics and, tentatively, to ecosystem processes. Production analyses of functional feeding groups indicated the importance of herbivory, and the likelihood that low-moderate metal contamination has far reaching effects on energy flow in these ecosystems.

Metal-induced reductions of heptageniid population density have been well documented in the Rocky Mountains. Clements et al. (2000) reported negative correlations of heptageniids and metal contamination across 80+ streams throughout Colorado. Similar findings were reported among six streams (Kiffney and Clements 1996), above and below metal inputs on a single stream (Clements 1994), before and after metal remediation (W. Clements, unpublished data), and in experimental microcosms (Kiffney and Clements 1996). These studies also reported that baetid mayflies tended to be more metal tolerant than heptageniids. Based on these studies we conclude that reductions in the productivity of metal-sensitive heptageniid mayflies was primarily due to reductions in population biomass resulting from toxicity.

Observed growth rates in the field generally support the conclusion that reductions in mayfly production were largely due to lower biomass in polluted streams. Because growth rates of metal-tolerant baetids and metal-sensitive *E. longimanus* were similar among streams, among-stream variation in production of these species was due to differences in population biomass. Higher production of *Cinygmula* spp. in reference streams relative to polluted streams was also due to higher biomass. Apparently high growth of *Cinygmula* spp. in the moderate-metals stream was due to a shorter larval period. In all other streams, *Cinygmula* spp. first instars appeared in fall, overwintered as early instars, and grew quickly the following spring and summer. In contrast, *Cinygmula* spp. in the moderate-metals stream appeared in spring and immediately began rapid growth, which resulted in a faster growth rate than in other streams. These differences in the life-histories of *Cinygmula* spp. may be due to taxonomic difficulties. Unfortunately, species-level identification of Rocky Mountain species is not possible for this genus (Ward and Kondratieff 1992). Slightly lower growth rates of *R. robusta* in the moderate-metals stream than in the reference streams may have contributed to lower production in the former, but because biomass was also much lower in the moderate-metals stream the effects of each mechanism cannot be separated.

Results from the growth experiment apparently contradict observed growth rates in the field. Our hypothesis that periphyton quality and quantity would be reduced in polluted sites was supported by the observed reduction in growth of *B. tricaudatus* in experimental microcosms. However, growth of *B. tricaudatus* and most other mayflies was similar among streams. Even though insects from the polluted streams had elevated metal concentrations in their food and tissues (D. Carlisle, unpublished data), they were still able to maintain growth rates similar to animals in unpolluted streams. There are at least two explanations for this contradiction. First, through either genetic or physiological acclimation these animals may be able to detoxify metals at no energetic cost. This is, however, contrary to the findings of others (Weis and Weis 1989, Beyers et al. 1999). A second possibility is that there is an energetic cost for living in a polluted environment, but individuals are able to compensate by consuming more food. Low population abundances in metal-polluted streams may allow greater per capita consumption, thereby offsetting the effects of lower food quality and quantity. Hawkins (1986) demonstrated a similar pattern in several Oregon streams that differed in food quality and quantity. Increased consumption has been observed in a variety of animals feeding on low quality food (Chen and Folt 1993, Wheeler et al. 1998).

Estimates of annual P/B ratios suggested that life-histories of sensitive taxa may have been altered in metal-polluted streams. Annual P/B ratios were variable, and higher in contaminated sites for only two taxa, *E. longimanus* and *Prosimulium* spp. However, closer examination of the interplay between life-histories and temporal trends in contamination lends additional insight. Early instar heptageniid mayflies may be more sensitive to metals than later instars (Kiffney and Clements 1996), and first appeared in the fall in reference and low-metals streams. Metal contamination in the moderate- and high-metals streams was highest in the fall. Heptageniid taxa that persisted in the moderate-metals stream had life different life histories than those in less polluted streams. *Epeorus longimanus* exhibited a 3-fold increase in population turnover time (compared to less polluted streams) because early instars appeared in the spring. Similarly, unlike in any other stream *Cinygmula* spp. early instars appeared in spring in the moderate-metals stream. *Rhithrogena robusta* exhibited a semi-voltine life cycle in streams adjacent to the moderate-metals stream. However, *R. robusta* in the moderate-metals stream exhibited a univoltine life cycle, in which larvae grew rapidly during the summer and reached late instars by autumn. Thus, through delayed hatching or altered voltinism, heptageniid taxa that persisted in the moderately polluted stream avoided exposure of early instars to high metal levels. Among-stream variation in life history for a given species is not uncommon and may result from adaptations to local temperature, food, and environmental stress (Wallace and Anderson 1996). If chronic metal contamination also applies selective pressure on life history, it is possible that life history alterations of sensitive mayfly taxa in polluted streams are the result of temporal dynamics of metal toxicity.

Huryn and Wallace (2000) hypothesized that assemblages in environments where the risk of larval mortality is high would posses life histories that maximize growth rate in lieu of body size. Our results indicate that on average, high growth rates and small body size may be optimal in moderately-polluted streams. However, results from the high-metals stream suggests that the environment may set limits on how far growth rates can be maximized. Extremely low primary productivity (D. Carlisle, unpublished data) is likely to limit growth much more than body size in highly polluted environments. Consequently, trade-offs between growth rate and body size may be limited in highly polluted environments.

Patterns of functional group production indicated that some ecosystem processes may be sensitive to metal contamination in Rocky Mountain streams. Functional composition and production of functional groups were similar between reference streams, which suggests a general pattern may be observable in unpolluted streams in this region. The dominance of scraper production highlights the importance of primary production in the ecosystem energetics of these high elevation streams (Minshall 1978, Fisher et al. 1982, Benke et al. 1988). The relatively minor role of shredders and filtering-collectors was also expected given the paucity of riparian vegetation and organic FPOM in these headwater streams (Vannote et al. 1980). Although assignment of taxa to functional feeding groups is based on morphology and behavior in addition to resource use (Merritt and Cummins 1996) and therefore has some limitations (Hawkins and MacMahon 1989, Statzner and Resh 1993), functional categories nevertheless indicate general patterns in both resource use among ecosystems (Merritt and Cummins 1996).

At Zn levels approaching the chronic criterion value (e.g., Buckskin Creek), few changes in the composition of functional groups were observed. However, total production of collector-gatherers, scrapers, predators, and to a lesser extent shredders was lower in this stream. This was largely due to reductions in the biomass of most taxa in these groups. Most measures of community structure in the low-metals stream were not different than in the reference streams, which implies that changes in community structure may not be reflected in ecosystem processes. It is possible that reductions in ecosystem process rates occur at Zn concentrations considered safe for aquatic life, and these changes occur through widespread reductions in population biomass rather than losses of entire populations.

A more drastic change was observed in the moderate-metals stream (Mosquito Creek). Large reductions in population biomass of metal-sensitive taxa (primarily heptageniids) led to much lower production of scrapers. Baetid mayflies and orthoclad midges are collector-gatherers and more tolerant of metals than heptageniids. As a result, this functional feeding group dominated assemblage productivity in the moderate-metals stream. Given the abundance of metal-tolerant primary consumers, the maintenance of the relative role of predator productivity in this stream was not surprising. However, total production of functional groups declined sharply, with the exception of collector-filterers and gatherers. Reduced scraper and shredder productivity implies that herbivory and coarse detritus processing was also reduced in the moderate-metals stream. Schultheis et al. (1997) also observed reductions in leaf-litter decomposition in metal-polluted streams in Virginia. Trophic structure was extremely simplified in the high-metals stream, where Zn concentrations were > 5X the chronic value. Functional composition was dominated by collector-gatherers, with equal contributions from predators, shredders, and collector-filterers. However, the actual production of these groups was a small fraction of what occurred in less-polluted streams. It is therefore likely that most, if not all, ecosystem processes are suppressed in systems where metals levels exceed 5X the chronic value. Hill et al. (1997) reported reductions in benthic primary production and respiration in a nearby Colorado stream with similarly high metal concentrations.

Our estimates of secondary production compare reasonably well with estimates from streams in other regions. Heptageniid mayfly production in our unpolluted streams was within the ranges reported for other western U.S. and Appalachian streams (Robinson and Minshall 1998, Stone and Wallace 1998) In contrast, our estimates of *Baetis* spp. production were generally lower than other reports (Peterson et al. 1993, Benke and Jacobi 1994, Robinson and Minshall 1998). Our estimates of Chironominae and Orthocladiinae production were equal to the modal values for estimates from around the world (Tokeshi 1995). This is not surprising because we used globally-averaged values of P/B to estimate production. Our estimates of chironomid production were clearly rough approximations, and growth estimates from high altitude systems are necessary before more accurate estimates can be made. Our results do support a general observation that although chironomids often dominate the macroinvertebrate assemblage in both biomass and density, production is generally quite low in colder climates (Tokeshi 1995). However, given the possibility of extremely high population turnover rates for chironomids (Benke 1998), it is imperative that better production estimates be made of this family to understand stream trophic dynamics. Our estimates of total invertebrate production were also similar to streams from many different regions. Mean annual temperatures in streams with similar productivity ranged from 8-12 °C (Benke 1993). These results suggest that sub-alpine streams in the Rocky Mountains are as productive as streams from warmer climates. An equally striking result is that our total production estimate for Snake River, the most polluted stream, is the lowest reported for any stream in the world (Benke 1993).

Despite their ecological and recreational importance, studies of ecosystem functions in headwater Rocky Mountain streams are rare. Our study was the first to estimate total macroinvertebrate assemblage productivity in Rocky Mountain streams, and to relate this functional measure to an environmental stressor. Although macroinvertebrate productivity in these streams is comparable to more thoroughly studied systems, our results suggest that ecosystem functions may be compromised in streams with low-moderate Zn levels. Given that >30% of streams in the southern Rocky Mountain ecoregion contain metals >2X the chronic criterion (Clements et al., 2000), the effects of metal pollution on stream energetics may be widespread.

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LITERATURE CITED

Benke, A.C. 1993. Concepts and patterns of invertebrate production in running waters. Edgardo Baldi Memorial Lecture. Verhandlungen Der Internationalen Vereinigung Fur Theoretische Und Angewandte Limnologie **25**:15-38.

Benke, A.C. 1996. Secondary production of macroinvertebrates. Pages 557-578 *in* F. R. Hauer and G.A. Lamberti, editors. Methods in stream ecology. Academic Press, San Diego, California, USA.

Benke, A.C. 1998. Production dynamics of riverine chironomids: Extremely high biomass turnover rates of primary consumers. Ecology **79**:899-910.

Benke, A.C., C.A.S. Hall, C.P. Hawkins, R.H. Lowe-McConnel, J.A. Stanford, K. Suberkopp, and J.V. Ward. 1988. Bioenergetic considerations in the analysis of stream ecosystems. Journal of the North American Benthological Society **7**:480-502.

Benke, A.C., A.D. Huryn, L.A. Smock, and J.B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society **18**:308-343.

Benke, A.C., and D.I. Jacobi. 1994. Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. Ecology **75**:1219-1232.

Benke, A.C., and J.B. Wallace. 1997. Trophic basis of production among riverine caddisflies: Implications for food web analysis. Ecology **78**:1132-1145.

Benke, A.C., and J.B. Wallace. 1997. Trophic basis of production among riverine caddisflies: Implications for food web analysis. Ecology **78**:1132-1145.

Beyers, D. W., J. A. Rice, W. H. Clements, and C. J. Henry. 1999. Estimating physiological cost of chemical exposure: Integrating energetics and stress to quantify toxic effects in fish. Canadian Journal of Fisheries and Aquatic Sciences **56**:814-822.

Brey, T. 1990. Confidence-limits for secondary production estimates - application of the bootstrap to the increment summation method. Marine Biology **106**:503-508.

Caruso, B. S., and R. C. Ward. 1998. Assessment of non-point source pollution from inactive mines using a watershed-based approach. Environmental Management **22**:225-243.

Chen, C. Y., and C. L. Folt. 1993. Measures of food quality as demographic-predictors in fresh- water copepods. Journal of Plankton Research **15**:1247-1261.

Clements, W. H. 1991. Characterization of stream benthic communities using substrate-filled trays: Colonization, variability, and sampling selectivity. Journal of Freshwater Ecology **6**:209-221.

Clements, W. H. 1994. Benthic invertebrate community response to heavy metals in the upper Arkansas River basin, Colorado. Journal of the North American Benthological Society **13**:30-84.

Clements, W. H., D. M. Carlisle, J. M. Lazorchak, and P. C. Johnson. 2000. Heavy metals structure benthic communities in Colorado mountain streams. Ecological Applications **10**:626-638.

Clements, W. H., and P. M. Kiffney. 1995. The influence of elevation on benthic community responses to heavy metals in Rocky Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences **52**:1966-1977.

Clesceri, L. S., A. E. Greenberg, and A.D. Eaton. 1998. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, D.C., USA.

CDPHE. 1999. Colorado Department of Public Health and Environment, Water Quality Control Commission. The basic standards and methodologies for surface water. **5 CCR 1002-31.**

Efron, B. 1982. The Jacknife, the bootstrap and other methods in statistics. Society for Industrial and Applied Mathematics. Philadelphia, Pennsylvania, USA.

Elliott, J. M. 1971. Some methods for the statistical analysis of samples of benthic macroinvertebrates. Freshwater Biological Association Scientific Publication 25.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs **52**:93-110.

Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224-239 *in* C. G. Jones and J.

H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Grime, J.P. 1997. Biodiversity and ecosystem function: The debate deepens. Science **277**:1260-1261.

Hatakeyama, S., H. Shiraishi, and S. Uno. 1997. Overall pesticide effects on growth and emergence of two species of Ephemeroptera in a model stream carrying pesticide-polluted river water. Ecotoxicology **6**:167-180.

Hauer, F. R., and A. C. Benke. 1991. Rapid growth of snag-dwelling chironomids in a blackwater river - the Influence of temperature and discharge. Journal of the North American Benthological Society **10**:154-164.

Hawkins, C.P. 1986. Variation in individual growth-rates and population-densities of ephemerellid mayflies. Ecology **67**:1384-1395.

Hawkins, C.P., and J. A. MacMahon. 1989. Guilds-the multiple meanings of a concept. Annual Review of Entomology **34**:423-451.

Hill, B. H., J. M. Lazorchak, F. H. Mccormick, and W. T. Willingham. 1997. The effects of elevated metals on benthic community metabolism in a Rocky Mountain stream. Environmental Pollution **95**:183-190.

Huryn, A. D. 1990. Growth and voltinism of lotic midge larvae - patterns across an Appalachian Mountain basin. Limnology and Oceanography **35**:339-351.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnology and Oceanography **41**:243-252.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology **45**:83-110.

Kiffney, P. F., and W. H. Clements. 1994. Effects of metals on a Rocky Mountain stream macroinvertebrate assemblage in experimental microcosms. Journal of the North American Benthological Society **13**:511-523.

Kiffney, P. D., and W. H. Clements. 1996. Effects of metals on stream macroinvertebrate communities from different altitudes. Canadian Journal of Fisheries and Aquatic Sciences **6**:472-481.

Koetsier, P., G. W. Minshall, and C. T. Robinson. 1996. Benthos and macroinvertebrate drift in six streams differing in alkalinity. Hydrobiologia **317**:41-49.

Krueger, C. C., and T. F. Waters. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology **64**:840-850.

Lawton, J. H. 1994. What do species do in ecosystems? Oikos **71**:367-374.

Lehmkuhl, D. M. 1979. Environmental disturbance and life histories: Principles and examples. Journal of the Fisheries Research Board of Canada **36**:329-334.

Leland, H. V., S. V. Fend, T. L. Dudley, and J. L. Carter. 1989. Effects of copper on species composition of benthic insects in a Sierra Nevada, California, stream. Freshwater Biology **21**:163-179.

Medley, C. N., and W. H. Clements. 1998. Responses of diatom communities to heavy metals in streams: The influence of longitudinal variation. Ecological Applications **8**:631-644.

Merritt, R. W., and K. W. Cummins. 1996. An Introduction to the Aquatic Insects of North America. Kendall/Hunt, Dubuque, Iowa, USA.

Meyer, J. S., C. G. Ingersoll, L. L. McDonald, and M. S. Boyce. 1986. Estimating uncertainty in population growth rates: Jacknife vs. bootstrap techniques. Ecology **67**:1156-1166.

Minshall, G. W. 1978. Autotrophy in stream ecosystems. BioScience **28**:767-771.

Mulvey, M., and S.A. Diamond. 1991. Genetic factors and tolerance acquisition in populations exposed to metals and metalloids. Pages 301-321 *in* M. C. Newman and A. W. McIntosh, editors. Metal ecotoxicology: Concepts and applications. Lewis Publishers, Chelsea, Michigan, USA.

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

Power, M. E. 1995. Floods, food chains, and ecosystem processes in rivers. Pages 52-60 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Robinson, C. T., and G. W. Minshall. 1998. Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. Archiv Fur Hydrobiologie **142**:257-281.

Schultheis, A. S., M. Sanchez, and A. C. Hendricks. 1997. Structural and functional responses of stream insects to copper pollution. Hydrobiologia **346**:85-93.

Statzner, B., and V. H. Resh. 1993. Multiple-site and multiple-year analyses of stream insect emergence-a test of ecological theory. Oecologia **96**:65-79.

Stone, M. K., and J. B. Wallace. 1998. Long term recovery of a mountain stream from clearcut logging: The effects of forest succession on benthic invertebrate community structure. Freshwater Biology **39**:151-169.

Tokeshi, M. 1995. Production Ecology. Pages 269-29 in P. D. Armitage, P. S. Cranston, and L. C. V. Pinder, editors. The Chironomidae: Biology and ecology of non-biting midges. Chapman and Hall, London, England.

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

Wallace, J. B., and N. H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-73 *in* R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa, USA.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology **41**:115-139.

Waters, T. F. 1969. The turnover ratio in production ecology of freshwater invertebrates. American Naturalist **103**:173-185.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research **10**: 91-164.

Weis, J. S., and P. Weis. 1989. Tolerance and stress in a polluted environment: The case of the mummichog. BioScience **39**:89-95.

Wheeler, G. S., T. K. Van, and T. D. Center. 1998. Herbivore adaptations to a low-nutrient food: Weed biological control specialist *Spodoptera pectinicornis* (Lepidoptera: Noctuidae) fed the floating aquatic plant *Pistia stratiotes*. Environmental Entomology **27**:993-1000.

Wilkinson, L. 1996. SYSTAT 8: Statistics. SPSS, Inc., Chicago, Illinois, USA.

Wilkinson, L., and L. Engelman. 1996. Bootstrapping and sampling. Pages 17-29 *in* SYSTAT 8: Statistics. SPSS, Inc., Chicago, Illinois, USA.

Wilson, J. B., 1988. The cost of heavy-metal tolerance: An example. Evolution **42**:408-413.

Table 2.1. Environmental conditions of five study streams in central Colorado, May 1998-May 1999. Zn ratio = the ratio of measured dissolved Zn concentrations to the hardness-adjusted chronic value.

Variable	Four-mile	East Fork	Buck-skin	Mos-quito	Snake
Median discharge (m^3/s)	0.241	0.168	0.270	0.428	0.198
Mean channel width (m)	3.86	3.57	4.16	3.96	4.81
Annual degree days	918	1201	939	1089	1007
Mean annual alkalinity (mg/l)	114	34	55	70	4
Mean annual total hardness (mg/l)	125	57	84	104	45
pH range	7.5-8.9	6.7-8.5	7.1-9.0	7.4-9.0	5.7-8.2
Mean annual dissolved [Zn](μg/l)	56	36	105	210	293
Mean annual Zn ratio	0.60	0.85	1.68	2.64	7.07
Mean annual conductivity	237	119	169	200	117
Watershed area (km^2)	23.32	31.16	22.10	32.20	28.99
Mean stream gradient (°)	22	25	30	26	26
Elevation (m)	3283	3202	3217	3249	3144

Table 2.2. Mean annual abundance and biomass of 18 dominant taxa in five Colorado streams, 1998.

Taxon	Abundance (No. /0.1 m^2)					Biomass (mg DM / 0.1 m^2)				
	East Fork	Fourmile	Buckskin	Mosquito	Snake	East Fork	Fourmile	Buckskin	Mosquito	Snake
Epeorus longimanus	56	57	28	13	<1	3.0	6.8	1.9	0.7	<0.1
Cinygmula spp.	162	24	9	27	<1	5.8	5.8	2.0	1.6	<0.1
Rhithrogena robusta	21	60	77	3	<1	17.6	31.9	20.0	2.2	0.2
Baetis bicaudatus	75	155	55	67	<1	1.9	10.5	3.1	3.4	<0.1
B. tricaudatus	101	32	26	66	<1	1.2	1.7	0.9	8.4	<0.1
Drunella doddsi	36	14	19	37	<1	2.6	2.9	1.3	2.5	<0.1
Megarcys signata	8	4	1	1	<1	17.4	7.3	2.7	5.8	<0.1
Kogotus modestus	4	0	0	0	0	2.56	0.0	0.0	0.0	0.0
Suwallia spp.	35	50	15	9	1	6.0	4.6	1.8	1.2	0.4
Sweltsa spp.	<1	31	16	<1	0	0.2	3.4	6.7	0.2	0.0
Zapada spp.	13	31	29	13	22	1.0	0.9	1.5	0.5	0.1
Paraleuctra spp.	13	<1	5	0	0	2.4	0.2	2.0	0.0	0.0
Taenionema pallidum	<1	23	<1	<1	0	<0.1	0.5	<0.1	<0.1	0.0
Doddsia occidentalis	57	23	19	7	0	0.9	0.5	0.4	0.0	0.0

Arctopsyche grandis	3	0	0	4	<1	9.7	0.0	0.0	3.5	<0.1
Rhyacophila spp.	23	3	2	3	<1	16.8	4.9	0.7	2.3	<0.1
Prosimulium spp.	25	22	3	120	1	0.2	0.6	2.9	0.8	0.1
Chironominae	665	1256	330	206	4	20.7	36.1	11.6	0.1	0.6
Orthocladiinae	381	388	140	327	56	3.0	2.1	1.6	2.4	0.5

Table 2.3. Growth statistics for mayfly taxa in four Colorado streams, 1998-1999. Note, mayfly taxa were absent from Snake. G = 100 k and $W_t = W_0e^{kt}$, where W_t = mean mass at time t, W_0 = mean mass at time 0, and k = instantaneous coefficient of growth. Also, n = number of sampling dates, and r^2 = coefficient of determination for fit of exponential growth model.

	B. bicaudatus			*B. tricaudatus*			*Cinygmula* spp.			*E. longimanus*			*R. robusta*			*D. doddsi*		
Site	G	n	r^2	G	n	r^2	G	n	r^2	G	n	r^2	G	n	r^2	G	n	r^2
East Fork	1.52	5	0.96	7.23	4	0.96	1.26	6	0.86	4.60	5	0.92	1.16	6	0.64	1.21	9	0.87
Fourmile	1.36	7	0.86	7.19	4	0.99	1.28	7	0.86	4.64	5	0.94	1.14	12	0.86	1.33	8	0.85
Buckskin	1.22	5	0.98	6.14	4	0.96	1.29	6	0.79	2.99	5	0.98	0.60	9	0.81	1.37	7	0.88
Mosquito	1.29	6	0.95	6.66	4	0.90	8.33	4	0.90	5.01	5	0.93	0.87	6	0.75	1.33	6	0.74
ANOVA*	F = 0.489			F = 0.364			F = 12.118			F = 2.516			F = 3.633			F = 0.116		
	P = 0.69			P = 0.78			P < 0.01			P = 0.11			P = 0.03			P = 0.95		

* F-statistic and P values reported are for tests of equal G's among streams in an ANCOVA model.

Table 2.4. Summary of production (mg DM/0.1 m^2/yr) for 18 taxa collected in five streams in central Colorado, 1998-1999. P= production, CI_{upper}, CI_{lower} = upper and lower, respectively 95% confidence levels.

	East Fork		Fourmile		Buckskin		Mosquito		Snake	
Taxon	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}
E. longimanus	28.4	19.9 36.8	54.5	42.1 66.3	10.4	7.1 15.2	8.7	3.0 15.2	0.000	— —
Cinygmula spp.	65.1	37.0 96.3	23.9	17.1 33.7	8.6	5.7 11.5	12.5	8.2 15.9	0.000	— —
R. robusta	35.6	26.4 46.8	136.6	104.4 173.4	72.1	58.3 87.1	10.3	7.7 13.7	0.000	— —
B. bicaudatus	12.9	7.1 17.8	52.7	37.1 75.2	20.2	12.5 30.7	19.2	14.8 24.4	0.000	— —
B. tricaudatus	26.9	19.8 34.4	18.0	13.4 23.0	9.9	6.4 13.3	48.4	26.6 69.1	0.000	— —
D. doddsi	17.1	13.6 21.3	14.5	8.4 21.2	8.1	6.0 10.0	13.6	8.2 19.6	0.000	— —
M. signata	40.8	22.1 75.0	37.7	37.6 37.8	10.6	3.3 18.1	18.3	7.1 31.8	0.000	— —
K. modestus	29.7	15.6 49.9	0.0	— —	0.0	— —	0.0	— —	0.000	— —

Suwallia spp.	17.7	11.9 26.5	21.5	16.7 29.4	5.9	2.7 11.0	3.0	1.3 5.2	0.462	0.0 1.4
Sweltsa spp.	0.0	— —	12.6	7.5 22.0	9.6	0.8 19.7	0.0	— —	0.0	— —
Zapada spp.	2.4	1.4 3.7	2.7	2.1 3.4	4.6	3.7 5.4	2.5	1.8 3.2	0.6	0.3 1.0
Paraleuctra spp.	6.3	5.2 7.7	0.0	— —	1.1	0.7 1.8	0.0	— —	0.0	— —
T. pallidum	<0.1	— —	5.9	2.8 8.9	<0.1	— —	0.0	— —	0.0	— —
D. occidentalis	13.3	3.2 24.0	5.9	2.8 8.9	6.5	4.6 8.6	0.0	— —	0.0	— —
A. grandis	18.3	12.0 23.8	0.0	— —	0.0	— —	13.1	6.1 24.1	0.0	— —
Rhyacophila spp.	78.1	36.1 133.8	48.2	0.0 145.1	29.4	21.4 42.2	10.2	4.3 17.8	0.0	— —
Prosimulium spp.	0.9	0.0 3.6	4.4	2.1 7.0	2.7	1.0 4.6	7.0	2.8 11.9	0.5	0.0 0.9
Chironominae	46.9	20.4 84.9	76.7	35.4 127.4	25.7	10.5 40.0	0.2	0.1 0.3	1.4	0.3 2.7
Orthocladiinae	6.125	2.2 10.7	3.934	2.6 5.9	3.0	2.6 5.9	4.6	1.7 9.0	0.9	0.6 1.3

Total	**446.5**	**519.7**	**228.4**	**171.8**	**3.9**

Table 2.5. Annual P/B ratios of 18 taxa in five Colorado streams, 1998. P/B = production:biomass ratio, CI_{upper}, CI_{lower} = upper and lower, respectively 95% confidence levels.

	East Fork		Fourmile		Buckskin		Mosquito		Snake	
Taxon	P/B	CI_{lower} CI_{upper}	P/B	CI_{lower} CI_{upper}	P/B	CI_{lower} CI_{upper}	P/B	CI_{lower} CI_{upper}	P/B	CI_{lower} CI_{upper}
E. longimanus	10	7 13	13	12 14	9	7 13	27	18 41	--	— —
Cinygmula spp.	8	6 11	6	5 7	5	3 6	12	1 29	--	— —
R. robusta	3	2 4	4	3 5	7	7 7	5	4 6	--	— —
B. bicaudatus	8	6 10	5	4 6	7	5 9	6	5 7	--	— —
B. tricaudatus	37	32 45	18	16 22	22	18 26	11	9 14	--	— —
D. doddsi	8	7 9	5	4 6	5	4 6	5	4 7	--	— —
M. signata	2	1 3	6	6 6	2	1 3	3	1 4	--	— —
K. modestus	19	9 60	—	— —	--	— —	--	— —	--	— —

Suwallia spp.	3	2 4	4	3 6	4	3 6	4	3 6	2	0 9
Sweltsa spp.	--	— —	4	2 6	2	1 4	--		--	— —
Zapada spp.	6	5 7	4	3 4	3	3 4	4	3 4	2	1 3
Paraleuctra spp.	2	1 4		— —	3	2 4	--		--	— —
T. pallidum	9	2 17	11	9 12	7	5 10	--		--	— —
A. grandis	1	1 2	--	— —	--	— —	3	2 4	--	— —
Rhyacophila spp.	4	2 5	3	1 6	4	1 5	4	3 5	--	— —
Prosimulium spp.	5	2 7	7	6 8	6	4 8	11	7 19	3	0 16
Total Community	3.54		4.37		3.26		6.14		2.0	

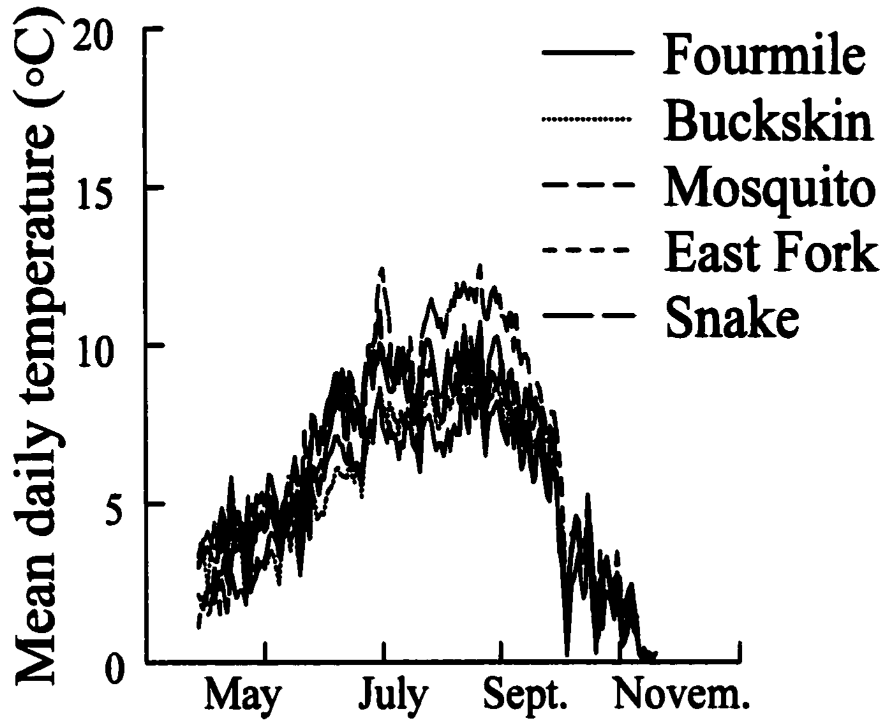

Figure 2.1. Mean daily temperature in five Colorado streams April-November 1998. Note, temperature in all streams was at or near 0° C from November-April.

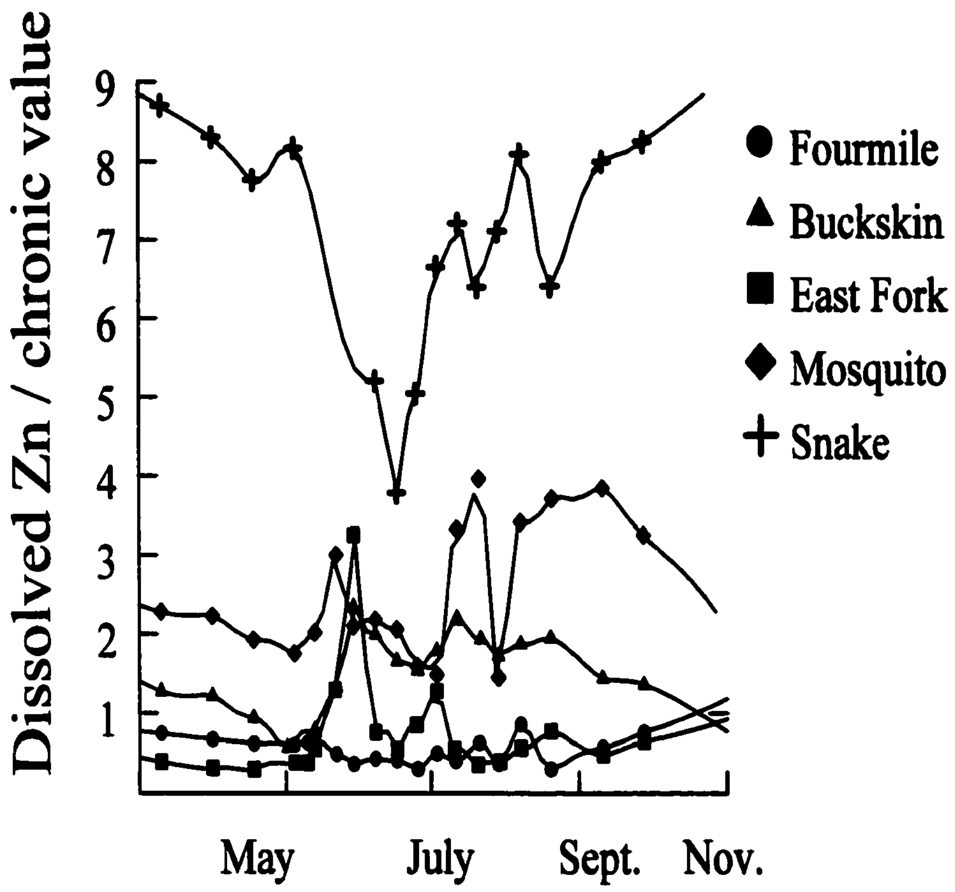

Figure 2.2. Seasonal variation in Zinc concentrations (as ratios measured dissolved Zn to the hardness-adjusted chronic criterion value) in five Colorado streams April 1998-March 1999.

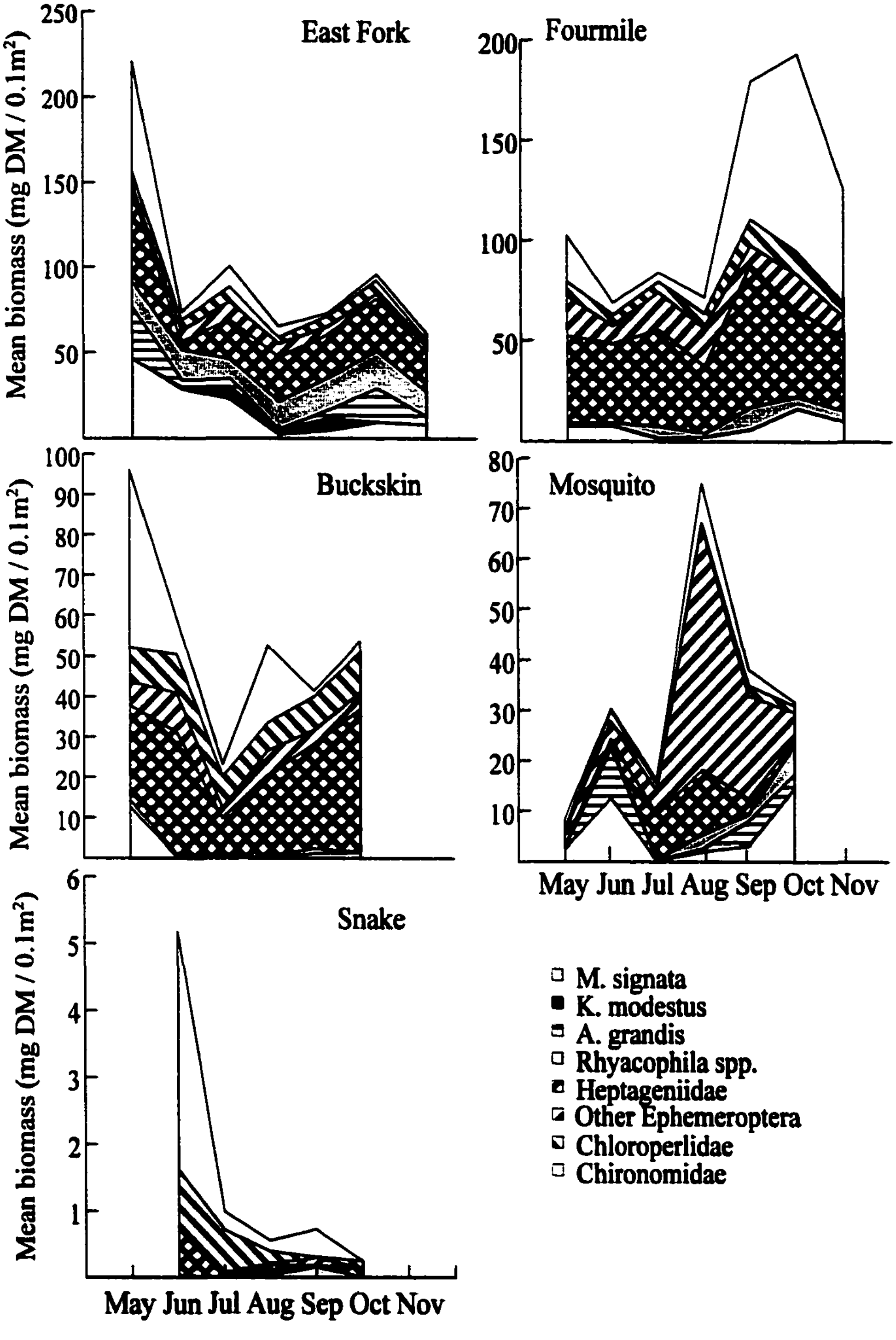

Figure 2.3. Temporal trends in the relative contribution of major taxonomic groups to total assemblage biomass in five Colorado streams, 1998. Note level of Zn contamination: East Fork = Fourmile < Buckskin < Mosquito < Snake.

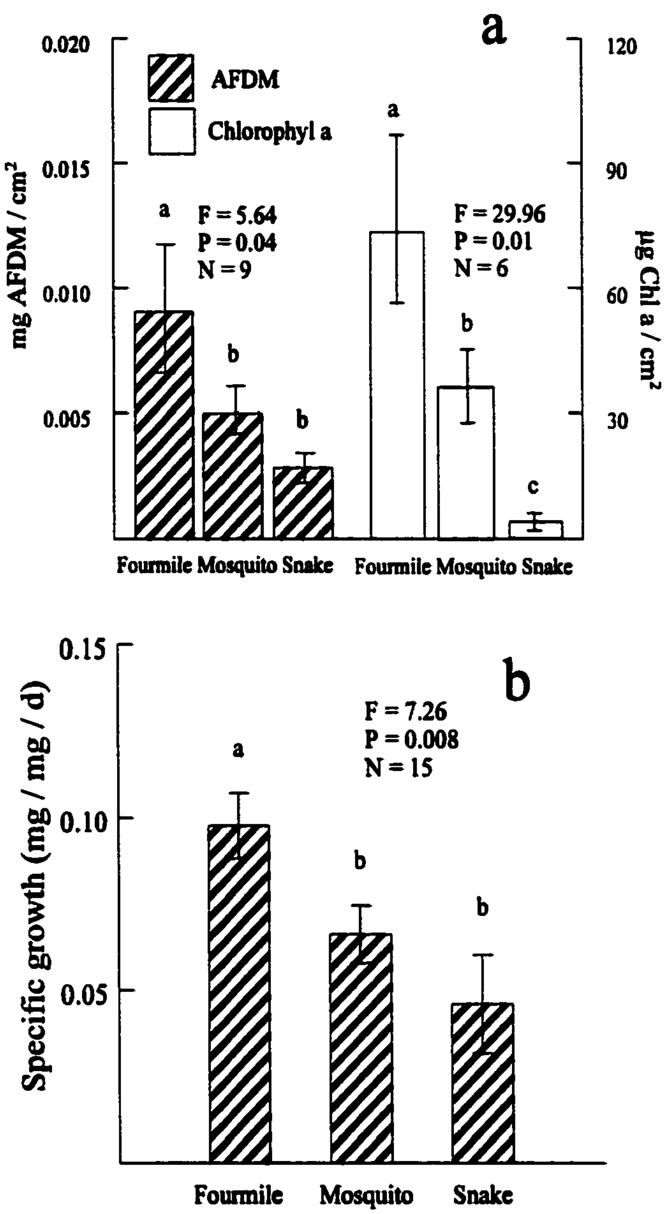

Figure 2.4. a) Periphyton biomass and chlorophyl a content ±(1se) on tiles colonized in Fourmile, Mosquito, and Snake. Bars with different letter superscripts are significantly different at $P<0.05$ (LSD post hoc test). b) Growth rates ±(1se) of *B. tricaudatus* after an eight day feeding trial on periphyton from Fourmile, Mosquito, and Snake. Bars with different letter superscripts are significantly different at $P<0.05$ (LSD post hoc test).

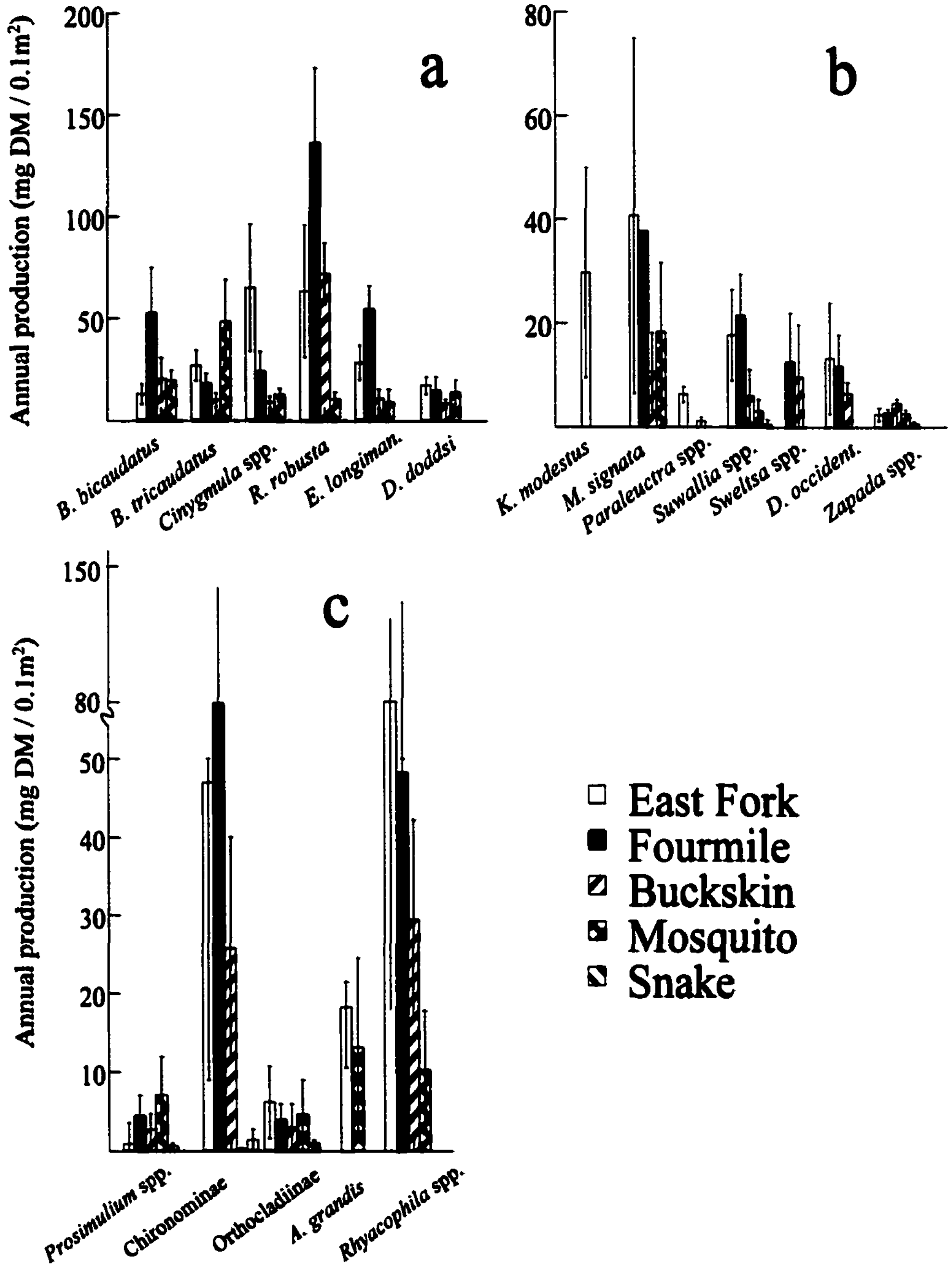

Figure 2.5. Annual production of 18 taxa in five Colorado streams, 1998. Error bars represent 95% confidence intervals derived from bootstrapping. Note level of Zn contamination: East Fork = Fourmile < Buckskin < Mosquito < Snake.

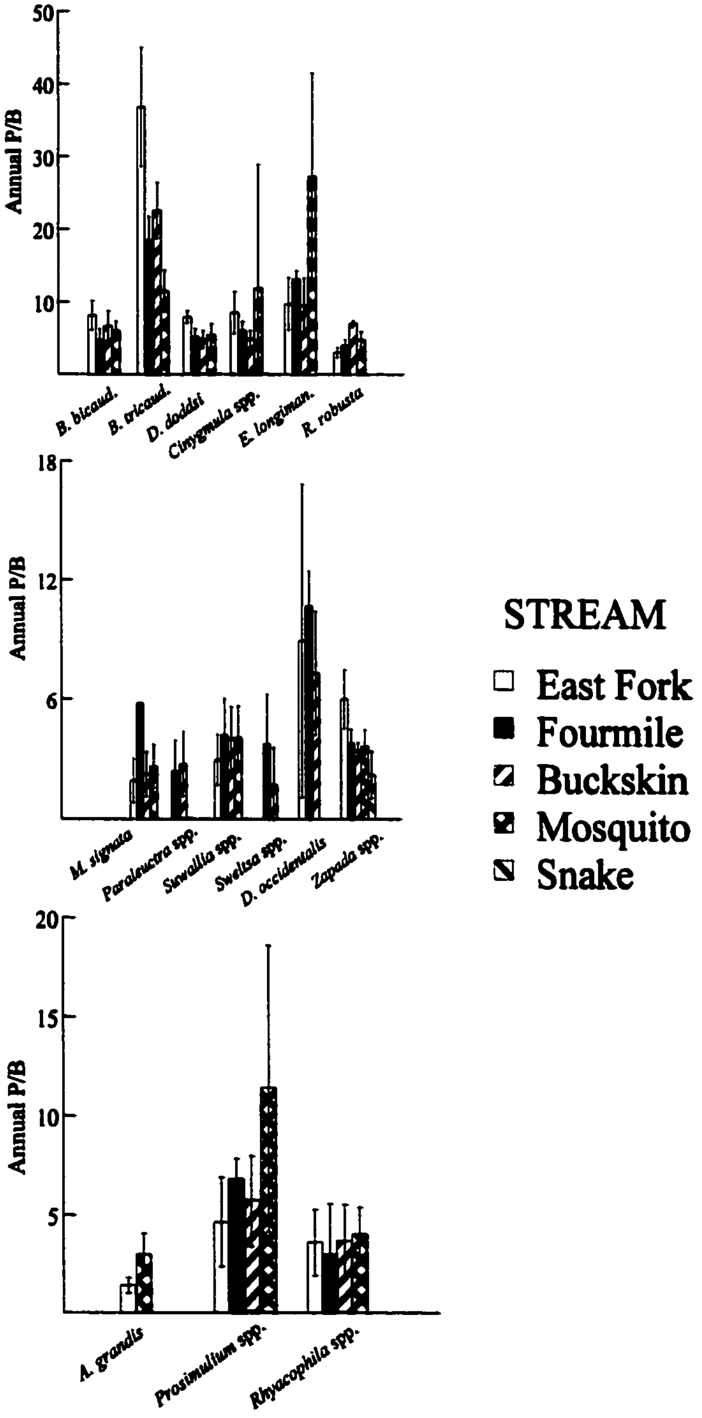

Figure 2.6. Annual P/B ratios of 18 taxa in five Colorado streams, 1998. Error bars represent 95% confidence intervals derived from bootstrapping. Note level of Zn contamination: East Fork = Fourmile < Buckskin < Mosquito < Snake.

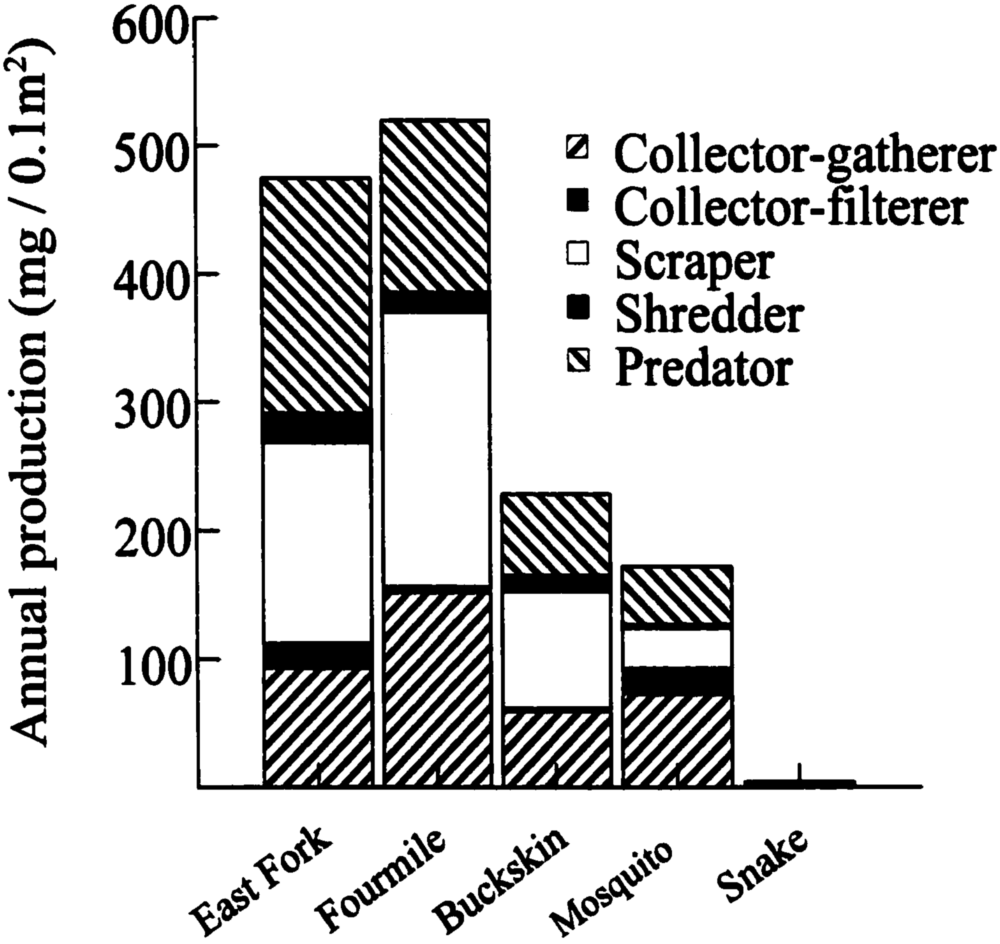

Figure 2.7. Relative contribution of functional groups to total macroinvertebrate production in five Colorado streams, 1998. Note level of Zn contamination: East Fork = Fourmile < Buckskin < Mosquito < Snake.

CHAPTER 3:

SPATIOTEMPORAL VARIATION OF ENERGETIC FOOD WEBS ALONG AN ENVIRONMENTAL GRADIENT

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ABSTRACT

Energetic-based food webs provide insights into trophic dynamics and the roles of species in ecosystem processes. We used energetic-based food webs to test several hypotheses about potential effects of chronic metal contamination on stream ecosystem structure and function. We quantified energetic food webs in five high elevation streams that were differentially affected by metal contamination. Seasonal estimates of consumption for each population were made by using energetic principles of assimilation and growth efficiency, and estimates of diet composition and secondary production. Uncertainty was quantified by bootstrapping estimates of production, diet composition, and energetic efficiencies. Connectance and linkage density were generally consistent among streams, but significantly different in the highly contaminated stream. Web linkage strength (measured as average energy flux / link) declined with increasing metal contamination. Results suggested that energy fluxes changed markedly along the contamination gradient even though trophic structure changed only in the most polluted site. Most energetic fluxes through food webs were dominated by a small number of species. Metal-sensitive Heptageniidae mayflies and Tanytarsini (Chironomidae) dominated energetic fluxes in reference streams. Energetic fluxes in low and moderately contaminated streams were limited to metal-tolerant mayflies. We conclude that ecosystem energetics in these streams is controlled by a few species and, consequently, do not exhibit redundancy when species are lost or populations decline as a result of human disturbance.

INTRODUCTION

Food webs are an intuitive approach to studying trophic and community dynamics (Pimm 1982, Levin 1992), and are the basis of intensive research and debate (see reviews by Pimm 1982, Cohen et al. 1990, Polis 1991, Polis and Winemiller 1996). Food web structure and dynamics may influence species diversity (Hutchinson 1959, Leibold 1996), ecosystem structure (Polis and Strong 1996, Hairston and Hairston 1997), ecosystem processes (Covich et al. 1999), and human use of natural systems (Winemiller and Polis 1996, Schlapfer and Schmid 1999).

The basic building blocks of food webs are links between nodes (usually species), and have been quantified in at least four ways. One approach is to represent each link on a binary (e.g., present/absent) scale. Scores of food webs from a variety of ecosystems have been assembled in this manner and have been used to search for broad patterns in food web structure (Pimm 1980, Pimm et al. 1991), relate food web structure to environmental gradients (Briand 1983, Briand and Cohen 1987), and relate food web structure to community stability (Auerbach 1984, DeAngelis et al. 1989). Aside from numerous methodological problems (Paine 1988, Polis 1991, Winemiller and Polis 1996), this approach provides no information on the importance of links. Nonetheless, food webs assembled with binary linkages provide an informative-- if not heuristic-- view of ecosystems and a source of hypotheses regarding community and ecosystem dynamics (Paine 1988).

Another method to quantify food web linkages is to weight each link based on its relative contribution to the consumer's diet (e.g.,Tavares-Cromar and Williams 1996).

Links quantified in this manner lend additional insight into the relative importance of trophic relationships, and some researchers (Taveres-Cromar and Williams 1996) have used these weights to identify linkage strength (sensu Paine 1992). However, this approach does not consider the relative importance of each food item to the consumer or the actual flux of materials through consumer populations. Furthermore, relatively rare food items that provide a disproportionate contribution to consumer growth are under-represented.

A more rigorous method of quantifying food web links is to manipulate populations in the food web (sensu Paine 1966, 1992). Links are established based on the relative importance of consumers in controlling their prey populations, and are indicative of species interactions that control community structure. This approach has led to the identification of keystone species in a variety of ecosystems (Power et al. 1996), and has significant applications in efforts to understand the role of species in controlling ecosystem structure and function (Covich et al. 1999). Although this approach reveals processes that control ecosystem structure, it does not indicate material fluxes that are ultimately manifested in ecosystem functions.

Food web links may also be quantified in terms of energy flow (Baird and Milne 1981, De Ruiter, et al. 1996, Ulanowicz 1997, Hall et al. 2000). Although less common than other approaches, quantification of energy fluxes is necessary to understand material flows and species interactions in ecosystems (Hairston and Hairston 1993 and 1997). The flow of energy among populations is manifested as consumption, which can be estimated using energetic principles at the individual and population levels. Although energetic pathways may not reveal the species interactions that control trophic structure (Paine 1992, Raffaelli and Hall 1996), they provide valuable information on the relative roles of populations in transferring energy and materials through ecosystems, which lends insights into the role of species in ecosystems (sensu Jones and Lawton 1995).

An aspect of food web research that has largely been ignored is the quantification (recognition?) of uncertainty associated with linkage estimates. Estimates of linkages based on observational data are no different than any other estimate based on sampling a population. In cases where linkages are quantified by experimentation, experimental error clearly cannot be ignored. Variance and associated confidence limits would facilitate more rigorous comparisons of linkages among and within food webs, and indicate the uncertainty with which linkages were quantified. Variation in linkage strengths has received only recent theoretical attention (Berlow et al. 1999), and we have not found an empirical study that reported uncertainty associated with linkage quantification.

Ecologists have begun to recognize the influence of spatiotemporal variation on trophic structure and function (Polis et al. 1996, Polis et al. 1997). Recent investigations have shown that seasonal changes in food availability (Closs and Lake 1994, Jaarsma et al. 1998) and ontogenic shifts in the diets and habitats of species (Tavares-Cromar and Williams 1996) are reflected in food web structure and dynamics. Spatial variation in trophic structure and dynamics may result from major environmental gradients such as productivity (Polis et al. 1996, Polis et al. 1997).

Ecological studies along environmental gradients can reveal the interplay between biotic and abiotic controls of trophic structure and dynamics (Dunson and Travis 1991, Menge et al., 1996). Ideally, controlled experiments are performed along dominant gradients such as disturbance regimes (e.g., Dayton 1971). However, because experiments are not always possible (Diamond 1984, Polis et al. 1996), comparative approaches augmented with more practical experiments are a necessary compromise.

Human perturbations are a major source of environmental gradients in nature (Vitousek et al. 1997). For example, more than 40% of surveyed rivers and streams in the United States are degraded by anthropogenic contaminants (U.S. EPA 1996). Discussion among the public, legislators (Clean Water Act 1977), and scientists (Lubchenco et al. 1991, Lubchenco 1998) has highlighted the need to apply basic ecological principles to identify and restore degraded ecosystems. Despite this widespread recognition, there is still a growing need to link population and ecosystem ecology with environmental toxicology (Levin et al. 1984, Levin 1992). Toward this goal, food web research can provide valuable insights into the ecological consequences of human disturbance.

Our overall research objective was to determine the ecological significance of a chronic anthropogenic stressor on stream ecosystems. Our main approach was to quantify temporally explicit food webs along a gradient of metal contamination in five Rocky Mountain watersheds. Metal pollution is a major factor structuring stream ecosystems in the southern Rocky Mountains (Clements et al., 2000). Further, the relatively simple food webs of high elevation ecosystems facilitate food web research (Pennak 1989). Food webs are useful for linking ecological sub-disciplines (Martinez 1995), and an energetics-based approach provides a common "currency" (e.g., energy) to link individual- and population-level dynamics to ecosystem structure and function. We tested three hypotheses relating environmental stress to aspects of ecosystem structure and function. Specifically, we predicted that 1) linkage strength and trophic complexity would decline in disturbed systems (Menge and Sutherland 1987, Ulanowicz 1996), 2) relative effects of disturbance (e.g., contamination) would differ across trophic levels (Power et al. 1996), and 3) energy flow would become dominated by detrital sources in polluted systems (Odum 1985). Based on previous studies we also predicted that trophic dynamics would be related to species' life histories (Polis et al. 1996, Polis et al. 1997), temporal scale (Polis et al. 1996, Polis et al. 1997), and food web structure (Covich 1996, Covich et al. 1999).

METHODS

Study sites

This study was conducted on five 2nd-3rd order streams in the Colorado Rockies (Figure 3.1). The watersheds are typical U-shaped glacial valleys containing high gradient streams. About 25% of the watershed land cover is bare rock, especially at high elevations (up to 4200 masl). Sub-alpine tundra and alpine willow (*Salix* spp.) are the dominant vegetation, and are accompanied by scattered evergreens in valley bottoms at lower elevations (<3300 masl). The geology is dominated by metamorphic gneisses and felsic composites, and is covered by a thin layer of loamy skeletal soils. Riparian vegetation is mostly *Salix* spp. and open meadow, and provides sparse canopy cover. Streams at this elevation are ice- and snow-covered for 6-7 months each year, followed by a characteristic snowmelt-driven hydrograph in late June-early July. The streams are dominated by small to large cobble substrate and riffles. We selected a 500 m study reach on each stream that was similar in elevation and valley form.

Field sampling

We sampled water chemistry bi-monthly from May-September and monthly throughout the rest of the year. Two 15 ml water samples were taken from a riffle. One was passed through a 0.45 um filter and used to measure dissolved metals. Both samples were then acidified with reagent grade nitric acid to $pH < 2$. A 1-l grab sample was also taken from mid-stream and stored on ice for laboratory determination of alkalinity and total hardness. Acidity was measured with a hand-held probe (Quickchek® models 106, 116, Orion Research, Inc., Beverly, MA). Temperature was monitored continuously with data loggers (Optic StowAway ®, Onset Computer Corp., Pocasset, MA). Discharge was estimated using the continuity equation: $Q=wdv$, where w = mean channel width, d = mean depth, and v = mean velocity. Width, depth, and velocity measurements were made at 20 cm increments at channel cross-sections free from turbulent flow and obstructions, and were made at the same location in each stream throughout the ice-free period.

Benthic insects were sampled monthly during the ice-free season using two methods. Five quantitative ($0.1 m^2$) Hess samples were collected with 150 μm mesh nets and preserved in 5% formalin. Other insects were collected bi-monthly for gut analyses. At least six riffles were sampled with a 1 m^2 kick net (1 mm mesh size). These insects were separated from debris in white enamel pans, anesthetized with CO_2, and preserved in 10% formalin.

Laboratory methods

Metal concentrations were measured on an atomic adsorption spectrophotometer. Because metal toxicity is influenced by water hardness (Sprague 1995), among-stream comparisons of actual metal concentrations do not reflect potential biological effects. Consequently, we standardized all metal concentrations using chronic criterion values (CCVs) recommended by U.S. EPA (CDPHE 1999). CCVs represent the contaminant concentration that, if exceeded, may cause ecological degradation. Location-specific CCVs for metals are calculated as the ratio of measured concentration and the hardness-adjusted CCV and represents the expected level of toxicity. For example, a ratio near unity implies that observed metal concentrations after adjusting for hardness are near the CCV, and are considered ecologically benign. In contrast, a ratio >1 implies that metal concentrations are potentially toxic to biological systems. Ratios of the CCV therefore allow coarse comparisons of metal toxicity among different streams. In this research, we present both the ratio of each metal to the CCV and the actual measured concentrations.

Benthic samples were processed using a two-step procedure. First, each sample was placed in a white enamel pan under intense light. All organisms > 1 mm were removed, as were large organic and inorganic debris. The remaining sample was then sub-sampled. Each sub-sample was examined under a 40X dissecting scope, and all organisms were removed. Sub-sampling continued until at least 300 individual organisms had been removed, or 12 sub-samples (collectively representing ≈20% of the whole sample) had been examined (Elliott 1971). A minimum of three sub-samples was taken from each sample. Insect taxa were identified to species or subfamily (chironomids).

Diet analyses were performed differently for non-predators and predators. Non-predator fore-guts were removed with surgical scissors and the homogenized contents mounted onto microscope slides (CMC-10 mounting media, Master Chemical, Elk Grove, IL). The guts of larger insects (>5 mm) were mounted individually, whereas guts of smaller species were often combined and homogenized with up to 20 individuals. The gut contents of at least 30 individuals from each taxon were represented for each sampling period. Chironomids were mounted whole using CMC-10, which increases the transparency of soft tissues and allows observation of gut contents. At 200X magnification, the proportion of the slide containing various food categories was estimated by tabulating the frequency of each food category in an ocular grid. These categories included: diatoms, other algae, animal matter, fine detritus, and course detritus. After 100 separate particles had been enumerated, the proportion of each food category was noted. This process continued by taking additional random fields across the slide until a total of 1000 food items had been counted. The mean (n=10) frequency of each food category was used in the analyses of consumption. For predators, guts of individual animals were removed as before, and the contents were examined under a 40X dissecting scope. Intact body parts and whole organisms were then identified to genus or sub-family, and body length was measured. Body-length was converted to dry mass using the equations of Benke et al. (1999) and used to calculate the relative biomass of each prey species in the predator gut.

Community ordination

We performed multivariate ordination to evaluate how community composition varied among seasons and streams. The dominant 18 taxa were considered for the analysis, and mean monthly biomass was calculated for each taxon. Principal components analysis was performed on log (x+1)-transformed data.

Production and consumption estimates

We calculated secondary production of aquatic insects using three methods. The increment-summation method was used for species exhibiting distinct cohorts (Benke 1996). The P/B method was used for Chironomidae, and the size-frequency method was used for all remaining taxa (Benke 1996). Detailed methods for production analyses are given in chapter 2.

Seasonal consumption was estimated using a bioenergetics mass-balance model: Ingestion = Wastes + Metabolism + Activity + Growth. The energetic "costs" other than growth were combined and defined as the assimilation efficiency, or the proportion of food ingested that was available for growth. Given that individual growth is expressed as production at the population level, we defined net production efficiency (NPE) as the mass increase in population production per unit mass of food assimilated. We followed the methods of Benke and Wallace (1980) to estimate consumption. First, the relative contribution of each food type to population production was calculated as the product of gross production efficiency and the percentage of that food type eaten. Second, the relative contributions were converted to percentages and multiplied by production to obtain the amount of production attributed to that food type. Third, dividing by the gross production efficiency yielded the amount of food consumed. Because we did not directly measure NPE, we made assumptions about our species based on a range of values taken from the literature (Benke and Wallace 1980, Huryn 1996). For species with distinct cohorts, seasonal production was obtained by summing interval production across sampling dates. For all other taxa, seasonal production was estimated by multiplying total annual production by the proportion of total annual biomass within each season. Seasons were differentiated as follows: summer = June-August, fall = September-November. Winter and spring were combined, and included November-May.

In addition to trophic pathways within food webs, we also present two other aspects of trophic dynamics using our consumption estimates. First, because consumption of aquatic insect functional groups represents broad patterns of resource use (Wallace and Webster 1996), we summed consumption estimates across taxa within the functional groups defined by Merritt and Cummins (1996a, 1996b). Second, we present data for the amount of secondary production attributable to each food type. Because food varies substantially in quality and quantity consumed, this representation indicates the relative importance of different food types to energetic processes within ecosystems (Benke and Wallace 1980, Benke 1996).

Estimating uncertainty

We used bootstrapping to estimate variance and associated confidence intervals for all energetic food web links. The bootstrap is a form of Monte Carlo simulation that re-samples observed data (Efron 1982), and has proved useful where data are of unknown distributions or sufficient replication is difficult. A set of 1000 bootstrap "samples" was generated for each variable used to estimate production and consumption. These variables included density and mean body mass estimates through time and the relative proportion of each food type in the diet for each season. Bootstrap samples were also generated from a range of estimates of cohort production intervals and NPE that were obtained from the literature. This procedure resulted in 1000 estimates of consumption for each food type*species*season combination in each stream. We computed 95% confidence intervals from this vector using a bias-corrected percentile approach described by Meyer et al.(1986). Although bootstrapping may not be reliable for small (e.g., $n < 20$) samples, it provides a relative measure of uncertainty given the ranges of variables used in making consumption estimates.

Linkage strength and trophic complexity

We defined linkage strength in terms of energetic fluxes. For the sake of simplicity in our food web diagrams, we categorized consumption estimates for each link into one of five levels: 1-50, 51-100, 101-150, 151-200, and >200 mg DM/m^2. Because energy fluxes are continuously distributed, categorization as "strong" or "weak" is clearly arbitrary. We therefore compared linkage strengths by calculating a mean flux per link (F_L) as:

$$F_L = TF / L,$$

where TF = total energy flux between prey and consumers, and L = total number of links between producers and consumers. A separate calculation was made for primary and secondary consumers for comparisons among trophic levels. These calculations were made for each season within each stream.

Trophic complexity was characterized as linkage density and connectance. Linkage density is the total number of links divided by the total number of species (Pimm 1982). We also calculated lower connectance (Pimm 1982, Briand 1983, Martinez 1991), which represents the observed number of interspecific interactions divided by the possible number of interspecific interactions:

$$C_L = L*2/S(S-1),$$

where L is the total number of links in the web and S is the total number of species. Because our food webs excluded rare species, fish, microbes, and meiofauna, we made no attempt to compare these metrics with literature values of more complete food webs. Rather, these metrics were used to compare temporal and spatial variation in trophic complexity among the food webs of this study. Mean annual values of taxa richness, linkage density, number of links, connectance, and linkage strength were analyzed with ANOVA ($p=0.10$). We relaxed a priori alpha levels in anticipation of low power ($n=3$ seasons / stream).

RESULTS

Physicochemical conditions

The strongest environmental gradient among streams was water chemistry, particularly metal concentrations (Table 3.1). Watershed area and slope, valley gradient, pH, channel width, annual degree days, mean annual temperature, and elevation varied less than 1.5-fold among streams. Median discharge and conductivity varied 2-fold. In contrast, alkalinity and Zn ratios varied 28- and 12-fold, respectively. Mean daily temperatures varied from 0° (November-April) to 11° C (August), but were similar among streams (Figure 3.2). However, East Fork and Fourmile Creeks were on average the warmest and coldest streams, respectively (Table 3.1, Figure 3.2). In general, water temperatures reached the seasonal maximum in late June as spring floods receded, remained steady through July and August, then declined in early September (Figure 3.3).

We report metals data only for Zn because other metals (Cd and Cu) generally occurred at concentrations near analytical detection limits (5 µg/l). Seasonal and spatial (among-stream) variation in Zn levels was substantial (Figure 3.4). Zn levels in Fourmile Creek were consistently below the CCV, as were levels in East Fork Creek except for a short increase during runoff. Zn levels in Buckskin Creek were consistently ≈2X the CCV, and also peaked during runoff. Zn levels in Mosquito Creek varied from 2-4X the CCV, but were highest during the fall. Zn levels in Snake River showed a similar temporal pattern, but were up to 9X the CCV. For simplicity, we hereafter refer to East Fork and Fourmile as reference streams, Buckskin as the "low-metals" stream, Mosquito as the "moderate-metals" stream, and Snake as the "high- metals" stream.

Community structure

Quantitative samples yielded 39 taxa over the course of this study. Fourteen taxa were rare, which prevented production calculations. Six species of *Rhyacophila* were lumped due to uncertainty associated with early instar identification. We calculated production for the remaining 19 taxa, which represented 85-95% of the total abundance and biomass collected at all sites.

Assemblage composition varied considerably among streams (Figure 3.5). The first two factors of principal components analysis explained 50% of the variation in community structure. Because most of the taxa that loaded on factor 1 were metal-sensitive (Kiffney and Clements 1994), this axis appeared to represent the metal gradient in the environment. Interpretation of factor 2 was less clear, but taxa positively correlated with this axis had high seasonal variations in abundance and biomass. The ordination revealed that both reference streams had virtually identical communities with respect to factor 1, although Fourmile had higher biomasses of the species represented by factor 2. The low-, moderate-, and high-metals streams had progressively lower biomasses of metal-sensitive species than reference streams.

Linkage strength and trophic complexity

Some measures of trophic complexity and linkage strength varied as predicted along the contaminant gradient (Figure 3.6). Food web taxa richness was similar among all but the high metal stream, which had 5X-fewer taxa. The number of primary consumer links was similar among reference and low-metal streams (East Fork, Fourmile, and Buckskin, respectively), ≈30% lower in moderate (Mosquito), and 5X lower in high-metals (Snake) streams. There were similar numbers of secondary consumer links among one reference, low-, and moderate-metals streams, and none in the high-metals stream. Connectance was 4X higher in the high-metals stream than all other streams, which were similar. Link density was similar among reference, low-, and moderate-metals streams, but was ≈50% lower in the high-metals stream. Linkage strengths of primary consumers were not statistically different among streams, but had a declining trend with increasing metal levels. In contrast, linkage strengths of secondary consumers were generally higher in unpolluted streams than in polluted streams.

Functional guild consumption

The association between functional guild consumption and metal contamination varied seasonally (Figure 3.7). Predator consumption was generally lower in low-, moderate-, and high-metals streams than in reference streams, but this pattern was less pronounced in spring than in other seasons. Predator consumption accounted for 5-28% of total energy consumed, but did not vary with season or along the metals gradient (except in the high-metals site, where predator consumption was zero). In summer, scraper consumption was lower in low-, moderate-, and high-metals streams than reference streams. Scraper consumption accounted for 15-40% of total energy consumed, and also declined along the metals gradient. Collector-gatherer consumption was not associated with metals or season, but was consistently the dominant contributor (10-60%) to energy consumption in moderate- and high-metals streams. Collector-filterer consumption contributed 2-76% of total energy consumed, and was lower in moderate- and high-metals streams than reference and low-metals streams during summer and spring. Shredder consumption was lower in moderate-high-metals streams than reference and low-metals streams during all seasons. Shredder consumption contributed <1- 86% of total energy consumed, and decreased along the metal gradient in spring.

Sources of energy

The contribution of general food categories to community secondary production varied among streams and seasons (Figure 3.8). No energetic contributions of animal tissue were observed in the high-metals stream, and this source generally declined with increasing pollutant levels in the fall in other streams. Primary producers contributed 12-60% of secondary production, and this contribution varied little among all but the high-metals stream. In contrast, these energy sources contributed 2-4X less production in low- and moderate-metals streams than the reference streams during summer and fall.

Food web structure and energetic fluxes

Seasonal, quantitative food web diagrams (Figures 3.9a-o) summarize trophic structure and energetic fluxes in each stream. Specific ingestion rates (and associated 95% confidence intervals) used to construct food web diagrams are included in Appendix I.

Four general patterns emerged in trophic structure and dynamics among streams. First, energy fluxes were dominated by a few taxa. In reference and low-metals streams, heptageniid mayflies (*E. longimanus, Cinygmula* spp., and *R. robusta*) were the dominant herbivores, and Tanytarsini dominated detritus-based energy fluxes. Second, energetic fluxes from primary producers generally declined in polluted streams, although this trend was partially reversed by *B. tricaudatus* in low- and moderate-metals streams. Third, generally 3-4 trophic levels were represented in all but the high-metals stream, which had only 2. Fourth, there was general decline in the number of major (e.g., >100 mg DM/m^2) energy pathways among the streams that correlated with stream metal contamination.

Life history influences

The life histories of several taxa influenced food web structure and energy flow. The life history of *Doddsia occidentalis* and *Taenionema pallidum* influenced energy flow from coarse, and to a lesser extent, fine detritus. Early instars first appeared in September, grew rapidly throughout the fall and winter, and emerged in late spring. Detritus consumption was therefore high during these seasons. The other major consumer of coarse detritus (*Zapada* spp.) exhibited slower growth and development (probably semi-voltine), lower productivity, and therefore lower consumption.

Energy flow from algae and diatoms was influenced by the life history of *Baetis tricaudatus*, particularly in light and moderately polluted streams (Buckskin and Mosquito Creeks, respectively). This species exhibited a rapid life cycle, wherein early instars first appeared in late summer, grew rapidly, and emerged in early fall. This species was a significant pathway for energy flow in polluted streams during the summer and fall.

The life history of the predator *Megarcys signata* altered trophic structure in some seasons. Early instars of this species appeared in late summer and consumed mostly small primary consumers (e.g., *Prosimulium* spp., Orthocladiinae, and Tanytarsini). Growth was rapid and nymphs reached ≈ 10 mm in early fall, when they began to consume larger-bodied predator species (e.g., *Suwallia* spp. and *Rhyacophila* spp.). Consumption of larger-bodied prey continued through winter and spring. Consumption of increasingly large prey items by *M. signata* through its life history created a third trophic level in some streams.

Few taxa exhibited distinct life history omnivory. *Drunella doddsi* early instars appeared in late summer and consumed mainly detritus and diatoms throughout the fall. As they increased in size during the following spring and summer, their diet shifted to a variety of insects. In contrast, the predator *M. signata* consumed a variety of insects throughout its life, with no apparent preferences for particular prey species at different life stages.

DISCUSSION

Our study is one of only a few that quantified linkages in a stream food web. Benke and Wallace (1997) were among the first to use the trophic basis of production to quantify food webs, but their study was limited to a guild of filter-feeding caddisflies. Hall et al. (2000) quantified organic matter flow in two headwater Appalachian streams. To our knowledge, no other energetic food webs have been reported for streams. It is probably impossible to quantify all linkages in a food web, but the production-based approach facilitates the quantification of major energetic pathways. Although our food webs were incomplete (e.g., no links to fish, microbes, meiofauna, and fungal components of the ecosystem), observed spatiotemporal patterns yielded important insights into the trophic dynamics of high elevation streams, the relationships between food web structure and ecosystem processes, and the possible ecosystem-level consequences of metal contamination in Rocky Mountain streams.

Two lines of evidence suggest that among-stream differences in ecosystem structure and function were most likely due to metal contamination. First, there was wide variation in the population biomass of metal-sensitive taxa. The sensitivity to metals of heptageniid mayflies, Tanytarsini, and some stonefly taxa has been substantiated by experimental and observational studies at multiple spatial and temporal scales (Leland et al. 1989, Clements 1994, Clements and Kiffney 1995, Clements et al. 2000, Clements and Courtney, in preparation). Likewise, shifts in community composition in polluted streams to metal-tolerant species (e.g., *B. tricaudatus* and *Prosimulium*) have been documented (Leland et al., 1989, Clements and Kiffney 1995).

The second piece of evidence is that the strongest environmental gradient among streams was Zn contamination. Degree days and discharge also varied substantially among streams and may have influenced the structure and dynamics of these food webs. Temperature exerts a strong influence on individual (Hawkins 1986) and population energetics (Benke and Jacobi 1994). However, growth rates of several mayfly species were similar among streams (Chapter 2), and discharge variability was greater among years in the same stream than among streams during this study (Carlisle et al., in preparation). Hence, relative to temperature and discharge, Zn played a more important role in explaining among-stream variation in food web structure and dynamics. Furthermore, Zn levels in our study reflected the range of contamination encountered in previous, spatially extensive surveys of metal-polluted Colorado streams (Kiffney and Clements 1996, Clements et al., 2000). Consequently, the associations between ecological conditions and metals that we reported are probably representative of much of the southern Rocky Mountain ecoregion.

Linkage strength and trophic complexity

Our hypothesis that linkage strength and trophic complexity would decline in contaminated streams was partially supported. Since connectance and linkage density are scaled to taxa richness, it is not surprising that these metrics changed only in the most contaminated site, where taxa richness was 4-5X less than in the other streams. Slight reductions in linkage strength among primary consumers along the contaminant gradient were the result of species replacement and reductions in total energy flow. Energy-rich primary consumer links were maintained in low to moderately polluted streams by metal-tolerant herbivores (e.g., *Baetis tricaudatus*) and detritivores (e.g., *Prosimulium* spp.). Productivity and consumption of these species increased in polluted streams relative to the reference streams. However, these tolerant species did not completely replace the energy flowing through their respective guilds because total energy flow (measured as consumption) was substantially lower in the low to moderate-metals streams than in the reference streams, especially in summer and fall. Hence, in polluted streams the structure of food webs changed less than the magnitudes of energy flowing through them. The general decline in predator consumption was associated with metal contamination, and corresponded to a decline in predator productivity (Chapter 2). Collectively, these results suggest that energetic linkage strength and trophic complexity are generally reduced in metal- polluted streams, but pollution-tolerant species may maintain some energy flow in low-moderately polluted systems.

We recognize that trophic pathways may not reflect the biotic interactions that structure food webs (Paine 1992, Raffaelli and Hall 1996). Clearly, experimental manipulations are necessary to understand how species are dynamically related. However, quantification of dominant trophic relationships may be a more realistic goal when experimental manipulations are impractical. Energetics-based estimates of food web linkage strength provide important information about ecosystem dynamics (Hairston and Hairston 1993, Polis 1994, Jones and Lawton 1995). Benke and Wallace (1997) suggested that consumption can provide evidence for possible dynamically important web linkages. In our study, most (>80%) of primary consumer productivity was assimilated by secondary consumers. Although this observation can occur when primary consumer productivity is underestimated, we are confident that our estimates are only slightly conservative due to the unknown growth rates of chironomids. All other abundant taxa exhibited distinct cohorts, which increases confidence in the accuracy of production estimates (Benke 1993). Hall et al. (2000) reported that up to 88% of invertebrate production was consumed in

Appalachian streams. These results suggest that primary consumer populations may be under top-down control.

Trophic levels and metal contamination

Trophic dynamics can be affected by environmental stress in at least two ways, depending on the relative sensitivities of organisms within trophic levels. First, the disproportionate removal of lower trophic levels may pose energetic deficits for consumers. Power et al. (1996) found that lower trophic levels were more susceptible to disturbances than higher trophic levels, largely because mobile predators (salmonids) were able to avoid flood events that scoured substrates. An alternative view is that higher trophic levels are more susceptible to disturbance, causing a variety of responses at lower trophic levels (Menge and Sutherland 1987). However, it is uncertain whether these models apply to long-term stresses.

Data from chronically polluted streams supports the former hypothesis. Numerous experimental studies using stream assemblages have shown that predatory stoneflies are less sensitive to metals than herbivorous mayflies (Leland et al. 1989, Clements 1994, Clements and Kiffney 1995, Courtney and Clements, 2000). Our results suggest that severe chronic metal contamination was associated with shortened food chains, possibly due to energetic limitations. Although herbivorous heptageniids were the most sensitive taxa to contamination, metal-tolerant herbivores and detritivores were capable of significant energy transfer in light to moderately-contaminated streams. Energy flow to secondary consumers was lower in light to moderately-contaminated streams than in reference streams, but was apparently adequate for predator production. However, most primary consumer taxa were unable to persist at higher levels of metal contamination. Production of the primary consumers that persisted in the most contaminated stream was two orders-of-magnitude lower than in less polluted streams. Therefore, the absence of predators in the most polluted stream may have resulted from inadequate energy resources.

Energy sources in stream ecosystems

Because we quantified food web linkages based on energetics, we were able to evaluate the relative importance of primary production and detritus in ecosystem energetics. Relative to detritus, primary production contributed an equal and sometimes greater proportion of energy to primary consumer production. Previous studies of stream food webs highlighted the dominance of detritus as a basal food source (Richardson 1991, Closs and Lake 1994, Tavares-Cromar and Williams 1996). However, these conclusions may be misleading because the energetic contributions of algae were not examined. Most primary consumers in our study consumed both algae and detritus. However, because algae have higher nutritional value than detritus, it contributed more energy to consumer growth.

Odum's (1985) prediction of increasing detrital-dominance in stressed ecosystems was supported only in the high-metals stream, largely because herbivores were absent there. Primary producers maintained their importance to secondary production in low-moderately polluted streams. Maintenance of primary production is perhaps not surprising given the existence of metal-tolerant algal assemblages (Medley and Clements 1998).

Seasonality and Life-Histories

There were distinct seasonal differences in structure and energetic fluxes of food webs, largely due to shifts in life-histories, diet, and production. The algal growing season is relatively short in high elevation streams because cold temperatures and darkness limit growth during winter, followed by a period of high hydraulic stress in early summer. During these periods the relative importance of algae to consumer production was lower than in summer. Several grazing mayfly species consumed large amounts of fine detritus throughout the year, but grew most rapidly during the summer when large amounts of algae were also consumed. In a similar fashion, the magnitude of energy flow from coarse detritus varied seasonally. The highest fluxes occurred in fall and winter, corresponding to litter inputs from deciduous riparian vegetation. Marked seasonality of energy fluxes were also observed in the Appalachians (Hall et al., 2000), and seasonal differences in food web structure were reported from intermittent streams in Australia (Closs and Lake 1994). In summary, life-histories of producers and consumers driven by a harsh seasonal climate contributed to the temporal dynamics of food web structure and organic matter flows.

Functional guilds and ecosystem redundancy

Although observed patterns in trophic complexity and linkage strength along the contaminant gradient are suggestive of functional redundancy, patterns in total energy flow and detritus processing show otherwise. Functional redundancy occurs when sequential reductions in species richness do not affect ecosystem process rates due to species replacement or compensation (Lawton and Brown 1993, Frost et al. 1995). Despite the maintenance of relatively strong trophic pathways in the presence of low-moderate pollution, overall energy flow declined sharply, especially from primary producers. The inability of herbivores to maintain energy flow indicates low redundancy in the grazing guilds of Rocky Mountain headwater streams. Preliminary estimates indicate that leaf litter breakdown was significantly lower in streams with low-moderate Zn levels and corresponding low shredder consumption rates (D. Carlisle unpublished data), suggesting that decomposition also lacks redundancy in these systems.

The evidence for functional redundancy in ecosystems is mixed (McNaughton 1993, Schulze and Mooney 1993, Grime 1997, Schlapfer and Schmid 1999), especially for aquatic systems. Howarth (1991) reviewed the literature on disturbed aquatic systems and concluded that functional redundancy was a widespread phenomenon. Schindler et al. (1985) also showed strong evidence that redundancy existed in lentic ecosystems. More recently, however, Schindler (1995) and Frost et al. (1995) proposed that relatively few species may control ecosystem processes in species poor systems. Clearly, sub-alpine streams are harsh and oligotrophic environments, and our data show that they are species poor relative to other streams (Mihuc and Minshall 1995, Whiles and Wallace 1995). Because only 4 species were known to shred leaves and feed on coarse detritus, and 5 species were herbivorous, it is likely that the reduction in biomass of one or more species could have dramatic effects on material and energy flow in these streams, especially if conditions were altered by natural or anthropogenic disturbances. Our relatively coarse taxonomic resolution for some taxa (e.g., Chironomidae) probably did not detract from these observations. Taxonomic resolution was to the species level for taxa that dominated energy flow through herbivory (except *Cinygmula* spp.) and coarse detritus consumption.

SUMMARY AND CONCLUSIONS

Metal contamination was the most prominent environmental difference among these streams, and therefore likely influenced among-stream variation in food web structure and dynamics. With the exception of Snake River, the most polluted site, the presence of species and their connectedness in the food webs changed little. Rather, the production and consumption of a few metal-sensitive species changed dramatically among streams with different metal contamination, which was associated with changes in energy flow. Although heptageniid mayflies dominated energy flow in unpolluted streams, these taxa were less dominant in polluted streams because of their inherent sensitivity to metals. Had we not quantified food web linkages, contaminant-induced changes in these ecosystems would have been severely underestimated because food web structure (as measured by food web indices) changed significantly only in the most contaminated stream. Our results also indicate that overall energy flow through grazing and detritus processing were controlled by a few species, and that redundancy is low in these high-elevation Rocky Mountain streams. We observed altered patterns of ecosystem processes in a stream where Zn concentrations were at the chronic threshold value. Because dominant trophic fluxes are confined to a few species and disturbance-tolerant assemblages are less energetically efficient, we predict that contaminants near chronic levels may adversely affect ecological processes in Rocky Mountain headwater streams.

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LITERATURE CITED

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371-395 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Allan, J. D. 1982. Feeding habits and prey consumption of three setipalpian stoneflies (Plecoptera) in a mountain stream. Ecology **63**:26-34.

Allan, J. D. 1995. Stream ecology: Structure and function of running waters. Chapman and Hall, New York, New York, USA.

Auerbach, M. J. 1984. Stability, probability, and the topology of food webs. Pages 413-436 *in* D. R. Strong, Jr., D. Simberloff, L .G. Abele, and A. B. Thistle, editors. Ecological communities: Conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Baird, D., and H. Milne. 1981. Energy flow in the Ythan Estuary, Aberdeenshire, Scotland. Estuarine, Coastal and Shelf Science **13**:455-472.

Benke, A. C. 1993. Concepts and patterns of invertebrate production in running waters. Edgardo Baldi Memorial Lecture. Verhandlungen Der Internationalen Vereinigung Fur Theoretische Und Angewandte Limnologie **25**:15-38.

Benke, A.C.. 1996. Secondary production of macroinvertebrates. Pages 557-578 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, San Diego, California, USA.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society **18**:308-343.

Benke, A. C., and D. I. Jacobi. 1994. Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. Ecology **75**:1219-1232.

Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology **61**:108-118.

Benke, A. C., and J. B. Wallace. 1997. Trophic basis of production among riverine caddisflies: Implications for food web analysis. Ecology **78**:1132-1145.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology **80**:2206-2224.

Briand, F. 1983. Environmental control of food web structure. Ecology **64**:253-263.

Briand, F., and J. E. Cohen. 1987. Environmental correlates of food chain length. Science **238**:956-960.

Clean Water Act. 1977. **33 U.S.C. s/s 1251 et seq.**

Clements, W. H. 1994. Benthic invertebrate community response to heavy metals in the Upper Arkansas River basin, Colorado. Journal of the North American Benthological Society **13**:30-84.

Clements, W. H., D. M. Carlisle, J. M. Lazorchak, and P. C. Johnson. 2000. Heavy metals structure benthic communities in Colorado mountain streams. Ecological Applications **10**:626-638.

Clements, W. H., and P. M. Kiffney. 1995. The influence of elevation on benthic community responses to heavy metals in Rocky Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences **52**:1966-1977.

Closs, G. P., and P. S. Lake. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. Ecological Monographs **64**:1-21.

CDPHE, 1999. Colorado Department of Public Health and Environment Water Quality Control Commission. The basic standards and methodologies for surface water. **5 CCR 1002-31.**

Covich, A. P. 1996. Stream biodiversity and ecosystem processes. Bulletin of the North American Benthological Society **13**:294-303.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in benthic ecosystems: Zoobenthic species influence energy flows and nutrient cycling. BioScience **49**: 119-127.

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351-389.

De Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1996. Energetics and stability in belowground food webs. Pages 201-210 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

DeAngelis, D. L., S. M. Bartell, and A. L. Brenkert. 1989. Effects of nutrient cycling and food-chain length on resilience. American Naturalist **134**:778-805.

Diamond, J. 1984. Overview: Laboratory experiments, field experiments, and natural experiments. Pages 3-22 in J. Diamond and T.J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist **138**:1067-1091.

Efron, B. 1982. The Jacknife, the bootstrap and other methods in statistics. Society for Industrial and Applied Mathematics. Philadelphia, Pennsylvania, USA.

Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224-239 in C. G. Jones and J. H. Lawton, editors. Linking Species and Ecosystems. Chapman and Hall, New York, New York, USA.

Grime, J. P. 1997. Biodiversity and ecosystem function: The debate deepens. Science 277:1260-1261.

Hairston, N. G. Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. American Naturalist 142:379-411.

Hairston, N. G. Jr., and N. G. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? American Naturalist 149:1001-1007.

Hall, R. O. Jr., J. B. Wallace, and S. L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology (in press).

Hall, S. J., and D. G. Raffaelli. 1993. Food webs: Theory and reality. Advances in Ecological Research 24:187-239.

Hawkins, C. P. 1986. Variation individual growth-rates and population densities of ephemerellid mayflies. Ecology 67:1384-1395.

Howarth, R. W. 1991. Comparative responses of aquatic ecosystems to toxic chemical stress. Pages 169-195 *in* J. Cole, G. Lovett, and S. Findlay, editors. Comparative analysis of ecosystems: Patterns, mechanisms, and theories. Springer-Verlag, New York, NewYork, USA.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnology and Oceanography 41:243-252.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145-159.

Jaarsma, N. G., S. M. De Boer, C. R. Townsend, R. M. Thompson, and E. D. Edwards. 1998. Characterising food-webs in two New Zealand streams. New Zealand Journal of Marine and Freshwater Research **32**:271-286.

Jones, C. G., and J. H. Lawton. 1995. Linking Species and Ecosystems. Chapman and Hall, New York, New York, USA.

Kiffney, P. F., and W. H. Clements. 1994. Effects of metals on a Rocky Mountain stream macroinvertebrate assemblage in experimental microcosms. Journal of the North American Benthological Society **13**:511-523.

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosytems. Pages 255-270 *in* E.-D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, London, England.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist **147**:784-812.

Leland, H. V., S. V. Fend, T. L. Dudley, and J. L. Carter. 1989. Effects of copper on species composition of benthic insects in a Sierra Nevada, California, stream. Freshwater Biology **21**:163-179.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1967.

Levin, S. A., K. D. Kimball, W. H. McDowell, and S. F. Kimbal. 1984. New perspectives in ecotoxicology. Environmental Management **8**:375-442.

Lubchenco, J. 1998. Entering the century of the environment: A new social contract for science. Science **279**:491-497.

Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The sustainable biosphere initiative: An ecological research agenda. Ecology **72**:371-412.

Martinez, N. D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecological Monographs **61**:367-392.

Martinez, N. D. 1995. Unifying ecological subdisciplines with ecosystem food webs. Pages 166-175 *in* C. G. Jones and J. H. Lawton, editors. Linking Species and Ecosystems. Chapman and Hall, New York, New York, USA.

McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystems. Pages 361-383 in E.-D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, London, England.

Medley, C. N., and W. H. Clements. 1998. Responses of diatom communities to heavy metals in streams: The influence of longitudinal variation. Ecological Applications **8**:631-644.

Menge, B. A., B. Daley, and P. A. Wheeler. 1996. Control of interaction strength in marine benthic communities. Pages 258-274 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist **130**:730-757.

Merritt, R. W., and K. W. Cummins. 1996a. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa, USA.

Merrit, R. W., and K. W. Cummins. 1996b. Trophic relations of macroinvertebrates. Pages 453-474 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology. Academic Press, San Diego, California, USA.

Meyer, J. S., C. G. Ingersoll, L. L. McDonald, and M. S. Boyce. 1986. Estimating uncertainty in population growth rates: Jacknife vs. bootstrap techniques. Ecology **67**:1156-1166.

Mihuc, T. B., and G. W. Minshall. 1995. Trophic generalists vs trophic specialists: Implications for food-web dynamics in postfire streams. Ecology **76**:2361-2372.

Odum, E. P. 1985. Trends expected in stressed ecosystems. BioScience **35**:419-422.

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

Paine, R. T. 1988. Food webs: Road maps of interactions or grist for theoretical development? Ecology **69**:1648-1654.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature **355**:73-75.

Pennak, R. W. 1989. Freshwater invertebrates of the United States. John Wiley and Sons, NewYork, New York, USA.

Pimm, S. L. 1980. Properties of food webs. Ecology **61**:219-225.

Pimm, S. L. 1982. Food Webs. Chapman and Hall, London, England.

Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature **350**:669-674.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature **307**:321-326.

Polis, G. A. 1991. Complex trophic interactions in deserts: An empirical critique of food-web theory. American Naturalist **138**:122-155.

Polis, G. A. 1994. Food webs, trophic cascades and community structure. Australian Journal of Ecology :121-136.

Polis, G. A., R. D. Holt, B. A. Menge, and K. O. Winemiller. 1996. Time, space, and life history: Influences on food webs. Pages 435-460 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**: 813-846.

Power, M. E., M. S. Parker, and J. T. Wootton. 1996. Disturbance and food chain length in rivers. Pages 286-297 *in* G. A. Polis and K. O. Winemiller, editors. Food webs:

Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

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

Raffaelli, D. G., and S. J. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185-191 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Schindler, D. W. 1995. Linking species and communities to ecosystem management: A perspective from the experimental lakes experience. Pages 313-325 in C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Schindler, D. W., K. H. Mills, D. F. Malley, D. L. Findlay, J. A. Shearer, I. J. Davies, M. A. Turner, G. A. Linsey, and D. R. Cruikshank. 1985. Long-term ecosystem stress: The effects of years of acidification on a small lake. Science **228**:1395-1401.

Schlapfer, F., and B. Schmic. 1999. Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. Ecological Applications **9**: 893-912.

Schulze, E.-D., and H. A. Mooney. 1993. Ecosystem function of biodiversity: A summary. Pages 497-510 *in* E.-D. Schulze and H. A. Mooney , editors. Biodiversity and ecosystem function. Springer-Verlag, London, England.

Sprague, J. B. 1995. Appendix C: Factors that modify toxicity. Pages 1012-1051 *in* G. M. Rand, editor. Fundamentals of aquatic toxicology: Effects, environmental fate, and risk assessment. Taylor and Francis, Washington, D.C., USA.

Tavares-Cromar, A. F., and D. D. Williams. 1996. The importance of temporal resolution in food web analysis: Evidence from a detritus-based stream. Ecological Monographs **66**:91-113.

U.S. EPA. 1996. U.S. EPA Office of Water. National Water Quality Inventory: Report to Congress. Washington, D.C.

Ulanowicz, R. E. 1996. Trophic flow networks as indicators of ecosystem stress. Pages 358-368 in G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and Dynamics. Chapman and Hall, New York, New York, USA.

Ulanowicz, R. E. 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York, New York, USA.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. Science **277**:494-499.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology **41**:115-139.

Ward, J. V., and B.C. Kondratieff. 1992. An illustrated guide to the mountain stream insects of Colorado. University Press of Colorado, Niwot, Colorado, USA.

Whiles, M. R., and J. B. Wallace. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. Canadian Journal of Fisheries and Aquatic Sciences **52**:2402-2422.

Winemiller, K. O., and G. A. Polis. 1996. Food webs: What can they tell us about the world? Pages 1-22 in G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Table 3.1. Environmental conditions of five study streams in central Colorado, May 1998-May 1999.

Variable	Fourmile	East Fork	Buckskin	Mosquito	Snake
Median discharge (m^3/s)	0.241	0.168	0.270	0.428	0.198
Mean channel width (m)	3.86	3.57	4.16	3.96	4.81
Annual degree days	11,910	15,327	12,153	14,378	13,029
Mean annual temperature (°C)	2.7	3.5	2.8	3.3	3.0
Mean annual alkalinity (mg/l)	114	34	55	70	4
Mean annual total hardness (mg/l)	125	57	84	104	45
pH range	7.5-8.9	6.7-8.5	7.1-9.0	7.4-9.0	5.7-8.2
Mean annual dissolved [Zn] (µg/l)	56	36	105	210	293
Mean annual Zn ratio	0.60	0.85	1.68	2.64	7.07
Mean annual conductivity	237	119	169	200	117
Watershed area (km^2)	23.32	31.16	22.10	32.20	28.99
Mean stream gradient (°)	22	25	30	26	26
Elevation (m)	3283	3202	3217	3249	3144

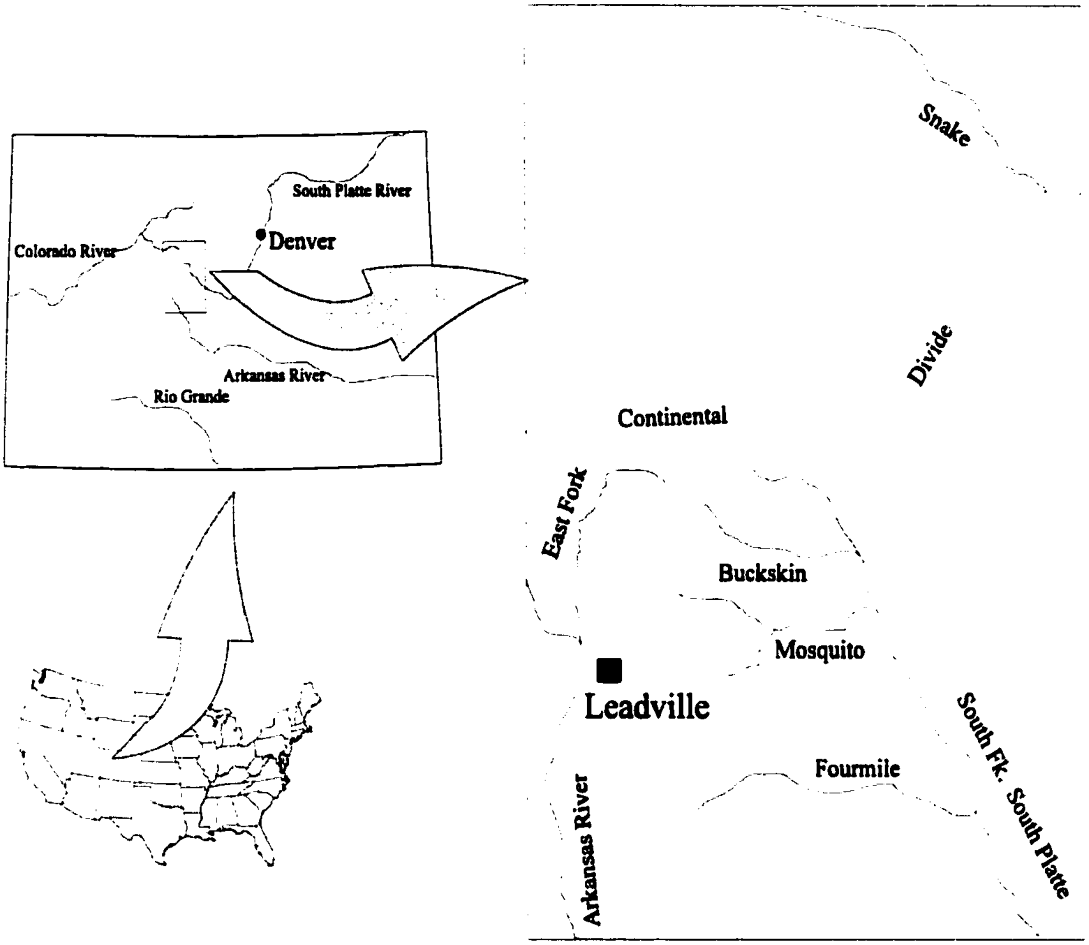

Figure 3.1. Study area in Colorado, U.S.A.

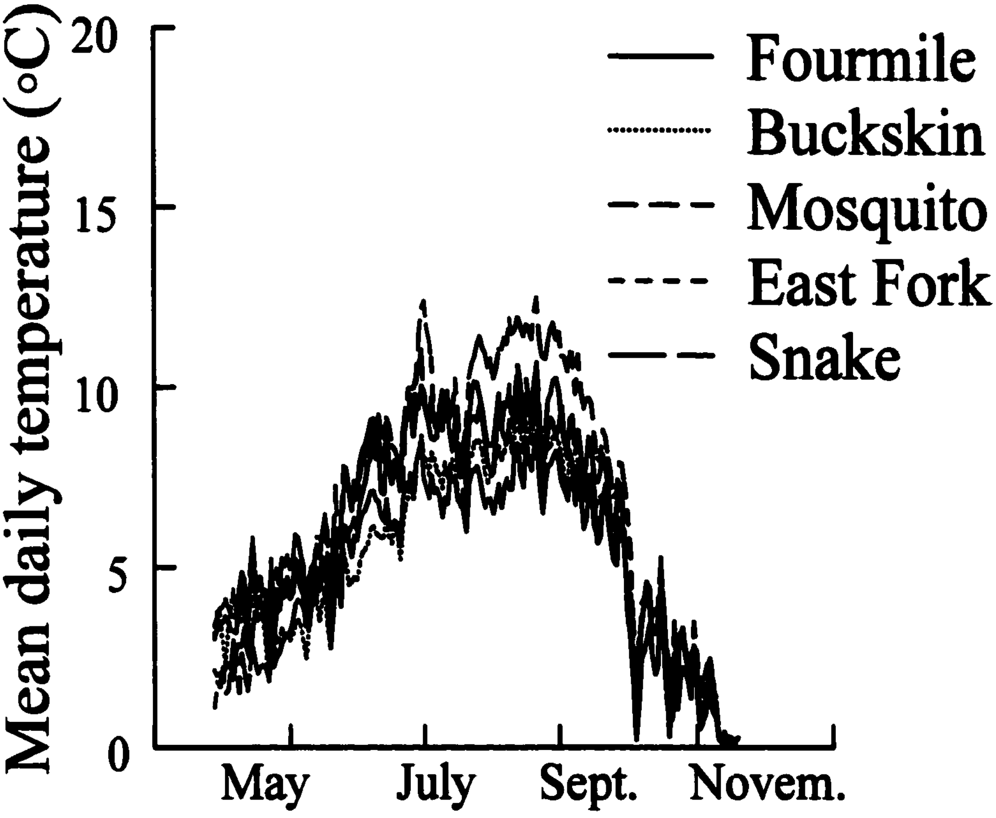

Figure 3.2. Seasonal variation of mean daily temperature in five Colorado streams, 1998.

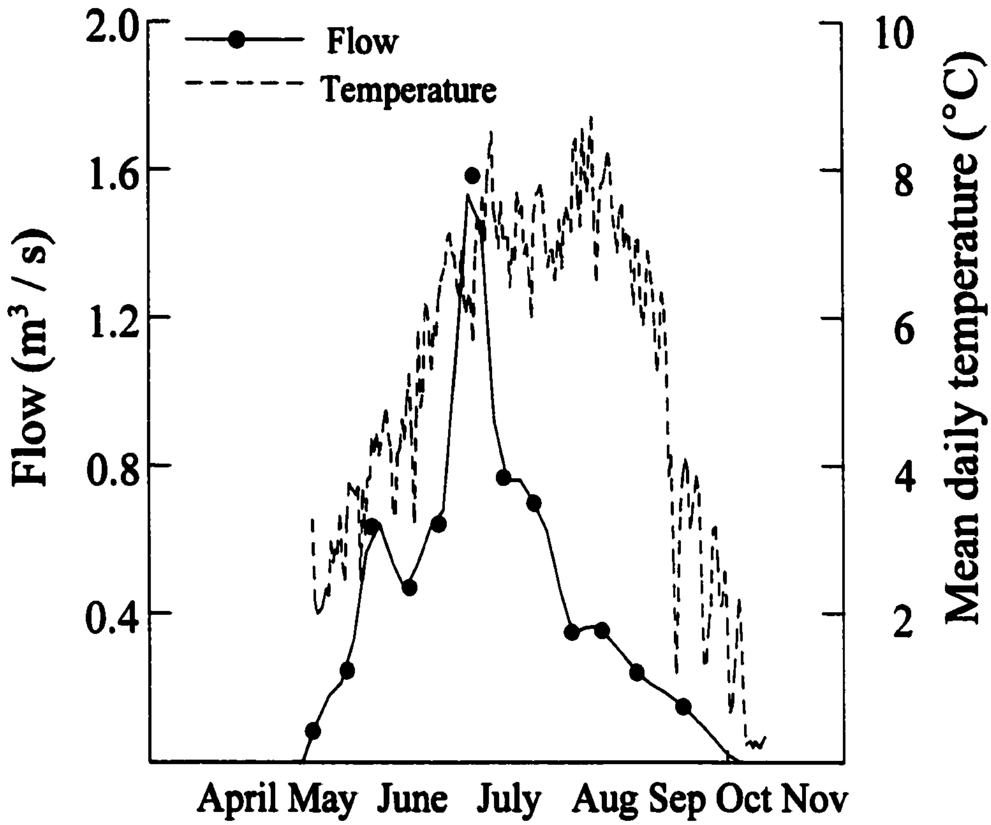

Figure 3.3. Representative seasonal variation of discharge and temperature in Fourmile Creek, Park County, Colorado, 1998.

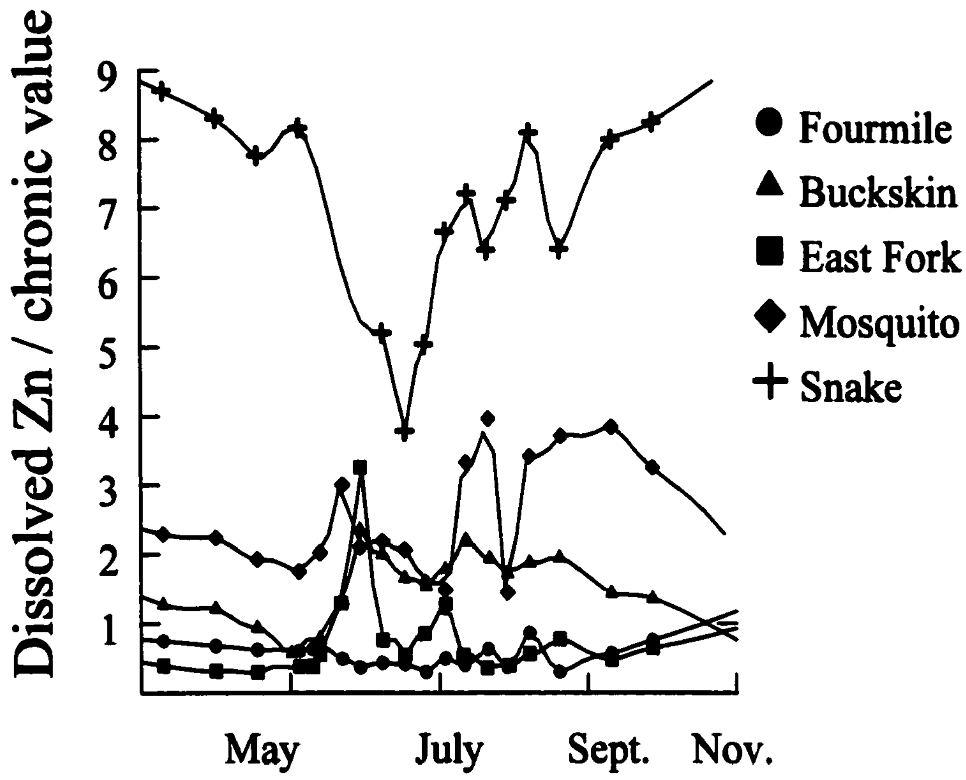

Figure 3.4. Seasonal variation in the ratio of measured dissolved Zn to the chronic value in five Colorado streams, 1998.

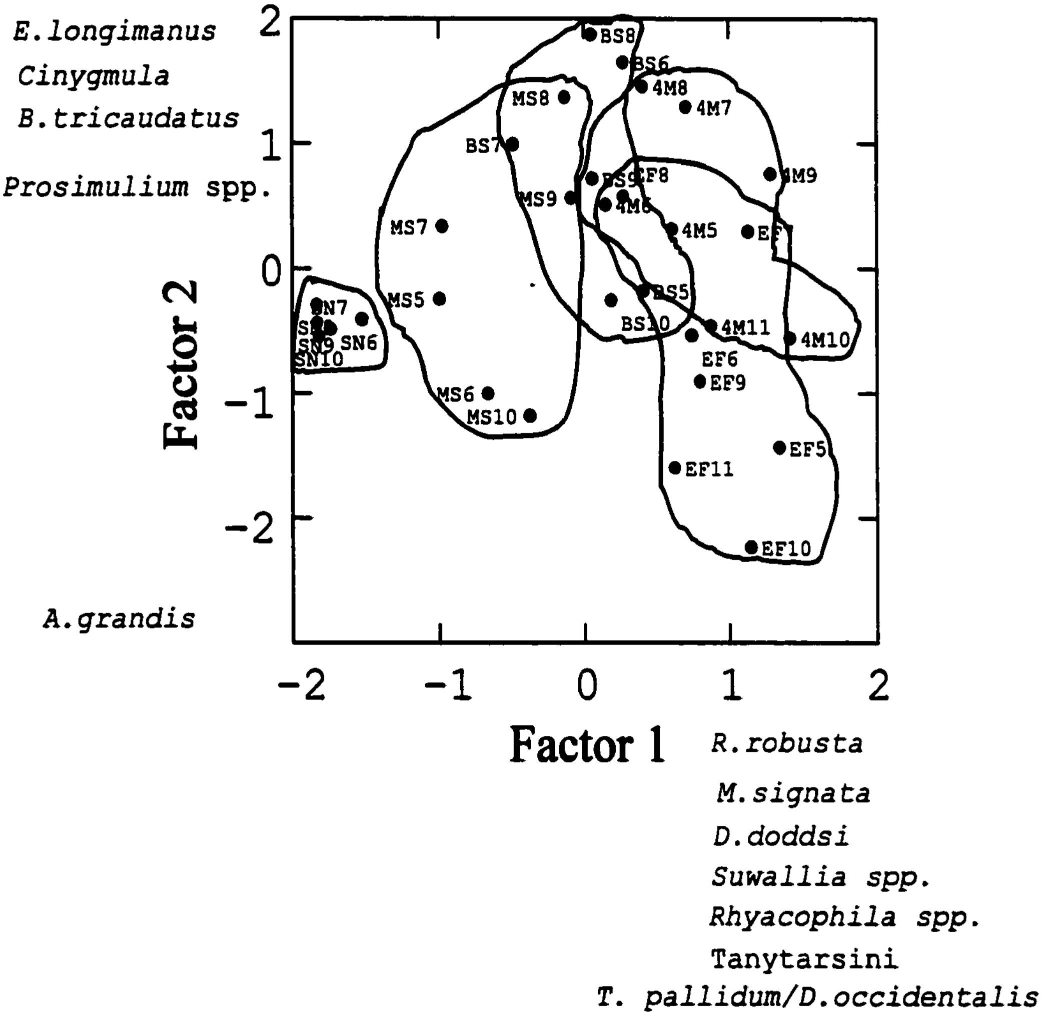

Figure 3.5. Ordination based on principle components analysis of assemblage structure in five Colorado streams. Taxa that loaded on factors 1 and 2 are indicated. Streams are coded as follows: EF=East Fork, 4M=Fourmile, BS=Buckskin, MS=Mosquito, and SN=Snake. Numbers following the stream code indicate month. Streams are enclosed for clarification. Zn levels were: East Fork = Fourmile < Buckskin < Mosquito < Snake.

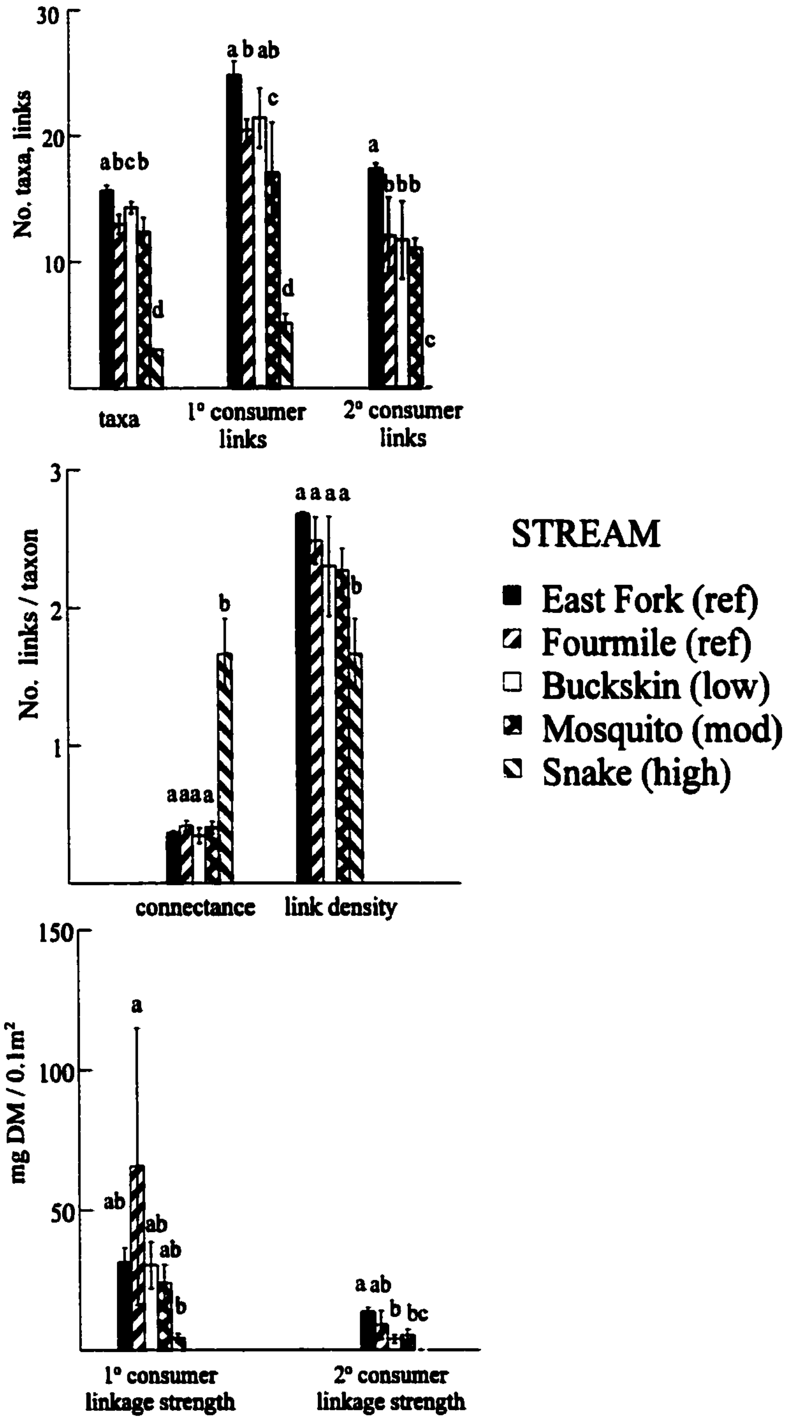

Figure 3.6. Values of various measures of trophic complexity among five Colorado streams. See text for definitions. Bars with different letters are significantly different ($P<0.10$) after LSD post-hoc test.

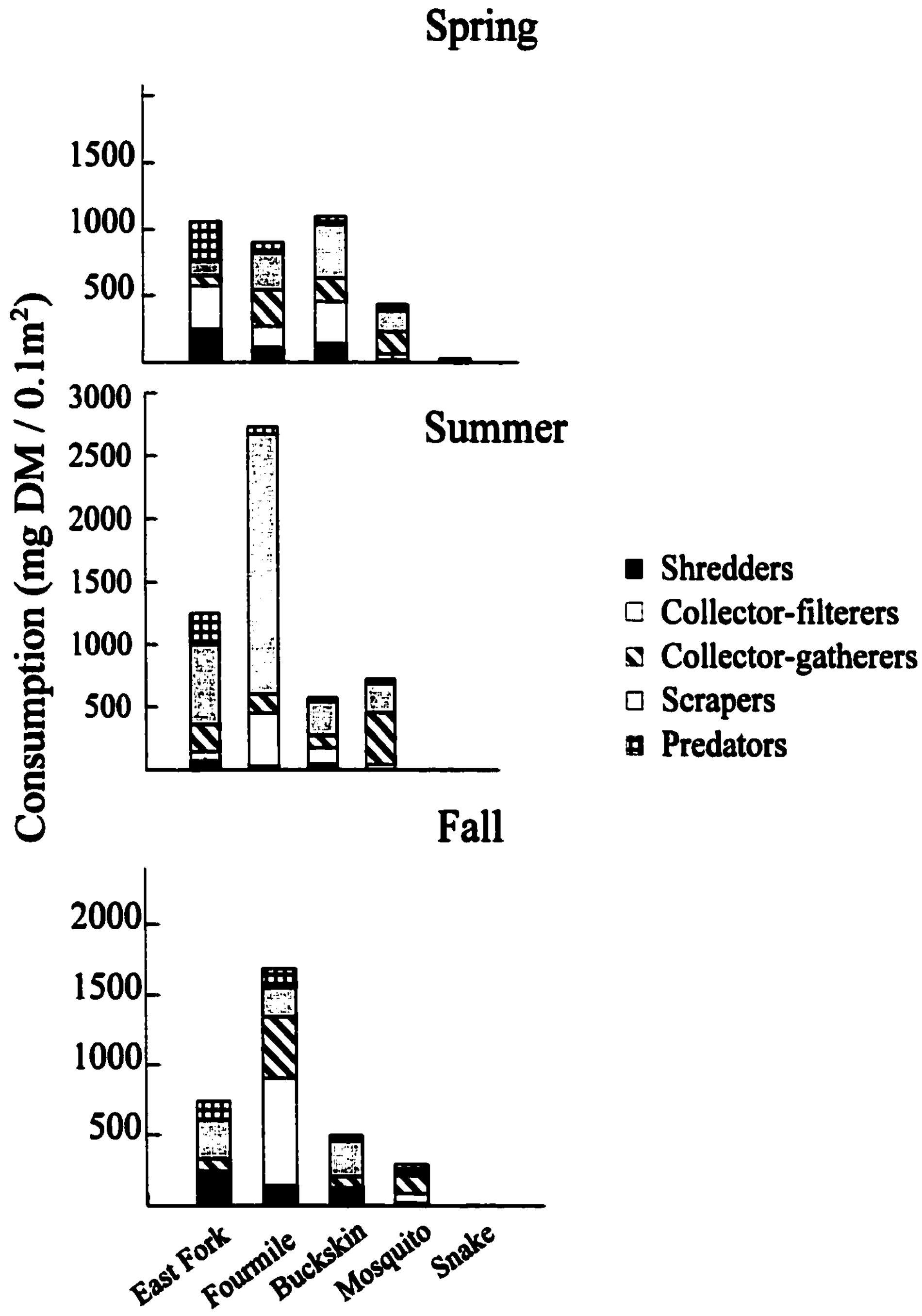

Figure 3.7. Seasonal consumption of insect functional feeding groups in five Colorado streams. Zn levels were: East Fork = Fourmile < Buckskin < Mosquito < Snake.

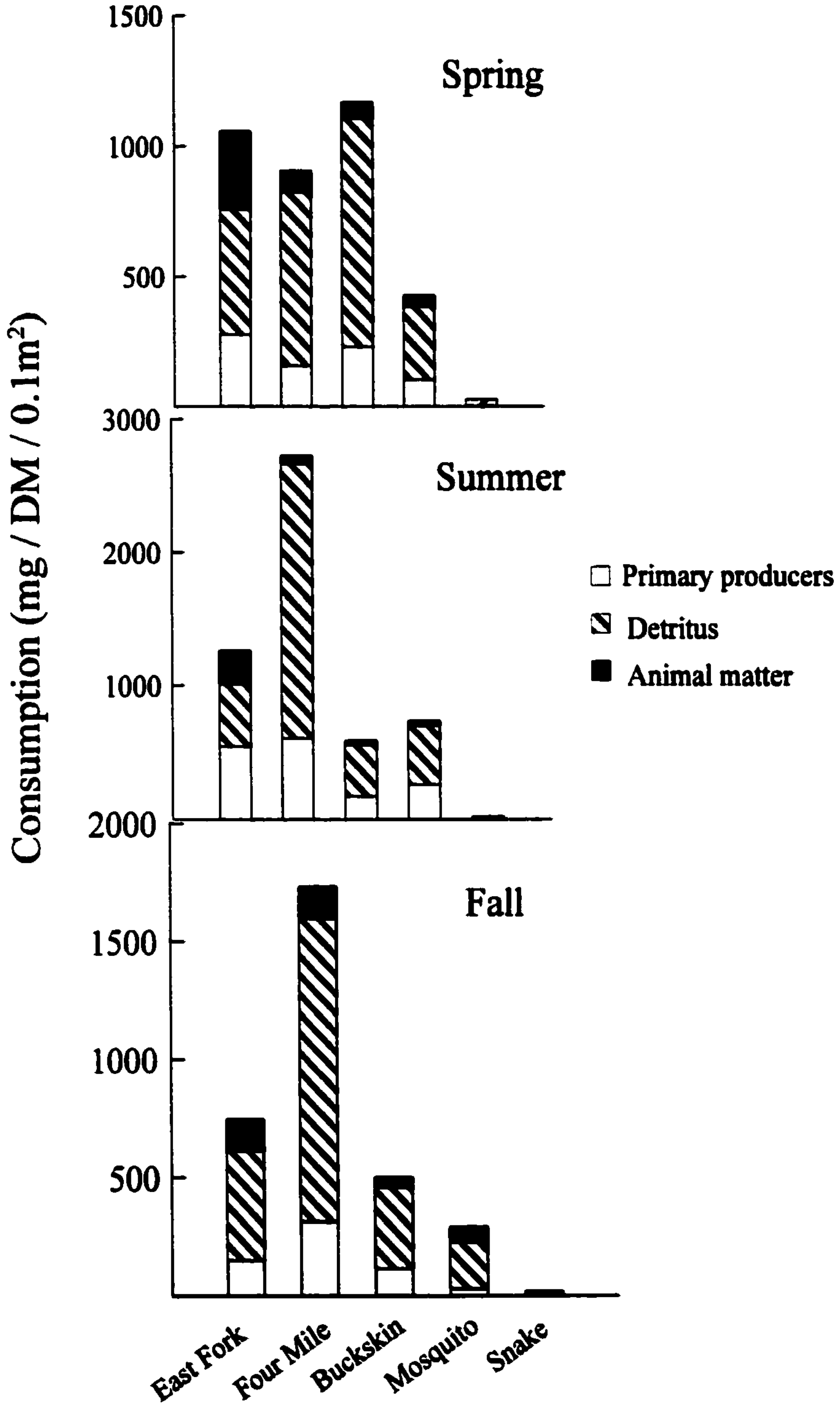

Figure 3.8. Seasonal contribution of various food sources to invertebrate secondary production in five Colorado streams, 1998. Zn levels were: East Fork=Fourmile<Buckskin<Mosquito<Snake.

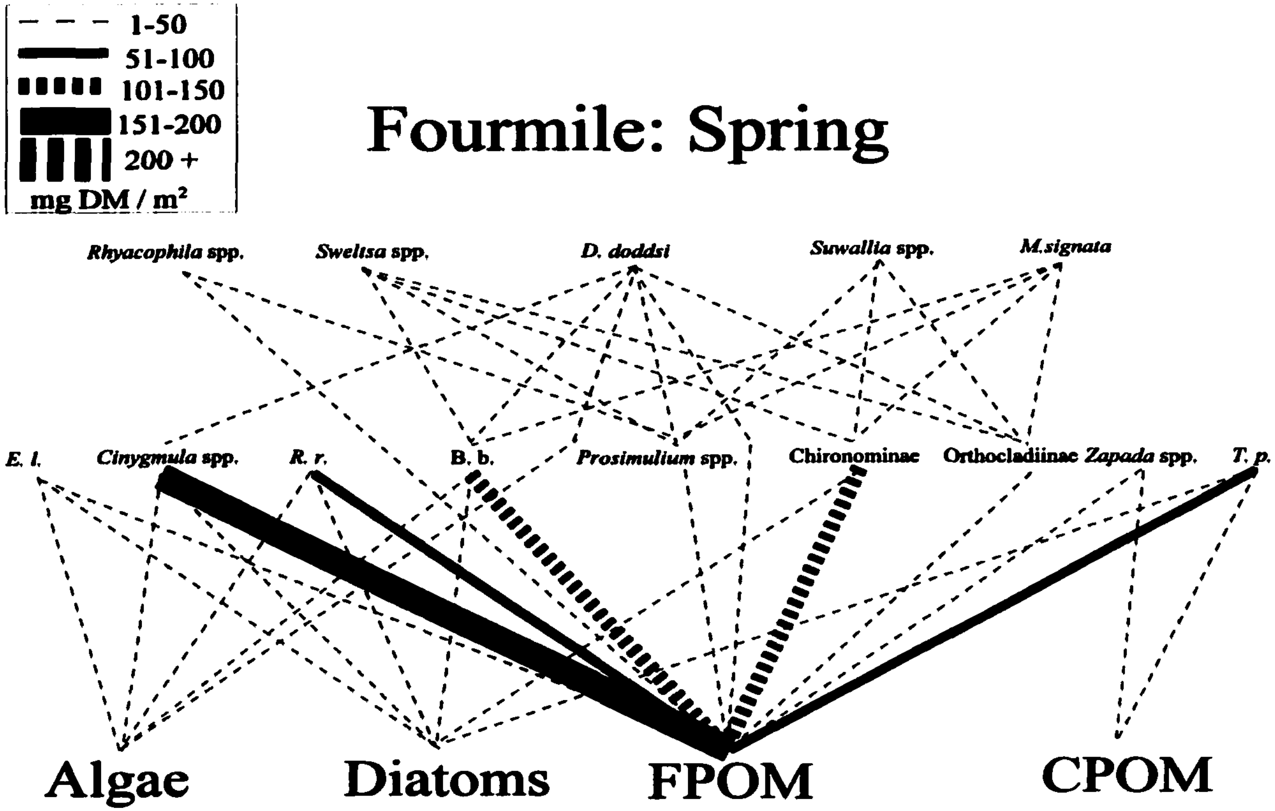

Figure 3.9.a. Food web diagram for Fourmile Creek, Colorado, spring 1998. E.l. = Epeorus longimanus, R.r. = Rhithrogena robusta, B.b. = Baetis bicaudatus, T.p. = Taenionema pallidum., *D.o.* = *Doddsia occidentalis.*

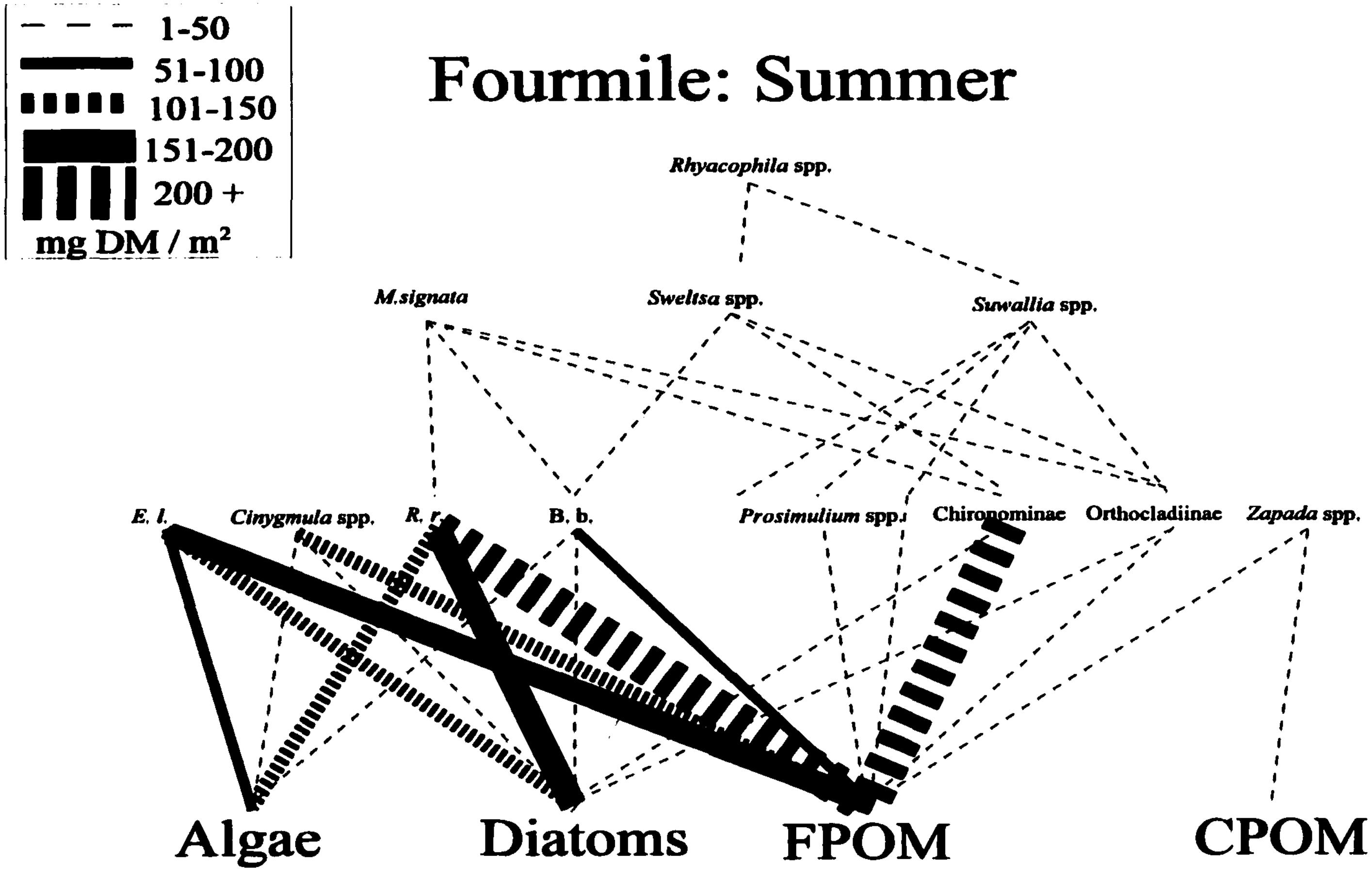

Figure 3.9.b. Food web diagram for Fourmile Creek, Colorado, summer 1998. Abbreviations are as in Figure 3.9.a.

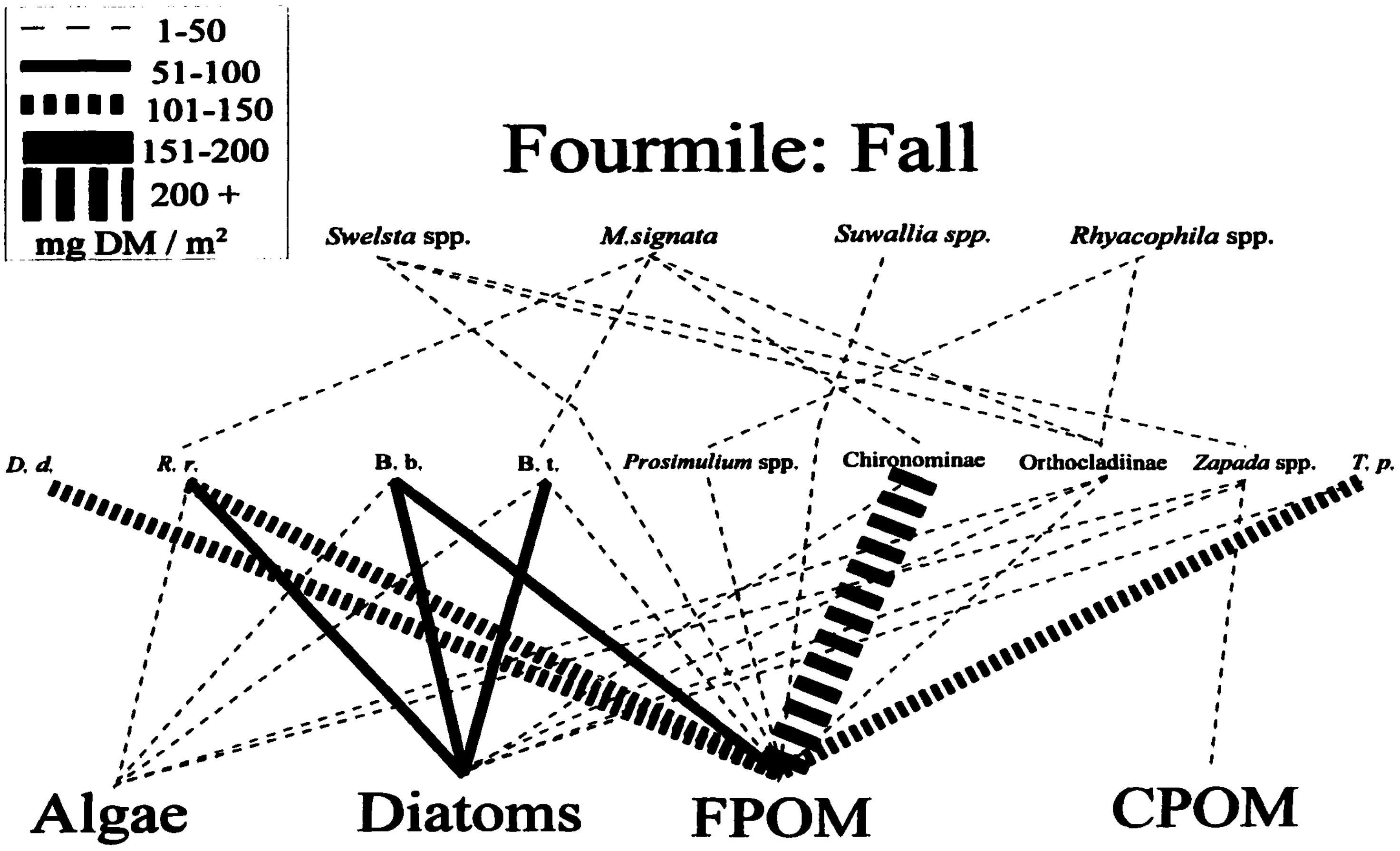

Figure 3.9.c. Food web diagram for Fourmile Creek, Colorado, fall 1998. Abbreviations are as in Figure 3.9.a.

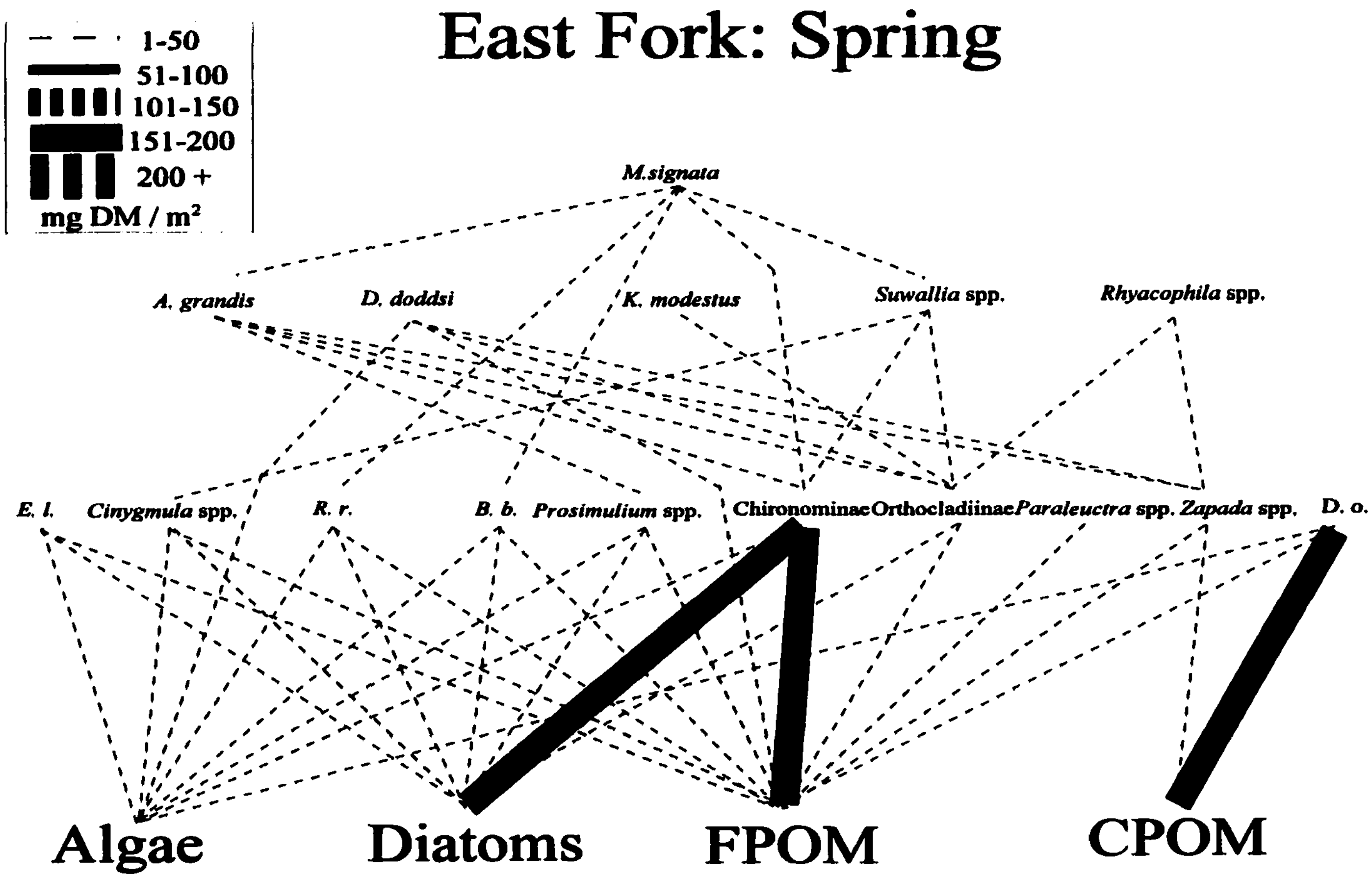

Figure 3.9d. Food web diagram for East Fork Creek, Colorado, spring 1998. Abbreviations are as in Figure 3.9.a.

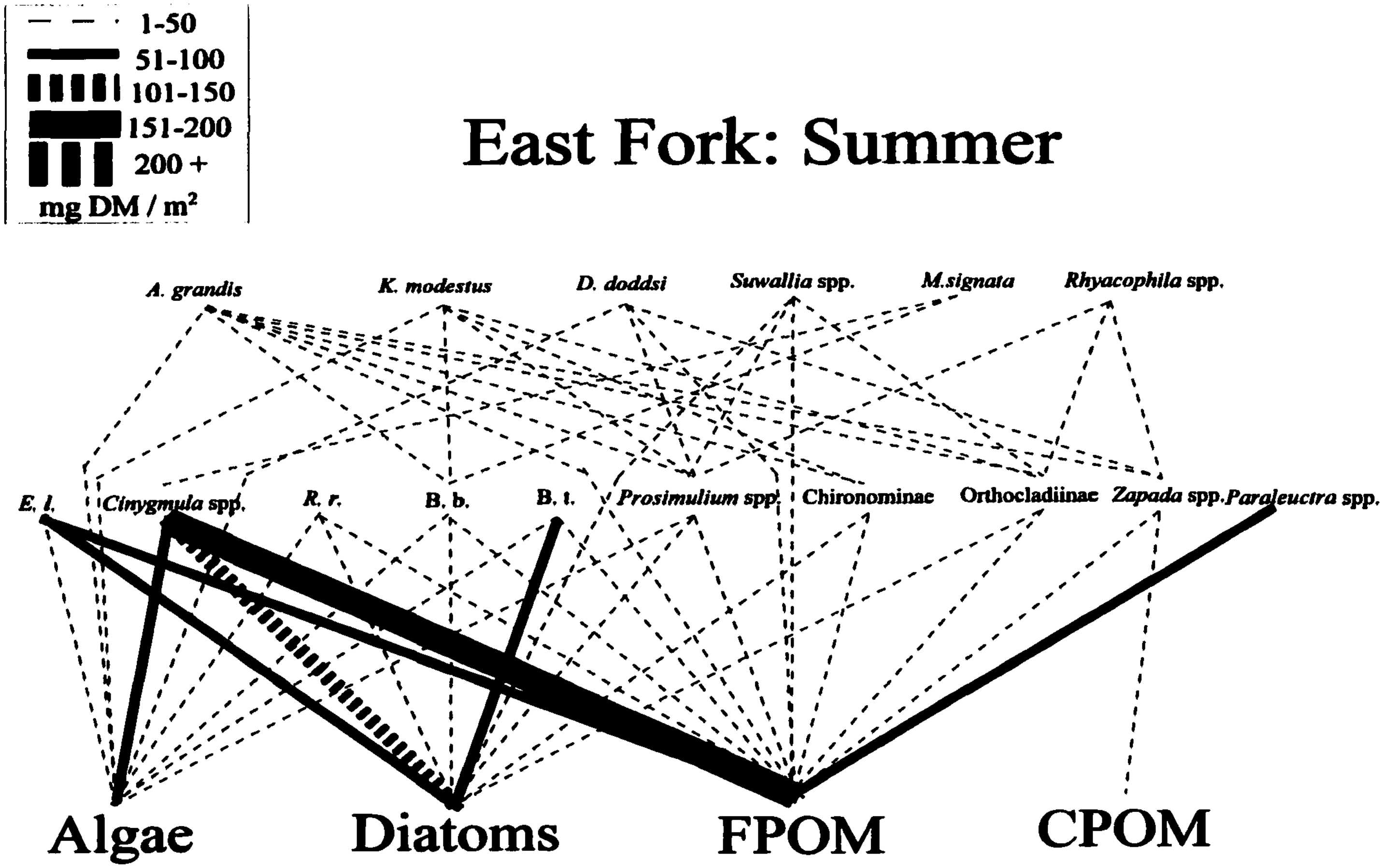

Figure 3.9.e. Food web diagram for East Fork Creek, Colorado, summer 1998. Abbreviations are as in Figure 3.9.a.

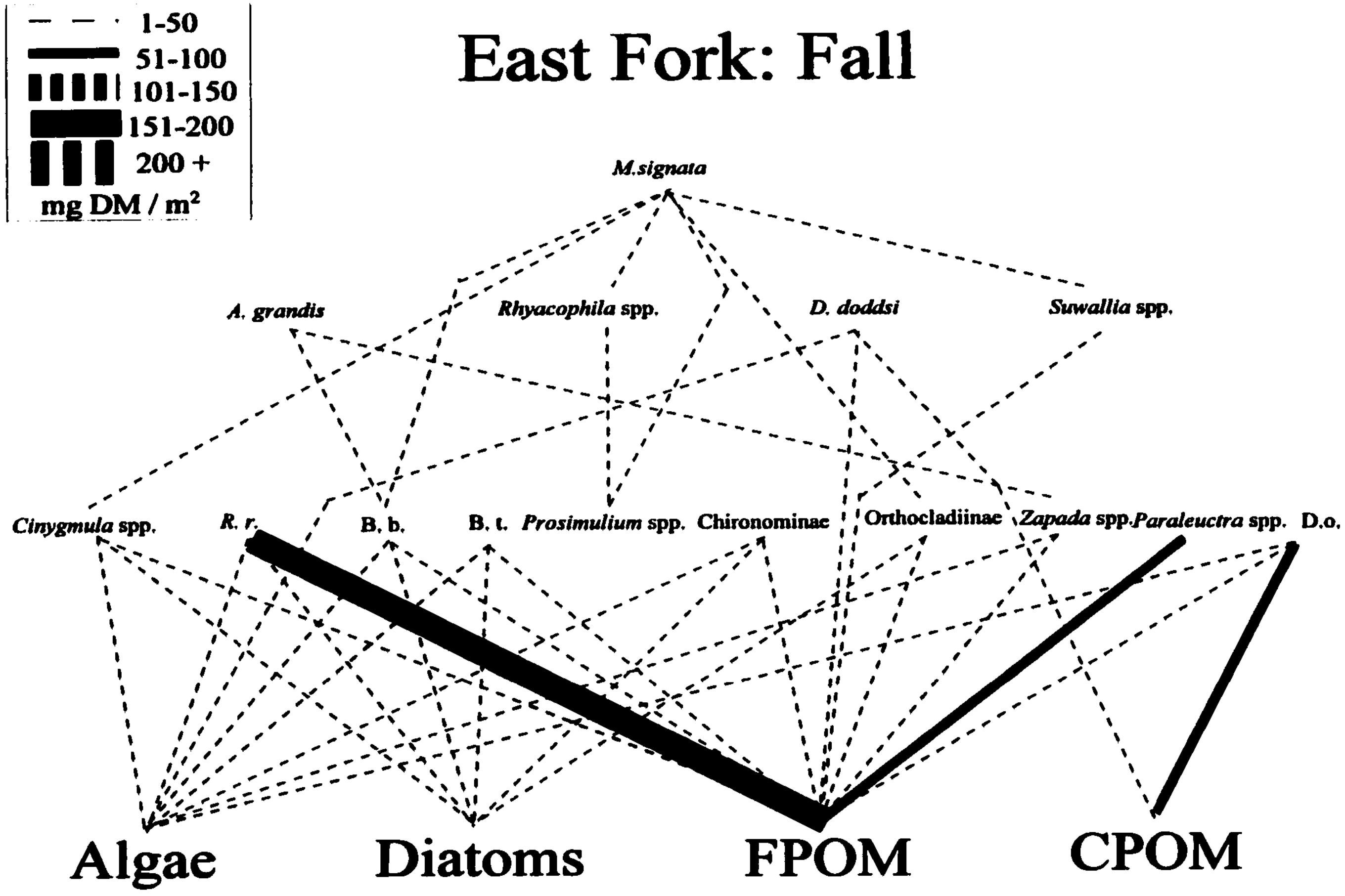

Figure 3.9.f. Food web diagram for East Fork Creek, Colorado, fall 1998. Abbreviations are as in Figure 3.9.a.

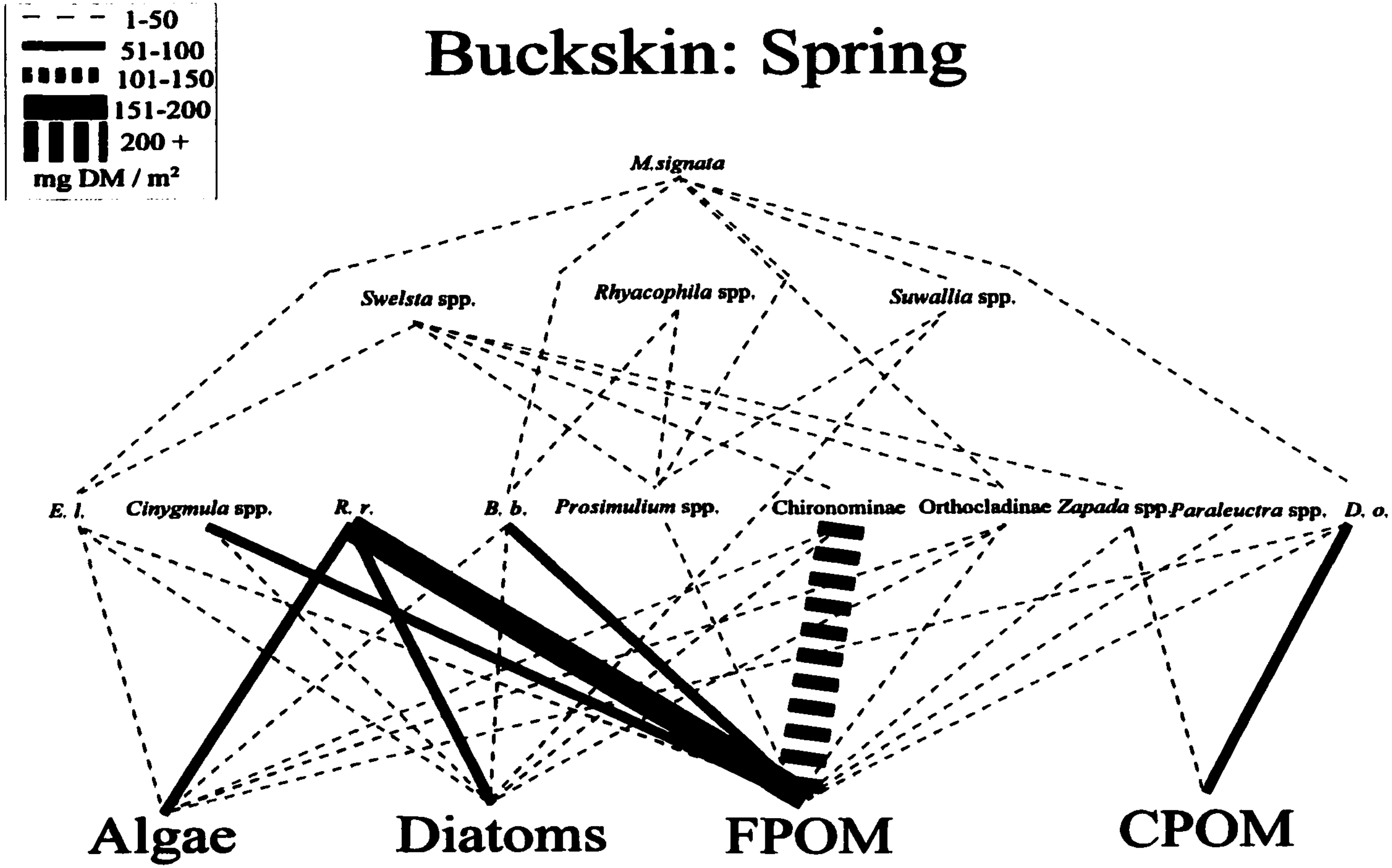

Figure 3.9.g. Food web diagram for Buckskin Creek, Colorado, spring 1998. Abbreviations are as in Figure 3.9.a.

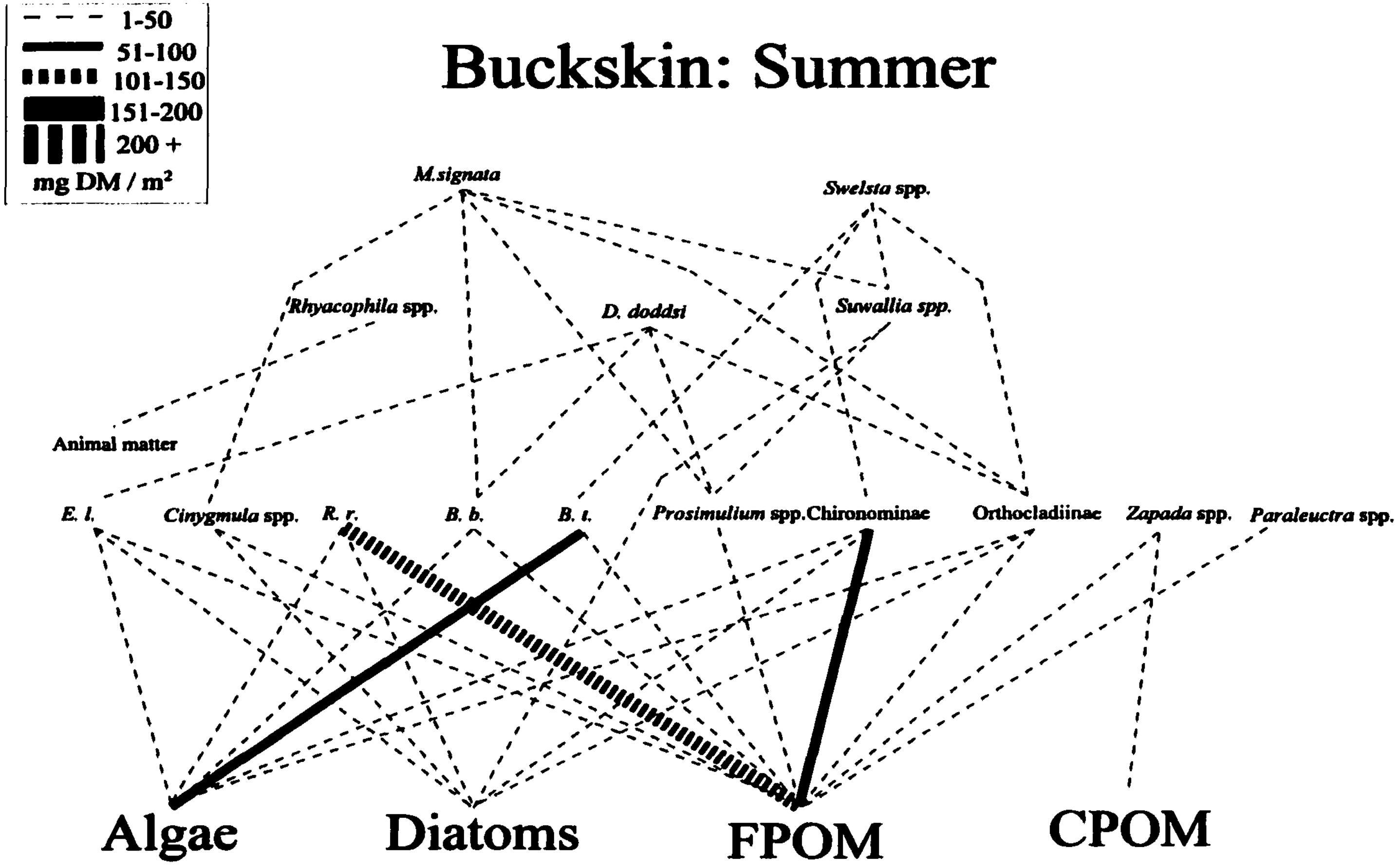

Figure 3.9.h. Food web diagram for Buckskin Creek, Colorado, summer 1998. Abbreviations are as in Figure 3.9.a.

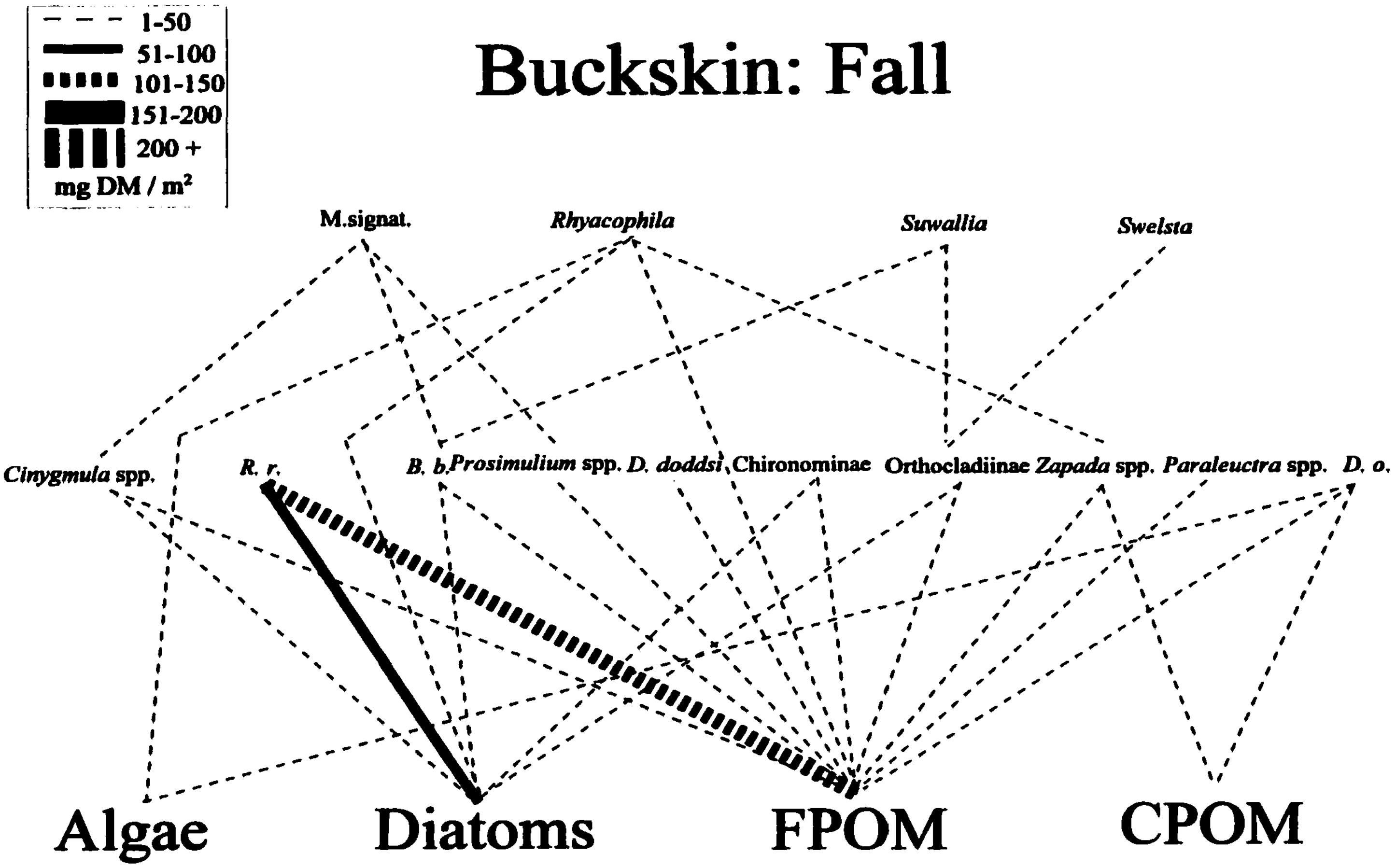

Figure 3.9.i. Food web diagram for Buckskin Creek, Colorado, fall 998. Abbreviations are as in Figure 3.9.a.

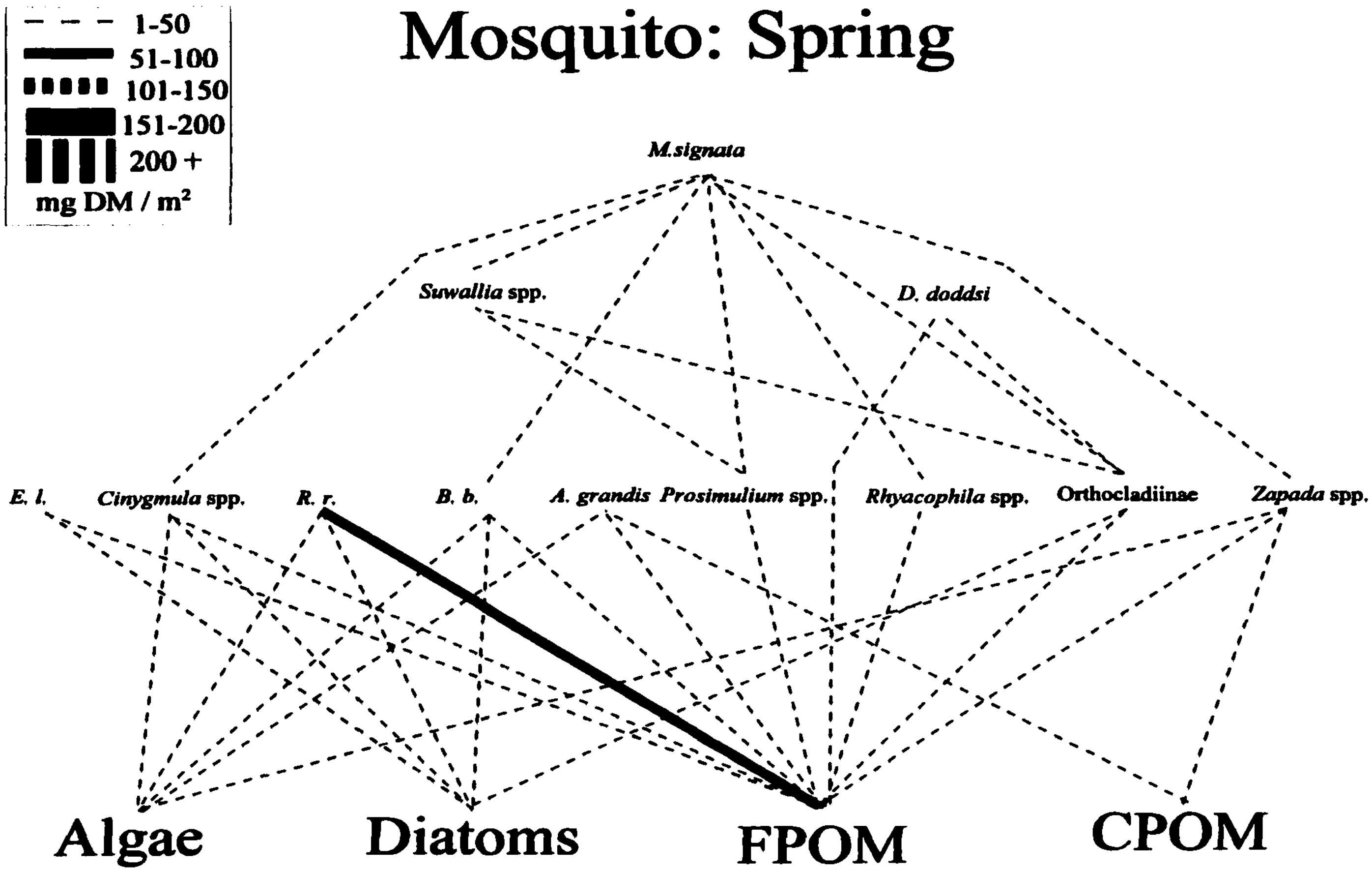

Figure 3.9.j. Food web diagram for Mosquito Creek, Colorado, spring 1998. Abbreviations are as in Figure 3.9.a.

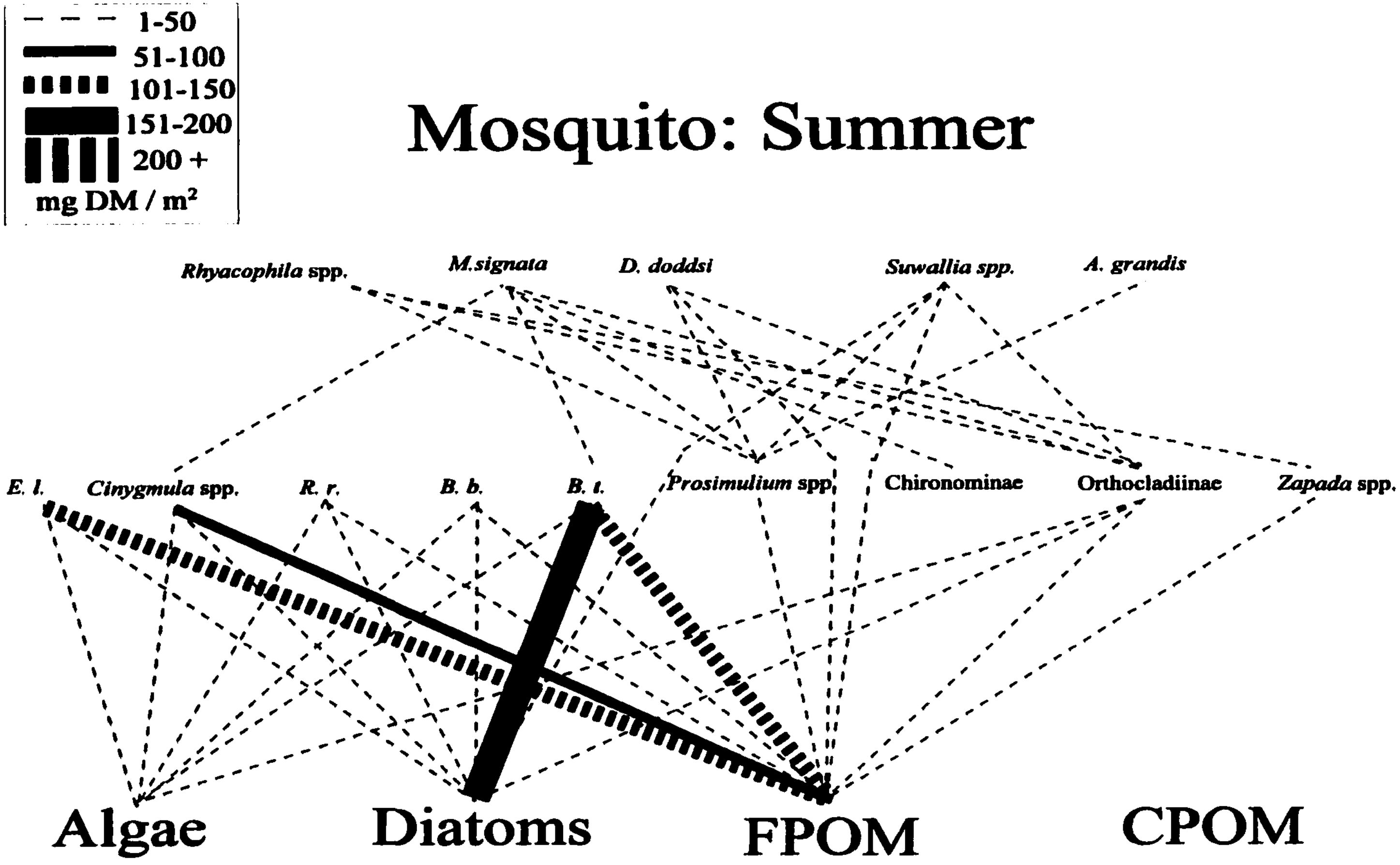

Figure 3.9.k. Food web diagram for Mosquito Creek, Colorado, summer 1998. Abbreviations are as in Figure 3.9.a.

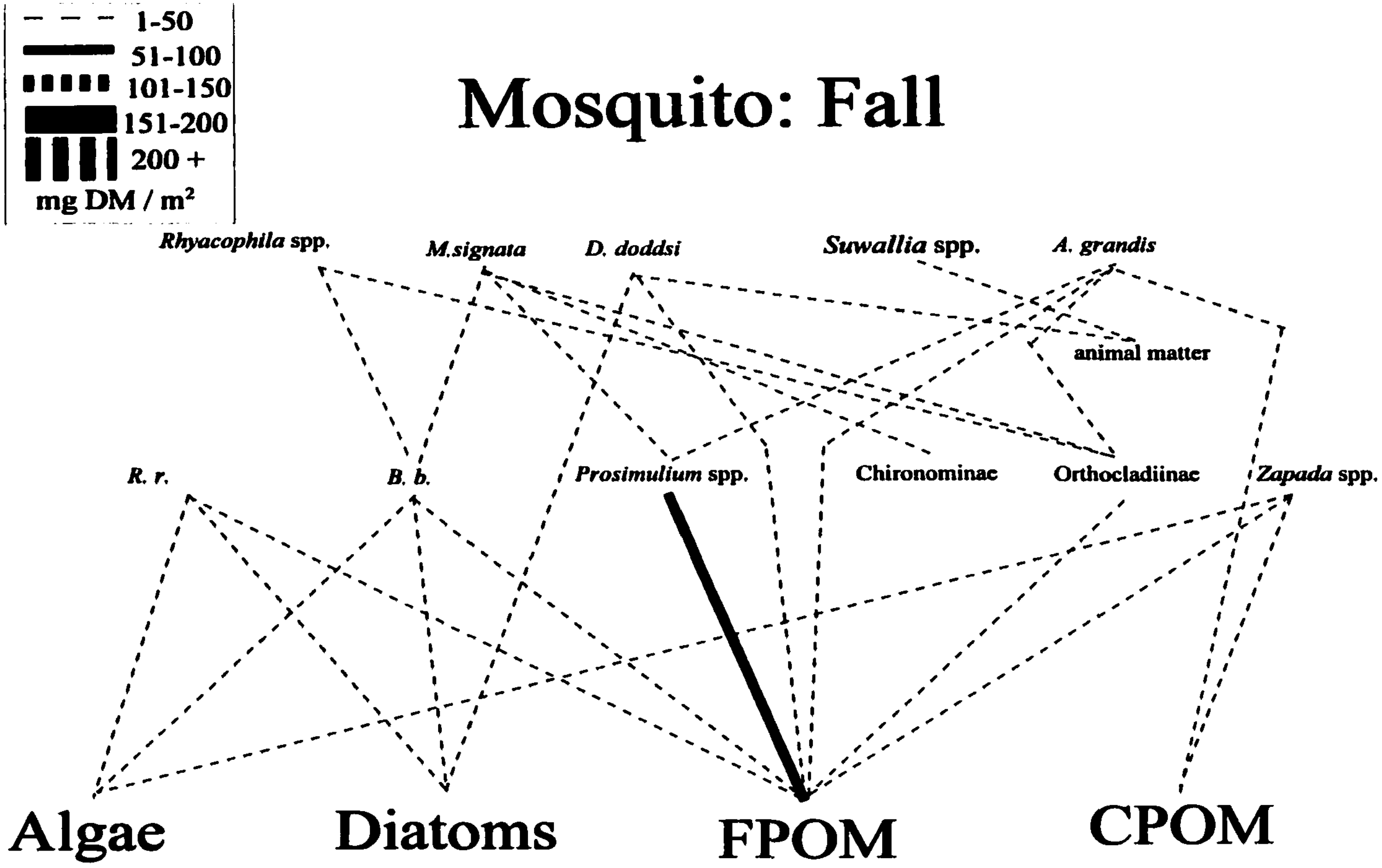

Figure 3.9.l. Food web diagram for Mosquito Creek, Colorado, fall 1998. Abbreviations are as in Figure 3.9.a.

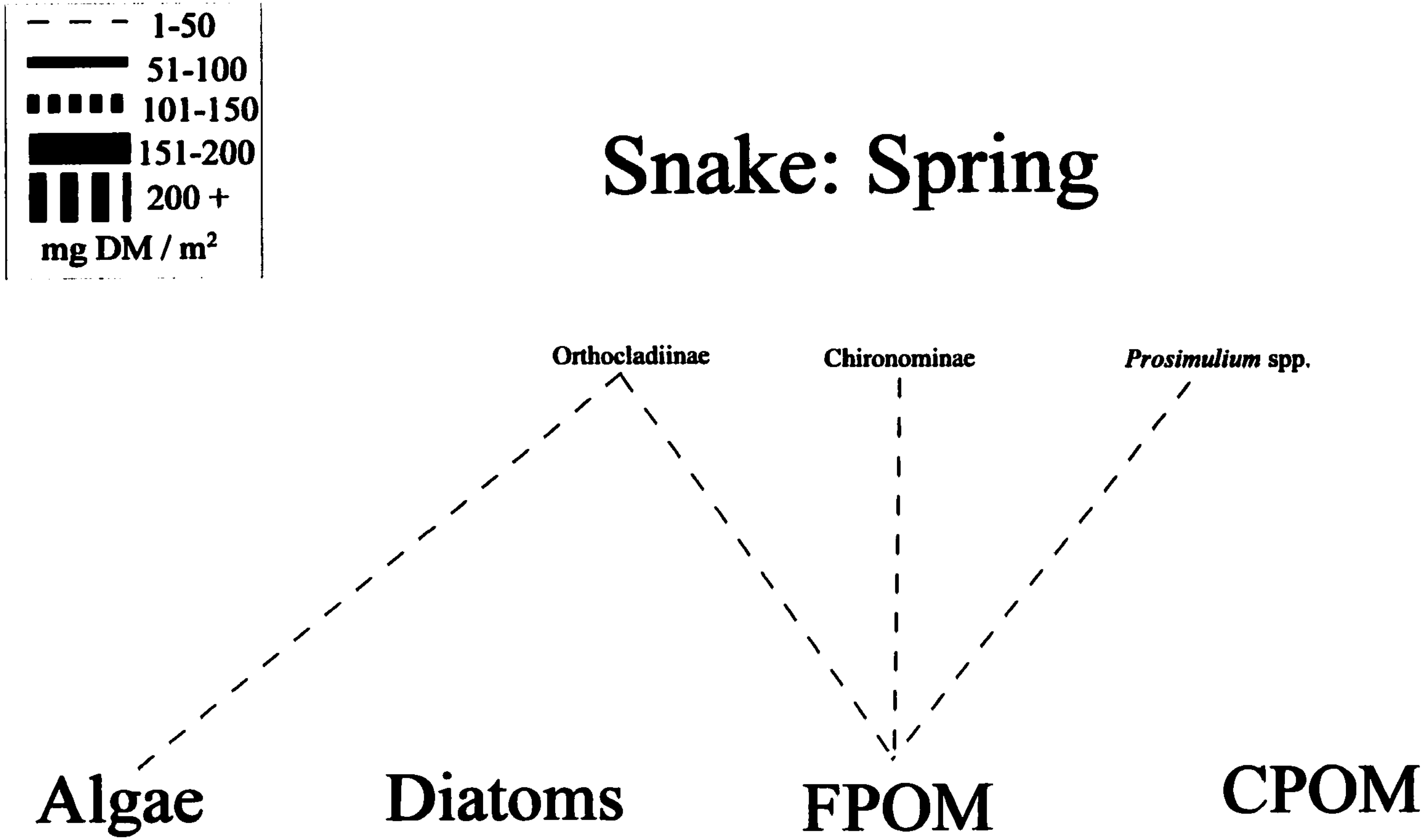

Figure 3.9.m. Food web diagram for Snake River, Colorado, spring 1998.

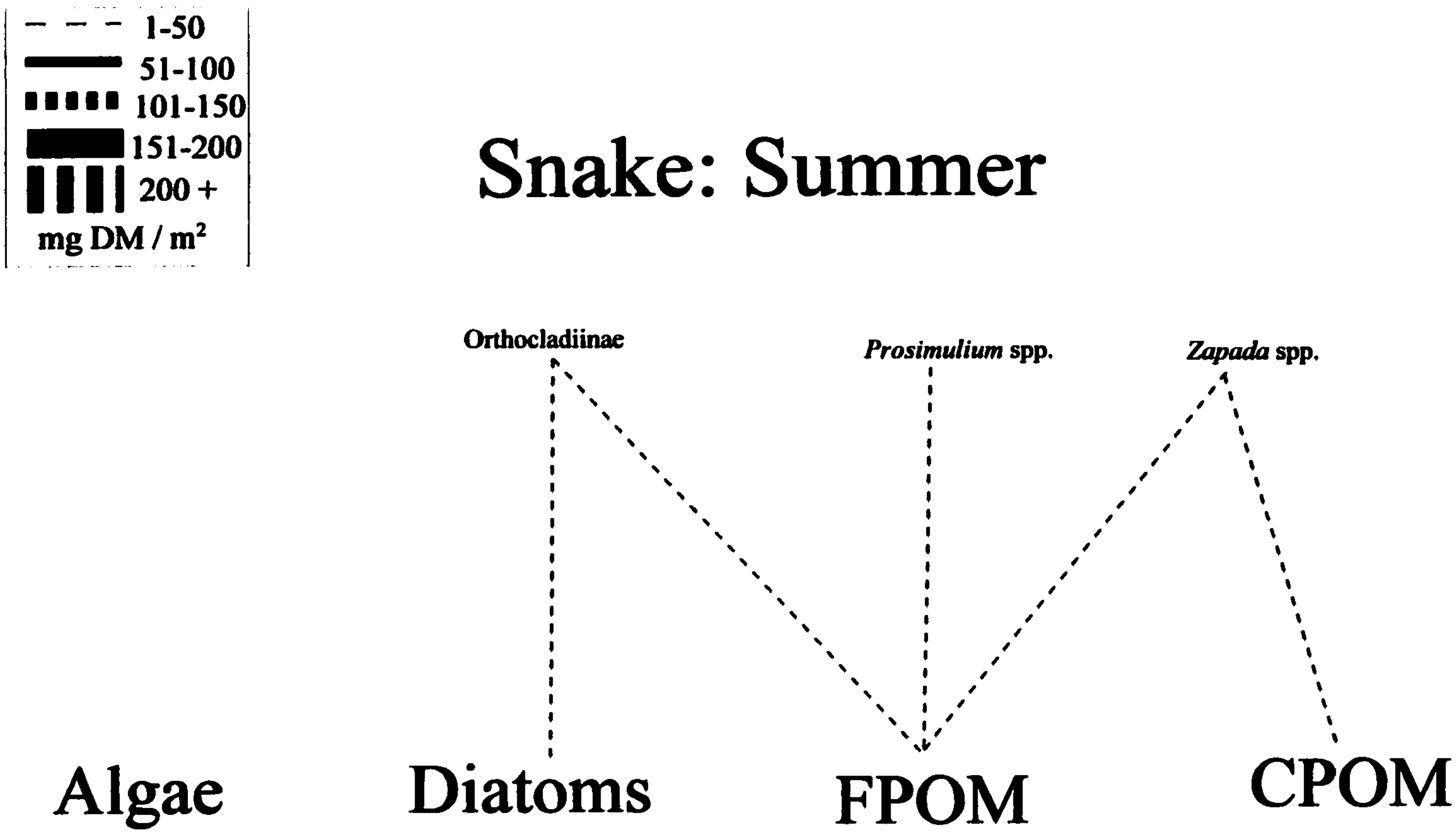

Figure 3.9.n. Food web diagram for Snake River, Colorado, summer1998.

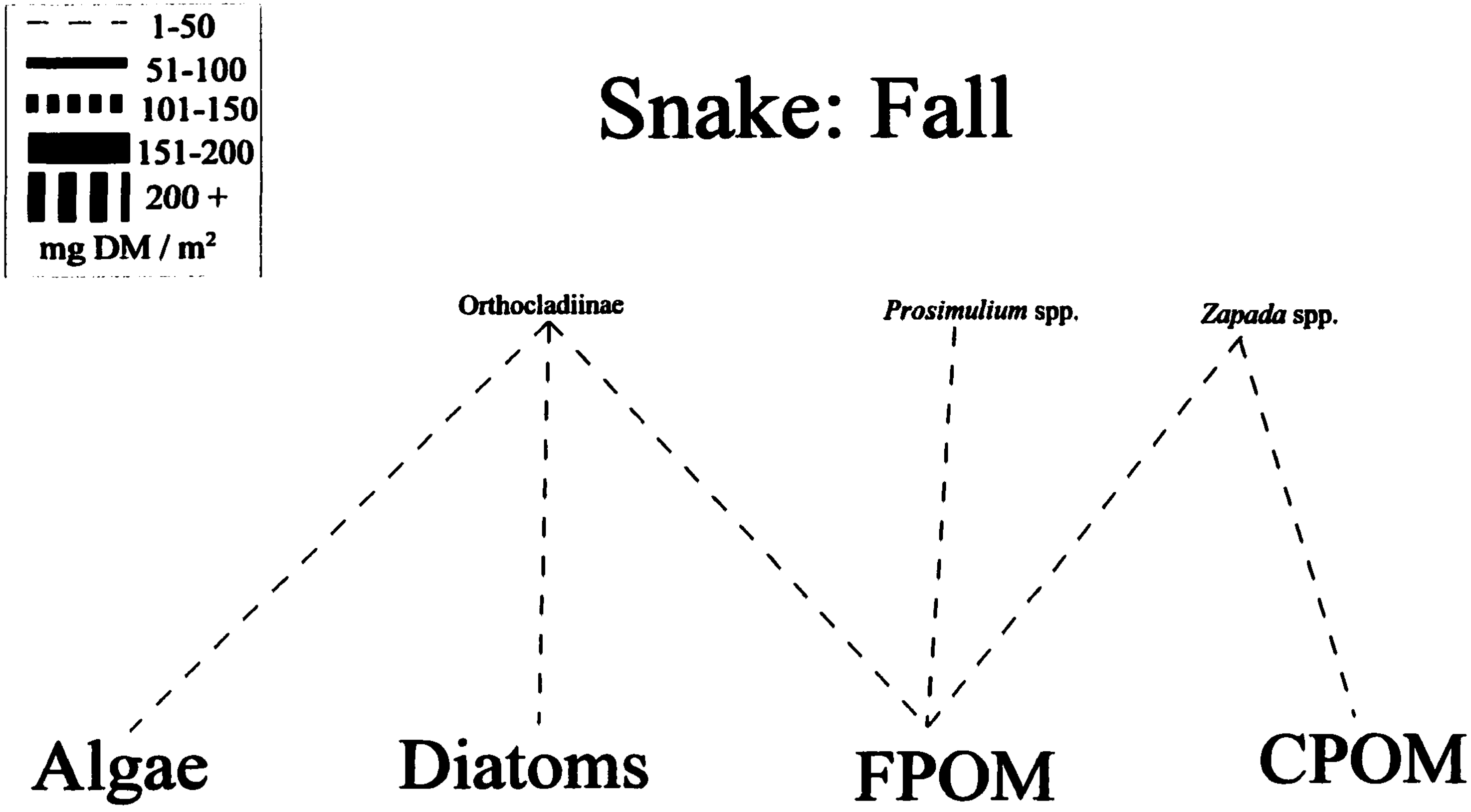

Figure 3.9.n. Food web diagram for Snake River, Colorado, fall 1998.

Appendix I

Consumption estimates of major food items by taxa

Consumption and 95% confidence intervals of major food items by taxa in Fourmile Creek, Colorado, 1998.

Taxon	Season	Algae	95% CI	Diatoms	95% CI	Animal	95% CI	Fine Detritus	95% CI	Coarse Detritus	95% CI
Baetis bicaudatus	Fall	14	4-32	81	39-145			58	21-120		
	Spring	55	24-105	29	10-60			144	45-304		
	Summer	48	31-67	5	2-8			76	46-107		
B. tricaudatus	Fall	22	8-46	60	36-92			39	17-69		
Chironominae	Fall			30	5-64			720	221-1427		
	Spring			5	1-11			120	37-238		
	Summer			15	4-34			360	110-714		
Cinygmula spp.	Spring	14	8-20	20	9-34			156	103-213		
	Summer	10	3-18	15	5-29			109	36-203		
Drunella doddsi	Fall							135	96-200		
	Spring	2	0-6			18	8-42	21	8-40		
Epeorus longimanus	Fall										
	Spring	1	0-2	2	1-3			3	1-5		
	Summer	87	32-171	148	91-209			211	126-311		
Megarcys signata	Fall					37	17-54				
	Spring					30	12-47				
	Summer					22	14-33				
Orthocladiini	Fall	2	0-5	1	1-2			24	16-34		
	Spring							16	10-24		
	Summer			2	0-2			18	12-26		
Prosimullim spp.	Fall							11	5-18		
	Spring							35	15-58		
	Summer							45	20-75		
Rhyacophila spp.	Fall					39	18-73				
	Spring					6	2-11	2	2-2		
	Summer					14	6-26				
Rhithrogena robusta	Fall	23	12-40	68	30-120			122	77-262		
	Spring	17	6-32	5	1-13			66	18-144		
	Summer	111	63-171	159	89-259			1226	699-1945		
Suwallia spp.	Fall					30	22-46	30	22-46		

	Spring					12	9-18	1	0-1		
	Summer			5	4-8	12	9-18	6	4-9		
Sweltsa spp.	Fall					28	20-52	4	0-10		
	Spring					12	9-23	1	0-4		
	Summer					9	6-17				
Taenionema pallidum	Fall			6	1-14			129	73-201		
	Spring	3	1-8	2	2-2			98	27-175	2	0-3
Zapada spp.	Fall	3	0-7	5	2-10					12	0-26
	Spring							4	4-6	3	3-5
	Summer	1	1-2					4	3-5	5	3-6

Consumption and 95% confidence intervals of major food items by taxa in Buckskin Creek, Colorado, 1998.

Taxon	Season	Algae	95% CI	Diatoms	95% CI	Animal	95% CI	Fine Detritus	95% CI	Coarse Detritus	95% CI
Baetis bicaudatus	Fall			6	3-11			27	13-45		
	Spring	16	4-28	34	17-52			109	46-189		
	Summer	8	3-12					2	0-6		
B. tricaudatus	Summer	65	43-82					24	6-56		
Chironominae	Fall		0-1	1	0-1			10	3-18		
	Spring	6	2-13	14	2-33			251	73-442		
	Summer	2	1-4	5	1-12			87	25-153		
Cinygmula spp.	Fall							9	3-13		
	Spring			15	6-26			56	25-92		
	Summer			5	1-10			18	1-51		
Drunella doddsi	Fall							35	22-55		
	Spring	2	1-3			12	8-16	2	1-3		
	Summer					3	2-5				
Epeorus longimanus	Spring	1	0-3	5	2-9			7	1-16		
	Summer	4	1-16	30	15-50			37	5-95		
Megarcys signata	Fall					6	0-12				
	Spring					19	1-36				
	Summer					3	2-5				
Orthocladiini	Fall		0-1	1	0-2			6	3-11		
	Spring	1	0-1	1	0-3			9	4-15		
	Summer	1	0-1	1	0-1			28	15-41		
Paraleuctra spp.	Fall							16	9-24		
	Spring							4	2-6		
	Summer							10	6-15		
Prosimulium spp.	Fall							12	7-16		
	Spring							44	26-60		
	Summer							34	20-46		
Rhyacophila spp.	Fall					8	3-18				
	Spring	12	4-26	3	1-6	3	1-7	13	5-29	42	15-95
	Summer					1	0-2				

Rhithrogena robusta	**Fall**			**105**	**67-154**			**138**	**90-203**		
	Spring	**57**	**37-77**	**51**	**26-77**			**216**	**119-372**		
	Summer	**43**	**25-65**	**5**	**3-7**			**126**	**81-185**		
***Suwallia* spp.**	**Fall**					**6**	**3-11**	**5**	**2-9**		
	Spring			**2**	**1-3**	**7**	**4-13**				
	Summer			**1**	**0-1**	**3**	**1-5**				
***Sweltsa* spp.**	**Fall**					**21**	**13-32**				
	Spring					**18**	**11-28**				
	Summer					**18**	**11-28**				
Taenionema pallidum	**Fall**	**3**	**2-5**					**13**	**1-38**	**21**	**12-29**
	Spring	**9**	**5-13**					**39**	**6-83**	**53**	**18-93**
***Zapada* spp.**	**Fall**							**25**	**15-36**	**26**	**12-41**
	Spring							**3**	**2-4**	**30**	**25-37**
	Summer							**4**	**1-9**	**16**	**11-21**

Consumption and 95% confidence intervals of major food items by taxa in East Fork Arkansas River, Colorado, 1998.

Taxon	Season	Algae	95% CI	Diatoms	95% CI	Animal	95% CI	Fine Detritus	95% CI	Coarse Detritus	95% CI
Arctopsyche grandis	Fall					5	2-12				
	Spring					34	21-54				
	Summer	2	0-3			41	14-73	11	5-30	5	1-55
Baetis bicaudatus	Fall	3	1-6	1	1-2			15	6 -26		
	Spring	8	2-15	14	4-28			4	1-7		
	Summer	14	2-15	21	11-33			14	5 -26		
Baetis tricaudatus	Fall	12	6-22	18	10-26			34	16-56		
	Summer	39	25-56	57	39-82			38	20-61		
Chironominae	Fall	1	0-2	6	1-13			7	1-16		
	Spring	12	0-47	138	15-301			157	17-363		
	Summer			7	0-16			24	5-49		
Cinygmula spp.	Fall	8	5-13	18	11-29			10	4-18		
	Spring	25	12-35	28	12-46			36	15-63		
	Summer	56	20-83	146	59-267			172	58-340		
Drunella doddsi	Fall	1	0-2			6	4-9	2	0-6		
	Spring	2	1??			12	8-14	4	2-8		
	Summer	9	3-18			18	13-25	13	5-26		
Epeorus longimanus	Fall										
	Spring	3	1??	4	2-7			2	1-3		
	Summer	31	19-47	89	54-133			63	25-118		
Kogotus modestus	Spring					58	35-72				
	Summer	8	2-19			19	4-44				
Megarcys signata	Fall					11	5-17				
	Spring					92	47-180				
	Summer					24	12-53				
Orthocladiini	Fall			1	0-2			1	0-5		
	Spring			20	7-36			26	4-101		
	Summer			1	0-2			2	0-5		
Paraleuctra spp.	Fall							73	46-112		
	Spring							13	7-18		

	Summer							55	35-84		
Prosimullim spp.	Spring	1	0-2	2	0-5			10	3-18		
	Summer	1	1-2	2	1-5			24	6-55		
Rhyacophila spp.	Fall					94	57-146				
	Spring					85	51-132				
	Summer					122	73-189				
Rhithrogena robusta	Fall	37	19-57	40	19-67			160	100-220		
	Spring	3	0-8	7	0-21			3	0-11		
	Summer	21	12-33	36	21-55			29	7-54		
Suwallia spp.	Fall					16	11-25	5	4-8	3	2-5
	Spring					16	10-23		0-1		
	Summer			1	0-2	26	18-39	1	0-1		
Taenionema pallidum	Fall	5	0-11					17	1-47	100	64-141
	Spring	10	2-19					32	2-86	187	51-329
Zapada spp.	Fall	2	0-3					14	7-22	21	12-32
	Spring	1	0-1					6	4-9	3	2-4
	Summer							9	5-15	7	4-10

Consumption and 95% confidence intervals of major food items by taxa in Mosquito Creek, Colorado, 1998.

Taxon	Season	Algae	95% CI	Diatoms	95% CI	Animal	95% CI	Fine Detritus	95% CI	Coarse Detritus	95% CI
Arctopsyche grandis	Fall	1	0-1			15	9-23	2	1-2	1	1-1
	Spring	1	0-2			12	0-32	5	1-11	2	0-5
	Summer					6	3-13				
Baetis bicaudatus	Fall	6	6-7	7	5-8			35	31-41		
	Spring	32	16-53	33	21-49			76	44-120		
	Summer	4	1-8	2	1-4			11	4-20		
Baetis tricaudatus	Summer	17	3-39	178	107-254			146	81-221		
Chironominae	Fall										
	Spring										
	Summer										
Cinygmula spp.	Spring	3	1-6	9	4-16			43	20-70		
	Summer	5	1-10	15	5-24			69	26-114		
Drunella doddsi	Fall			7	0-14	10	4-17	68	43-98		
	Spring					6	2-9	12	4-16		
	Summer			1	0-1	4	3-6	6	4-9		
Epeorus longimanus	Spring			2	0-3			18	5-37		
	Summer	1	0-4	9	2-19			111	31-198		
Megarcys signata	Fall					16	5-37				
	Spring					21	10-30				
	Summer					9	1-28				
Orthocladiini	Fall							2	1-4		
	Spring			1	0-2			11	2-27		
	Summer	2	1-4	9	2-21			34	9-76		
Prosimullim spp.	Fall							66	23-111		
	Spring							38	13-62		
	Summer							36	13-64		
Rhyacophila spp.	Fall					18	10-28				
	Spring					3	1-5	2	0-6		
	Summer					13	7-21				
Rhithrogena robusta	Fall	2	0-4	3	0-6			13	1-32		

Consumption and 95% confidence intervals of major food items by taxa in Snake River, Colorado, 1998.

Taxon	Season	Algae	95% CI	Diatoms	95% CI	Animal	95% CI	Fine Detritus	95% CI	Coarse Detritus	95% CI
Chironominae	Spring							20	1-49		
Orthocladiini	Fall										
	Spring							4			
	Summer										
Prosimullim spp.	Fall							1	0-3		
	Spring										
	Summer							10	1-51		
Suwallia spp.											
Zapada spp.	Fall									14	11-19
	Spring										
	Summer							6	3-9	2	0-4