ABSTRACT OF THE DISSERTATION OF

Kristopher Keith Wright for the degree of Doctor of Philosophy in Fisheries Science presented on April 28 2000. Title: From Continua to Patches: Longitudinal Patterns in the Middle Fork of the John Day River, Oregon.

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The Middle Fork John Day River is composed of low gradient, alluvial valley segments separated by constrained, canyon-like reaches, and has a history of multiple land-uses. These factors can alter the physical and biological structure of streams, and disrupt the longitudinal river continuum. I examined habitat, fish, macroinvertebrates, and primary production at 20 sites along a 1st–5th order gradient of this eastern Oregon river during summer low flow in 1996-1998. Using non-parametric, multivariate ordination, I examined longitudinal patterns of physical and biological characteristics by rotating ordinations to a common set of variables. Three *a priori,* qualitative null hypotheses of ordination patterns were established: 1) an ideal longitudinal continuum, 2) a highly variable distribution and 3) discrete patches. Effects of spatial perspective on longitudinal patterns were considered by comparing site- and reach–scale patterns. The potential influence of abiotic factors and trophic interactions were examined using correlations with ordination coordinates and regressions with individual parameters. Despite variations in valley constraint and land-use, both physical and biological elements occurred along longitudinal gradients. The most consistent longitudinal gradients were observed for physical characteristics, and there was no evidence of subsurface water upwelling associated with discontinuities in valley constraint. Fish and macroinvertebrate communities were more strongly correlated with landscape scale, geomorphic gradients than with site-

scale habitat variability. Algal biomass and productivity were highly variable. Most individual physical and biological variables (e.g. substrates or insect taxa) reflected discontinuous or patchy gradients from a site-scale perspective, and more continuous gradients from a reach-scale perspective. There was little evidence of trophic interactions affecting community structure in a consistent pattern. The spatial scope and breadth of measures in my study revealed how perceptions of stream gradients absolutely depend upon the spatial extent of our observations. This study illustrates that continuous and patchy aspects of both physical and biological parameters occur together in stream systems and are not mutually exclusive.

From Continua to Patches: Longitudinal Patterns in the Middle Fork of
the John Day River, Oregon

by

Kristopher Keith Wright

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Doctor of Philosophy dissertation of Kristopher Keith Wright presented on April 28, 2000.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Kristopher Keith Wright, Author

ACKNOWLEDGMENT

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FROM CONTINUA TO PATCHES: LONGITUDINAL PATTERNS IN THE MIDDLE FORK OF THE JOHN DAY RIVER, OREGON

1. INTRODUCTION

Understanding the structure of ecological communities across temporal and spatial gradients has been the subject of theoretical debates (e.g. Gleasonian vs. Clementsian views), the template for classic community ecology studies (e.g. work by Joseph Connell and Robert Paine), and the foundation of ecological conceptual frameworks (e.g. Trophic Cascading, River Continuum Concept). As a topic of ecological research, the study of community structure incorporates various physiochemical and biological interactions over multiple temporal and spatial scales. Perhaps it is this imposing complexity associated with community structure that has lured ecologists into focusing so much attention on the topic.

In the past two decades, multiple theoretical concepts have been developed to explain structure and processes in stream ecosystems. These concepts include, but are not limited to, the River Continuum Concept (Vannote et al. 1980, Minshall et al. 1985), the Nutrient Spiralling Concept (Newbold et al. 1982, Elwood et al. 1983), Patch Dynamics in streams (Pringle et al. 1989, Townsend 1989), the Flood Pulse Concept (Junk et al. 1989), stream flow predictability (Poff & Ward 1989), the Riparian Corridor Concept (Gregory et al. 1991), the Hyporheic Corridor Concept (Stanford & Ward 1993), the Hierarchical Habitat Classification (Frissel et al. 1986), and Process Domains (Montgomerey 1999). While each concept presents a particular perspective of lotic systems, they all emphasize that streams are physically and biologically connected to their respective landscapes through multiple pathways. This implies that the structure of stream communities is a function of both in-stream and landscape physical and biological factors. Presumably, when connections between streams and their landscapes are severed through natural or anthropogenic alterations,

the physical and biological structure within those streams will be altered (e.g. Minshall et al. 1985, Allan et al. 1997, Brunke & Gonser 1997).

A stream devoid of riparian vegetation that has been channelized, incised and simplified would be disconnected from the surrounding landscape. This image depicts a river as a simple, closed system (much like a canal). Without variation in landscape interactions, the stream and its biota would be predicted to remain relatively homogeneous along its profile. In contrast, a stream that is connected to the landscape would vary according to the predictions of current theoretical models.

Because of their longitudinal connectivity, river networks are unlike most other ecosystems. This was perhaps best illustrated by the development of the River Continuum Concept (RCC) in the early 1980's (Vannote et al. 1980). The RCC and its corollaries emphasize the longitudinal and lateral connectivity of stream systems in terms of riparian influences, energy sources, nutrient spiraling, primary production and stream biota. This concept predicts that as a stream progresses downstream from its headwaters, the sources of energy within the system change. Headwaters and low order sections are predicted to be driven by allochthonous, coarse particulate matter (CPOM) inputs from streamside vegetation (Figure 1.1, from Vannote et al. 1980). In mid-order reaches, the stream widens allowing more sun to reach the stream where autochthonous processes and periphyton become more prevalent. Finally, in high order reaches the system becomes predominately driven by fine particulate matter (FPOM) within the system. Because of these changes in energy sources, the RCC suggests that biota within these different reaches also will reflect a longitudinal progression (Figure 1.1).

According to the RCC predictions on community structure, low order (1-3) heterotrophic segments would have relatively large proportions of shredding and collecting macroinvertebrates, and a low proportion of grazers. In mid-order (4-6) autotrophic segments, collectors and grazers are predicted to dominate the macroinvertebrate assemblage, with a low proportion represented by shredders. Finally, in higher order (7-12) segments, the macroinvertebrate community would be primarily composed of collectors.
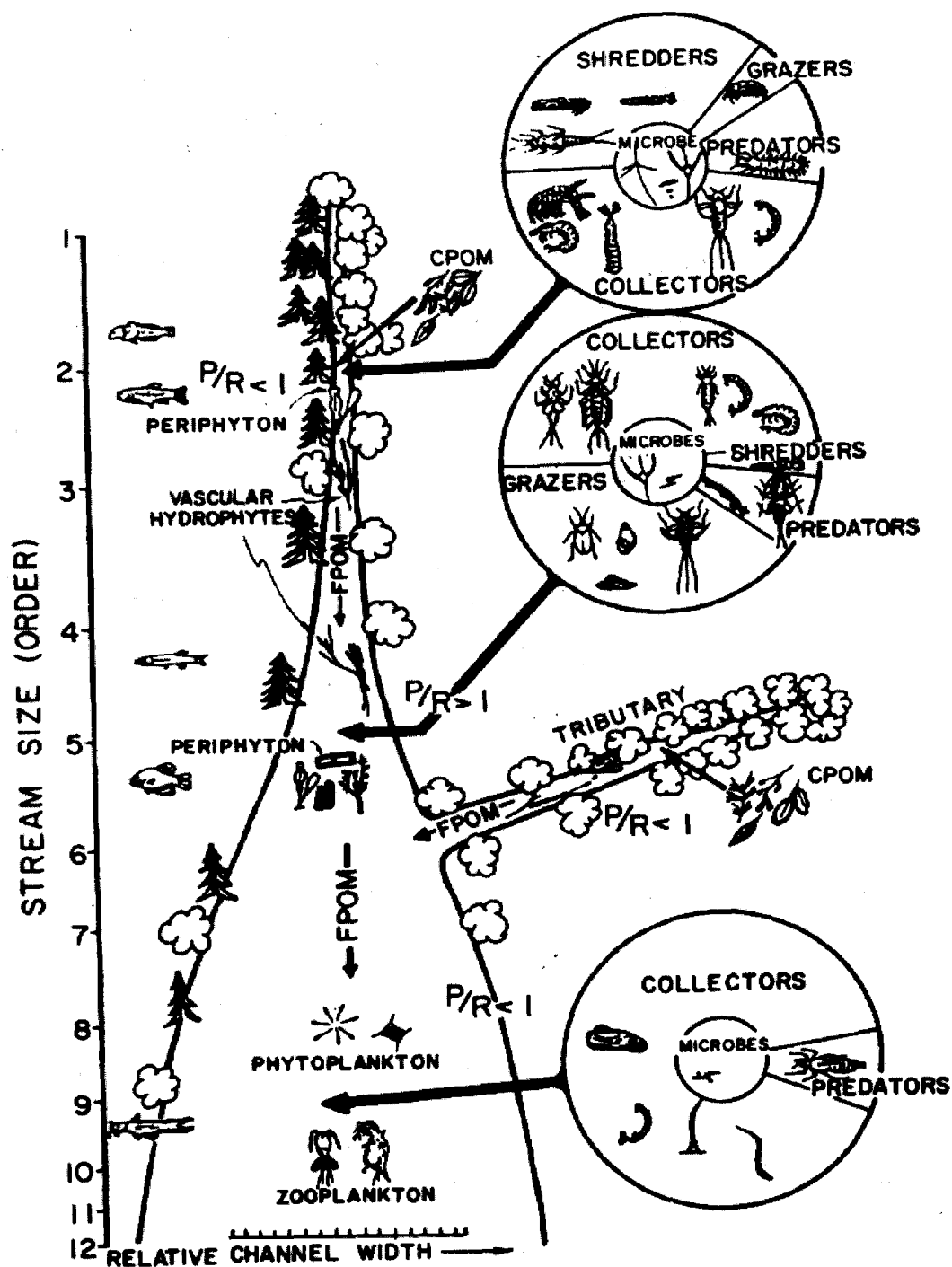
Figure 1.1. An illustration describing the proposed relationships within the River Continuum Concept (from Vannote et al. 1980).

The RCC was primarily based on continuous, longitudinal progressions within undisturbed, temperate, montane systems. Therefore, streams that: 1) are located within different ecotypes, 2) have patchy or discontinuous geomorphic features, or 3) have been altered through anthropogenic influences, may reflect variations on the RCC predictions (Ward & Stanford 1983, Minshall et al. 1983, 1985, & 1992, Brussock et al. 1985, Statzner & Higler 1985, Huryn & Wallace 1987, Brussock & Brown 1991, Luthgart & Wallace 1992, Stanford and Ward 1993, Grubaugh et al. 1996, Allan et al. 1997, Townsend et al. 1997, Delong & Brusven 1998). Within the arid interior of the Pacific Northwest, the longitudinal profiles of many streams are composed of large, low gradient, alluvial valley segments separated by constrained, canyon-like reaches. In addition, many of the watersheds have been subjected to a history of various land-use practices including grazing, mining, channelization, irrigation and forestry. Such influences can alter the physical and biological structure within stream systems, and presumably disrupt the predicted longitudinal succession (Minshall et al. 1985, Allan et al. 1997).

While current theoretical models consider how community structure can be determined by geomorphology, hydrology and riparian conditions longitudinally, little work has been done on the influence of trophic interactions affecting longitudinal trends in community structure. Top-down and bottom-up trophic interactions have been shown to influence community structure within lentic systems (e.g. Carpenter et al. 1985, Kitchell & Crowder 1986) and under experimental conditions in stream reaches (e.g. Power 1990 & 1992, Wooton et al. 1996). In other reach scale experiments, grazing pressure from benthic macroinvertebrates has been shown to influence both algal biomass (Jacoby 1987, Lamberti et al. 1987, Lamberti et al. 1995, Walton et al. 1995) and primary production (Jacoby 1987, Lamberti et al. 1987) by reducing algal standing crop and increasing turnover rates. Fishes also may influence aquatic community structure by preying on invertebrates and thereby reducing the grazing pressure on primary producers (Carpenter et al. 1985, Power 1990, Wooton et al. 1996), or by grazing directly on algae (Gelwick & Matthews 1992). Nevertheless,

we know little about how such biological interactions may influence community structure along a natural stream continuum, within the context of abiotic constraints.

This study had two primary objectives. First, I examined the applicability of the RCC to fish, macroinvertebrate, and algal communities in a high-desert stream in eastern Oregon, within the context of multiple physical and anthropogenic constraints. The second objective of this study was to examine the potential role of trophic interactions in community structure along the longitudinal profile of a high-desert stream within the context of physical and anthropogenic constraints.

2. A NEW APPROACH TO EXAMINE ENVIRONMENTAL GRADIENTS USING NON-PARAMETRIC, MULTIVARIATE ORDINATION

"In biological sciences…inherent variation must be accepted as basic, and must be handled as such."
- Norman T. J. Bailey, from Statistical Methods in Biology

In the search for ecosystem patterns and processes, ecologists consider the influence of multiple large and small scale factors, combinations of abiotic and biotic factors, and often numerous taxa and organisms. To account for such considerations ecologists may focus studies to address one or two of these considerations, narrow their scope to specific taxa or habitats, or rely on multivariate analysis techniques to address all considerations simultaneously. Multivariate techniques are popular with ecologists because, by definition, this approach depends on numerous variables and incorporates the inherent variation within community data. However, one concern with multivariate analyses in ecology is that for any given analysis there may be numerous possible interpretations (e.g. patterns in an ordination plot) (sensu Austin 1985). In this paper, I describe a conceptual framework and methodological approach for examining community patterns at multiple scales using multivariate ordination techniques. This approach is generally applicable to any ecosystem or community, can be used for both biotic and abiotic gradients over multiple scales, utilizes numerous taxa and variables, and provides a set of qualitative, *a priori* hypotheses regarding community structure.

I define a community as a collection of living organisms found at a specific place and time, with no implication of whether or not the species are independent or interacting (modified from Krebs 1994, McCune 1999). Determining the structure of a community typically follows an observational approach which is inductive, non-experimental, and multivariate (Noy-Meir & Austin1970, Ludwig & Reynolds 1988), because community ecologists obtain information pertaining to a large number of variables in a community without manipulating these variables (Ludwig & Reynolds

1988). Consequently, much work in community ecology attempts to elucidate and describe patterns from empirical data, rather than formally testing *a priori* hypotheses (Green 1980, Ludwig & Reynolds 1988). In some cases, the detection of specific patterns across samples may lead to the formation of causal hypotheses about the underlying structure of the ecological community (Noy-Meir 1970), which may then be tested with future work (Ludwig & Reynolds 1988).

The structure of a given community is a function of multiple environmental (biotic and abiotic) gradients ranging from large to local in scale, relative to the organisms involved (Wiens 1976, Levin 1992). How organisms respond (or have responded) to this spectrum of sometimes opposing, correlated, or individual gradients determines the community structure at any given point in time and space (Austin 1985). Consider a single, large-scale environmental gradient (e.g. from alpine slopes to valley plains, from lake surface to bottom depth, from headwater streams to large rivers). If factors driving community structure along this gradient are continuous and linear (Figure 2.1), the changes in community structure along this gradient should be continuous (sensu Whittaker 1975, Vannote et al. 1980). On the other hand, if the factors driving community structure along this gradient are discontinuous or patchy (Figure 2.1), community structure along this gradient should be patchy (sensu Wiens 1976). While both continuous and patch-like patterns in community structure have been observed, the ability of ecologists to examine and deal with both types of patterns simultaneously has been limited. I believe this limitation is due in part to the lack of a conceptual or theoretical framework that allows one to create and test hypotheses and consequently develop community ecological theory.

Adding further complexity to the issue of community structure is the recognition that environmental gradients include abiotic and biotic components (e.g. temperature and predation pressure) that also operate across a range of scales. If we consider a gradient from alpine to valley, structure of small mammal communities will respond differently than terrestrial insect communities to the same suite of environmental gradients. In addition, biotic and abiotic factors that influence these communities are often correlated (e.g. tree species and elevation). Various
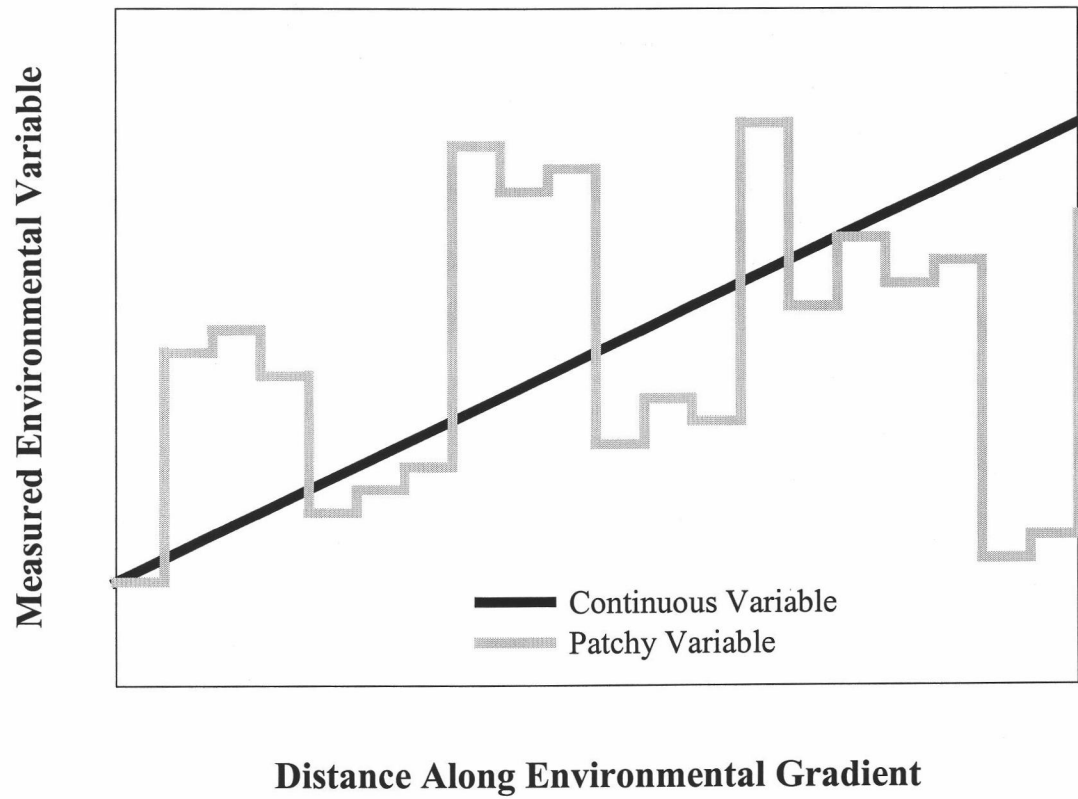
Figure 2.1. Theoretical distributions of continuous and patchy variables along an environmental gradient.

interpretations of these kinds of correlations have led to major ecological paradigms in terrestrial and aquatic systems (e.g. Whittaker 1975, Connell 1978). However community ecologists lack a consistent, widely applicable approach that simultaneously incorporates both biotic and abiotic factors across scales into the structure of communities. Although many studies have been successful at this integration using various techniques (e.g. Richards et al. 1997, Wiley et al. 1997, Poff & Huryn 1998), the applicability of these approaches has been limited to the systems under consideration.

What would it take to develop such an approach? First, the approach must be able to describe different community structures along environmental gradients at multiple spatial scales. One should be able to make general comparisons of community structure across different ecosystems and community types. Second, the approach should identify those physical and biological factors potentially influencing community structure. This includes being able to identify those factors that are correlated with each other. Finally, the approach would indicate the scale(s) at which those different factors may influence members of the community.

This chapter describes an initial attempt to develop such an approach. I begin by creating a conceptual framework based on multivariate ordination that can be used to describe structures of various community types. Although this framework was based on my experience with stream ecosystems, it is applicable to any ecotype or environmental gradient. The next stage describes the data sets and analytical methods I used to expand this approach beyond the conceptual framework. I propose the means to not only integrate the conceptual framework with actual community data, but also how to: 1) identify both physical and biological factors potentially influencing community structure and 2) incorporate a multiple spatial scale perspective. Finally, I discuss some of the potential applications and limitations of the approach.

The proposed approach is directly linked to multivariate, non-parametric, ordination techniques. It is important to understand why such techniques are used. First, I used multivariate analyses because we are examining multiple sample units, taxa, and environmental variables. Second, I used non-parametric methods because

community data rarely meets the normality and independence requirements of traditional parametric statistics. Finally, I used ordination (indirect gradient analysis) because we are interested in community patterns across multiple environmental gradients. Ordination in this context measures the similarity in communities among sample units, and then ordinates the units in multi-dimensional space such that sites with most similar communities are close together and the variance is minimized among the environmental gradients (or axes).

The Conceptual Framework

While this framework is not restricted in the number of dimensions used in an ordination, for the purpose of simplicity, I limit this discussion to examples using two dimensions where:

Axis 1 = primary axis

Axis 2 = secondary axis.

Primary and secondary refer to the amount of variance explained (i.e. r^2) by each of the axes, such that the primary axis has the highest r^2 value.

Consider 30 sample units distributed along a longitudinal profile of a hypothetical stream from 1st order headwaters to 5th order mid-size reaches. At each sample unit, the same suites of physical and biological variables are measured. Let us first assume this hypothetical stream is an 'ideal' continuum. All biological and physical variables are strongly correlated, because all variables consistently and gradually change along this profile. The only variation among the sample units is along the longitudinal gradient. If I were to run an ordination of the sample units using either the physical or biological variables, I would get an ordination that looks like Figure 2.2. Each symbol represents a given sample unit, and the color and shape indicate the stream order (i.e. stream size). (Note: Sites may be grouped to any variable. While the use of elevation, discharge, or drainage area would work equally well, I used stream order because it is strongly correlated with these other physical
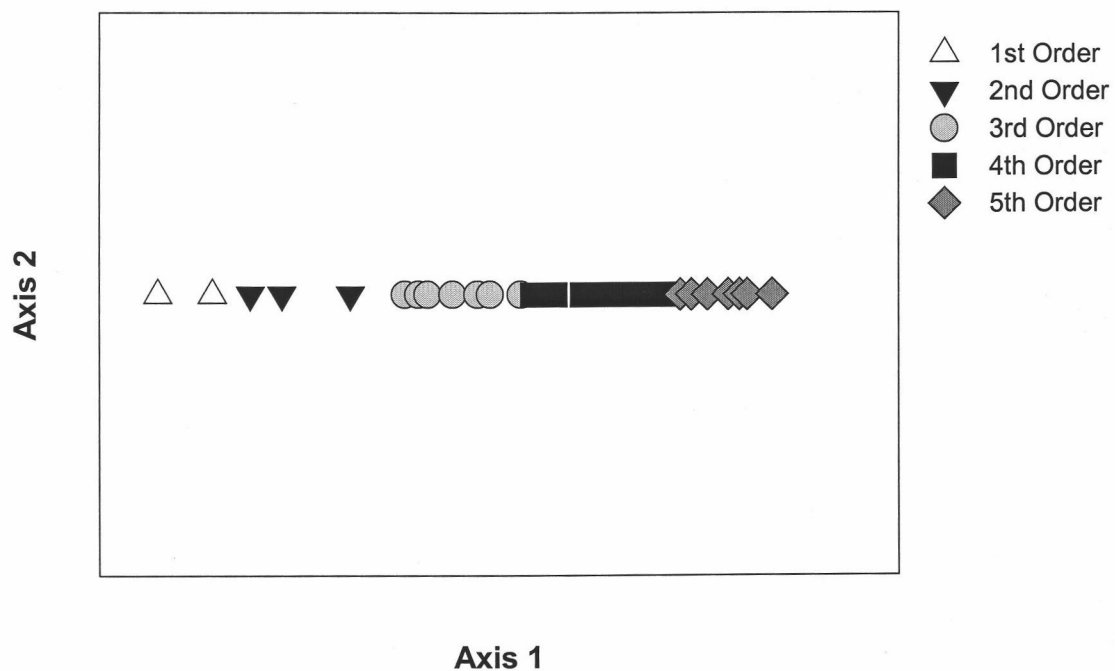
Figure 2.2. Conceptual ordination pattern of sample units from an 'ideal' stream continuum. Each symbol represents a given sample unit; shade and shape indicate stream order. The sample units are arranged continuously along the first axis, because there is only one gradient, the longitudinal progression from headwaters down stream.

variables in our watershed, and is easier to represent graphically). Notice that for our ideal continuum, there is only one dimension. Axis 1, the primary axis, explains 100% of the variation, because in an ideal continuum there is only one gradient: the longitudinal gradient.

At another extreme, let us assume the hypothetical stream is simply a random assortment of physical and biological variables. There are no strong correlations between or among the physical and biological variables, and no variable consistently changes along the longitudinal profile. If I were to run an ordination of the sample units using either the physical or biological variables, I would get an ordination that looks like Figure 2.3. The sites are spread out in ordination space and there is no longitudinal gradient. The ordination indicates that there is a high degree of variability among the sample units along both axes. Neither axis is primary, and the cumulative r^2 for both axes is negligible (i.e. approaching zero). In this case, I either assume the sample units are so similar they cannot be distinguished from one another or, they are so different that no similarities exist.

To visualize a "patchy model", we can modify the latter example. Again in our hypothetical stream, no variable changes consistently along the longitudinal profile; however, there are strong correlations between certain physical and biological variables. While there is no longitudinal gradient, there are other discontinuous or smaller scale gradients that cause the sites to group together in clusters (Figure 2.4). The sites within a cluster are more similar to each other than to sites in any other cluster. Thus, there is no longitudinal continuum, but a series of discrete patches along the longitudinal profile. The configurations of patchy systems can vary greatly. In this example I have four clusters, but there can be other numbers and arrangements of clusters (Figure 2.5). The basic premise is that large-scale gradients are not correlated with community patterns in these patchy models, rather small-scale or discontinuous gradients are most strongly correlated with the patterns. The result, in our example, is a patchy distribution of sample units in ordination space with no longitudinal gradients.
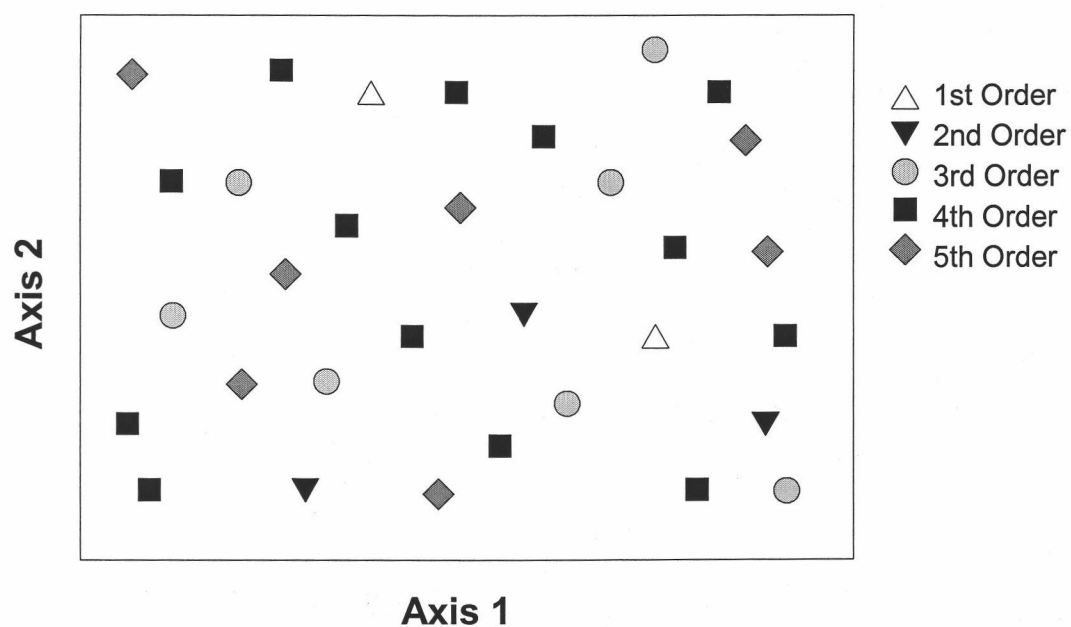
Figure 2.3. Conceptual ordination pattern of sample units from a discontinuous, highly variable stream gradient. Each symbol represents a given sample unit; shade and shape indicate stream order. The sample units are scattered randomly throughout the plot because there are no distinctive gradients.
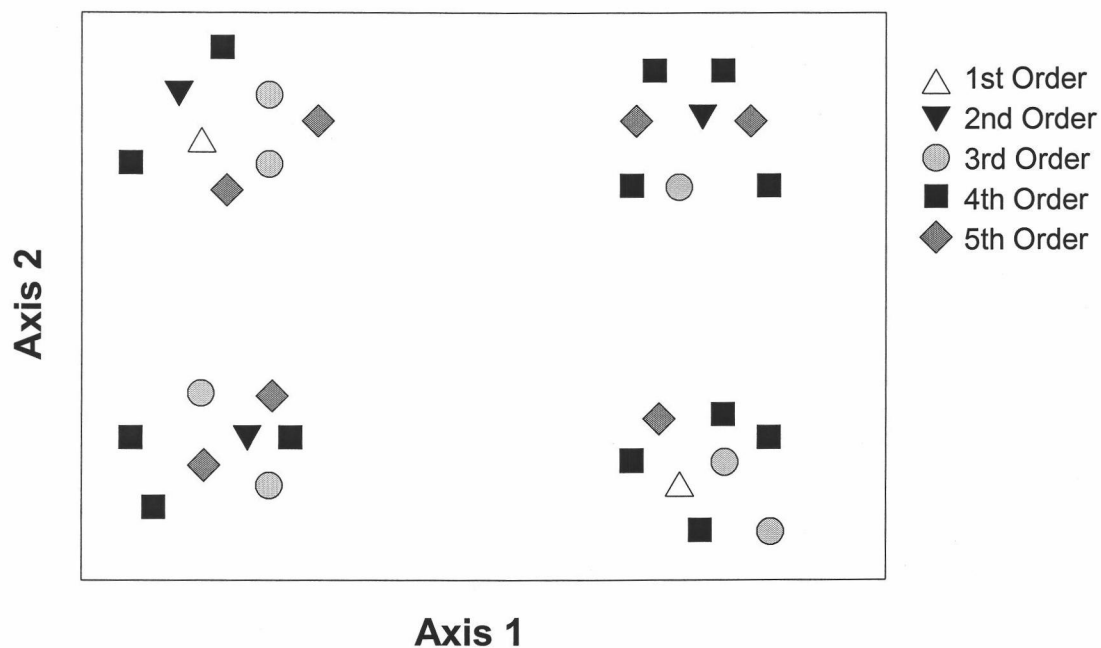
Figure 2.4. Conceptual ordination pattern of sample units from a patchy stream gradient. Each symbol represents a given sample unit; shade and shape indicate stream order. The sample units are arranged in clusters or groups, because the gradient is a series of discrete patches. The sample units within each group are more similar to each other than to those in other groups.
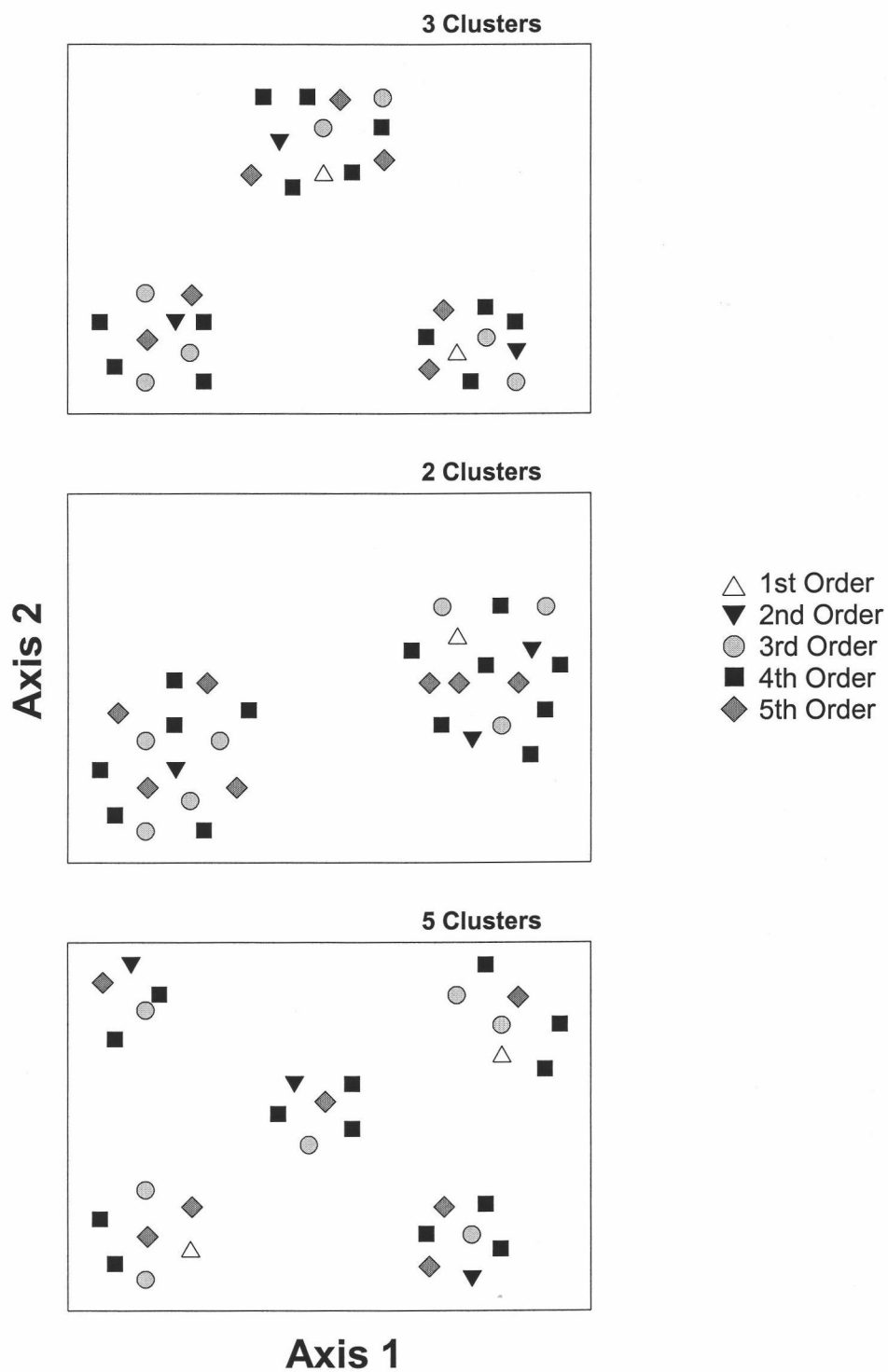
Figure 2.5. Conceptual ordination patterns showing example variations on the patchy model. Sample units may group together in any number of clusters or arrangements.

These conceptual representations provide a framework within which to examine actual community structures. Basically each model may be viewed as a null hypothesis for the ordination of communities along a gradient. In most cases, one would not expect a situation that corresponds directly to one of the above models. Rather, because communities are influenced by a combination of relatively large- and small-scale variables, I would expect to see a combination of the models when I use real data (Figure 2.6). For example, the central ordination in Figure 2.6, represents a situation in which there is evidence of a continuous gradient from headwaters to 5th order sites, some variability, and also patchiness represented by clusters of sample units.

This conceptual framework can be used to describe community patterns along a gradient regardless of system or spatial scale. By asking, "How much do ordinations of actual communities vary from the proposed conceptual models?" and "*Why* do ordinations of actual communities vary from the proposed conceptual models?", one can begin to integrate the factors influencing community structure and the spatial scales at which they operate. In the next section, I use an example from an actual stream gradient to describe how these questions may be addressed.

Example from a Stream: Introduction

Stream ecosystems are ideal for examining changes in community structure along environmental gradients, because they possess both continuous and patchy characteristics (e.g. Vannote et al. 1980, Minshall et al. 1985, Statzner & Higler 1985, Pringle et al. 1988, Townsend 1996, Montgomery 1999). The progression from headwaters down stream can be a continuous longitudinal gradient for factors like discharge and elevation that tend to change steadily downstream, whereas, gradient, depth, and benthic substrates may be downstream series of heterogeneous patches. In addition, members of the stream communities, including fish, macroinvertebrates, and algae, each respond differently to the same suite of environmental gradients from headwaters downstream (Fisher 1994).
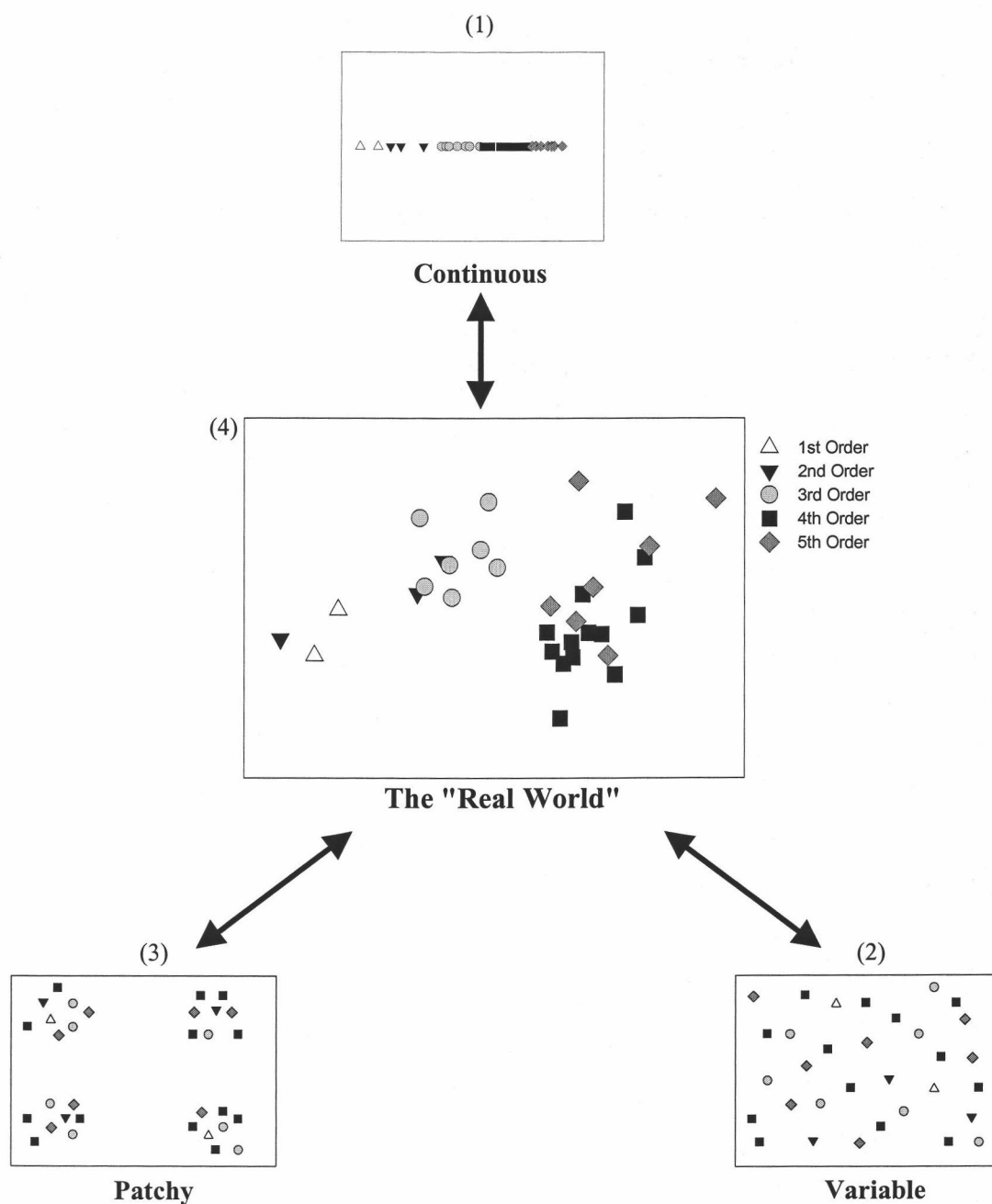
Figure 2.6. A conceptual framework based on ordination patterns that provides three *a priori* conceptual, null hypotheses of ordination patterns: (1) an ideal continuum, (2) highly variable, and (3) discrete patches. Ordinations from actual data would be expected to contain elements of all three conceptual patterns (4).

In this example, we examined longitudinal patterns of physical habitat, fishes, and macroinvertebrates along a 1st through 5th stream order gradient. I hypothesized that ordination patterns of the three data sets would contain elements of all three distributions presented in the conceptual framework. I also expected that ordination of physical variables would be more strongly correlated with large-scale, longitudinal gradients than either biotic community ordination. Finally, I hypothesized that ordination of the larger-bodied, more mobile fish communities would be more strongly correlated with continuous, landscape scale longitudinal gradients than the smaller-bodied, less mobile benthic macroinvertebrate communities.

Example from a Stream: Data and Analysis

Sampling

I sampled physical variables, fishes and benthic macroinvertebrates at 32 sites along a 100 km section of the Middle Fork of the John Day River in eastern Oregon, during summer low flow conditions in 1996-1998. This section ranges from 1st to 5th stream order, has no impoundments or dams, but has been influenced by grazing, timber harvest, and mining. All sites were 50-100 m in length and dominated by riffle and run habitats. Twelve sites were sampled in 1996, 10 sites were sampled in 1997, and 10 sites were sampled in 1998. Some sites were represented in each of the three years of sampling, however for this example I considered each sample year independently.

Macroinvertebrates were sampled with a (0.1 m^2) modified Surber sampler. Six samples were collected within each site; sampling locations were determined arbitrarily but without preconceived bias. Each sample was counted individually and macroinvertebrates were identified to genus. Approximately 109 taxa have been identified from the samples. For analysis, I used the mean densities of each taxon (no./m^2) from the six samples at each site.

Fish were sampled using a backpack electro-shocker, two dip nets and a 5 mm mesh, 2 m wide, block net. For each pass, the block net was set 10 m downstream from the electro-shocker. Sampling progressed downstream toward the block net within a 2m wide frame outlined by the block net. Substrates were disturbed along the pass to ensure burrowing fishes were dislodged. Fish were captured along the pass by dip nets and any missed fish were retained in the block net. Passes were made within a site until at least 15 of the two most common taxa were collected. All collected fish were counted. For analyses I used relative abundance of each species at each site. A total of 10 species of fish were identified in the study.

Variables in the environmental matrix were used to assess the distribution of sites in ordination space. The variables ranged from landscape (e.g. valley slope) to site-specific (e.g. depth) in scale (Table 2.1). Typically landscape features do not change at a given site from year to year; in contrast site-specific features may vary seasonally and/or annually. Because the River Continuum Concept (Vannote et al. 1980) focused on continuous longitudinal gradients, particularly stream size, I used stream order (Order) as the primary environmental gradient for comparisons between matrices.

Analysis

I used non-metric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976) for ordination of biological and physical data. NMS relieves the zero-truncation problem for heterogeneous community data, and relaxes assumptions of normality because it uses a rank-ordering procedure for sample unit distances (Beals 1984, Austin 1985, Ludwig & Reynolds 1988, Tabachnick & Fidell 1996). In addition, it is a robust ordination method that could be consistently applied to data sets with a varying range in the number of attributes across sample units (i.e. 109 invertebrate taxa vs. 10 fishes) (Austin 1985, Faith et al. 1987, Faith & Norris 1989).

Table 2.1. Abiotic environmental variables used in analysis of 32 Middle Fork John Day River sites. All measurements were made during summer low-flow periods from 1996-1998.

Environmental Variable	Source
Elevation (m)	Topographic Maps, GPS
Discharge (m^3/s)	Field Measurements (3 per site)[1,2]
Valley Slope (degrees)	Topographic Maps
Stream Gradient (degrees)	Clinometer[2,3]
Wetted Channel Width (m)	Field Measurements (3 per site)[1,2]
Depth (m)	Field Measurements (>25 per site)[1,2]
Width:Depth	Calculated
Average Weekly Temperature (°C)	Onset®, Thermal Data Loggers
Average Weekly Minimum Temperature (°C)	Onset®,Thermal Data Loggers
Average Weekly Maximum Temperature (°C)	Onset®,Thermal Data Loggers
Average Weekly Difference of Maximum and Minimum Temperatures (°C)	Onset®,Thermal Data Loggers
Solar Input to Stream (h)	SolarPathfinder® (9 per site)[3]
Percent of Available Solar Input Reaching Stream	SolarPathfinder® (9 per site)[3]
Aspect (radians)	Compass Reading
Constrained vs Unconstrained	Topographic Maps, Field Observations
Percent of Riffle Habitat in Site	Field Measurements (>25 per site)[4]
Percent of Cobbles/Gravels in Site	Field Measurements (>25 per site)[4]
Percent of Sands/Silts in Site	Field Measurements (>25 per site)[4]
Percent of Boulders in Site	Field Measurements (>25 per site)[4]
Percent Macrophyte Cover	Field Measurements (>25 per site)[4]

* Complete description of methods found in: [1] Hauer & Lamberti 1996, [2]Gordon et al. 1992, [3]Platts et al. 1987, [4]Wright 1997

Each data matrix was analyzed separately using NMS in PC-ORD, version 3.2. I used Sorensen's distance measure with settings for each analysis at: 30 runs with original data, 30 Monte Carlo simulations, and a 0.20 step length. Sorensen's distance was chosen because it remains sensitive to differences between communities at large environmental distances (Beals 1984, Faith et al. 1987). Final configurations were limited to three dimensions.

Data matrices contained site level information. The three data matrices included: 1) mean macroinvertebrate taxa densities (32 site by 109 taxa matrix), 2) relative abundance of fishes (32 site by 10 taxa matrix), and 3) environmental variables (32 site by 20 matrix). Densities of macroinvertebrates (mean no./m^2) were calculated for each taxon by averaging densities from all 6 samples at each site. I calculated relative abundance of fishes in each site by dividing the total number of each species by the total number of all species. All data were transformed by $\ln(x + 1)$.

To compare ordinations I examined cumulative variance explained (R^2), and correlation between the site's ordination coordinates and environmental gradient variables. To examine the correlation between site ordination coordinates and environmental gradients, each ordination was rotated to a common set of environmental variables. For a given ordination, the primary (1°) and secondary (2°) axes were identified using incremental r^2 values determined by a correlation between ordination and original matrix distances. Each ordination was then rotated such that the 1° axis represented large-scale, longitudinal gradients and the 2° axis represented small-scale, site-specific gradients:

In the plane of axes 1 and 2: 1° axis was rotated to stream order, and 2° axis was rotated to percent riffle habitat.

I used riffle habitat for the 2° axis because it was a site-specific, physical habitat variable that was not correlated with stream order. Any similar variables may be used however, for different ordinations to be compared, rotations **must** be consistent from one ordination to the next. After the three ordinations were oriented according to the

same gradients, I compared Pearson correlation coefficients between the 1° and 2°
axes with the environmental variables from the environmental matrix.

Example from a Stream: Results and Discussion

A visual comparison of the MFJD ordination patterns to the conceptual
diagrams illustrated that patterns from all three ordinations contain aspects from all
three conceptual models (Figure 2.7). While there is generally a consistent
longitudinal gradient along the first axes from low order headwater sites to larger 5th
order sites, there are also varying degrees of variability (scatter) and patchiness among
the ordinations. Ordination of the physical variables appears to have the most
continuum-like pattern and the least amount of variability and patchiness among the
three ordinations. In contrast, the macroinvertebrate ordination appeared to have the
most variable and patchy pattern among ordinations (Figure 2.7). Ordination of fishes
suggests that along the longitudinal gradient of axis 1 there is little difference among
3rd through 5th order sites, and that the headwater sites in 1st and 2nd order reaches are
driving the longitudinal gradient.

Perhaps the most important part of this step is to recognize the inconsistencies
between the ordinations of data and the conceptual diagrams. In all cases, there are
aspects of the ordinations that do not conform to the conceptual distributions. For
example, many of the 4th and 5th order sites are not consistently arranged by stream
size along axis 1. There may have been a problem using stream order as a gradient or
grouping variable; however, results from preliminary analyses were similar using
elevation, discharge, etc. Why do such inconsistencies occur? The physical habitat
ordination suggests that size of the stream is less indicative of the physical
characteristics at downstream sites than for low order, upstream sites.

The next step directly compares ordination patterns and examines the strength
of continuous versus patchy environmental gradients. Because I have rotated the
ordinations to the same variables, I can compare cumulative r^2 values, r^2 values of the
individual axes, and the correlations between the different axes and environmental
variables.
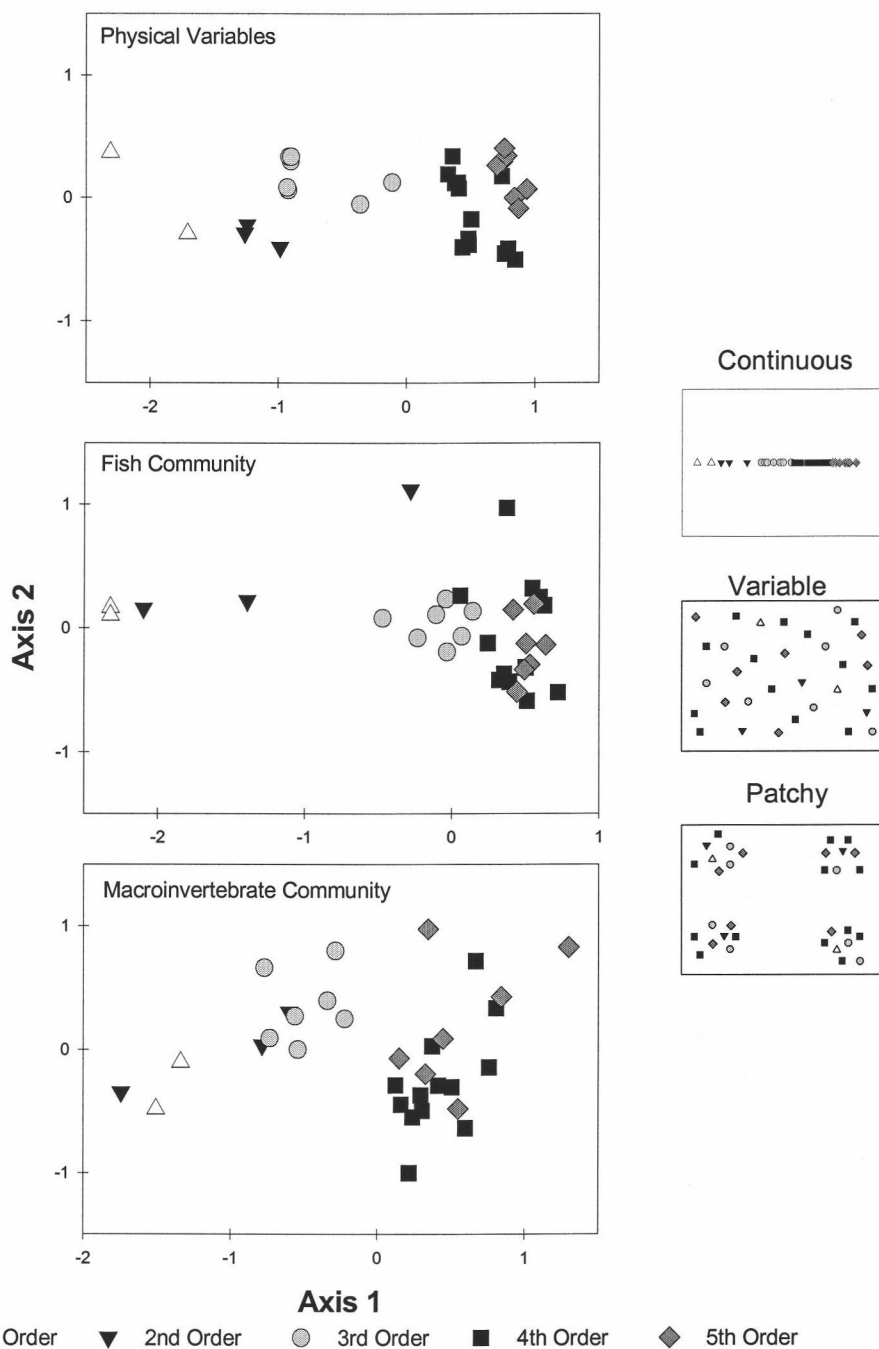
Figure 2.7. Two dimension plots of the NMS ordination of physical variables, relative abundance of fishes, and macroinvertebrate densities in the MFJD. Each symbol represents a given site; the color and shape indicate stream order. Miniature versions of the conceptual framework are shown on the right. Configurations have been rotated such that axis 1 represents large-scale, longitudinal gradients, and axis 2 represents small-scale, site-specific gradients.

Each of the ordinations of physical habitat, fish, and macroinvertebrates explained over 90% of the variation (cumulative r^2 values = 0.994, 0.987, and 0.926 respectively). Along axis 1 (the longitudinal gradient), the individual r^2 values for the physical, fish, and macroinvertebrate ordinations were 0.942, 0.848, and 0.608, respectively. These values suggested that most of the variability in all 3 ordinations was explained by large-scale, longitudinal gradients. As observed in the visual comparisons, macroinvertebrates were the least strongly correlated with large-scale variables. Along axis 2 (site-specific gradients), the r^2 values for physical, fish, and macroinvertebrate ordinations were 0.032, 0.099, and 0.162 respectively. Again this supports the visual comparisons; there is greater variation among more local scale than large, landscape scale variables and local scale variables explain more of the variation in macroinvertebrates than in physical habitat and fishes.

If the MFJD were an ideal continuum, the cumulative r^2 values would equal 1.00 and axis 1 would have an individual r^2 of 1.00 (i.e. all the variance could be explained by the longitudinal gradient). In contrast, if there were no large- or small-scale gradients in the MFJD and there was no correlation among variables, the cumulative r^2 values would approach 0 and all axes would have an individual r^2 approaching 0 (i.e. very little of the variance could be explained at all). Finally, if the MFJD followed the patchy model, the cumulative r^2 values would approach 1.00. Both axes would have individual r^2 approaching 0.50 because half the variance would be explained by local scale variables (axis 2) and half would be explained by discontinuous, landscape variables (axis 1) (In the ideal patchy model there are no continuous longitudinal gradients). It appears the macroinvertebrate ordination most closely represents the patch-like model compared to physical variables and fish abundance.

To examine differences in response to scale, one can look at the correlations between ordination axes and individual physical variables from the environmental matrix. Table 2.2 shows the five environmental variables that were most strongly correlated with each axis for each of the 3 different ordinations. This portion of the analysis is a useful tool for developing hypotheses directed toward the mechanisms

underlying the community structures. Not only does one notice which variables are most strongly correlated with the community patterns, but we can also examine the correlations among the physical variables themselves. Because rotations were organized according to landscape and local scales, we predicted that axis 1 would be most strongly correlated with large scale variables that correspond to the longitudinal gradient, and axis 2 would be most strongly correlated with variables that had patchy distributions along the longitudinal gradient (Table 2.2). In the MFJD, four physical variables that were highly correlated with axis 1 in all 3 ordinations could be interpreted as large scale: elevation, discharge, and average and minimum temperatures (Table 2.2). In contrast, site-specific variables that correlated with axis 2 were more unique to each ordination (Table 2.2).

Implications, Limitations and Further Applications

Rotating the different ordinations to the same set of variables is a critical component of this approach. While I focused on large and small scale variables, rotations may be performed on any set of variables that represent different aspects along a gradient. Rotations may also be made for more than one set of variables to further examine community structure in ordination space. For example, I could have rotated to the variables for average temperature and diel temperature range if I were focusing on temperature gradients. Although I focused on ordination patterns using the first and second axes, there is no reason to limit the number of axes/dimensions other than ease of interpretation. As long as the rotations for those axes represent varying degrees of scale along the greatest environmental gradient, the framework would still be applicable. For example, a 3 dimensional ordination could be rotated such that axis 1 is correlated with large-scale gradients, axis 2 is correlated with patch-like variables, and axis 3 is correlated with highly variable or more random variables.

Table 2.2. Correlation values between the physical, fish and macroinvertebrate ordinations' axes and individual physical variables from the environmental matrix. Only the six environmental variables most strongly correlated with each axis for the 3 different ordinations are shown.

Physical Variables		Fish		Macroinvertebrates	
Axis 1		**Axis 1**		**Axis 1**	
Variable	r-value	Variable	r-value	Variable	r-value
Ave. Temperature	0.964	Valley Slope	-0.891	Discharge	0.832
Discharge	0.932	Minimum Temperature	0.889	Ave. Temperature	0.833
Elevation	-0.932	Ave. Temperature	0.883	Macrophyte Cover	-0.793
Max Temperature	0.906	Stream Gradient	0.850	Elevation	-0.789
Minimum Temperature	0.869	Elevation	-0.827	Max Temperature	0.778
Valley Slope	-0.863	Discharge	0.754	Minimum Temperature	0.740
Axis 2		**Axis 2**		**Axis 2**	
Variable	r-value	Variable	r-value	Variable	r-value
Width:Depth	-0.615	Riffle Habitat	-0.453	Width:Depth	-0.457
Hours of Solar Input	0.569	Macrophyte Cover	0.397	Width	-0.382
Depth	0.505	Minimum Temperature	0.351	Cobble/Gravel	-0.354
Width	-0.431	Elevation	0.35	Boulders	-0.333
Solar Input	0.409	Ave. Temperature	0.305	Riffle Habitat	0.321
Temperature Range	0.323	Hours of Sun	0.298	Constrained or No	0.17

The examination of correlations, between the ordination axes and other variables, is not limited to physical variables. Correlations may also be examined using biological data. For example, the macroinvertebrate ordination axes may be examined for correlations with physical, algal, fish, and riparian vegetation variables. In this manner ecologists may simultaneously consider abiotic and biological factors driving community structure, leading to more inclusive hypotheses regarding community ecology. Chapters 3 and 4 explore further correlations of the MFJD ordinations with both physical and biological variables.

This approach also can be used to examine the effects of different aggregation metrics to represent taxa in the community matrices. Would I get the same patterns and interpretations of community structure if I represent communities using mean densities, relative abundance, coefficients of variation, etc.? How ecologists choose/have chosen to aggregate community data may influence interpretations of community structure and ecological theory (e.g. Faith & Norris 1989, Pascual & Levin 1999, Micheli et al. 1999). I suggest this method can help ecologists better understand the effect of various metrics on the development of ecological theory.

To take the comparisons among ordinations further, I could compare ordination scores using canonical correlation (Tabachnick & Fidell 1996). Canonical correlation would allow us to compare similarities between two ordination patterns using all axes simultaneously, rather than separately. For example I could compare a multi-dimension ordination pattern of either fish or macroinvertebrate community data to the multi-dimension ordination pattern of environmental data. A comparison of the canonical correlations may suggest that the overall fish community ordination pattern is more strongly correlated with the environmental ordination pattern than the macroinvertebrate pattern. I can also compare biological data to biological data (e.g. fish and macroinvertebrate data) as long as each ordination has the same number of dimensions and sample units (Tabachnick & Fidell 1996).

As with any technique, there are limitations and assumptions that must be recognized. Variations from the conceptual framework or from expected results may be a consequence of sampling error, limited number of variables, nonlinear

relationships or gradients, just to name a few. Ideally samples would be collected continuously along the gradients in question. However, practical limitations (i.e. funding, logistics, time, etc.) often force ecologists to sample at intervals or selected locations along the gradients. The problem becomes how to extrapolate patterns observed at certain locations across an entire environmental gradient (Levin 1992, Wiley et al. 1997). Can I tell whether community structure changes are continuous or patchy along an environmental gradient using data from a limited number of sites? This too may be examined further using the proposed framework. For example, one could compare community ordination patterns between two or more different sets of hierarchically arranged sample units along the same gradient.

The number of variables measured along a gradient will also influence interpretations of community structure (sensu Faith & Norris 1989). Selection of these variables should not be done without familiarity of the literature regarding the study area and organisms involved. Even then a complete list of variables would be unlikely. Therefore, I recommend preliminary analyses in the early part of the study be used to illustrate potentially significant variables as well as apparent voids.

The influence of scale is prevalent throughout ecology and dominates the way we perceive ecosystems. Obviously the scales over which samples are taken will affect patterns and interpretations of community structure (e.g. Wiens 1976, Levin 1992, Wiley et al. 1997). Recognition of scale and scope of inference is critical for comparisons among ecosystems, study sites, sample units and species. Using this proposed approach, sampling units of different sizes along the same gradients may be used to examine the effect of scale on the structure of various communities. For example, do stream communities sampled at the landscape scale (100s of Km) have more continuous patterns than those sampled at the micro-habitat scale (<1m) along the same gradient, or vice versa? As long as the same suite of variables and rotations are used, such questions may be addressed within the proposed framework.

Aside from the recently proposed Principal Curvature method (De'ath 1999), most ordination techniques are dependent on some degree of linearity (Austin 1985, De'ath 1999). This linearity assumption also is present using correlation coefficients

to determine potential relationship strengths in NMS ordinations. Thus, any relationships or gradients that may be exponential, curvilinear, parabolic, etc., may not be apparent using this approach. However, other methods, such as the Principal Curvature method, exponential transformations of variables, or other nonlinear multivariate techniques may be used to examine these possibilities and supplement findings within the context of the proposed approach.

This proposed approach to examining community structure establishes a series of conceptual, *a priori* hypotheses that can be used to examine the structure of community data along any number of environmental gradients. Through the use of non-parametric multivariate ordination techniques, this approach enables us to integrate the influence of multiple physical and biological factors influencing community structure across spatial scales. In addition, ecologists may examine large empirical data sets, within the context of current ecological theory and without manipulation or aggregation of the study organisms or sample units (sensu Faith & Norris 1989, Pascual & Levin 1999). While I believe this approach provides a much needed tool for multivariate examinations in community ecology, I recognize it as a starting place rather than a conclusion.

3. LONGITUDINAL PATTERNS OF PHYSICAL HABITAT AND INSTREAM COMMUNITIES IN A HIGH DESERT STREAM

Introduction

In the past two decades, multiple theoretical concepts have been developed to explain structure and processes in stream ecosystems. These concepts include, but are not limited to, the River Continuum Concept (Vannote et al. 1980, Minshall et al. 1985), the Flood Pulse Concept (Junk et al. 1989), the Nutrient Spiralling Concept (Newbold et al. 1982, Elwood et al. 1983), stream flow predictability (Poff & Ward 1989), the Riparian Corridor Concept (Gregory et al. 1991), the Hyporheic Corridor Concept (Stanford & Ward 1993), the Hierarchical Habitat Classification (Frissel et al. 1986), and Process Domains (Montgomerey 1999). While each concept presents a particular perspective of lotic systems, they all emphasize that streams are physically and biologically connected to their respective landscapes through multiple pathways. This implies that the structure of stream communities is a function of in-stream and landscape physical and biological factors. The River Continuum Concept (RCC) is unique among the above frameworks in that it attempted to link the physical, geomorphic template with trophic and community structure in streams. The RCC predicted how continuous longitudinal gradients in stream geomorphology directly or indirectly influence the primary sources of available energy (i.e. allochthonous vs. autochthonous) and the structure of in-stream communities.

The RCC was primarily based on continuous, longitudinal progressions within undisturbed, temperate, montane systems. Therefore, streams that: 1) are located within different ecotypes, 2) have patchy or discontinuous geomorphic features, or 3) have been altered through anthropogenic influences may reflect variations on the RCC predictions (Ward & Stanford 1983, Minshall et al. 1983, 1985, & 1992, Brussock et al. 1985, Statzner & Higler 1985, Huryn & Wallace 1987, Brussock & Brown 1991, Lugthart & Wallace 1992, Stanford and Ward 1993, Grubaugh et al. 1996, Townsend et al. 1997, Delong & Brusven 1998). Within the arid interior of the Pacific Northwest, the longitudinal profiles of many streams are composed of large, low

gradient, alluvial valley segments separated by constrained, canyon-like reaches. In addition, many of the watersheds have been subjected to a history of various land-use practices including grazing, mining, channelization, irrigation and forestry. Such influences can alter the physical and biological structure within stream systems, and presumably disrupt the predicted longitudinal succession (Minshall et al. 1985, Allan et al. 1997). The purpose of this study was to examine the applicability of the RCC in a high-desert stream subjected to these multiple physical and anthropogenic constraints.

I examined longitudinal patterns of both physical and biological variables along a 1st through 5th order gradient of the Middle Fork of the John Day River (MFJD) in semi-arid eastern Oregon. The upper reaches of the MFJD are a series of broad, unconstrained, alluvial floodplains and narrow, constrained valley segments. Within the last century, the MFJD also has been influenced by multiple land-use practices such as mining, timber harvest, grazing, and channelization; grazing and timber harvest are the only land-uses currently practiced. Grazing is most prevalent in the unconstrained, valley segments but exists throughout the watershed; timber harvest is limited to primarily 1st and 2nd order headwater reaches.

The first objective of this study was to describe changes in aquatic community structures along a 1st through 5th stream order longitudinal gradient of the MFJD. These patterns were then used to: 1) test the applicability of the River Continuum Concept to the MFJD, 2) explore correlations between changes in community structure with both local and landscape scale physical habitat variables, and 3) generate hypotheses regarding the underlying mechanisms of community structure within the context of ecological theory. I hypothesized that physical habitat characteristics, structures of fish and macroinvertebrate communities, and algal abundance would not reflect continuous longitudinal gradients from headwaters to downstream reaches. Based on the MFJD's geomorphic template and history of land-use impacts, I expected to find extremely patchy and variable patterns rather than continuous gradients along the longitudinal profile. Therefore, I hypothesized that the MFJD would not follow predictions of the RCC. Finally, I expected that the changes

in community structures along the MFJD would be more strongly correlated with local-scale physical habitat characteristics than landscape-scale features.

Methods

Site selection

I sampled 20 sites along a 100 km section of the Middle Fork of the John Day River in eastern Oregon, during the summers of 1996-1998 (Figure 3.1). This section ranges from 1st to 5th stream order and has no impoundments or dams, but has been influenced by grazing, timber harvest, and mining. All sites were 50-100 m in length and dominated by riffle and run habitats. Sampling occurred during low flow conditions (late July-early August) and some sites were sampled in multiple years; twelve sites were sampled in 1996, 10 sites were sampled in 1997, and 10 sites were sampled in 1998 (Table 3.1).

Physical Habitat

At each site, I measured a suite of physical variables ranging from large-scale landscape features such as valley slope and stream order, to local scale, site-specific characteristics like depth and substrate type (see Table 3.2). Stream velocity (m/s) and discharge (m^3/s) were measured along 3 transects per site using a digital flow meter held at a depth of 1/8 of the water column. Available solar radiation and canopy cover (calculated using a Solar Pathfinder (Platts et al. 1987)) were measured at 9 locations within each site. Habitat type, substrate and depth (m) were recorded with each Surber sample, and at 1 m intervals along 5 random transects spanning the wetted width at each site. Habitats were classified as riffle, glide(run), pool, backwater, and edge habitat. Edge habitat was defined as any location that was within 30 cm of a bank, gravel bar, or island. Substrates were classified as bedrock, large boulder, small

Oregon

N

Upper Drainage of the Middle Fork of the John Day River (~100km in length)

20
19
18
16
17
15
14
12
13
10
11
9
8
6
7
5
2
4
3
1

1st Order = 1, 2
2nd Order = 3, 4, 5
3rd Order = 6*, 7*, 8*, 9
4th Order = 10, 11*, 12*, 13, 14*, 15*, 16*
5th Order = 17*, 18*, 19*, 20
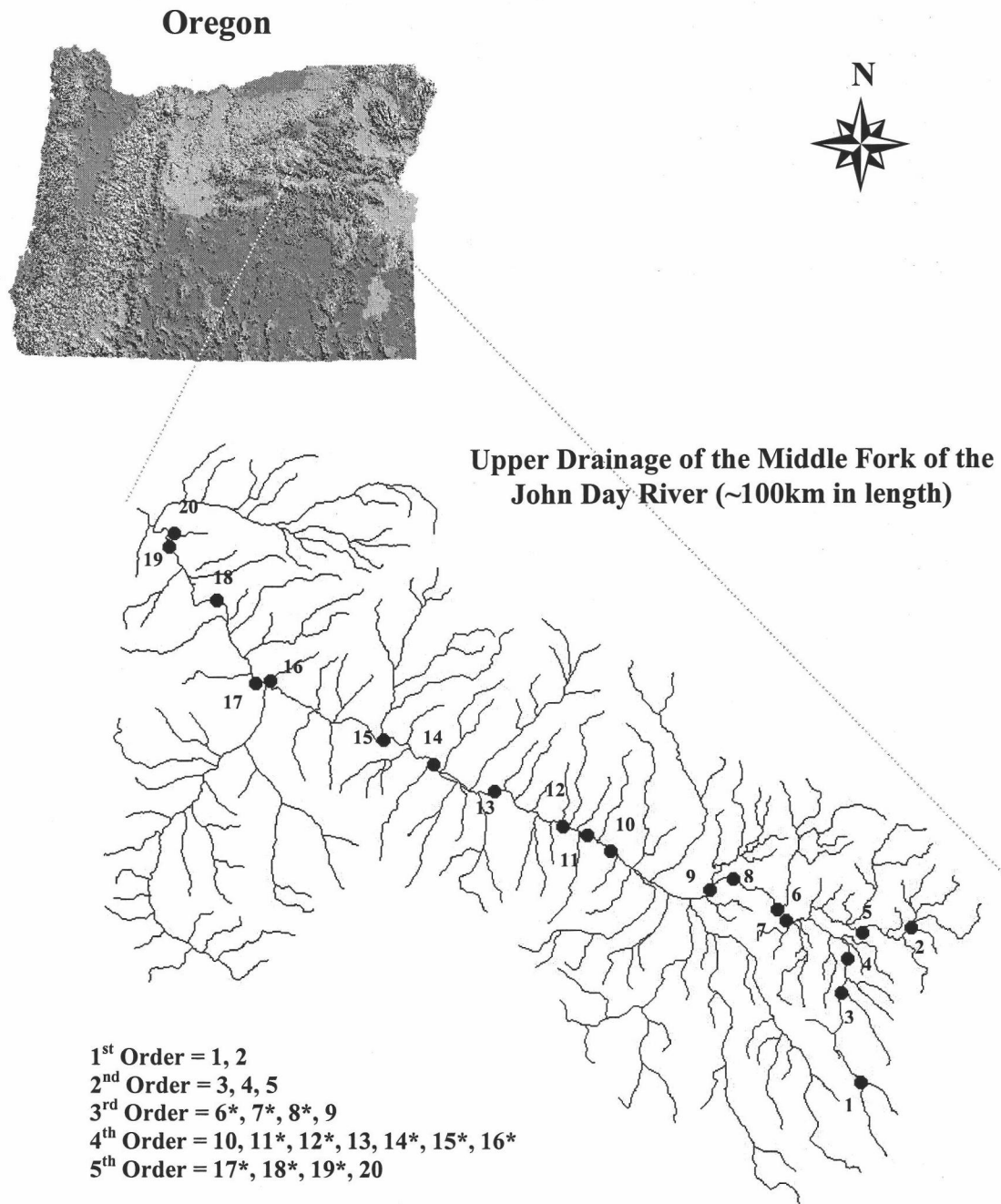
Figure 3.1. Shaded relief map of the state of Oregon and a map of the upper 100 river kilometers of the Middle Fork of the John Day River basin in eastern Oregon. Locations of study sites along the MFJD are indicated. Sites sampled in multiple years are indicated by an asterix in the stream order breakdown. Basin coverage provided by Christian Torgersen, Oregon State Univesity.

Table 3.1. Stream order and year of sampling for the 20 study sites in the Middle Fork of the John Day River.

Site	Stream Order	Year Sampled		
		1996	1997	1998
1	1			X
2	1			X
3	2			X
4	2			X
5	2			X
6	3	X	X	X
7	3	X	X	
8	3	X		
9	3	X		
10	4	X		
11	4	X	X	X
12	4	X	X	X
13	4	X		
14	4		X	
15	4	X	X	X
16	4		X	
17	5	X	X	
18	5	X	X	
19	5		X	X
20	5	X		

Table 3.2. Mean values (± 1 SE) for measured summer, low flow condition physical parameters in the Middle Fork of the John Day River according to sites in 1st + 2nd, 3rd, 4th, and 5th order reaches (averaged over all years). All measurements were taken within a 2 week sample period in late July-early August of each year.

	Site Groups							
	1st + 2nd	(SE)	3rd	(SE)	4th	(SE)	5th	(SE)
Number of Sites	5		7		13		7	
Elevation (m)	1402	(80)	1277	(15)	1156	(56)	1020	(20)
Drainage Area (km^2)	29	(12)	139	(19)	474	(82)	830	(29)
Wetted Width (m)	2.0	(0.5)	2.8	(0.2)	11.8	(4.7)	11.3	(2.1)
Valley Slope (%)	1.8	(0.7)	1.2	(0.2)	0.7	(0.2)	0.5	(0.0)
Stream Gradient (°)	1.72	(0.96)	1.00	(0.00)	0.56	(0.26)	0.50	(0.33)
Aspect (radians)	286	(60)	279	(51)	265	(30)	267	(49)
Summer Discharge (m^3/s)	0.01	(0.01)	0.16	(0.03)	0.97	(0.37)	1.31	(0.20)
Duration of Solar Exposure (h)	5.4	(1.0)	8.8	(2.0)	9.5	(1.7)	11.3	(0.4)
Available Solar Energy Reaching Stream (%)	54	(14)	75	(21)	86	(11)	97	(3)
Mean Depth (m)	0.16	(0.04)	0.24	(0.05)	0.25	(0.06)	0.34	(0.06)
Width : Depth	13.3	(4.5)	12.3	(3.4)	51.3	(26.5)	35.0	(11.1)

Table 3.2. (cont.)

	1st + 2nd	(SE)	3rd	(SE)	4th	(SE)	5th	(SE)
Percent Riffle Habitat	57	(33)	83	(18)	82	(22)	83	(28)
Percent Cobble/Gravel Substrate	63	(19)	74	(15)	95	(8)	67	(22)
Percent Fines Substrate	33	(18)	29	(32)	14	(28)	2	(6)
Percent Boulder Substrate	17	(21)	29	(21)	10	(12)	36	(23)
Percent Macrophyte Cover	33	(24)	31	(19)	0	(0)	0	(0)
Mean Daily Stream Temperature (°C)	15.8	(1.8)	17.9	(0.7)	19.9	(0.3)	20.9	(0.2)
Maximun Daily Stream Temperature (°C)	21.5	(2.5)	22.6	(1.1)	25.3	(0.7)	25.9	(0.6)
Minimum Daily Stream Temperature (°C)	11.2	(1.2)	13.7	(0.2)	14.6	(0.3)	15.4	(0.9)
Daily Range of Stream Temperature (°C)	10.3	(1.5)	8.8	(1.2)	10.7	(0.7)	10.6	(1.4)
Accumulated Exposure over 22° per Day (h)	0.95	(0.80)	3.20	(3.62)	10.06	(0.56)	10.96	(0.69)
Accumulated Exposure over 24° per Day (h)	0.00	(0.00)	1.30	(1.93)	6.00	(0.84)	7.43	(0.68)
Accumulated Exposure over 25° per Day (h)	0.00	(0.00)	0.54	(1.31)	2.79	(1.89)	4.32	(1.41)

boulder, cobble, gravel, sand and silt based on a modified Wentworth scale (1922). At each site wetted channel widths were recorded at 10 m intervals and averaged for each date. Channel gradient was measured using a clinometer, and channel aspect was determined from 3 compass measurements. Stream order (Strahler), valley slope, valley width, drainage area, and elevation were determined from 7.5 minute USGS topographic maps.

I measured stream temperatures using Onset Optical Thermal Data Loggers. Measurements were recorded at 15 minute intervals for a period of two weeks that included all sampling dates. Temperature data were represented as weekly mean, minimum, maximum, and the average amount of time each site exceeded 22°, 24° and 25° C in a 24 hr period.

Fish and fish diets

Fishes were sampled using a backpack electro-fisher, two dip nets and a 5 mm mesh, 2 m wide block net. For each pass, the block net was set 10 m downstream from the electro-fisher. Sampling progressed downstream toward the block net within a 2 m wide frame outlined by the block net. Substrates were disturbed along the pass to ensure burrowing fishes were dislodged. Fish were captured along the pass by dip nets and any missed fish were retained in the block net. Passes were made within a site until at least 15 of each of the two most common taxa were collected. All fish were counted and measured for total length and fork length. Fishes were identified to species and also categorized according to thermal guilds (Hokanson 1977, Zaroban et al. 1998): (1) warm water fishes: redside shiners (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), and northern pike minnow (*Ptychocheilus oregonensis*); (2) cool water fishes: torrent sculpin (*Cottus rhotheus*), bridgelip and mountain suckers (*Catostomus columbianus* and *platyrhynchus*), Pacific lamprey (*Entosphenus tridentatus*), and longnose dace (*Rhinischthys cataractae*); and (3) cold water fishes: rainbow trout (*Oncorhynchus mykiss*) and chinook salmon (*Oncorhynchus tshawytsch*a).

Macroinvertebrates

Benthic macroinvertebrate samples were collected at each site using a 0.093 m^2 modified Surber sampler with a 250 μm mesh net. Six random sample locations within the sites were determined using a ten-sided die. Substrates were disturbed for 30 seconds to a depth of 10 cm where possible. Samples were sieved through a 250 μm screen and were preserved in 95% ethanol. Depth, habitat and substrate were also recorded with each sample. Each sample was counted individually using a 300 count subsampling method (Vinson & Hawkins 1996) in which rare, large individuals were counted separately and later added to the total count. Invertebrates were identified to genus in the laboratory using a Zeiss dissecting microscope. Macroinvertebrates were categorized according to functional feeding groups based on Merritt & Cummins (1996). Standard metrics of total abundance, taxa richness, Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa richness, percent dominance, percent EPT taxa, and Shannon's diversity were calculated for each site.

Algae

Chlorophyll *a* biomass samples were collected by randomly selecting 18 rocks (approximately 10 cm in diameter) from each site. Algae was brushed and/or scraped off a 3 cm^2 area of each rock. The 18 scrapings were divided into sets of 3, and each set was individually stored in water within a light-sealed bottle and frozen for transportation. In the laboratory, chlorophyll *a* biomass was extracted by filtering the water from each bottle through glass fiber filters and then soaking the filters in 90% buffered acetone in the laboratory. The acetone solution was analyzed by spectrophotometry (Strickland & Parsons 1968).

Algal primary production was measured using self-contained, circulating production chambers at each site. Chambers were constructed from clear plexiglass pipe 30 cm long and 12.5 cm in diameter. The chambers were sealed with modified, water-tight caps that had outlets with 6.25 mm surgical tubing which connected to Teal submersible pumps that recirculated water. At each site, three rocks of approximately 5 cm diameter were placed in each of six chambers. Three chambers

were run for one hour in direct sunlight while three chambers were simultaneously run in complete darkness (provided by an opaque plastic container). Water was collected from each chamber after every run, and dissolved oxygen was determined using a dissolved oxygen meter. Water temperature within and outside the chambers also was recorded to correct for any warming effect the pumps may have had. In general, temperatures were approximately 2° C warmer in the chambers than the ambient stream water. Net primary production was calculated as the average amount of oxygen production from photosynthesis minus the average amount of oxygen consumption of respiration. To account for any differences in algal biomass among the sites, calculations of production per unit biomass were determined for each site using chlorophyll *a* biomass measurements from the rocks in each chamber. Surface area of the rocks was determined by wrapping the rocks in foil and trimming off any excess. The foils were then weighed, and a regression of foil weight to known surface area was used to calculate the rock's surface area.

Data Analysis

To examine broad, stream order reach patterns, I defined 4 groups of sites based on $1^{st} + 2^{nd}$, 3rd, 4th, and 5th order reaches of the MFJD. Comparisons of physical and biological characteristics among the site groups were made both graphically and by analysis of variance (ANOVA). Those sites that were sampled in multiple years were averaged across all sample dates prior to analyses. Because the number of sites varied among site groups, I determined statistically significant differences among site groups using Bonferroni's multiple comparison procedure (MCP). When data violated the assumption of equal variance, I used a Kruskal-Wallis test. All analyses were performed using StatGraphics version 3 statistical software. Reach scale comparisons included physical habitat measurements, relative abundance of fish thermal guilds and individual taxa, macroinvertebrate metrics and taxa, functional feeding group abundance, chlorophyll *a* biomass, and algal primary production.

I used non-metric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976), to examine longitudinal patterns of physical and biological variables at the site scale. Non-parametric methods relax the assumption of independence, which can be problematic for longitudinally stream communities. NMS relieves the zero-truncation problem for heterogeneous community data, and relaxes assumptions of normality because it uses a rank-ordering procedure for sample unit distances (Beals 1984, Ludwig & Reynolds 1988). In addition, this robust ordination method could be consistently applied to data sets that vary in the number of attributes across the sample units (i.e. 109 invertebrate taxa vs. 10 fishes) (Faith & Norris 1989).

Analyses were conducted at the sample unit (site) level using each sample date per site as an individual sample unit. The five data matrices included: 1) a 32 site by 20 environmental variable matrix, 2) a 32 site by 10 taxa matrix containing relative abundance of fishes, 3) a 32 site by 109 taxa matrix containing mean macroinvertebrate taxa densities, 4) a 32 site by 6 variable matrix containing mean macroinvertebrate functional feeding group densities and 5) a 32 site by 6 variable matrix containing measurements of algal chlorophyll a biomass, production, and respiration. Relative abundance of fishes in each site were calculated by dividing the total catch of each species by the total catch of all species. Mean site densities of macroinvertebrates (no./m^2) were calculated for each taxon and functional feeding group by averaging densities from all 6 samples at each site. Mean values of algal biomass for each site were calculated by averaging the measured biomass from the 6 sets of algal scrapings. Mean rates of algal primary production (and respiration) were determined at each site by averaging rates of oxygen production (and consumption) from the three chambers. All data were transformed by $\ln(x + 1)$.

Each data matrix was analyzed separately using NMS in PC-ORD, version 3.2. I used Sorensen's distance measure with settings for each analysis at: 30 runs with original data, 30 Monte Carlo simulations, and a 0.20 step length. Sorensen's distance was chosen because it remains sensitive to differences between communities at large environmental distances (Beals 1984, Faith et al. 1987). Final configurations were limited to three dimensions. I determined the appropriateness of 3 dimensions by

comparing the reductions in stress from a 1 dimensional solution to the 3 dimensional one. Stress is an inverse measure of fit to the data. A significant reduction in stress from a low dimension solution to a higher dimension solution would indicate a significant increase in the amount of variance explained (Faith & Norris 1989).

I compared the different community ordinations using cumulative variance explained (r^2), qualitative conformity with conceptual patterns, and correlation of ordination coordinates with variables in the physical habitat and other community matrices. To make these direct comparisons among ordinations, I rotated each ordination to a common set of variables from the physical habitat matrix. For a given ordination, I identified the primary (1°), secondary (2°), and tertiary (3°) axes using incremental r^2 values determined by a correlation between ordination and original matrix distances. Each ordination was then rotated such that the 1° axis represented large scale, longitudinal physical gradients and the 2° and 3° axes represented local scale, site-specific physical gradients:

> 1) In the plane of axes 1 and 2: 1° axis was rotated to stream order, and 2° axis was rotated to percent riffle habitat.
>
> 2) In the plane of axes 1 and 3: 1° axis was rotated to stream order, and 3° axis was rotated to percent of macrophyte cover.
>
> 3) In the plane of axes 2 and 3: 2° axis was rotated to percent of riffle habitat, and 3° axis was rotated to percent of macrophyte cover.

I used riffle habitat and macrophyte cover for the 2° and 3° axes because they were site-specific, physical habitat variables that were not correlated with stream order or each other. Any similar variables may be used however, for different ordinations to be compared, rotations **must** be consistent from one ordination to the next.

After all ordinations were oriented according to the same physical habitat gradients, I followed the same procedures with each ordination on an individual basis. First, I determined the individual and cumulative r^2 values for each axis. Second, I determined the Pearson correlation coefficients comparing the coordinate scores from each axis with the variables from the original data matrix. I then calculated the Pearson correlation coefficients comparing the coordinate scores from each axis with

the variables from the physical habitat matrix. This was a way of comparing physical and biological gradients in the same environmental space (i.e. the longitudinal profile of the MFJD).

Interpretations and qualitative examinations of the different ordinations were made using the conceptual framework developed in Chapter 2. This framework provides three *a priori* conceptual, null hypotheses of ordination patterns: 1) an ideal continuum, 2) highly variable, and 3) discrete patches (Figure 3.2). Although ordinations from actual data might contain elements of all three conceptual patterns, the degree to which they conform to the different conceptual patterns may vary from one community to the next (Chapter 2).

Lastly, I compared longitudinal trends of physical and biological variables from both site and reach scale perspectives. Comparisons were made both graphically and by using results from the ordinations' axes correlations. For the reach scale, I used the previously defined 4 groups of sites based on $1^{st} + 2^{nd}$, 3rd, 4th, and 5th order reaches. For the site scale perspective, those sites that were sampled in multiple years were averaged across all sample dates, resulting in 20 individual sites. Correlations between axis 1 coordinates and stream order and elevation also were used as indicators of reach versus site scale perspectives respectively. Arranged from high to low elevation, the sites in the MFJD would be sorted consecutively along the longitudinal gradient. Arranged from low to high stream order, sites are sorted only in consecutive reaches along the longitudinal gradient. Therefore, if the correlation between axis 1 coordinates and stream order equaled that of the correlation between axis 1 coordinates and elevation, one could assume sites were consecutively arranged along the longitudinal gradient from headwaters downstream in ordination space. If the correlation with elevation was lower than with stream order, there was a relatively stronger longitudinal gradient from a reach perspective than from a site scale perspective.
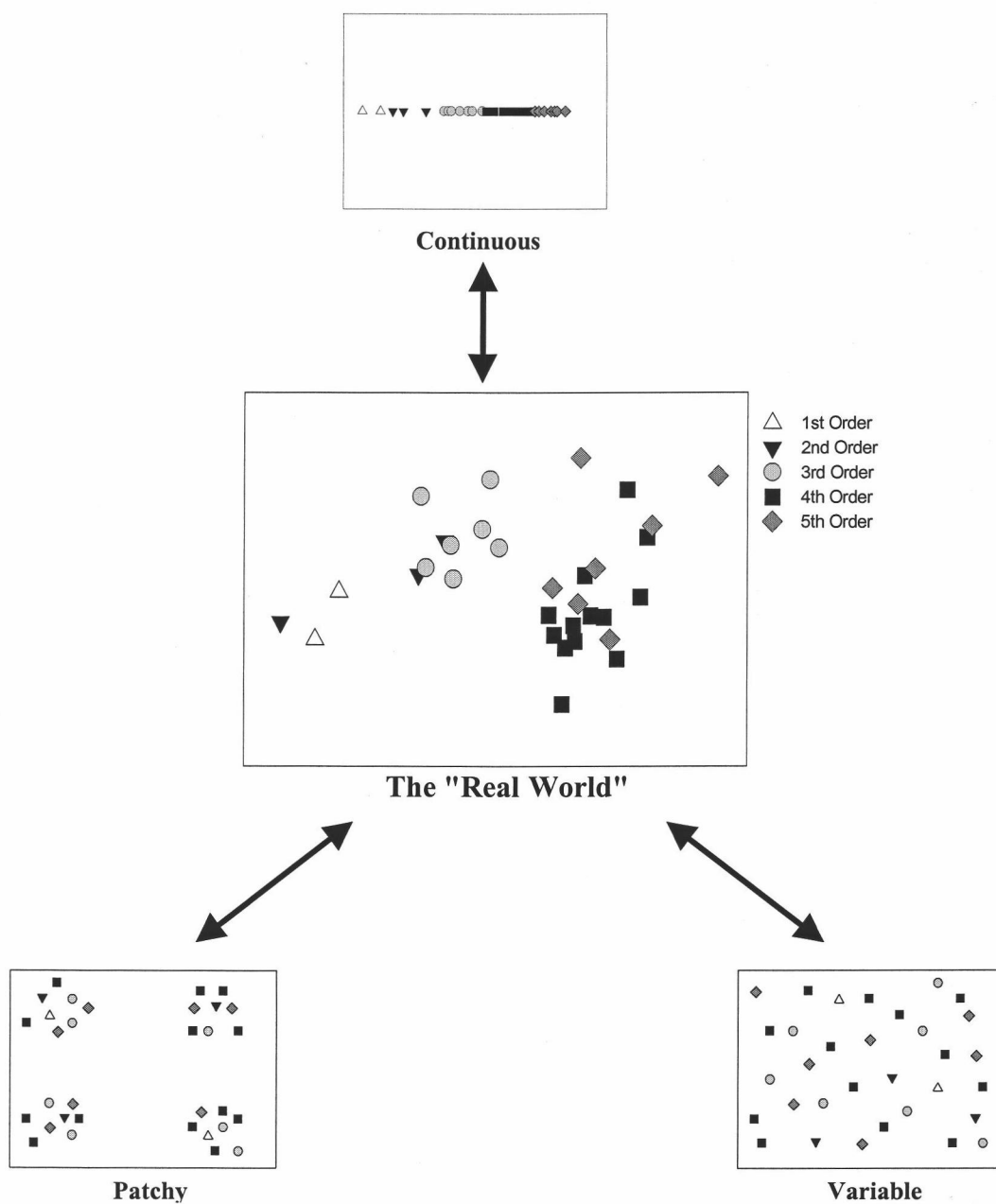
Figure 3.2. A conceptual framework developed in Chapter 2. The framework provides three *a priori* conceptual, null hypotheses of ordination patterns: 1) an ideal continuum, 2) highly variable, and 3) discrete patches. Ordinations from actual data would be expected to contain elements of all three conceptual patterns.

Results

Physical Habitat

Sites along the MFJD ranged from 1550 m to 990 m in elevation with mean summer low-flow discharge ranging from 0.005 m³/s (± 0.002 SE) in the headwaters to 1.4 m³/s (± 0.05 SE) downstream. Mean values of all measured physical parameters for the site groups (by stream orders 1+2, 3, 4, and 5) are shown in Table 3.2.

Ordination of the physical data resulted in a cumulative r^2 value of 0.994. There was a significant reduction in stress going from a 1 to 3 dimension NMS solution; the final stress for the 3 dimensional solution was 2.83. Axis 1 explained the majority of the variance in the data set ($r^2 = 0.942$), while axes 2 and 3 combined explained approximately 5% of the variance. Visual examination of the ordination pattern revealed a relatively consistent longitudinal gradient along axis 1 in physical variables from headwaters downstream (Figure 3.3). However, there was variability expressed along each of the three axes. Along axis 1, the 4th and 5th order sites were closely grouped together on the right side, whereas the 1st through 3rd order sites were more widely distributed along the axis. In addition, the progression of sites from 1st to 5th order was not consistent along axis 1, because sites in different orders overlapped along the gradient. Axis 2 was highly variable, with no distinct longitudinal gradient and high scatter within a limited range (Figure 3.3). Along axis 3 there was a weak gradient from headwaters downstream (Figure 3.3); sites in the upper and lower reaches were each arranged on opposite ends of the gradient. However, there was much more variability associated with the third axis than along the first.

Absolute values of correlations between axes coordinates and individual physical variables were higher for axis 1 and 3 than axis 2 (Table 3.3). As expected from the rotations, the first axis was most strongly correlated with primarily large-scale variables; correlations > 0.9 were with average temperature (+), stream order (+), time over 22°C (+), elevation (-), discharge (+), and maximum temperature (+) (Table 3.3). Axis 2 was most strongly correlated (r > 0.5) with small scale, site-specific variables of width to depth ratio (-), solar input (+), and average depth (+) (Table 3.3).
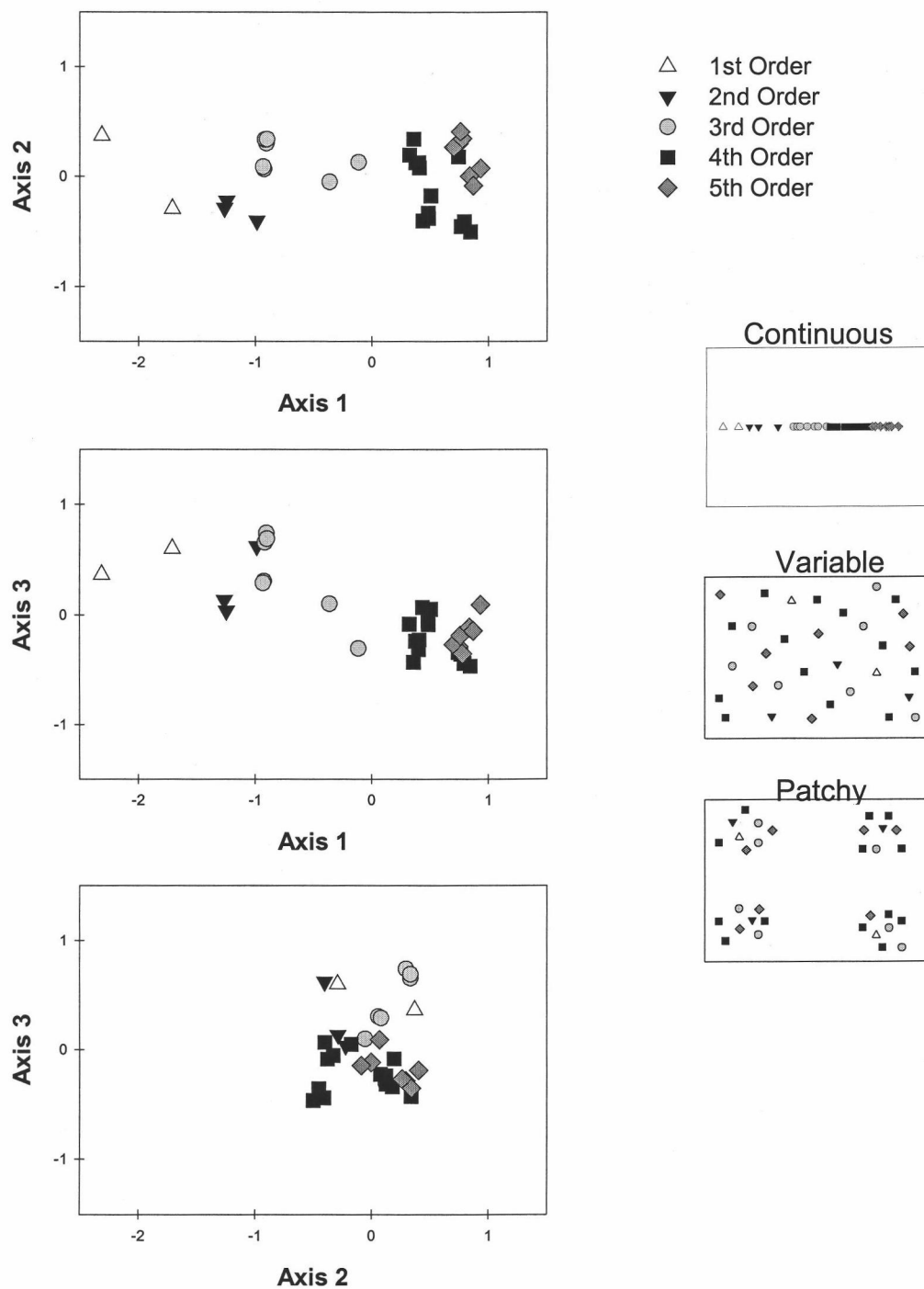
Figure 3.3. Two dimension plots of the NMS ordination of physical variables in the MFJD. Each symbol represents a given site; the shade and shape indicate stream order. Miniature versions of the conceptual framework presented in Chapter 1 are shown on the right. Configurations have been rotated such that axis 1 represents large-scale, longitudinal gradients, and axes 2 and 3 represent small-scale, site-specific gradients.

Table 3.3. Correlation between axes coordinates from the physical variable NMS ordination and individual physical parameters. The 10 highest correlations greater than 0.40 are shown.

Axis 1	r	Axis 2	r	Axis 3	r
Mean Temperature	0.964	Width : Depth	-0.615	Time Over 22°	-0.859
Stream Order	0.939	Hours of Solar Input	0.569	Time Over 24°	-0.855
Time Over 22°	0.939	Mean Depth	0.505	Maximum Temperature	-0.800
Elevation	-0.932	Stream Width	-0.431	Macrophyte Cover	0.799
Discharge	0.932	Solar Input	0.409	Time Over 25°	-0.789
Maximum Temperature	0.906			Temperature Range	-0.709
Minimum Temperature	0.869			Mean Temperature	-0.707
Valley Slope	-0.863			Stream Width	-0.659
Stream Width	0.820			Elevation	0.649
Stream Gradient	-0.788			Stream Order	-0.649

Axis 3 was strongly correlated with both large and local scale variables; correlations > 0.8 were with time over 22°C (-), time over 24°C (-), and maximum temperature (-) (Table 3.3).

There was only a difference of 0.007 in the absolute values of the correlation coefficients for stream order (reach-specific) and elevation (site-specific) with the first axis (Table 3.3). A small difference between such high r values (> 0.932) indicates strong longitudinal gradients in the physical habitat from both reach and site scale perspectives. Further comparisons of site versus reach scale patterns revealed that there were three groups of physical variables based on longitudinal trends (Figure 3.4). Certain variables (e.g. elevation, discharge) reflected a relatively continuous gradient at both scales, others (e.g. width, depth, and slope) had patchy distributions at the site scale but were more continuous at the reach scale, and finally some variables (e.g. aspect and mean daily temperature range) were patchy along the longitudinal gradient at both scales (Table 3.4, Figure 3.4).

Fishes

We recorded a total of 10 different fish species in the MFJD. The number of fish species in any given site ranged from 1 to 8 along the longitudinal profile. The most abundant species among all sites were torrent sculpin, speckled dace and rainbow trout (Appendix 1). Examination of the relative abundance of thermal guilds among site groups, revealed a gradual decrease in cold water fishes and an inverse increase in warm and cool water fishes from headwaters down to 5th order sites (Figure 3.5). There were significant differences among stream order sites groups based on relative abundance of both cold and cool water fish. Relative abundance of cold water species in 1st + 2nd order sites was significantly higher than in all higher order sites and 3rd order sites had significantly more cold water fishes than sites in 5th order reaches (ANOVA p-value < 0.001, F-Ratio = 28.68, df = 19; Bonferroni MCP). There were significantly less cool water fish in 1st +2nd order sites than in other sites (ANOVA p-value < 0.001, F-Ratio = 21.29, df = 19; Bonferroni MCP).
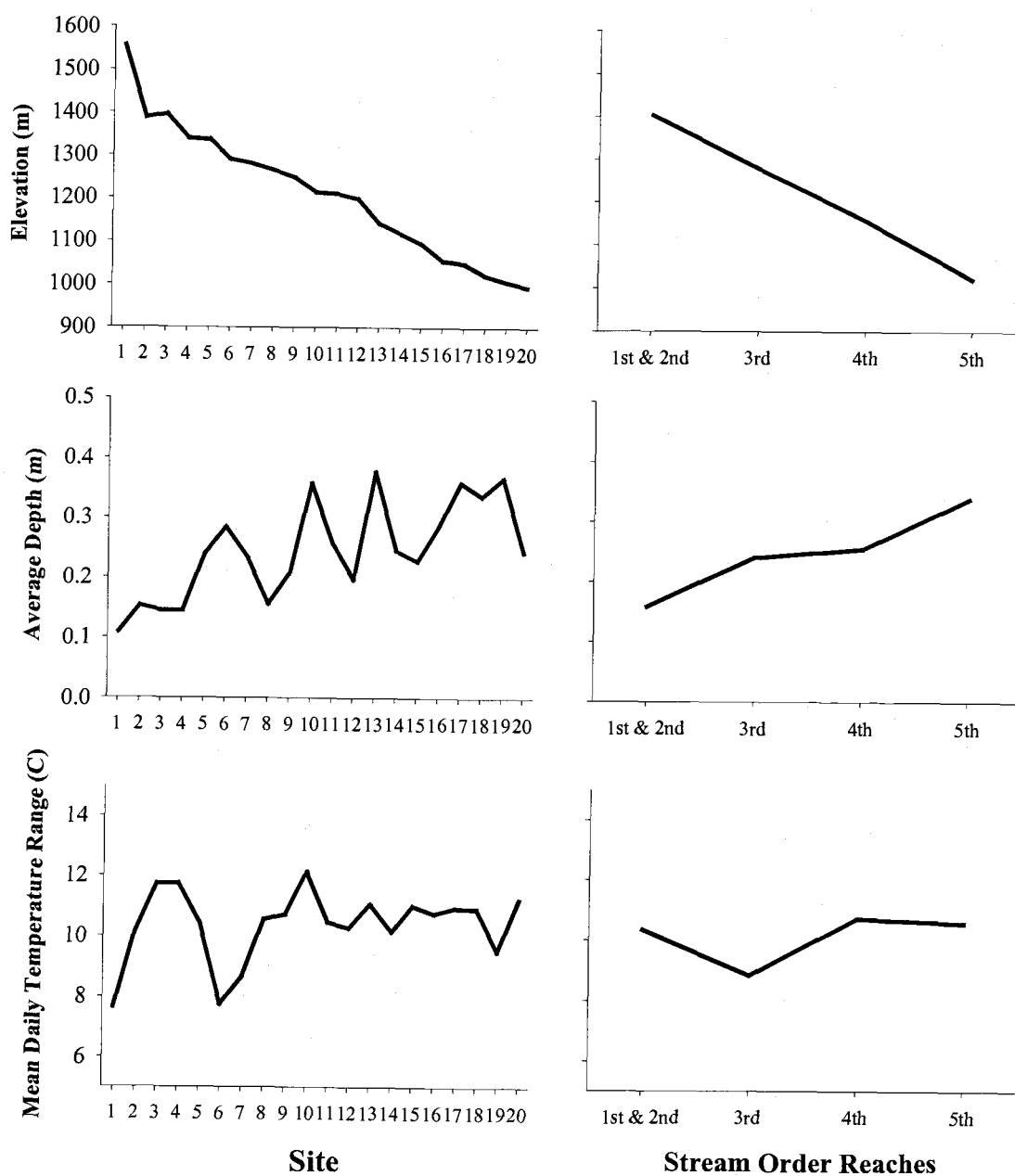
Figure 3.4. Examples of physical habitat characteristics in the Middle Fork of the John Day River that reflect relatively: 1) continuous trends at both site and reach scales (Elevation), 2) patchy trends at the site scale but continuous trends at the reach scale (Average Depth), and 3) patchy trends at both scales (Mean Daily Temperature Range). Figures represent a downstream gradient of approximately 100km (left to right).

Table 3.4. Comparison of site and reach scale patterns of physical habitat parameters from the Middle Fork of the John Day River, Oregon. Examples of the three trend types: continuous at both scales, patchy at the site scale but continuous at the stream order reach scale, or patchy at both scales.

Scale		Trends	
Site	Continuous	Patchy	Patchy
Stream Order	Continuous	Continuous	Patchy
	Elevation	Wetted Width	Aspect
	Discharge	Mean Depth	Width : Depth
	Stream Order	Valley Slope	Temperature Range
		Stream Gradient	Percent Riffle Habitat
		Solar Input	Percent Boulders
		Time of Solar Input	Percent Cobbles/Gravels
		Mean Temperature	
		Maximum Temperature	
		Minimum Temperature	
		Time Over 22	
		Time Over 24	
		Time Over 25	
		Percent Fines	
		Percent Macrophyte Cover	
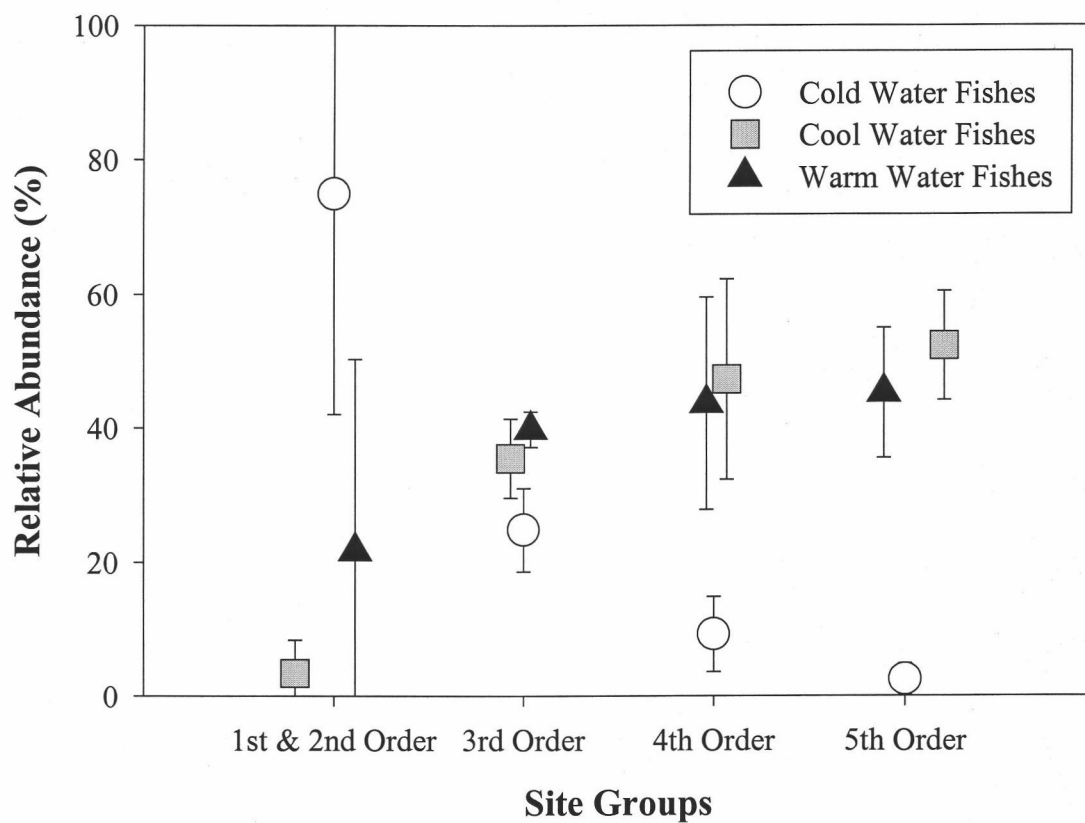
Figure 3.5. Relative abundance (± 1 SE) of fishes according thermal guilds from the stream order site groups in the MFJD 1996-1998. Cold water fishes are rainbow trout and chinook salmon; cool water fishes are torrent sculpin, bridge lip and mountain suckers, lamprey and long nosed dace; warm water fishes are red-side shiners, speckled dace and squaw fish.

Ordination of the relative abundance of fish species data resulted in a cumulative r^2 value of 0.987. There was a significant reduction in stress going from a 1 to 3 dimension solution (Monte Carlo test p-values < 0.05); the final stress of the 3 dimensional NMS solution was 4.27. Axis 1, representing the large-scale, longitudinal gradient, explained the majority of the variance in the data set ($r^2 = 0.848$), while axes 2 and 3 explained 10% and 4% of the variance respectively. The ordination pattern contained aspects of all three of the conceptual models: a longitudinal gradient, patchiness and high variability (Figure 3.6). There was a longitudinal gradient along axis 1 in fish communities from headwaters downstream; however, there also was a high degree of variability expressed along the first axis particularly among higher order sites (3rd-5th). In general, the 1st and 2nd order sites are most dissimilar from 3rd, 4th, and 5th order sites along axis 1, and there was little distinction between sites in 4th and 5th order reaches. Axis 2, representing more site-specific characteristics, primarily illustrated local variability among higher order sites (Figure 3.6). Axis 3 expressed a weak distinction of 4th order sites from those in 3rd and 5th order reaches along axis 3 (Figure 3.6).

The first axis was most strongly correlated with relative abundance of rainbow trout (-), torrent sculpin (+), and speckled dace (+) (Table 3.5). Axis 2 was most strongly correlated with torrent sculpin (-) and long nose dace (-) (Table 3.5), while axis 3 was most strongly correlated with red side shiners (+) and rainbow trout (-).

Correlations between axes coordinates and physical variables were generally higher along axis 1 than either axis 2 or 3 (Table 3.5). Axis 1 coordinates of the fish abundance ordination were most strongly correlated with large-scale physical variables; correlations > 0.85 were with valley slope (-), minimum and mean temperatures (+), stream order (+), and stream gradient (-) (Table 3.5). Axis 2 coordinates were not strongly correlated (r > 0.5) with any physical habitat variables (Table 3.5). Axis 3 coordinates were most strongly correlated with both site-specific and large-scale physical variables; correlations > 0.6 were with minimum temperature (+), solar input (+), and average depth (+) (Table 3.5).
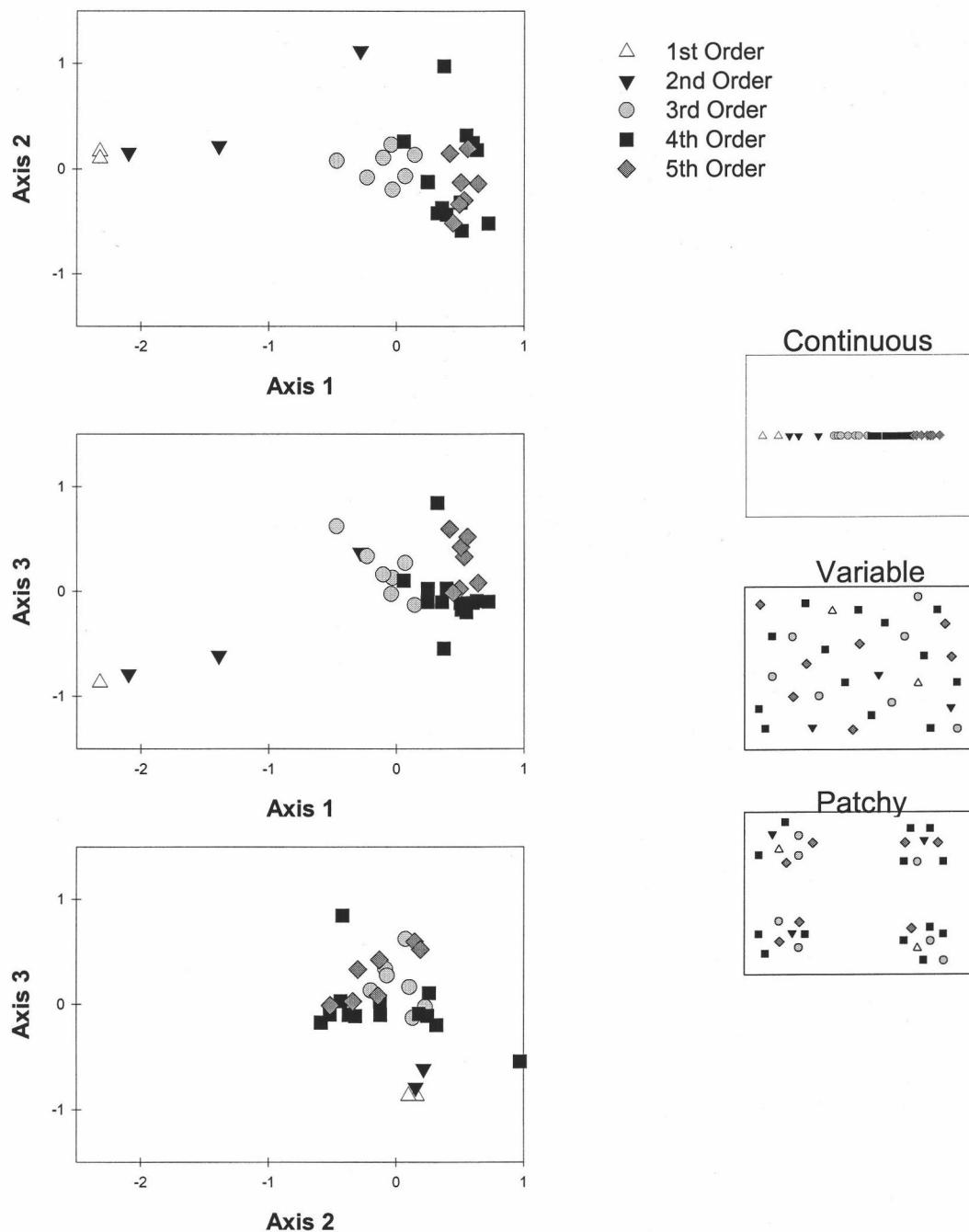
Figure 3.6. Two dimension plots of the NMS ordination of fish relative abundance in the MFJD. Each symbol represents a given site; the shade and shape indicate stream order. Miniature versions of the conceptual framework presented in Chapter 1 are shown on the right. Configurations have been rotated such that axis 1 represents large-scale, longitudinal gradients, and axes 2 and 3 represent small-scale, site-specific gradients.

Table 3.5. Correlation between axes coordinates from the fish relative abundance NMS ordination and individual fish species abundance, physical parameters, and macroinvertebrate taxa densities. The 10 highest correlations greater than 0.40 are shown.

Fish Species

Axis 1	r	Axis 2	r	Axis 3	r
Rainbow Trout	-0.981	Torrent Sculpin	-0.761	Red Side Shiner	0.780
Torrent Sculpin	0.793	Long Nose Dace	-0.511	Rainbow Trout	-0.712
Speckled Dace	0.623	Speckled Dace	0.497		
Long Nose Dace	0.487	Bridge Lip Sucker	0.469		

Physical Parameters

Axis 1	r	Axis 2	r	Axis 3	r
Valley Slope	-0.891	Percent Riffle Habitat	-0.453	Minimum Temperature	0.645
Minimum Temperature	0.889			Solar Input	0.626
Mean Temperature	0.883			Mean Depth	0.621
Stream Order	0.870			Valley Slope	-0.590
Stream Gradient	-0.850			Stream Gradient	-0.566
Elevation	-0.827			Time of Solar Input	0.557
Maximum Temperature	0.765			Stream Order	0.542
Discharge	0.754			Mean Temperature	0.520
Time Over 24°	0.743			Elevation	-0.510
Time of Solar Input	0.687				

There was a difference of 0.043 in the absolute values of the correlation coefficients for stream order and elevation with the first axis, suggesting longitudinal gradients in fish communities were more apparent from a reach scale perspective than from the site scale. Further comparisons of site versus reach scale patterns also revealed fishes (i.e. thermal guilds and individual species) reflected relatively patchy distributions at the site scale but were more continuous at the reach scale (Figure 3.7).

Macroinvertebrate Taxa

In the MFJD, macroinvertebrate taxa richness ranged from 38 to 62 individual taxa per site, EPT taxa richness ranged from 13 to 37 taxa per site, and percent dominance ranged from 9% to 27% per site. Total abundance of macroinvertebrates among the sites ranged from 2,316 to 22,463 individuals/m^2 (Appendix 2). There were no significant differences among sites grouped by orders 1+2, 3, 4, and 5 based on standard macroinvertebrate metrics of total abundance, taxa richness, percent dominance, percent EPT taxa, and Shannon's diversity of macroinvertebrates (ANOVA p-values >0.1). However, sites in 3rd order sites had significantly lower mean numbers of EPT taxa than other site groups (ANOVA p-value < 0.001, F-Ratio = 21.54, df = 31; Bonferroni MCP).

NMS Ordination of the macroinvertebrate density data resulted in a cumulative r^2 value of 0.926. There was a significant reduction in stress going from a 1 to 3 dimension NMS solution (Monte Carlo test p-values < 0.05); the final stress of the 3 dimensional solution was 8.75. Axis 1, representing the large-scale, longitudinal gradient, explained the majority of the variance in the data set (r^2 = 0.608), while axes 2 and 3 explained 16% and 15% of the variance respectively. There was evidence of a longitudinal gradient along axis 1 in macroinvertebrate communities from headwaters downstream; however, there also was patchiness and variability expressed along the first axis (Figure 3.8). In general, sites were grouped according to 1st and 2nd order sites, 3rd order sites, and 4th and 5th order sites along axis 1. Axis 3 tended to differentiate 3rd order sites from the others, and 4th order sites from 5th order sites (Figure 3.8).
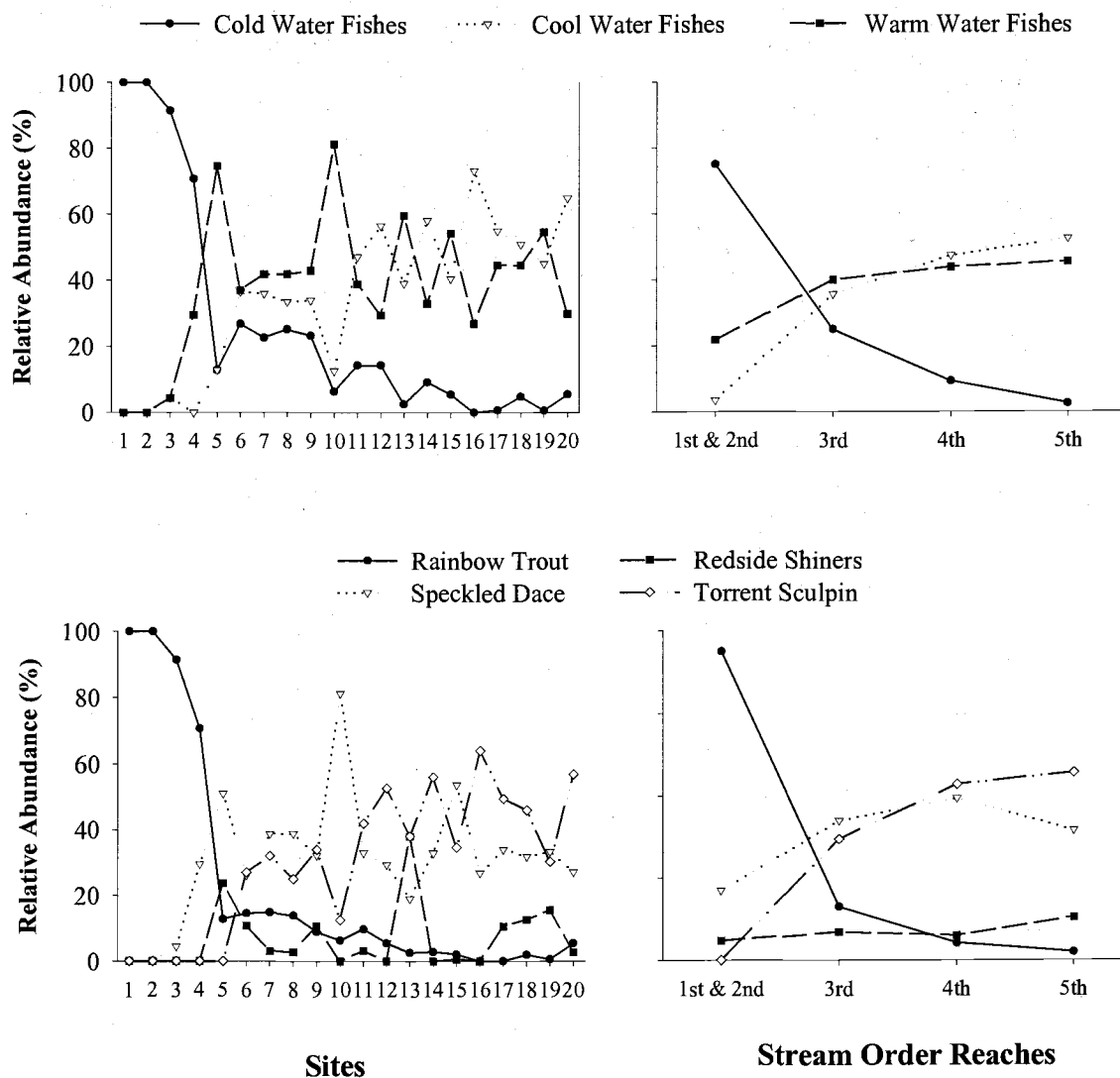
Figure 3.7. Site and reach scale trends in the relative abundance of fish thermal guilds (top) and the four most common species (bottom) in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).
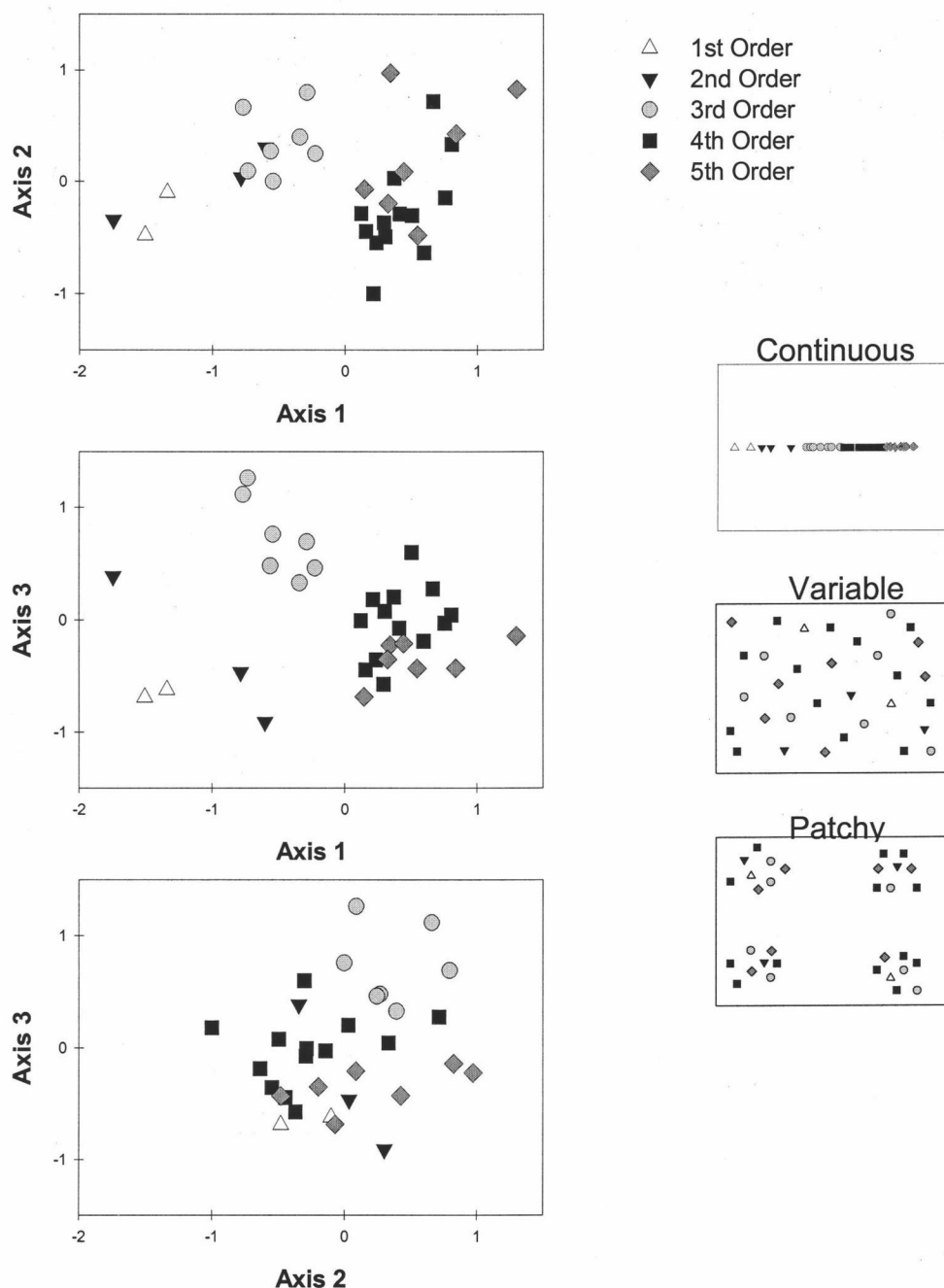
Figure 3.8. Two dimension plots of the NMS ordination of macroinvertebrate densities in the MFJD. Each symbol represents a given site; the shade and shape indicate stream order. Miniature versions of the conceptual framework presented in Chapter 1 are shown on the right. Configurations have been rotated such that axis 1 represents large-scale, longitudinal gradients, and axes 2 and 3 represent small-scale, site-specific gradients.

The first axis was most strongly correlated with taxa that were distributed in skewed fashion from either headwaters downstream or vice versa; correlations > 0.7 were with ostracods (-), amphipods (-), Sphaeriidae sp. (-), *Procloeon* (-), and *Micrasema* (-) (Table 3.6). Axis 2 was most strongly correlated with taxa that had more patch-like distributions from headwaters downstream; correlations > 0.575 were with *Epeorus* (-), *Wormaldia* (-), and Plecoptera sp. (-) (Table 3.6, Figure 3.9). Axis 3 was primarily correlated with taxa that had highest densities in 3rd order sites; correlations > 0.75 were with *Ophiogomphus* (+), Physid snails (+), and *Trichorythodes* (+) (Table 3.6).

Absolute values of correlations between axes coordinates and individual physical variables were much higher for axis 1 than for axes 2 and 3 (Table 3.6). Axis 1 coordinates of the macroinvertebrate density ordination were most strongly correlated with the large-scale physical variables; correlations > 0.8 were with stream order (+), discharge (+), time over 24°C (+), and mean temperature (+) (Table 3.6). Axes 2 and 3 were most highly correlated with site-specific variables such as width:depth ratio and average width (Table 3.6). However, no correlations between axes 2 and 3 coordinates and physical variables were greater than 0.5 (Table 3.6).

There was a difference of 0.09 in the absolute values of the correlation coefficients for stream order and elevation with the first axis (Table 3.6), indicating longitudinal gradients of macroinvertebrates were more apparent from a reach scale perspective than from the site scale. Further comparisons of site versus reach scale patterns revealed that those taxa most strongly correlated with axis 1 generally reflected relatively patchy distributions at the site scale but were more continuous at the reach scale (Figure 3.9). In contrast, those taxa that were most strongly correlated with axis 2 reflected relatively patchy distributions at both scales (Figure 3.9). No taxon had continuous patterns from both site and reach scale perspectives.

Macroinvertebrate Functional Feeding Groups
The highest percentage of shredders was found in 1st + 2nd and 4th order sites (Figure 3.10); relative abundance of shredders was significantly lower in 5th order sites than in

Table 3.6. Correlation between axes coordinates from the macroinvertebrate density NMS ordination and individual macroinvertebrate taxa densities and physical parameters. The 10 highest correlations greater than 0.40 are shown.

Macroinvertebrate Taxa

Axis 1	r	Axis 2	r	Axis 3	r
Ostracods	-0.834	*Epeorus*	-0.619	*Ophiogomphus*	0.823
Amphipods	-0.745	*Wormaldia*	-0.578	Physidae	0.776
Sphaeridae	-0.745	Plecoptera	-0.577	*Trichorythodes*	0.761
Procloeon	-0.704	*Ephemerella*	-0.573	*Hydroptilla*	0.641
Micrasema	-0.701	*Glossosoma*	-0.564	*Argia*	0.632
Paraleptophlebia	-0.678	*Antocha*	-0.555	Ephemerellidae	0.621
Hydropsychidae	0.650	*Serratella*	-0.546	Limpets	0.617
Chironomidae	-0.647	*Pteronarcys*	-0.524	*Brychius*	0.597
Tanypodinae	-0.602	*Drunella*	-0.519	Nemouridae	-0.594
Malenka	-0.598	Perlodidae	-0.512	*Juga*	0.592

Physical Parameters

Axis 1	r	Axis 2	r	Axis 3	r
Stream Order	0.879	Width : Depth	-0.457		
Discharge	0.854	(Stream Width)	(-0.382)		
Time Over 24°	0.835				
Mean Temperature	0.833				
Macrophyte Cover	-0.793				
Elevation	-0.789				
Maximum Temperature	0.778				
Minimum Temperature	0.740				
Valley Slope	-0.702				
Stream Width	0.662				
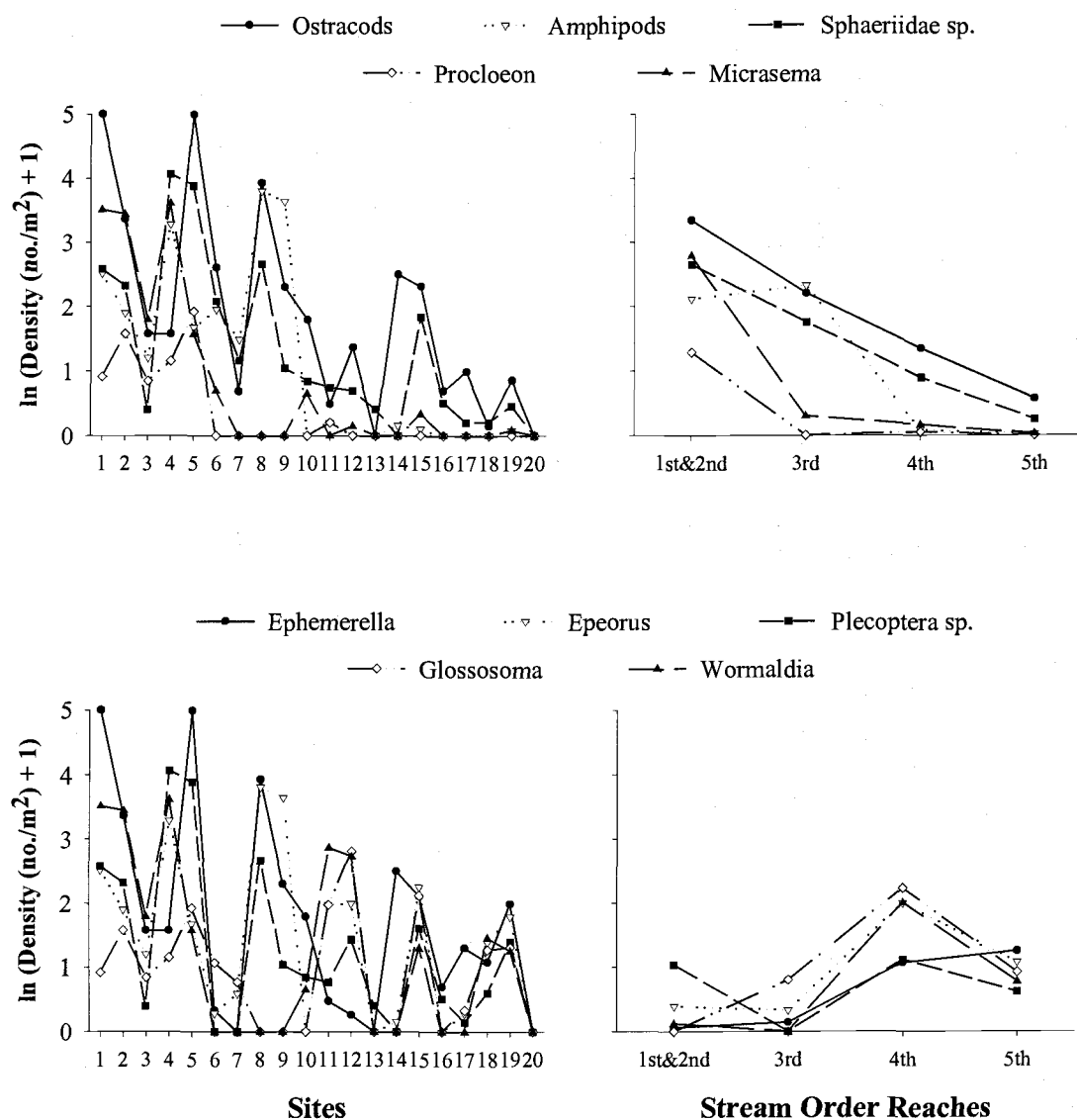
Figure 3.9. Site and reach scale trends in the densities of the five macroinvertebrate taxa most strongly correlated with axis 1 (top) and axis 2 (bottom) from the NMS ordination. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).
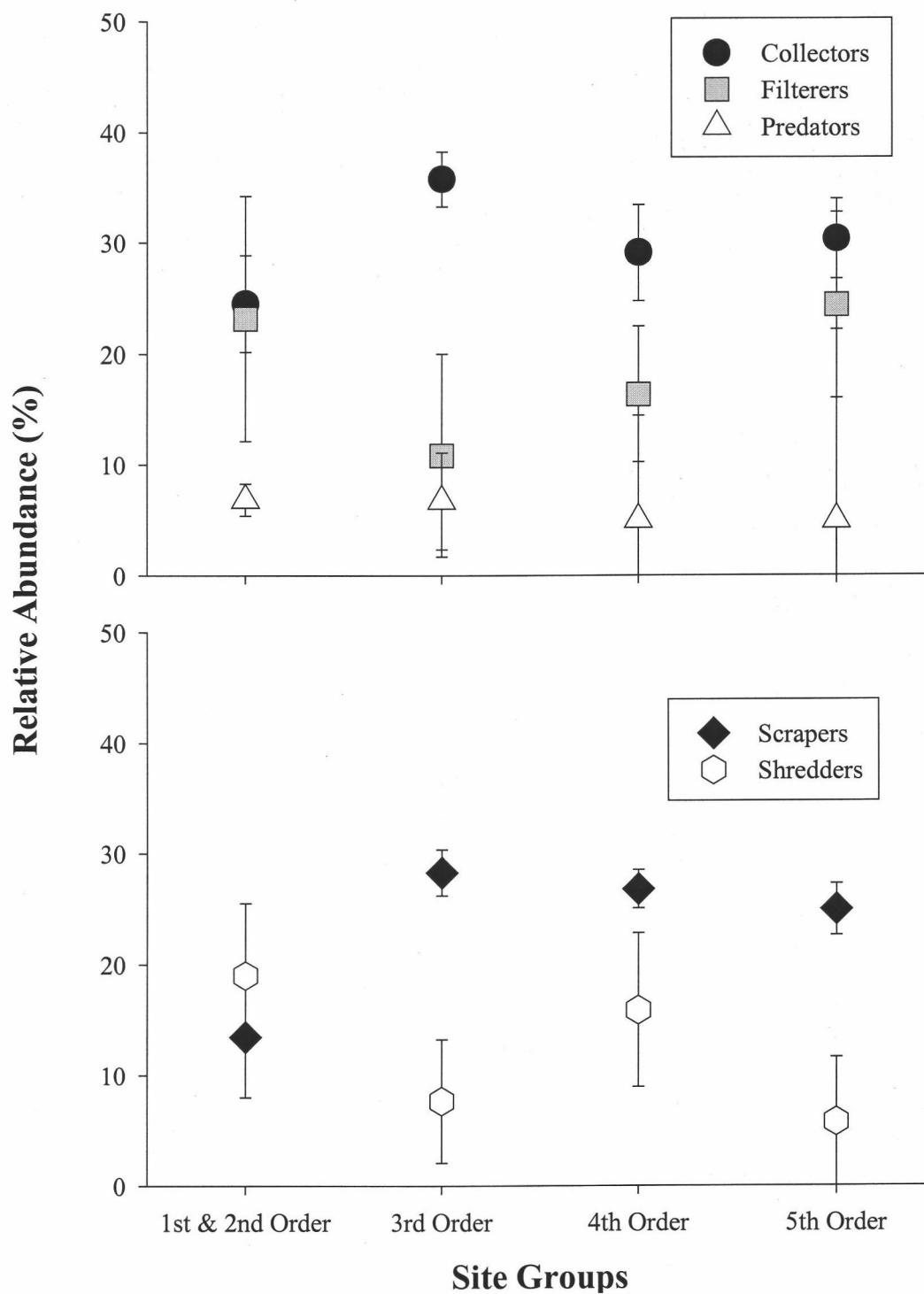
Figure 3.10. Relative abundance (± 1 SE) of macroinvertebrate functional feeding groups from stream order site groups in the MFJD.

1st + 2nd and 4th order sites (ANOVA p-value = 0.004, F-Ratio = 5.67, df = 31; Bonferroni MCP). The highest percentage of scrapers was in 3rd - 5th order sites (Figure 3.10); relative abundance of scrapers was significantly lower in 1st + 2nd order reaches than in higher order sites (ANOVA p-value = 0.003, F-Ratio = 6.01, df = 31; Bonferroni MCP). Collectors were the most dominant functional feeding group among all site groups and were highest in 3rd order sites (Figure 3.10). There were no significant differences among sites grouped by stream order based on relative abundance of collector, filterer, or predator functional feeding groups (ANOVA p-values >0.1).

Ordination of functional feeding group data resulted in a cumulative r^2 value of 0.966. There was a significant reduction in stress going from a 1 to 3 dimensional solution (Monte Carlo test p-value < 0.05); the final stress was 6.87. Axis 1 explained the majority of the variance in the data set (r^2 = 0.606), while axes 2 and 3 explained 21% and 15% of the variance respectively. The ordination pattern was highly variable, with no evidence of a longitudinal gradient (Figure 3.11). Sites were arranged as a single group with 1st and 5th order sites distributed at opposite ends along axis 1 (Figure 3.11).

The first axis was negatively correlated with densities of predators, shredders, and collectors (Table 3.7). Axis 2 was most strongly correlated with scrapers (+) and collectors (+), and axis 3 was positively correlated with filterers (Table 3.7).

Absolute values of correlations between axes coordinates and individual physical variables were similar among all axes (Table 3.7), however correlation values with axis 1 coordinates were lower than all previous ordinations. Axis 1 coordinates of the functional feeding group ordination were strongly correlated (r > 0.5) with only one physical variable: stream order (Table 3.7). Coordinates of axes 2 and 3 were not strongly correlated with any of the physical variables.

Compared to the previous ordinations, the relatively low correlations for stream order and elevation with the first axis coordinates (Table 3.7), indicated longitudinal gradients in functional feeding group abundance were not as consistent from either a reach and site scale perspective. Functional feeding groups generally reflected relatively patchy distributions at both the site and reach scales, except predators that had relatively continuous distributions at the reach scale (Figure 3.12).
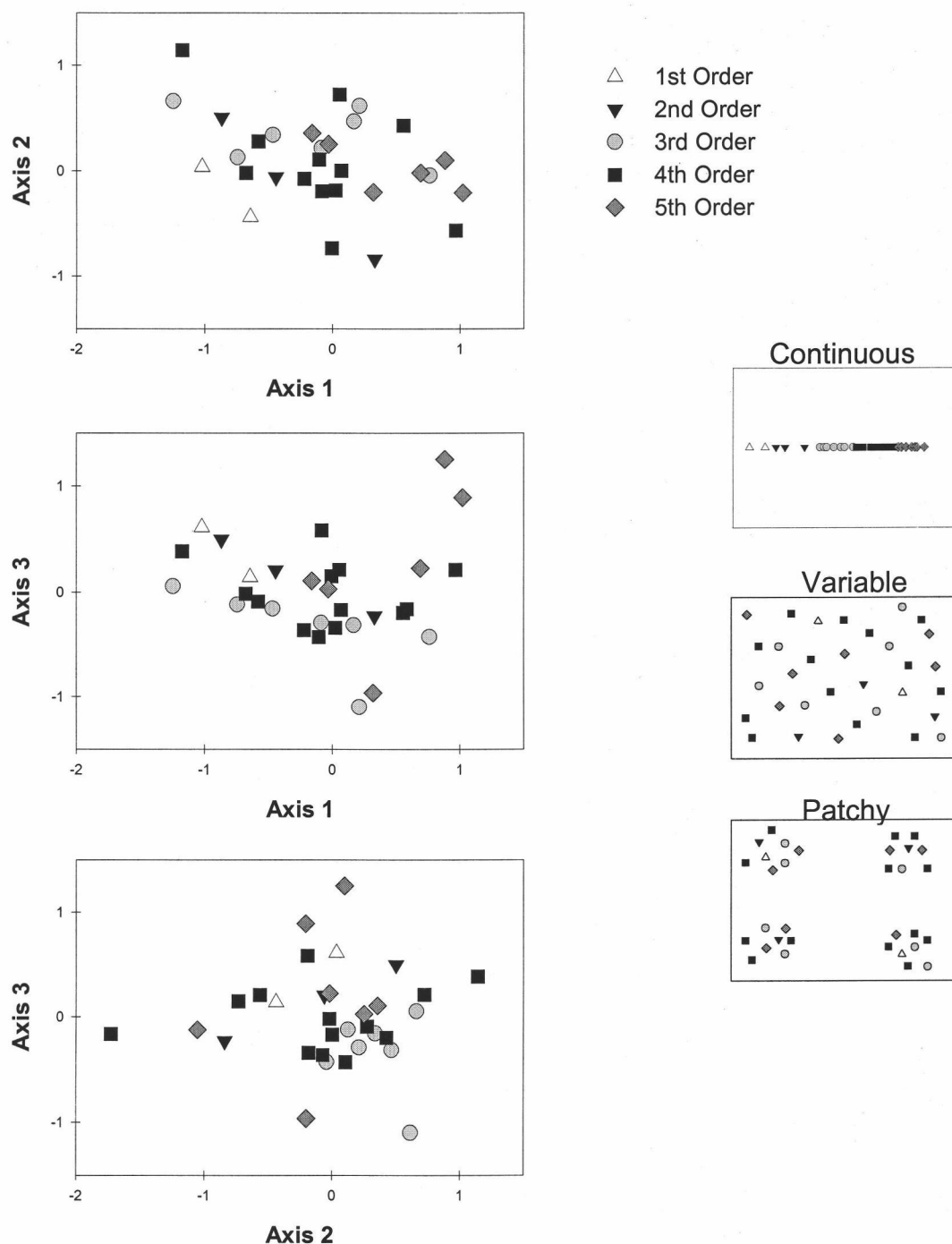
Figure 3.11. Two dimension plots of the NMS ordination of macroinvertebrate functional feeding group densities in the MFJD. Each symbol represents a given site, and the shade and shape indicate stream order. Miniature versions of the conceptual framework presented in Chapter 1 are shown on the right. Configurations have been rotated such that axis 1 represents large-scale, longitudinal gradients, and axes 2 and 3 represent small-scale, site-specific gradients.

Table 3.7. Correlation between axes coordinates from the macroinvertebrate functional feeding group density NMS ordination and individual functional feeding group densities and physical parameters. The 10 highest correlations greater than 0.40 are shown.

Functional Feeding Groups

Axis 1	r	Axis 2	r	Axis 3	r
Predators	-0.848	Scrapers	0.779	Filterers	0.718
Shredders	-0.813	Collectors	0.770		
Collectors	-0.748	Predators	0.635		
Unknown	-0.645	Filterers	0.617		
Filterers	-0.620				

Physical Parameters

Axis 1	r	Axis 2	r	Axis 3	r
Stream Order	0.526	Percent Riffle Habitat	0.448		
Mean Depth	0.488				
Elevation	-0.472				
Maximum Temperature	0.432				
Discharge	0.428				
Mean Temperature	0.427				
Time of Solar Input	0.418				
Time Over 24°	0.410				
Time Over 25°	0.403				
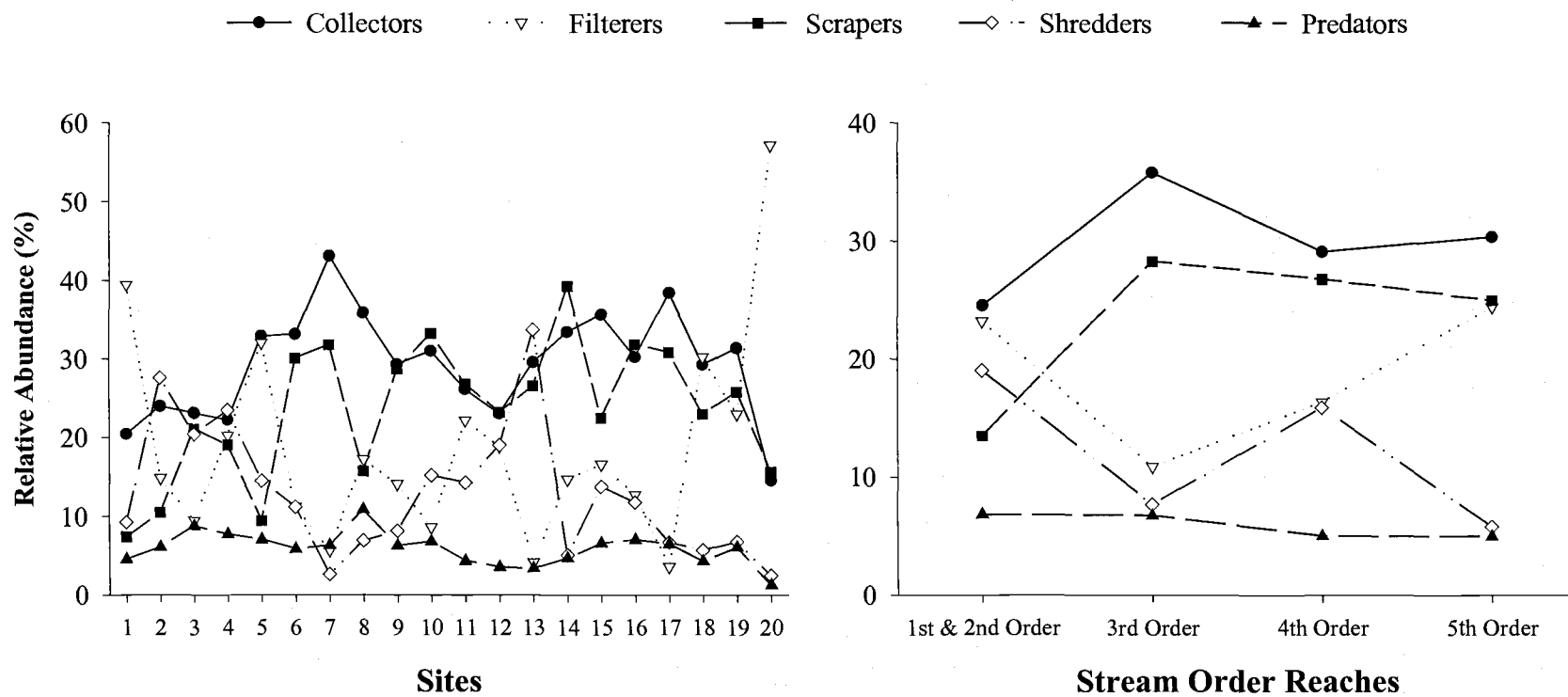
Figure 3.12. Site and reach scale trends in the relative abundance of macroinvertebrate functional feeding groups in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).

Algae

Chlorophyll *a* biomass was highly variable among sites in the MFJD with values ranging from 2.4 to 176.3 mg/m^2 (Figure 3.13). There was no significant difference among site groups (by stream order) based on median chlorophyll *a* biomass (Kruskal-Wallis test statistic = 3.77, p-value = 0.29, df = 31). Gross primary production (GPP) also was highly variable among sites however, average rates of GPP did increase from low order site groups to higher order groups. Sites in 4th order reaches had the highest mean rates of GPP (Table 3.8). Statistically significant differences were between 4th order reaches and both 1st + 2nd and 3rd order reaches (ANOVA p-value = 0.01, F-ratio = 4.62, df = 31; Bonferroni MCP).

Ordination of algal biomass and production data resulted in a low cumulative r^2 value of 0.009 and a relatively high three dimensional stress of 16.03. Axis 1, representing the large-scale, longitudinal gradient, explained the majority of the variance in the data set (r^2 = 0.009), while axes 2 and 3 explained less than 1% of the variance combined. The ordination pattern for the algal data was highly variable with little evidence of either a longitudinal gradient or discrete patches (Figure 3.14). Due to the extremely low R^2 value of the ordination, examination of any correlations with the axes coordinates was inappropriate.

Longitudinal trends in chlorophyll *a* biomass, GPP, and gross respiration were generally patchy from both site and reach scale perspectives (Figure 3.13). Trends of GPP expressed more variability at both scales along the longitudinal gradient than either biomass or respiration (Figure 3.13).

Discussion

The utility of a meaningful model is not its ability to precisely predict reality, but to enable researchers to question if and why their systems do not follow model predictions. Within this context, I applied the RCC to the MFJD, a stream in the semi-arid interior Pacific Northwest that has been subjected to multiple land-use practices. By integrating a new multivariate approach with more traditional parametric methods, this study suggested there were longitudinal gradients expressed by both individual
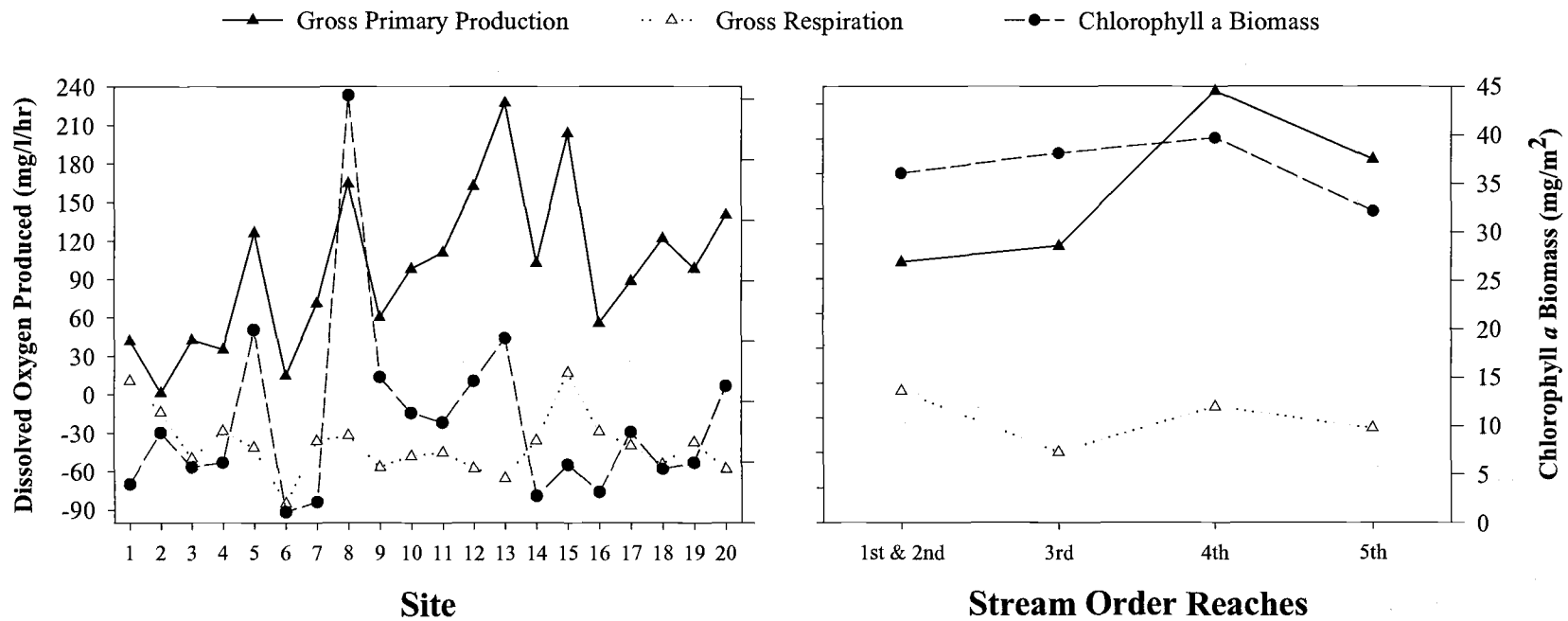
Figure 3.13. Site and reach scale trends in gross primary production, gross respiration, and chlorophyll *a* biomass in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).

Table 3.8. Mean estimates (± 1 SE) of algal chlorophyll *a* biomass, primary production, and respiration according to stream order site groups in the MFJD.

Algal Parameter	Site Groups			
	1st & 2nd	3rd	4th	5th
Chlorophyll *a* Biomass (mg/m^2)	35.99	38.07	39.64	32.09
(± 1 SE)	(22.81)	(59.49)	(23.57)	(19.30)
Gross Primary Production (mg DO/l/hr)	49.20	58.43	147.05	108.12
(± 1 SE)	(41.24)	(49.88)	(76.32)	(31.48)
Gross Respiration (mg DO/l/hr)	-24.70	-59.99	-33.69	-46.04
(± 1 SE)	(21.52)	(27.52)	(53.06)	(22.97)
Gross Production per Algal Biomass (mg DO/l/hr)/(mg/m^2)	0.05	4.47	5.11	6.50
(± 1 SE)	(0.03)	(4.28)	(4.24)	(4.27)
Gross Respiration per Algal Biomass (mg DO/l/hr)/(mg/m^2)	-0.02	-16.77	-2.26	-1.98
(± 1 SE)	(0.03)	(20.66)	(2.04)	(1.30)

Figure 3.14. Two dimension plots of the NMS ordination of algal biomass and production in the MFJD. Each symbol represents a given site; the color and shape indicate stream order. Miniature versions of the conceptual framework presented in Chapter 1 are shown on the left. Configurations have been rotated such that axis 1 represents large-scale, longitudinal gradients, and axes 2 and 3 represent small-scale, site-specific gradients.

and combined physical and biological elements in the MFJD. However, the integrated analyses also indicated sufficient variability among the study sites such that the MFJD does not follow the RCC for some parameters. This approach also was used to examine correlations between in-stream community structures and physical habitat gradients at stream order reach and site-specific scales. Fish and macroinvertebrate community structures along the MFJD were more strongly correlated with landscape scale, longitudinal gradients that than site scale variability. Much like the findings of Richards et al. (1997) and Wiley et al. (1997), this study illustrates how our ability to recognize and interpret environmental gradients in stream systems will change depending on the scale and type of variables under consideration.

Physical Habitat

Of the different data sets collected in the MFJD, the most consistent longitudinal gradients were observed for physical characteristics. As suggested by the strong correlations between axis 1 coordinates and the variables for stream order (reach-scale) and elevation (site-scale), overall physical habitat reflected longitudinal gradients from both reach and site scale perspectives in NMS ordination. Variability in physical habitat along the longitudinal profile (i.e. axis 1) was related to patchy, site-specific characteristics expressed along the 2nd and 3rd axes. However, many of the variables that contributed to this site scale variability also were strongly correlated with axis 1 (e.g. stream width and maximum temperature). Within any ecosystem, physical and biological variables may interact with and reflect various environmental gradients at many different scales (Levin 1992). Unlike other ordination techniques, each axis in an NMS ordination is calculated independently of the other axes such that all input variables are used to determine each axis (Kruskal 1964, Mather 1976). This characteristic allows individual variables to be correlated along more than one axis or environmental gradient (i.e. physical habitat variables can simultaneously express different gradients at large and small scales). Indeed, when considered individually, most physical habitat variables measured along the MFJD were discontinuous gradients from a site scale perspective and more continuous from a reach scale

perspective (Table 3.4). This 'dual nature' of most habitat parameters would account for the strong correlations of certain variables with axis 1 as well as axes 2 and 3 coordinates. Interpretations of physical habitat gradients will vary not only depending on the spatial scale but also on whether individual or multiple parameters were considered. After considering variables individually and collectively from site and reach scale perspectives, the physical stream template along the MFJD depicted by these 20 study sites was a generally continuous longitudinal gradient with localized patchiness and variability. This gradient forms the primary template for the structure of biotic communities examined in the MFJD.

Fish

As expected by the conceptual framework (Chapter 2), the structure of fish communities along the MFJD reflected patterns of longitudinal gradients, localized patchiness, and high variability. Ordination of the individual fish species along the MFJD contained convincing patterns of a longitudinal gradient, with most variability and patchiness associated with sites in higher order reaches. The ordination structure of fish communities along axis 1 was driven primarily by the distribution of rainbow trout, torrent sculpin, and speckled dace. Rainbow trout was the most abundant species in 1st and 2nd order reaches but rare in higher order reaches, whereas sculpin and dace were absent or rare in the headwaters but comprised about 80% of the fish community in 4th and 5th order sites. This dichotomy is a consequence of general life history requirements; trout prefer cold water systems with higher gradients, while torrent sculpin and speckled dace are found in cool or warm water areas with lower gradients (Li et al. 1987, Zaroban et al. 1998). This pattern was also expressed through correlations with environmental variables, where valley slope, temperature, stream size, and elevation were most strongly correlated with longitudinal gradients of fish communities in the MFJD.

The more site-specific axes, 2 and 3, were also strongly correlated with fish species and physical habitat variables that were strongly correlated with axis 1. Torrent sculpin, in particular, was correlated with all three axes. As indicated above,

for the physical habitat ordination, this occurs when a variable is expressed along more than one dimension (gradient) in a NMS ordination. In this case, the relative abundance of torrent sculpin is correlated with a longitudinal gradient (axis 1), and both site-specific gradients (axes 2 and 3). These site-specific gradients in turn, may represent variables that were either continuous, patchy, or absent along the longitudinal gradient (Table 3.4).

In general, thermal guilds and individual species of fish had rather discontinuous longitudinal patterns at the site scale and more continuous trends from a reach perspective. I believe the site to site variation is a consequence of the sampling method and interpretations of the resulting fish community. Most of the fish collected in this study were either benthic dwelling species or were small enough (< 200 mm) to take advantage of primarily riffle/run habitats. If large scale (>100 m) movements were limited during low flow conditions, but movements within sites were unrestricted, fish communities would be expected to be correlated with site-specific habitat features. The strong correlations between axis 3 coordinates and physical habitat variables support this idea. In addition, the apparent similarity among 4th and 5th order sites in the fish ordination is indicative of the relative similarities in the localized, physical habitat at these sites (see Table 3.2).

Macroinvertebrates

Ordination of macroinvertebrate taxa densities along the MFJD contained a longitudinal gradient, with variability and patchiness expressed in all dimensions. The ordination structure of macroinvertebrates along axis 1 was driven primarily by the distribution of those taxa with skewed distributions from headwaters downstream or vice versa. As shown in Figure 3.9 however, most of the taxa correlated with axis 1 also had relatively patchy longitudinal distributions from a site scale perspective. Again, this dichotomy is a consequence of taxa responding to multiple gradients at different scales. In contrast, taxa most strongly correlated with axes 2 and 3 had relatively discontinuous longitudinal distributions at both site and reach scales. Although there is a great deal of scatter along both axes 2 and 3 in the ordination of

macroinvertebrate taxa, 3rd order sites were distinguished from the rest of the MFJD along axis 3. The taxa most strongly correlated with axis 3 were either most abundant or only present in 3rd order sites. Many of these taxa represent sediment tolerant invertebrates such as *Trichorythodes*, Odonata sp., and Ephemerellidae sp. The sites in 3rd order reaches have been heavily grazed during the last decade and have incised banks, heavy macrophyte cover, and are strongly influenced by a large groundwater spring.

Ordination of macroinvertebrate taxa, as with fish species, was strongly correlated with large scale, physical habitat features along axis 1. Unlike the fish community however, correlations between axes 2 and 3 with individual, site-specific physical variables were generally lower for the macroinvertebrate taxa ordination than for the fish community ordination. I believe there are two possible reasons why the correlations between the macroinvertebrate ordination and the site scale, physical variables were low. Perhaps the physical variables measured did not directly influence the abundance and distribution of macroinvertebrates within sites; however, this would appear unlikely because depth, habitat type, and substrates have all been shown to either correlate with or influence macroinvertebrate communities elsewhere (e.g. Cummins & Lauff 1969, Rabeni & Minshall 1977, Williams 1980, Hawkins et al. 1982, Minshall 1984, Brussock & Brown 1991, Death 1995, Richards et al. 1997, Beisel et al. 1998). Another possible reason would be the scale at which measurements were made. Although I recorded depth, habitat type, and substrate with each macroinvertebrate sample, I also used additional habitat measurements that were not measured with each sample (see Poff & Ward 1992). Because of their high diversity, smaller body size, and limited mobility, macroinvertebrates may be more indicative of micro-habitat (< 1 m^2) characteristics than site scale (>10 m^2) ones. In a system like the MFJD that is dominated by riffle habitat and cobble/gravel substrates, these and other site-scale variables used in my analysis may have been too general to be strongly correlated with site to site variability of macroinvertebrate communities.

While localized characteristics (e.g. mean depth, stream width, and channel gradient) influence micro-habitat availability, landscape scale features determine the

general in-stream habitats along the longitudinal profile (Frissel et al. 1986, Montgomerey 1999). In the MFJD, community structure of macroinvertebrate taxa was primarily a reflection of this overall, longitudinal physical template with variability expressed by micro-habitat requirements of individual taxa. Similarly, Richards et al. (1997) found the macroinvertebrate communities were correlated with both catchment and reach scale habitat characteristics.

When I used functional feeding groups instead of individual taxa to represent the macroinvertebrate community, these patterns and their interpretations were much different. Because functional feeding groups are classified on a basis of energy consumption, changes of functional feeding group composition may not correspond to stream size. First, the RCC used stream order as a proxy for continuous changes of in-stream energy sources (i.e. allochthonous vs. autochthonous) used by different functional feeding groups. However, the riparian zone throughout the MFJD has been significantly influenced by grazing, timber harvest, and mining, which has potentially severed the relationship between energy sources and stream size. In systems where stream size and energy sources are not directly related, individual taxa still respond to other environmental gradients associated with stream order such as discharge, temperature, and gradient. Second, abundance of functional feeding groups is compromised by taxa with high densities. In the MFJD, those taxa that had the highest overall densities, also were most ubiquitous (e.g. Chironomidae sp. and Elmidae sp.). Therefore abundant, common taxa may have limited the expression of a strong longitudinal gradient in the ordination of functional feeding group densities. Finally, differences in resolution between individual taxa and functional feeding group also may have contributed to the different longitudinal patterns. By grouping taxa into functional feeding groups, I lost much of the among-taxa variability related to stream order. Therefore sites that differ greatly in taxa composition but have similar functional feeding group composition will have larger distances between them in taxa ordinations versus those in functional feeding group ordinations.

Algae

Algal data expressed the most variable pattern with little evidence of a longitudinal gradient. Many possible reasons exist for why the algal data were so variable, but there are two hypotheses I believe most probable. First, I used biomass and productivity variables rather than community composition variables. Because rates of production and biomass accumulation may be similar for multiple algal types, the variables I used may not represent actual changes in community structure. Second, reach and site scale gradients in the biomass and production of algal communities along the MFJD are simply not significant enough to be identified in an ordination (as indicated by the low r^2). No doubt gradients exist within the algal community, but perhaps the scales at which I sampled limited my ability to detect them.

The MFJD and the River Continuum Concept

By integrating a multivariate approach with more traditional parametric analyses, I was able to examine longitudinal patterns of both individual and combined stream parameters with the context of the RCC. In general, the MFJD is a mosaic of continuous and patchy gradients at both stream order reach and site scales, combining aspects of the River Continuum (Vannote et al. 1980) and Patch Dynamics (Pringle et al. 1989, Townsend 1989) concepts in stream ecology. The combined physical habitat parameters of the MFJD reflected a relatively consistent, continuous longitudinal gradient from a stream order perspective as predicted by the RCC, whereas among site variability along this gradient was expressed by individual, site-specific parameters, such as depth, substrate, and habitat.

The RCC suggested that fishes, macroinvertebrates, and algae also would reflect gradients from headwaters downstream (Vannote et al. 1980). From a stream order perspective, the distribution of fish thermal guilds in the MFJD changed continuously along the longitudinal profile. Contrary to RCC predictions, relative abundances of cool and warm water fishes were similar throughout the MFJD. This suggests that either the identification of cool and warm water fishes was ambiguous, or there was sufficient thermal heterogeneity in the lower reaches of the MFJD to

allow both fishes to co-exist. I believe the latter explanation is most probable because Torgersen et al (1999) found extensive thermal heterogeneity in 3rd - 5th order reaches of MFJD. In addition, the multiple land-uses in the MFJD have resulted in a highly variable riparian canopy cover in the lower reaches which may cause differential heating throughout the system.

According to the RCC, macroinvertebrate functional feeding groups would respond to changes along a stream by exploiting allochthonous and autocthonous energy sources. From a stream order perspective, the macroinvertebrate community in the MFJD reflected a longitudinal gradient using individual taxa but not functional feeding groups. I believe this difference occurred because individual taxa may respond to a suite of physical and biological variables ranging from landscape to micro-habitat in scale, whereas distributions of functional feeding groups respond primarily to changes in energy sources alone. Scraper and shredder communities lacked longitudinal gradients and were relatively homogeneous throughout the MFJD. Such distributions may be indicative of a system like the MFJD that has abundant, productive algae and variable riparian canopy cover throughout. Because functional feeding groups limit the expression of longitudinal gradients, I would suggest expanding predictions of macroinvertebrate communities along a longitudinal gradient to include individual taxa and their relationships to physical habitat gradients (sensu Statzner & Borchardt 1994). However, as this study illustrates, such an approach would require a more intimate understanding of the individual systems and taxa involved.

Lastly, the RCC predicted that both abundance and production of algae would increase from headwaters to mid-sized reaches (i.e. 4th -6th order) due to increased solar input (Vannote et al. 1980). While there was evidence of increasing biomass and production along the MFJD from a stream order perspective, the trends were not entirely consistent with the RCC. The lack of a significant difference in biomass and production among $1^{st} + 2^{nd}$, 3rd, and 5th order sites suggests that solar input is not a limiting factor in the MFJD. Again, this illustrates a possible connection between land-use practices and the highly variable riparian canopy cover throughout the MFJD.

Results from this study suggest that interpretations of longitudinal gradients are dependent on the type of community in question and the scale of observation used to determine those gradients. Contrary to my initial hypotheses, fish and macroinvertebrate communities were more strongly correlated with larger scale, more continuous physical variables than local scale, patchy variables. In addition, the fish community was strongly correlated with more local scale, site-specific variables than the macroinvertebrate community, suggesting micro-habitat preferences of macroinvertebrates were not expressed.

Despite variable valley geomorphology and extensive land-use, there were strong physical and biological longitudinal gradients in the MFJD. Nevertheless, I do believe grazing, mining, timber harvest, and channelization have affected the habitat and biota within this system. Most importantly, these activities have resulted in a sparse and highly variable riparian canopy cover throughout the MFJD. Reduction or discontinuity in the riparian corridor directly affects allochthonous inputs, exposure, sedimentation, and channel structure, which in turn affect communities of fishes, macroinvertebrates and algae.

Few studies have considered such a breadth of physical and biological components along such an extensive longitudinal profile of a stream. While I have certainly excluded numerous biotic and abiotic factors, I believe this study provides a unique and expansive foundation for multivariate examinations of stream communities. The spatial scope and breadth of measures in my study revealed how perceptions of stream gradients absolutely depend upon the spatial extent of our observations. This study illustrates that continuous and patchy aspects of both physical and biological parameters occur together in stream systems and are not mutually exclusive.

4. LONGITUDINAL PATTERNS OF TROPHIC RELATIONSHIPS IN A HIGH DESERT STREAM

Introduction

While the River Continuum Concept (Vannote et al. 1980) set the stage for considering how in-stream community structure may be influenced by geomorphic, hydrologic, and other physical factors (e.g. Minshall et al. 1989, Chapter 3), little work has been done on the influence of trophic interactions affecting longitudinal trends in stream community structure. Currently there are two different conceptual frameworks that attempt to link the physical template, trophic interactions, and community structure over large environmental gradients in aquatic systems: 1) the River Continuum Concept (RCC), and 2) the Geomorphic-Trophic Hypothesis of Hershey et al. (1999). Hershey et al. (1999) described a conceptual framework that interprets the community structures of lakes and ponds as a result of trophic interactions constrained by the position of the particular water body in a geomorphic context. The RCC describes how continuous longitudinal gradients in stream geomorphology influence the primary sources of available energy (i.e. allochthonous vs. autochthonous) and ultimately the structure of in-stream communities. One primary difference between these conceptual models is that one pertains to relatively closed systems (Hershey et al. 1999) and the other to more open systems (RCC). The trophic interactions predicted by these models further express this dichotomy. While the model of Hershey et al. (1999) incorporated both bottom-up and top-down influences on community structure, the RCC relied solely on bottom-up processes to determine consumer community structures.

Both top-down and bottom-up trophic interactions have been shown to influence community structure within lentic systems (e.g. Carpenter et al. 1985, Kitchell & Crowder 1986) and under experimental conditions in stream reaches (e.g. Power 1990 & 1992, Wooton et al. 1996, Englund & Evander 1999, Forrester et al. 1999). In other experiments, grazing pressure from benthic macroinvertebrates has been shown to influence both algal biomass (Jacoby 1987, Lamberti et al. 1987,

Lamberti et al. 1995, Walton et al. 1995) and primary production (Jacoby 1987, Lamberti et al. 1987) by reducing algal standing crop and increasing turnover rates. Fishes also may influence aquatic community structure by preying on invertebrates, thereby reducing the grazing pressure on primary producers (Carpenter et al. 1985, Power 1990, Wooton et al. 1996), or by grazing directly on algae (Gelwick & Matthews 1992). Nevertheless, within the context of geomorphic constraints, we know little about how bottom-up and top-down trophic interactions influence community structure along a natural stream continuum.

Although fish and macroinvertebrate communities in the Middle Fork of the John Day River (MFJD) reflected longitudinal gradients, there also was a great deal of patchiness and variability (Chapter 3). Large-scale patterns of stream communities along primarily the longitudinal gradient were strongly correlated with many physical habitat characteristics that reflected upstream-downstream trends (e.g. elevation, stream order, etc.). In addition, many site-specific habitat features (e.g. depth and substrate type) were correlated with the variability among communities expressed at the local scale. However, much of the variability in community structure at the local scale could not be explained by physical habitat alone. This suggests that the proper physical habitat measures were either lacking, or that physical habitat was not the only mechanism influencing stream community structure. While the former idea is certainly probable, this study explores the possibility that trophic interactions also play an important role in structuring MFJD stream communities.

Stream community patterns were either continuous or patchy along the longitudinal profile of the MFJD according to the scale and community type under consideration (Chapter 3). In addition, relationships between community structures and environmental gradients varied with scale because many physical habitat variables could simultaneously express different gradients at large and small scales. Could it be that the expression of top-down or bottom-up trophic interactions along a stream profile is also influenced by scale? If expression of top-down interactions is limited to closed, local habitats, then the bottom-up perspective of the RCC would be most appropriate from an open, stream order perspective. However if geomorphic

constraints primarily influence community structure at the scale of stream order reaches (like the lake groups in Hershey et al. 1999), then one would expect bottom-up **and** top-down trophic interactions to be expressed within each stream order reach (e.g. Forrester et al. 1999).

This project examined potential trophic relationships between the fish, macroinvertebrate, and algal communities along a 1st through 5th order gradient of the Middle Fork of the John Day River (MFJD) in semi-arid eastern Oregon. Although the RCC primarily presented two inversely related, bottom-up trophic relationships (Figure 4.1a, b), the potential suite of trophic interactions within any stream community far exceeds two simple chains (Figure 4.1c). This study focused on the relationships between: 1) fishes, macroinvertebrate scrapers, and algal biomass (Figure 4.1d), 2) solar input, algal biomass, and macroinvertebrate scrapers (Figure 4.1e), 3) canopy cover (a surrogate for allochthonous input) and macroinvertebrate shredders (Figure 4.1f), and 4) fishes and macroinvertebrate predators (Figure 4.1g). In addition, I explored how the interpretations of these potential trophic relationships would change according to longitudinal position given stream order reach and site based perspectives.

Methods

Site selection

I sampled 20 sites along a 100 km section of the Middle Fork of the John Day River in eastern Oregon, during the summers of 1996-1998. This section ranges from 1st to 5th stream order and has no impoundments or dams, but has been influenced by grazing, timber harvest, and mining. All sites were 50-100 m in length and dominated by riffle and run habitats. Sampling occurred during low flow conditions (late July-early August) and some sites were sampled in multiple years; twelve sites were sampled in 1996, 10 sites were sampled in 1997, and 10 sites were sampled in 1998 (Table 4.1).

(a) **Scrapers**

↑

**Autochthonous
Production**

(b) **Shredder**

↑

**Allochthonous
Production**

(c)

Fishes

**Large Invertebrate
Predators**

**Small Invertebrate
Predators**

Scrapers   **Collectors**   **Filterers**   **Shredders**

**Autochthonous
Production**

**Allochthonous
Production**

(d) **Fishes**

↓

Scrapers

↓

**Algal
Biomass**

(e) **Scrapers**

↑

**Algal
Biomass**

↑

Solar Input

(f)

Shredders

↑

**Canopy Cover /
Riparian
Vegetation**

(g) **Fish**

↓

**Large Invertebrate
Predators**

↓

**Small Invertebrate
Predators**

Figure 4.1. Diagrams of conceptual lotic food chains and webs. Arrows are drawn to represent either top-down (↓) or bottom-up (↑) relationships. Chains (a) and (b) represent bottom-up trophic links proposed in the River Continuum Concept (Vannote et al. 1980). Web (c) is a simplified, top-down food web based on observations from the MFJD. Chains (d), (e), (f), and (g) are those trophic relationships examined in this study; (d) and (g) indicate top-down interactions, while (e) and (f) are bottom-up interactions.

Table 4.1. Stream order and year of sampling for the 20 study sites in the Middle Fork of the John Day River.

		Year Sampled		
Site	Stream Order	1996	1997	1998
1	1			X
2	1			X
3	2			X
4	2			X
5	2			X
6	3	X	X	X
7	3	X	X	
8	3	X		
9	3	X		
10	4	X		
11	4	X	X	X
12	4	X	X	X
13	4	X		
14	4		X	
15	4	X	X	X
16	4		X	
17	5	X	X	
18	5	X	X	
19	5		X	X
20	5	X		

Physical Habitat

I measured a suite of physical habitat variables at each site. Variables ranged from large-scale landscape features such as valley slope and stream order, to small-scale site-specific characteristics like depth and substrate type. A description of all variables and the methods used to measure them is in Chapter 3.

Fish and fish diets

Fishes were sampled using a backpack electro-fisher, two dip nets and a 5 mm mesh, 2 m wide block net (Chapter 3). Passes were made within a site until at least 15 of the two most common taxa were collected. All fish were counted and measured for total and fork length. Fishes were identified to species and also categorized according to thermal guilds (Hokanson 1977, Zaroban et al. 1998): (1) warm water fishes: redside shiners (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), and northern pike minnow (*Ptychocheilus oregonensis*); (2) cool water fishes: torrent sculpin (*Cottus rhotheus*), bridgelip and mountain suckers (*Catostomus columbianus* and *platyrhynchus*), Pacific lamprey (*Entosphenus tridentatus*), and longnose dace (*Rhinischthys cataractae*); and (3) cold water fishes: rainbow trout (*Oncorhynchus mykiss*) and chinook salmon (*Oncorhynchus tshawytscha*). Catch per unit effort was calculated by dividing the total number of each fish species by the summed length of passes made at each site.

Stomach contents were collected from anesthetized fish (except chinook salmon) by flushing the stomachs with water into standard coffee filter papers. Fish were released upon recovery from the anesthetic. Stomach contents were stored in 95% ethanol for later laboratory examination. Other fishes caught in the net and not used for diet analysis, were enumerated and immediately released after recovery in a separate holding bucket. Stomach contents were examined under a dissecting microscope (25 X) and individual items were identified to the lowest possible taxonomic level and then counted according to number of head capsules. I recorded numbers of individuals and point volume estimates (Hynes 1950) for all taxa groups in each stomach. Using proportions of macroinvertebrate availability and consumption, I

calculated electivities (Ivlev 1961) for all macroinvertebrate taxa and each functional feeding group found in the stomachs. Electivities at both site and stream order reach scales were determined for all fish species combined.

Macroinvertebrates

Benthic macroinvertebrate samples were taken at each site, using a (0.093 m^2) modified Surber sampler with a 250 μm mesh net. Six random sample locations within the sites were determined using a ten-sided die. Substrates were disturbed for 30 seconds to a depth of 10 cm where possible. Samples were sieved through a 250 μm screen and were preserved in 95% ethanol. Depth, habitat and substrate were also recorded with each sample. Each sample was counted individually using a 300 count subsampling method (Vinson & Hawkins 1996) in which rare, large individuals were counted separately and later added to the total count. Invertebrates were identified down to genus in the laboratory using a Zeiss dissecting microscope. Macroinvertebrates were categorized according to functional feeding groups based on Merritt & Cummins (1996).

Visual counts of large-bodied invertebrates were made using a 0.1 meter water scope (Li 1990). Five transects perpendicular to shore, extending the wetted channel width, were randomly chosen, using a random number generator computer, within each of the sites. Counts were made at 1 meter intervals along each transect, resulting in no less than 16 observation points per site.

Algae

Chlorophyll *a* biomass samples were collected by randomly selecting 18 rocks (approximately 10 cm in diameter) from each site. Algae was brushed and/or scraped off a 3 cm^2 area of each rock. The 18 scrapings were divided into sets of 3, and each set was individually stored in water within a light-sealed bottle and frozen for transportation. In the laboratory, chlorophyll *a* biomass was extracted by filtering the water from each bottle through glass fiber filters and then soaking the filters in 90%

buffered acetone in the laboratory. The acetone solution was analyzed by spectrophotometry (Strickland & Parsons 1968).

Algal primary production was measured using self-contained, circulating production chambers at each site. At each site, three rocks of approximately 5 cm diameter were placed in each of six chambers. Three chambers were run for one hour in direct sunlight while three chambers were simultaneously run in complete darkness (provided by an opaque plastic container). Water was collected from each chamber after every run and dissolved oxygen concentration was determined using an Orion oxygen meter. Water temperature within and outside the chambers also was recorded to correct for any warming effect the pumps may have had. Net primary production was calculated as the average amount of oxygen production from photosynthesis minus the average amount of oxygen consumption of respiration. To account for any differences in algal biomass among the sites, calculations of production per unit biomass were determined for each site using chlorophyll *a* biomass measurements from the rocks in each chamber. Surface area of the rocks was determined by wrapping the rocks in foil and trimming off any excess. The foils were then weighed, and a regression of foil weight to surface area was used to calculate the rock's surface area.

Riparian Vegetation

Canopy cover over the channel was used as a surrogate for the potential of allochthonous input, and was measured using a Solar Pathfinder (Platts et al. 1987) at 9 locations within each site. In addition, the species and length of influence were determined for all vegetation hanging over the wetted channel. Typically these species were large shrubs and trees.

Data Analysis

I examined patterns of community structures using non-metric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976) at the site scale. I also used NMS to determine the physical and biological variables most strongly correlated

with those patterns (Chapter 3). All sites and sample dates were considered independently in the ordination analysis. The five data matrices included: 1) a 32 site by 20 environmental variable matrix, 2) a 32 site by 10 taxa matrix containing relative abundance of fishes, 3) a 32 site by 109 taxa matrix containing mean macroinvertebrate taxa densities, 4) a 32 site by 6 group matrix containing mean macroinvertebrate functional feeding group densities, and 5) a 32 site by 6 variable matrix containing measurements of algal chlorophyll a biomass, gross and net rates of production and respiration, and primary production : respiration (P:R) ratios. Variables in the physical matrix were transformed by $\ln(x + 1)$. I calculated relative abundance of fishes in each site by dividing the total catch of each species by the total catch of all species. Mean site densities of macroinvertebrates (no./m^2) were calculated for each taxon by averaging densities from all 6 samples at each site; data were transformed by $\ln(x + 1)$. Mean values of algal biomass for each site were calculated by averaging measured biomass from the 6 primary production chambers. I determined mean rates of algal primary production (and respiration) at each site by averaging rates of oxygen production (and consumption) from the three chambers. Algal data were transformed by $\ln(x + 1)$. Each data matrix was analyzed separately using NMS in PC-ORD, version 3.2 (Chapter 3).

In Chapter 3, I compared the different community ordinations using cumulative variance explained (r^2), qualitative conformity with conceptual patterns, and correlation of ordination coordinates with variables in the physical habitat matrix. To make these direct comparisons among ordinations, I rotated each ordination to a common set of variables from the physical habitat matrix. For a given ordination, I identified the primary (1°), secondary (2°), and tertiary (3°) axes using incremental r^2 values determined by a correlation between ordination and original matrix distances. Each ordination was then rotated such that the 1° axis represented large-scale, longitudinal physical gradients and the 2° and 3° axes represented smaller scale, site-specific physical gradients (Chapter 3). After all ordinations were oriented according to the same physical habitat gradients, I calculated the Pearson correlation coefficients comparing the coordinate scores from each axis with the variables from the different

community matrices. This analysis compared gradients of a particular community with the distribution of organisms from a different community in the same environmental space (i.e. the longitudinal profile of the MFJD). Only those correlations with absolute values greater than 0.50 were identified in the results.

Biotic and abiotic relationships among sites and stream order reaches were determined graphically, by linear regression, and using multivariate ordination. To graphically examine broad, reach-scale patterns I defined 4 groups of sites based on 1st + 2nd, 3rd, 4th, and 5th order reaches. Sites in 1st and 2nd order reaches were lumped because of the limited number of sites within lower order reaches. For graphs and regressions at the site scale, I used data from each of the 20 individual sites; sites that were sampled in multiple years were averaged across all sample dates prior to analyses. All regressions were performed using StatGraphics version 3 statistical software.

Results

Fish

I collected a total of 10 different fish species in the MFJD. The number of fish species in any given site ranged from 1 to 8 along the longitudinal profile. The most abundant species among all sites were torrent sculpin, speckled dace and rainbow trout (Appendix 1, Chapter 3). The NMS ordination pattern of the fish community was described in Chapter 3 and contained aspects of a consistent longitudinal gradient, patchiness, and variable scatter (Chapter 3, Figure 3.6). Axis 1, representing the large-scale, longitudinal gradient, explained the majority of the variance in the data set (r^2 = 0.848), while axes 2 and 3 explained 10% and 4% of the variance respectively.

Biological variables that were most strongly correlated with axes coordinates of the fish ordination were those of individual macroinvertebrate taxa densities and canopy cover (Table 4.2). There were no strong correlations with any of the algal parameters or macroinvertebrate functional feeding group densities ($r < 0.5$). Percent

Table 4.2. Correlations between axes coordinates from the fish relative abundance NMS ordination and individual biological variables (percent canopy cover and macroinvertebrate taxa densities).

Axis 1	r	Axis 2	r	Axis 3	r
Canopy Cover	-0.680			Canopy Cover	-0.626
Micrasema	-0.869	*Paraleptophlebia*	0.577	Nemouridae	-0.679
Rhyacophila	-0.854	*Cordulegaster*	0.545	*Rhyacophila*	-0.662
Procloeon	-0.733	Hydrophilidae	0.541	*Micrasema*	-0.647
Peltoperlidae	-0.721	Ostracoda	0.538	*Peltoperla*	-0.549
Ameletus	-0.694	Aesniidae	0.533	*Ameletus*	-0.540
Malenka	-0.690	Coenagrionidae	0.533	*Haliplus*	-0.506
Haliplus	-0.683	*Procloeon*	0.517		
Zaitzevia	0.679	Sphaeriidae	0.513		
Polycentropus	-0.637	Dytiscidae	0.511		
Skwala	0.590				
Amphipods	-0.586				
Ostracods	-0.513				

canopy cover was strongly correlated with coordinates of both axes 1 and 3 (Table 4.2). Axis 1 coordinates were negatively correlated with macroinvertebrate densities of *Micrasema, Rhyacophila, Procloeon*, and Peltoperlidae (Table 4.2). Axis 2 coordinates were positively correlated with densities of *Paraleptophlebia, Cordulegaster*, and Hydrophillidae (Table 4.2), and axis 3 coordinates were most strongly negatively correlated with Nemouridae, *Rhyacophila*, and *Micrasema* (Table 4.2).

Diets of fishes in the MFJD were highly variable; all fish from 1997 and 1998 (n = 592) consumed 42 different invertebrate taxa. According to numbers of individuals found in the stomachs, the most abundant taxa groups were Baetid mayflies, Chironomid midges, Simulid larvae, Heptageniid mayflies, terrestrials, and Ephemerellid mayflies (Table 4.3). By volume, the most prevalent taxa groups in the stomachs were Baetid mayflies, Heptageniid mayflies, Perlid stoneflies, Hydropsychid caddisflies, terrestrials, and Ephemerellid mayflies (Table 4.3). Terrestrial invertebrates were the primary diet item (numbers and volume) for fishes in 1st and 2nd order reaches (Figure 4.2, Tables 4.4 & 4.5). In higher order sites, Baetid mayflies were much more common than other taxa found in fish stomachs (Table 4.4). The relative abundance and volume of Perlid stoneflies, Hydropsychid caddisflies, and Ephemerellid and Heptageniid mayflies in the stomachs were highest in 4th and 5th order sites (Tables 4.4 & 4.5). Terrestrials and Baetids were primary diet items of rainbow trout and redside shiners, whereas speckled dace and torrent sculpin commonly consumed Baetids, Chironomids, Ephemerellids, and Simulids (Table 4.6).

In this study, electivity indices > 0.5 indicated selection and those < 0.5 indicated avoidance by fishes. Fishes did not select for any functional feeding group within particular stream order reaches (Table 4.7); electivity indices for most functional feeding groups were negative. Collectors were the most abundant functional feeding group found in the stomachs of fishes in 3rd-5th order sites (Figure 4.2). At the site scale, electivities were less than 0.5 for all functional feeding groups at all sites. However, fish did appear to select for individual macroinvertebrate taxa within the stream order reaches (Table 4.8). The highest positive electivities were

Table 4.3. Stomach contents for all fish species at all sites according to individual numbers and point volume estimates (n =592).

Individual Numbers		Point Volume Estimates	
Taxa	%	Taxa	%
Baetidae sp.	28.43	Baetidae sp.	14.98
Chironomidae sp.	11.05	Heptageniidae sp.	10.96
Simulidae sp.	9.99	Perlidae sp.	8.98
Heptageniidae sp.	8.86	Hydropsychidae sp.	7.26
Terrestrial	6.58	Terrestrial	7.02
Ephemerellidae sp.	6.10	Ephemerellidae sp.	6.82
Hydropsychidae sp.	3.77	Annelids	5.52
Annelids	2.46	Chironomidae sp.	4.97
Trichorythodes	2.42	Fish	3.63
Misc. Inverts	2.25	Misc. Inverts	3.22
Perlidae sp.	1.86	Simulidae sp.	3.07
Perlodidae sp.	1.78	*Trichorythodes*	2.49
Adult Chironomidae	1.57	Perlodidae sp.	2.04
Antocha	1.30	Adult Trichoptera	2.01
Miscellaneous	1.24	Philopotomadae sp.	1.82
Physiidae sp.	1.05	Physiidae sp.	1.69
Philopotomadae sp.	1.03	*Glossosoma*	1.40
Glossosoma	0.85	*Antocha*	1.36
Diptera	0.83	Miscellaneous	1.21
Elmid sp.	0.77	Tipulidae sp.	0.89
Adult Trichoptera	0.66	Adult Chironomidae	0.85
Plecoptera	0.66	Elmid sp.	0.84
Fish sp.	0.54	Zygoptera sp.	0.66
Paraleptophlebia	0.43	Plecoptera	0.65
Ephemeroptera sp.	0.35	*Lepidostoma*	0.58
Planorbidae sp.	0.33	*Paraleptophlebia*	0.56
Tipulidae sp.	0.31	*Psychoglypha*	0.49
Zygoptera sp.	0.25	*Brachycentrus*	0.43
Corixidae sp.	0.25	*Dicosmoecus*	0.34
Mites	0.23	Planorbidae sp.	0.29
Brachycentrus	0.21	Diptera	0.27
Sialis	0.17	Dytiscidae sp.	0.26
Hydroptillidae sp.	0.17	Trichoptera	0.26
Trichoptera	0.15	Anisoptera sp.	0.24
Rhyacophila	0.14	Ephemeroptera sp.	0.24
Atherix	0.14	Hydroptillidae sp.	0.22
Dytiscidae sp.	0.14	Mites	0.19
Amphipods	0.12	*Sialis*	0.17
Psychoglypha	0.10	*Atherix*	0.15
Anisoptera sp.	0.08	Corixidae sp.	0.15
Dicosmoecus	0.08	Hemiptera	0.14
Juga	0.06	*Petrophila*	0.14
Petrophila	0.06	*Juga*	0.14
Lepidostoma	0.04	*Rhyacophila*	0.12
Gomphidae sp.	0.02	Gomphidae sp.	0.07
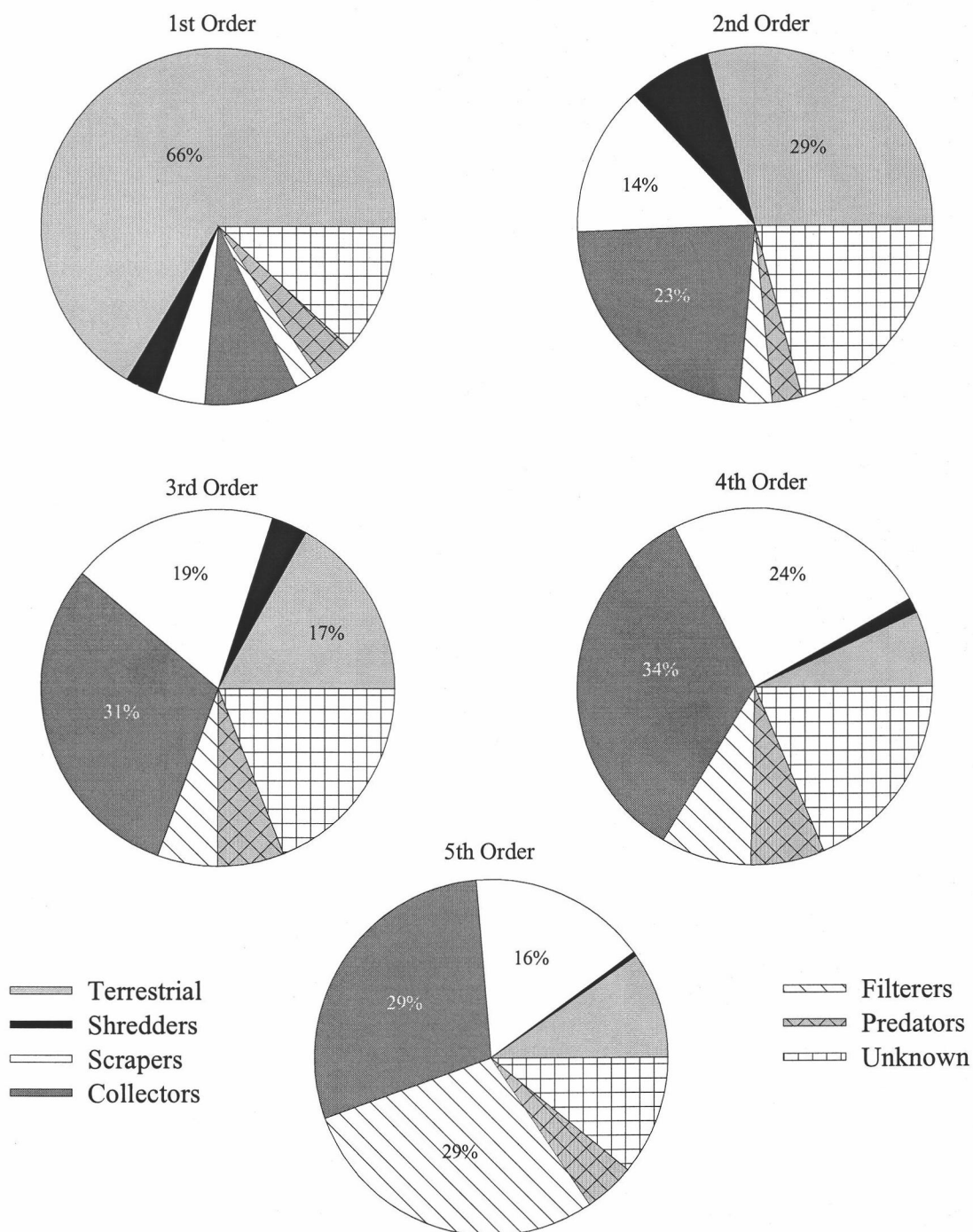
Figure 4.2. Proportions of aquatic macroinvertebrate functional feeding groups and terrestrial invertebrates found in the stomachs of all fishes collected within each stream order segment of the MFJD (*n* = 12, 46, 107, 262, and 161 respectively).

Table 4.4. Number of individual diet items found in the stomachs of all fish collected at sites in 1st, 2nd, 3rd, 4th, and 5th order reaches in the Middle Fork of the John Day River (n = 12, 46, 107, 262, and 161 respectively)

1st Order		2nd Order		3rd Order		4th Order		5th Order	
Taxa	**No.**	**Taxa**	**No.**	**Taxa**	**No.**	**Taxa**	**No.**	**Taxa**	**No.**
Terrestrial	82	Terrestrial	80	Baetidae sp.	373	Baetidae sp.	818	*Simulium*	372
Adult Midges	45	Chironomidae sp.	78	Terrestrial	108	Heptageniidae sp.	335	Baetidae sp.	190
Chironomidae sp.	24	Baetidae sp.	71	Chironomidae sp.	101	Chironomidae sp.	285	Ephemerellidae sp.	114
Baetidae sp.	17	Misc. Inverts	38	*Trichorythodes*	92	Ephemerellidae sp.	156	Heptageniidae sp.	102
Paraleptophlebia	8	Ephemerellidae sp.	28	*Simulium*	80	Hydropsychidae sp.	133	Chironomidae sp.	83
Rhyacophila	5	Elmidae sp.	19	Physiidae sp.	36	Annelids	104	Hydropsychidae sp.	58
Simulium	3	Planorbidae sp.	16	Misc.	30	Perlidae sp.	75	Misc. Inverts	37
Dytiscidae sp.	2	Physiidae sp.	13	Misc. Inverts	20	Perlodidae sp.	57	*Glossosoma*	27
Lepidostoma	2	Heptageniidae sp.	13	Annelids	19	*Simulium*	54	Perlodidae sp.	27
Psychoglypha	2	*Paraleptophlebia*	8	Ephemeroptera sp.	18	Terrestrial	46	Terrestrial	24
Heptageniidae sp.	2	*Simulium*	7	Ephemerellidae sp.	17	*Antocha*	43	Perlidae sp.	20
Nemouridae sp.	2	Mites	5	Corixidae sp.	11	Philopotomadae sp.	43	Antocha	18
Dixa	1	Trichoptera	4	Fish	11	Diptera	43	Adult Caddis	15
Trichoptera	1	Hydropsychidae sp.	4	Zygoptera sp.	10	Adult Midges	29	Tipulidae sp.	13
Mites	1	Psychoglypha	3	*Sialis*	8	Plecoptera	23	*Trichorythodes*	12
Hemiptera	1	Plecoptera	3	Elmidae sp.	7	Misc. Inverts	21	Misc.	12
Brachycentrus	1	Annelids	3	Perlodidae sp.	7	Misc.	21	Philopotomadae sp.	10
		Fish	2	Adult Midges	7	*Trichorythodes*	21	Elmidae sp.	9
		Rhyacophila	2	Amphipods	6	Adult Caddis	19	Plecoptera	8
		Corixidae sp.	2	Heptageniidae sp.	6	*Glossosoma*	14	*Brachycentrus*	7
		Dicosmoecus	2	Paraleptophlebia	5	Fish	12	Fish	3
		Antocha	2	Hydroptillidae sp.	5	Mites	6	Trichoptera	2

Table 4.4. (cont.)

1st Order		2nd Order		3rd Order		4th Order		5th Order	
Taxa	No.	Taxa	No.	Taxa	No.	Taxa	No.	Taxa	No.
		Misc.	1	*Atherix*	4	Dytiscidae sp.	5	Annelids	1
		Perlodidae sp.	1	*Antocha*	4	Physiidae sp.	5	Paraleptophlebia	1
		Perlidae sp.	1	*Juga*	3	Elmidae sp.	5	Hydroptillidae sp.	1
		Ameletus	1	*Glossosoma*	3	Zygoptera sp.	3	*Atherix*	1
		Brachycentrus	1	Anisoptera sp.	3	Tipulidae sp.	3		
				Tabanidae sp.	2	Hydroptillidae sp.	3		
				Trichoptera	1	*Petrophila*	3		
				Gomphidae sp.	1	*Atherix*	2		
				Odonata	1	*Dicosmoecus*	2		
				Brachycentrus	1	Planorbidae sp.	1		
						Brachycentrus	1		
						Anisoptera sp.	1		
						Sialis	1		

Table 4.5. Total point volume estimates of individual diet items found in the stomachs of all fish collected at sites in 1st, 2nd, 3rd, 4th, and 5th order reaches in the Middle Fork of the John Day River (n = 12, 46, 107, 262, and 161 respectively)

1st Order Taxa	Pts.	2nd Order Taxa	Pts.	3rd Order Taxa	Pts.	4th Order Taxa	Pts.	5th Order Taxa	Pts.
Terrestrial	104	Terrestrial	112	Baetidae sp.	183	Baetidae sp.	450	Heptageniidae sp.	195
Lepidostoma	34	Baetidae sp.	67	Annelids	92	Heptageniidae sp.	408	Baetidae sp.	167
Adult Midges	24	Ephemerellidae sp.	52	*Trichorythodes*	88	Perlidae sp.	408	Ephemerellidae sp.	167
Psychoglypha	16	Misc. Inverts	49	Physiidae sp.	61	Hydropsychidae sp.	279	Hydropsychidae sp.	142
Baetidae sp.	12	Chironomidae sp.	43	Terrestrial	56	Annelids	225	Perlidae sp.	118
Hemiptera	8	Fish	32	Chironomidae sp.	49	Ephemerellidae sp.	160	*Simulium*	97
Chironomidae sp.	7	Elmid sp.	27	Fish	45	Chironomidae sp.	137	Misc. Inverts	67
Paraleptophlebia	7	Heptageniidae sp.	22	Misc. Inverts	45	Fish	110	Adult Caddis	64
Rhyacophila	5	Physiidae sp.	21	*Simulium*	43	Terrestrial	90	Chironomidae sp.	55
Simulium	4	Planorbidae sp.	16	Zygoptera sp.	29	Philopotomadae sp.	89	Terrestrial	50
Nemouridae sp.	3	*Paraleptophlebia*	14	Misc.	21	Perlodidae sp.	68	*Glossosoma*	46
Dytiscidae sp.	3	*Psychoglypha*	13	Ephemerellidae sp.	21	Adult Caddis	54	Tipulidae sp.	40
Dixa	1	*Dicosmoecus*	12	Heptageniidae sp.	17	*Antocha*	47	Perlodidae sp.	38
Heptageniidae sp.	1	Trichoptera	6	Ephemeroptera sp.	14	*Trichorythodes*	37	*Antocha*	28
Mites	1	Hydropsychidae sp.	5	Anisoptera sp.	12	*Simulium*	31	Fish	26
Brachycentrus	1	*Simulium*	5	Perlodidae sp.	12	*Glossosoma*	29	Misc.	23
Trichoptera	1	Annelids	5	*Paraleptophlebia*	10	Misc. Inverts	28	*Trichorythodes*	21
		Mites	5	*Sialis*	8	Plecoptera	26	*Brachycentrus*	19
		Misc.	4	*Juga*	8	Misc.	23	Philopotomadae sp.	18
		Antocha	3	*Glossosoma*	7	Adult Midges	22	Plecoptera	9
		Plecoptera	3	Elmid sp.	7	Physiidae sp.	17	Elmid sp.	8
		Perlodidae sp.	2	Corixidae sp.	7	Diptera	16	Trichoptera	6

Table 4.5. (cont.)

1st Order		2nd Order		3rd Order		4th Order		5th Order	
Taxa	Pts.	Taxa	Pts.	Taxa	Pts.	Taxa	Pts.	Taxa	Pts.
		Corixidae sp.	2	Hydroptillidae sp.	7	Dytiscidae sp.	12	Annelids	2
		Rhyacophila	2	*Atherix*	6	Tipulidae sp.	12	*Paraleptophlebia*	2
		Ameletus	1	Adult Midges	4	Zygoptera sp.	10	Hydroptillidae sp.	1
		Brachycentrus	1	Odonata	4	*Petrophila*	8	*Atherix*	1
		Perlidae sp.	1	Gomphidae sp.	4	*Dicosmoecus*	8		
				Amphipods	3	Elmid sp.	7		
				Brachycentrus	2	Hydroptillidae sp.	5		
				Tabanidae sp.	2	Mites	5		
				Antocha	2	*Atherix*	2		
				Trichoptera	2	Anisoptera sp.	2		
						Sialis	2		
						Brachycentrus	2		
						Planorbidae sp.	1		

Table 4.6. Proportions of the 10 most common macroinvertebrate taxa found in the stomachs of rainbow trout (*Oncorhynchus mykiss*), redside shiners (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), and torrent sculpin (*Cottus rhotheus)* in 1st-5th order reaches of the MFJD.

Rainbow Trout

1st Order		2nd Order		3rd Order		4th Order		5th Order	
Terrestrial	41.2	Baetidae sp.	23.2	Baetidae sp.	38.4	Baetidae sp.	17.2	Hydropsychidae sp.	23.2
Adult Midges	22.6	Terrestrial	21.5	Terrestrial	18.9	Annelids	15.6	Heptageniidae sp.	21.4
Chironomidae sp.	12.1	Chironomidae sp.	12.4	*Trichorythodes*	15.1	Heptageniidae sp.	12.4	Terrestrial	10.7
Baetidae sp.	8.5	Ephemerellidae sp.	7.7	Chironomidae sp.	4.6	Chironomidae sp.	10.2	Philopotomadae sp.	8.9
Paraleptophlebia	4.0	Misc. Inverts	7.3	*Simulium*	4.6	Adult Midges	9.2	Adult Caddis	8.9
Rhyacophila	2.5	Heptageniidae sp.	5.2	Physiidae sp.	4.1	Hydropsychidae sp.	8.6	Ephemerellidae sp.	7.1
Simulium	1.5	Physiidae sp.	4.7	Corixidae sp.	3.0	Terrestrial	7.0	*Antocha*	3.6
Lepidostoma	1.0	Planorbidae sp.	2.1	Misc.	2.7	Ephemerellidae sp.	3.8	*Simulium*	3.6
Nemouridae sp.	1.0	Mites	1.7	Adult Midges	1.9	Perlidae sp.	3.8	Baetidae sp.	1.8
Heptageniidae sp.	1.0	*Simulium*	1.7	Perlodidae sp.	1.4	Philopotomadae sp.	2.5	*Glossosoma*	1.8

Redside Shiners

1st Order	2nd Order		3rd Order		4th Order		5th Order	
	Terrestrial	36.6	Terrestrial	30.1	Annelids	31.7	Baetidae sp.	19.8
	Elmidae sp.	25.4	*Trichorythodes*	14.6	Heptageniidae sp.	26.8	Heptageniidae sp.	19.1
	Chironomidae sp.	15.5	Ephemeroptera sp.	10.7	Hydropsychidae sp.	14.6	*Glossosoma*	11.1
	Misc. Inverts	7.0	Baetidae sp.	8.7	Philopotomadae sp.	9.8	Tipulidae sp.	6.8
(No fish)	Baetidae sp.	4.2	Annelids	8.7	*Glossosoma*	7.3	Chironomidae sp.	6.2
	Simulium	2.8	Misc. Inverts	7.8	Terrestrial	2.4	Terrestrial	5.6
	Paraleptophlebia	2.8	Ephemerellidae sp.	4.9	Baetidae sp.	2.4	Elmidae sp.	4.9
	Antocha	1.4	Chironomidae sp.	3.9	Adult Caddis	2.4	*Antocha*	4.3
	Brachycentrus	1.4	Elmidae sp.	2.9	Misc. Inverts	2.4	Ephemerellidae sp.	4.3
	Psychoglypha	1.4	Physiidae sp.	2.9			Perlodidae sp.	3.7

Table 4.6. (cont.)

Speckled Dace

1st Order	2nd Order		3rd Order		4th Order		5th Order	
	Chironomidae sp.	36.5	Baetidae sp.	26.8	Chironomidae sp.	38.3	Chironomidae sp.	18.9
	Misc. Inverts	15.4	Chironomidae sp.	22.3	Annelids	11.4	Misc. Inverts	18.1
	Baetidae sp.	13.5	*Simulium*	20.8	Baetidae sp.	9.6	*Simulium*	11.8
	Planorbidae sp.	10.6	Physiidae sp.	6.0	*Simulium*	6.8	Baetidae sp.	9.4
No Fish	Ephemerellidae sp.	9.6	Annelids	3.8	Misc. Inverts	5.6	Hydropsychidae sp.	7.9
	Terrestrial	3.8	Fish	3.4	Misc.	5.2	Terrestrial	6.3
	Trichoptera sp.	1.9	Misc.	3.4	Heptageniidae sp.	4.6	Ephemerellidae sp.	5.5
	Paraleptophlebia	1.9	Ephemeroptera sp.	2.6	Philopotomadae sp.	3.4	Heptageniidae sp.	3.9
	Physiidae sp.	1.9	*Trichorythodes*	2.3	Hydropsychidae sp.	3.1	Misc.	3.1
	Misc.	1.0	Misc. Inverts	1.9	*Antocha*	2.2	*Antocha*	3.1

Torrent Sculpin

1st Order	2nd Order	3rd Order		4th Order		5th Order	
		Baetidae sp.	59.4	Baetidae sp.	43.5	Baetidae sp.	28.9
		Chironomidae sp.	6.4	Heptageniidae sp.	15.5	Ephemerellidae sp.	24.0
		Trichorythodes	6.0	Ephemerellidae sp.	9.3	Heptageniidae sp.	12.9
		Sialis	3.2	Chironomidae sp.	7.3	Chironomidae sp.	8.0
No Fish	No Fish	Ephemerellidae sp.	3.2	Hydropsychidae sp.	6.0	Hydropsychidae sp.	5.4
		Misc. Inverts	2.8	Perlidae sp.	4.4	Perlodidae sp.	4.4
		Simulium	2.8	Perlodidae sp.	3.7	Perlidae sp.	3.1
		Amphipods	2.4	*Antocha*	2.1	*Trichorythodes*	3.1
		Misc.	2.4	Plecoptera sp.	1.5	Adult Caddis	2.6
		Terrestrial	2.0	*Trichorythodes*	1.2	*Antocha*	1.3

Table 4.7. Electivity indices (Ivlev 1961) of macroinvertebrate functional feeding groups based upon all fish stomach contents at sites in each stream order of the Middle Fork of the John Day River (n = 12, 46, 107, 262, and 161 respectively).

	1st Order	2nd Order	3rd Order	4th Order	5th Order
Unknown	-0.58	-0.32	-0.30	-0.16	-0.42
Collectors	-0.55	0.03	0.06	0.08	-0.01
Filterers	-0.30	0.45	0.55	0.14	0.10
Predators	-0.42	-0.53	-0.05	-0.11	-0.38
Scrapers	-0.51	-0.08	-0.24	-0.01	-0.12
Shredders	-0.48	-0.35	0.10	-0.85	-0.84

Table 4.8. Five highest fish electivity indices (Ivlev 1961) for macroinvertebrates based upon all fish stomach contents at sites in each stream order of the Middle Fork of the John Day River (n = 12, 46, 107, 262, and 161 respectively).

1st Order	Electivity	2nd Order	Electivity
Rhyacophila	0.54	*Dicosmoecus*	0.63
Brachycentridae sp.	0.50	Ephemerellidae sp.	0.46
Hemiptera sp.	0.50	*Psychoglypha*	0.43
Dixa	0.50	Brachycentrid sp	0.33
Dytiscidae sp.	0.50	Hydropsychidae sp.	0.25

3rd Order	Electivity	4th Order	Electivity
Annelids	0.97	Annelids	0.57
Ephemerellidae sp.	0.90	Heptageniidae sp.	0.54
Anisoptera sp.	0.67	Perlidae sp.	0.53
Trichorythodes	0.63	*Trichorythodes*	0.43
Simulium	0.62	Baetidae sp.	0.38

5th Order	Electivity
Trichorythodes	0.75
Heptageniidae sp.	0.58
Baetidae sp.	0.35
Hydropsychidae sp.	0.31
Perlidae sp.	0.28

found in 3rd order sites where fish preferred annelid earthworms and Ephemerellid mayflies. Electivities in general were lower in 1st and 2nd order reaches than in higher order sections of the MFJD (Table 4.8).

Macroinvertebrate Taxa

In the MFJD, macroinvertebrate taxa richness ranged from 38 to 62 individual taxa per site, EPT taxa richness ranged from 13 to 37 taxa per site, and percent dominance ranged from 9% to 27% per site. The most common taxa throughout the MFJD were Chironomid midges, mayflies, and Elmid beetles (Table 4.9, Appendix 2). The NMS ordination pattern of macroinvertebrate taxa contained aspects of all three of the conceptual models: a longitudinal gradient, some patchiness and high variability (Chapter 3, Figure 3.8). Axis 1, representing the large-scale, longitudinal gradient, explained the majority of the variance in the data set (r^2 = 0.608), while axes 2 and 3 explained 16% and 15% of the variance respectively.

Biological variables that were most strongly correlated with axes coordinates of the macroinvertebrate density ordination were those of fish species abundance (Table 4.9). Axis 1 coordinates were strongly correlated with abundance of torrent sculpin (+), rainbow trout (-), and longnose dace (+). Axis 3 coordinates were highly correlated with abundance of juvenile chinook salmon (+); axis 2 coordinates were not strongly correlated with fish data. In addition, axis 1 coordinates of the macroinvertebrate density ordination were negatively correlated with percent canopy cover and densities of the invertebrate predator functional feeding group (Table 4.10). There were no strong correlations (r > 0.5) with any of the algal parameters.

Functional Feeding Groups

The highest percentage of shredders was found in 1st + 2nd and 4th order sites and the highest percentage of scrapers was in 3rd and 4th order sites (Chapter 3, Figure 3.10). Collectors were the most dominant functional feeding group among all site groups and were highest in 3rd order sites (Chapter 3, Figure 3.10). NMS ordination of functional feeding group data was highly variable, with no evidence of a longitudinal

Table 4.9. Mean densities (± 1SE) of the twenty five most abundant taxa in 1st, 2nd, 3rd, 4th, and 5th order sites in the Middle Fork of the John Day River during summer low flow conditions, 1996-98. The number of samples taken in each stream order equals 12, 18, 42, 78, and 42 respectively.

1st Order	No./m^2	±1SE	2nd Order	No./m^2	±1SE	3rd Order	No./m^2	±1SE
Ostracods	1141	841	Orthocladinae sp.	1032	538	Orthocladinae sp.	1100	857
Chironominae sp.	975	670	Chironominae sp.	665	613	Chironominae sp.	1083	750
Orthocladinae sp.	935	330	Oligochaeta	581	603	Baetidae sp.	885	504
Ephemeroptera	858	326	Baetidae sp.	576	157	Elmidae sp.	696	341
Baetidae sp.	565	23	Ostracods	552	722	Tanypodinae sp.	572	776
Mites	463	75	Tanypodinae sp.	442	86	*Juga*	523	528
Micrasema	337	13	Sphaeriidae sp.	379	268	Oligochaeta	463	252
Tanypodinae sp.	287	27	Mites	300	178	*Optioservus*	457	259
Nemouridae sp.	285	113	Planorbidae sp.	280	396	*Diphetor*	410	382
Paraleptophlebia	273	230	Elmidae sp.	277	257	Mites	334	325
Simulium	239	111	*Diphetor*	257	227	*Labiobaetis*	293	151
Ephemerellidae sp.	227	46	*Optioservus*	216	147	*Hydroptilla*	276	395
Malenka	152	152	Ephemeroptera	216	47	Physidae sp.	226	285
Elmidae sp.	149	117	*Paraleptophlebia*	208	180	Tanytarsini sp.	213	338
Tanytarsini sp.	126	38	Nemouridae sp.	164	117	*Simulium*	191	181
Sphaeriidae sp.	115	16	*Micrasema*	161	160	Amphipods	177	173
Diphetor	113	54	Amphipods	116	114	Ephemeroptera	175	162
Oligochaeta	103	24	Corixidae sp.	95	134	*Trichorythodes*	167	81
Labiobaetis	92	74	*Labiobaetis*	90	18	Ostracods	158	170
Amphipods	91	30	*Lepidostoma*	87	19	*Zaitzevia*	136	119
Chironomidae sp.	82	6	*Zaitzevia*	59	74	*Paraleptophlebia*	104	81
Heptageniidae sp.	65	14	Physidae sp.	57	59	Sphaeriidae sp.	98	134
Yoraperla	63	63	Heptageniidae sp.	51	31	*Atherix*	91	117
Optioservus	56	50	*Malenka*	50	19	*Heter/Optio*	48	24

Table 4.9. (cont.)

4th Order	No./m^2	±1SE	5th Order	No./m^2	±1SE
Orthocladinae sp.	832	465	Chironominae sp.	534	636
Oligochaeta	669	984	Orthocladinae sp.	487	300
Elmidae sp.	609	682	*Zaitzevia*	402	251
Lepidostoma	577	599	Elmidae sp.	395	162
Optioservus	500	217	*Optioservus*	272	196
Baetidae sp.	449	257	*Hydropsyche*	236	212
Zaitzevia	395	232	Baetidae sp.	227	108
Diphetor	357	291	Oligochaeta	221	236
Hydropsyche	266	593	Mites	209	168
Mites	211	263	*Brachycentrus*	206	344
Chironominae sp.	202	147	*Lepidostoma*	159	112
Labiobaetis	188	121	Ephemeroptera	141	112
Tanypodinae sp.	165	76	*Diphetor*	115	31
Hydropsychidae sp.	164	214	*Labiobaetis*	114	39
Ephemeroptera	144	154	Ephemerellidae sp.	113	126
Ephemerellidae sp.	131	142	Tanypodinae sp.	80	52
Wormaldia	128	188	Heptageniidae sp.	68	38
Antocha	120	105	*Simulium*	63	94
Glossosoma	110	63	*Heter/Optio*	61	32
Heter/Optio	107	87	Hydropsychidae sp.	57	57
Epeorus	85	50	Perlodidae sp.	56	56
Planorbidae sp.	84	132	*Ephemerella*	55	62
Atherix	82	90	*Acentrella*	54	47
Tanytarsini sp.	82	96	*Antocha*	50	45

Table 4.10. Correlation between axes coordinates from the macroinvertebrate density NMS ordination and individual biological variables (percent canopy cover, fish species abundance, and macroinvertebrate functional feeding group densities).

Axis 1	r	Axis 2	r	Axis 3	r
Canopy Cover	-0.581				
Torrent Sculpin	0.767	Chinook Salmon	0.583		
Rainbow Trout	-0.651				
Longnose Dace	0.636				
Predators	-0.611			Collectors	-0.583
Unknown	-0.559				

gradient (Chapter 3, Figure 3.11). Axis 1 explained the majority of the variance in the data set ($r^2 = 0.606$), while axes 2 and 3 explained 21% and 15% of the variance respectively. There were no strong correlations between the axes coordinates of this ordination and any of the biological variables considered in this study.

Algal Biomass and Production

Chlorophyll *a* biomass was highly variable among sites in the MFJD with values ranging from 2.4 to 176.3 mg/m^2. Gross primary production (GPP) also was highly variable among sites however, average rates of GPP did increase from low order site groups to higher order groups. Sites in 4th order reaches had the highest mean rates of GPP followed by 5th order, 3rd order, and finally 1st and 2nd order sites (Table 4.11). NMS ordination of algal biomass and production data resulted in a low cumulative r^2 value of 0.009 (Chapter 3). Axis 1, representing the large-scale, longitudinal gradient, explained the majority of the variance in the data set ($r^2 = 0.009$), while axes 2 and 3 explained less than 1% of the variance combined. The ordination pattern for the algal data was highly variable with little evidence of either a longitudinal gradient or discrete patches (Chapter 3, Figure 3.14). Due to the extremely low r^2 value of the ordination, examination of any correlations with the axes coordinates were inappropriate.

Trophic Relationships

Regressions of potential trophic interactions were grouped according to top-down or bottom-up processes (Table 4.12). Regression analysis indicated that the trophic relationships depicted in Figures 1d-g were neither consistent nor significant among all sites (Table 4.12). The significant relationship between densities of large and small invertebrate predators was positive rather than negative. There also was no consistent evidence of the proposed trophic relationships based on trends for stream order reaches (Figures 4.3-4.7). However, graphs of the different food chains did reveal both inverse and positive relationships among trophic levels at certain individual sites.

Table 4.11. Mean estimates (± 1 SE) of algal chlorophyll *a* biomass, primary production, and respiration according to stream order site groups in the MFJD.

Algal Parameter	Site Groups			
	1st & 2nd	3rd	4th	5th
Chlorophyll *a* Biomass (mg/m^2)	35.99	38.07	39.64	32.09
(± 1 SE)	(22.81)	(59.49)	(23.57)	(19.30)
Gross Primary Production (mg DO/l/hr)	49.20	58.43	147.05	108.12
(± 1 SE)	(41.24)	(49.88)	(76.32)	(31.48)
Gross Respiration (mg DO/l/hr)	-24.70	-59.99	-33.69	-46.04
(± 1 SE)	(21.52)	(27.52)	(53.06)	(22.97)
Gross Production per Algal Biomass (mg DO/l/hr)/(mg/m^2)	0.05	4.47	5.11	6.50
(± 1 SE)	(0.03)	(4.28)	(4.24)	(4.27)
Gross Respiration per Algal Biomass (mg DO/l/hr)/(mg/m^2)	-0.02	-16.77	-2.26	-1.98
(± 1 SE)	(0.03)	(20.66)	(2.04)	(1.30)

Table 4.12. Results of the regressions relating the site-specific abundance of the individual components for the potential top-down and bottom-up trophic interactions shown in Figure 1d-g. Regressions compared the mean values of the x and y components for each of the 20 sites along the Middle Fork of the John Day River.

x	y	p-value	Slope	R^2	df
Top-Down					
Fish Predators	Invertebrate Scrapers	0.91	N/A	0.07	19
Fish Predators	Large Invertebrate Predators	0.99	N/A	0.00	19
Fish Predators	Small Invertebrate Predators	0.71	N/A	0.80	19
Large Invertebrate Predators	Small Invertebrate Predators	0.005	+	36.47	19
Invertebrate Scrapers	Algal Biomass	0.71	N/A	0.80	19
Invertebrate Scrapers	Algal Production	0.22	N/A	8.30	19
Bottom-Up					
Algal Biomass	Invertebrate Scrapers	0.71	N/A	0.80	19
Canopy Cover	Invertebrate Shredders	0.23	N/A	7.80	19
Canopy Cover	Algal Biomass	0.38	N/A	4.20	19
Canopy Cover	Algal Production	0.40	N/A	3.90	19
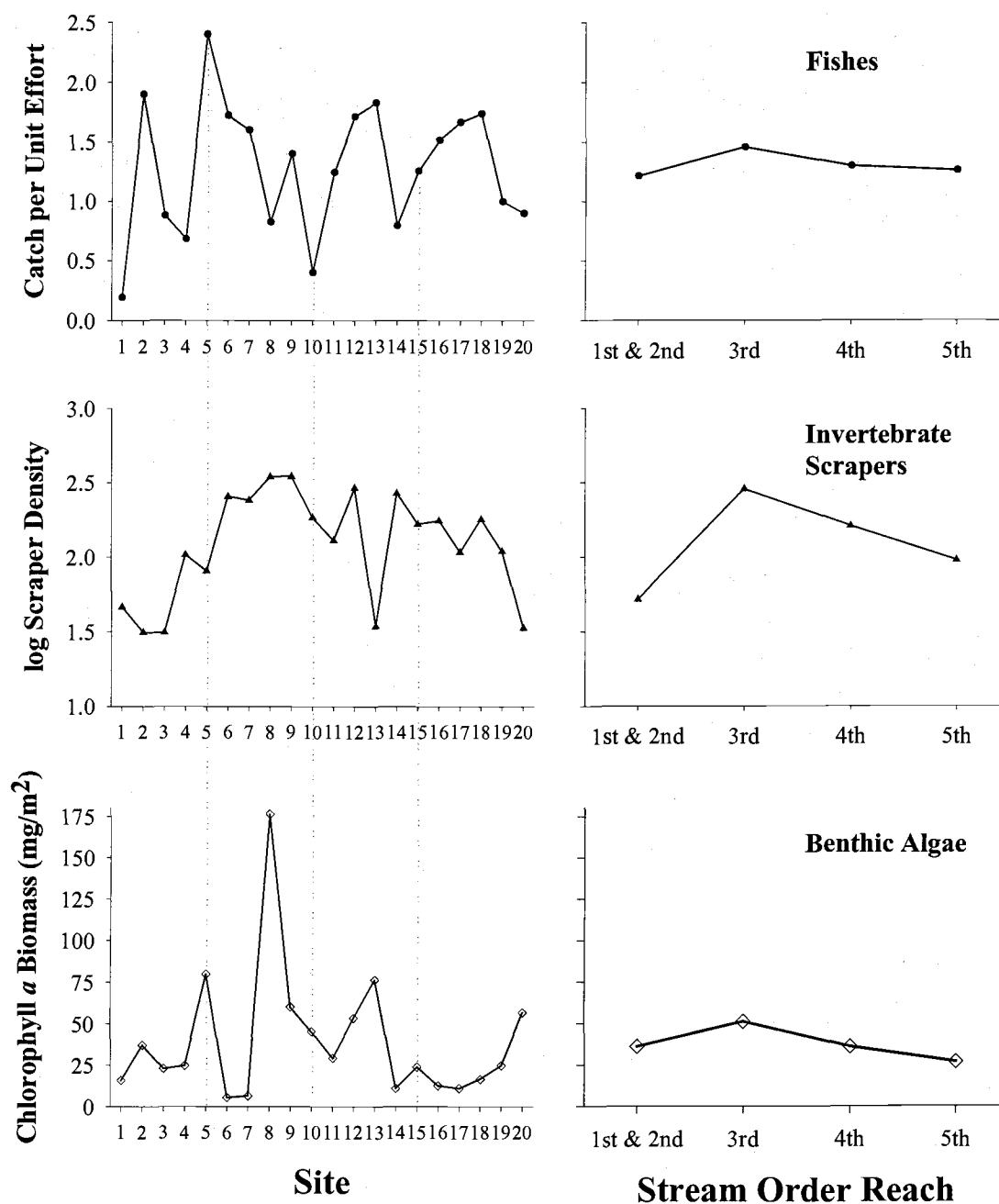
Figure 4.3. Site and reach scale trends in the mean values of fish caught per unit effort, densities of macroinvertebrate scrapers, and chlorophyll *a* biomass in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).
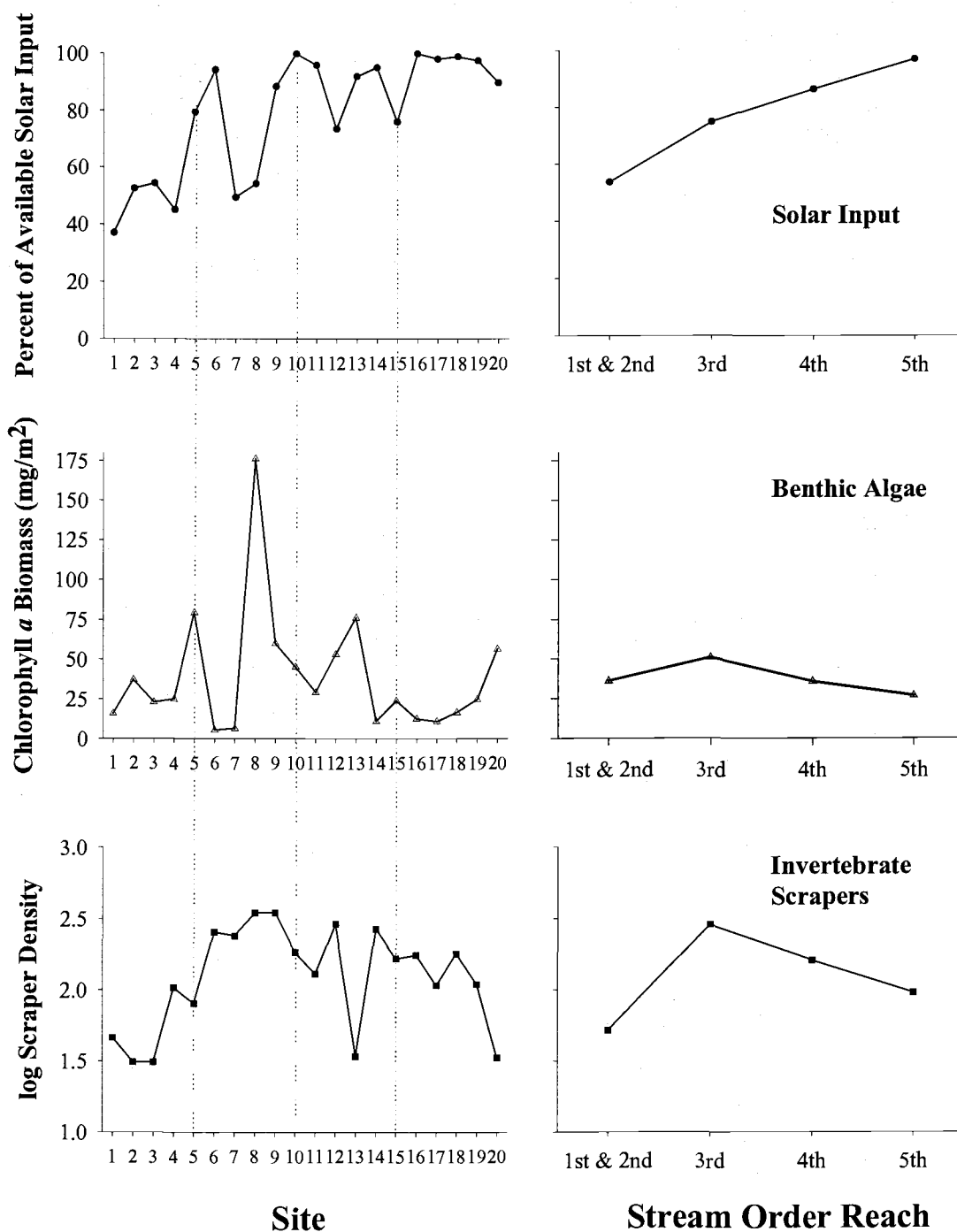
Figure 4.4. Site and reach scale trends in the mean values of available solar input, chlorophyll *a* biomass, and densities of macroinvertebrate scrapers in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).
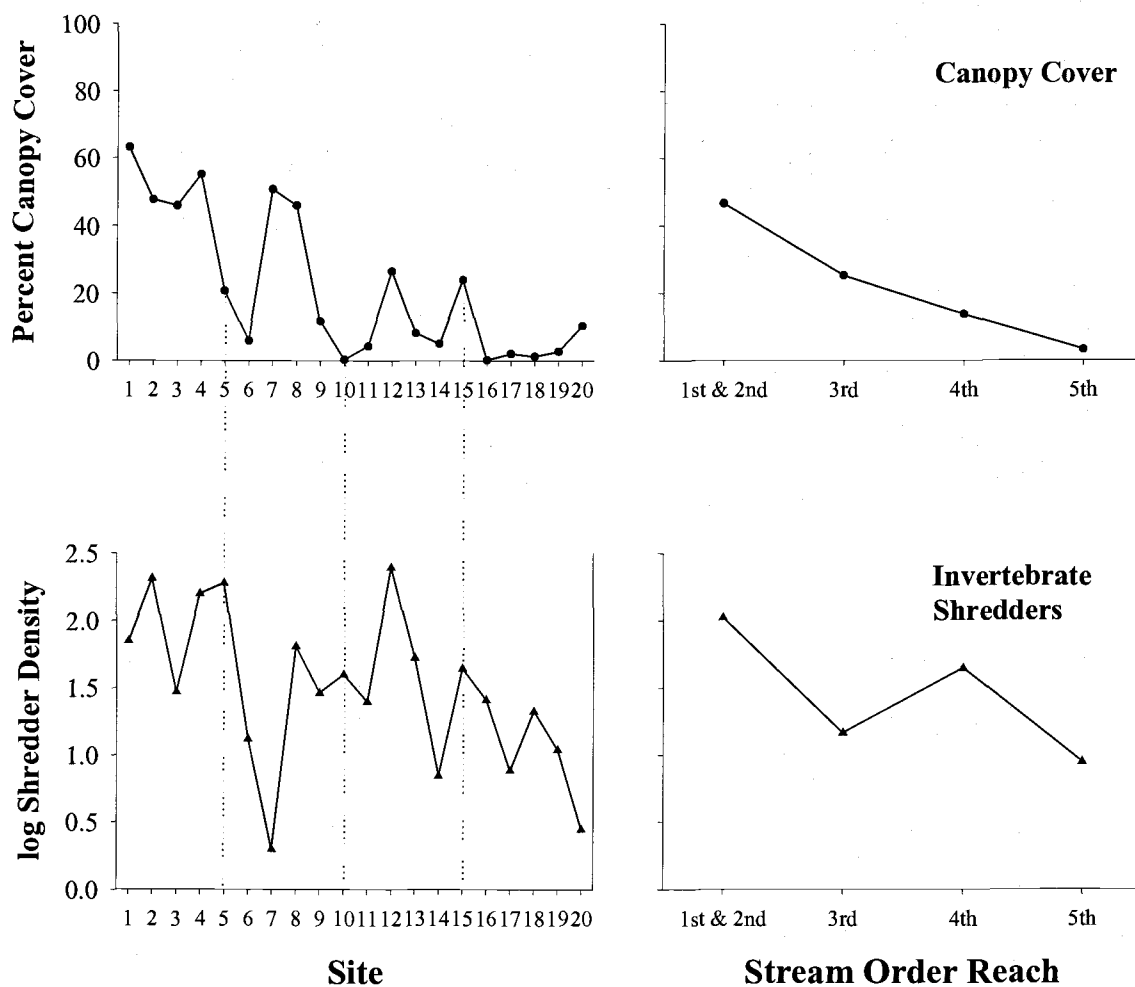
Figure 4.5. Site and reach scale trends in the mean values of riparian canopy cover and densities of macroinvertebrate shredders in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).
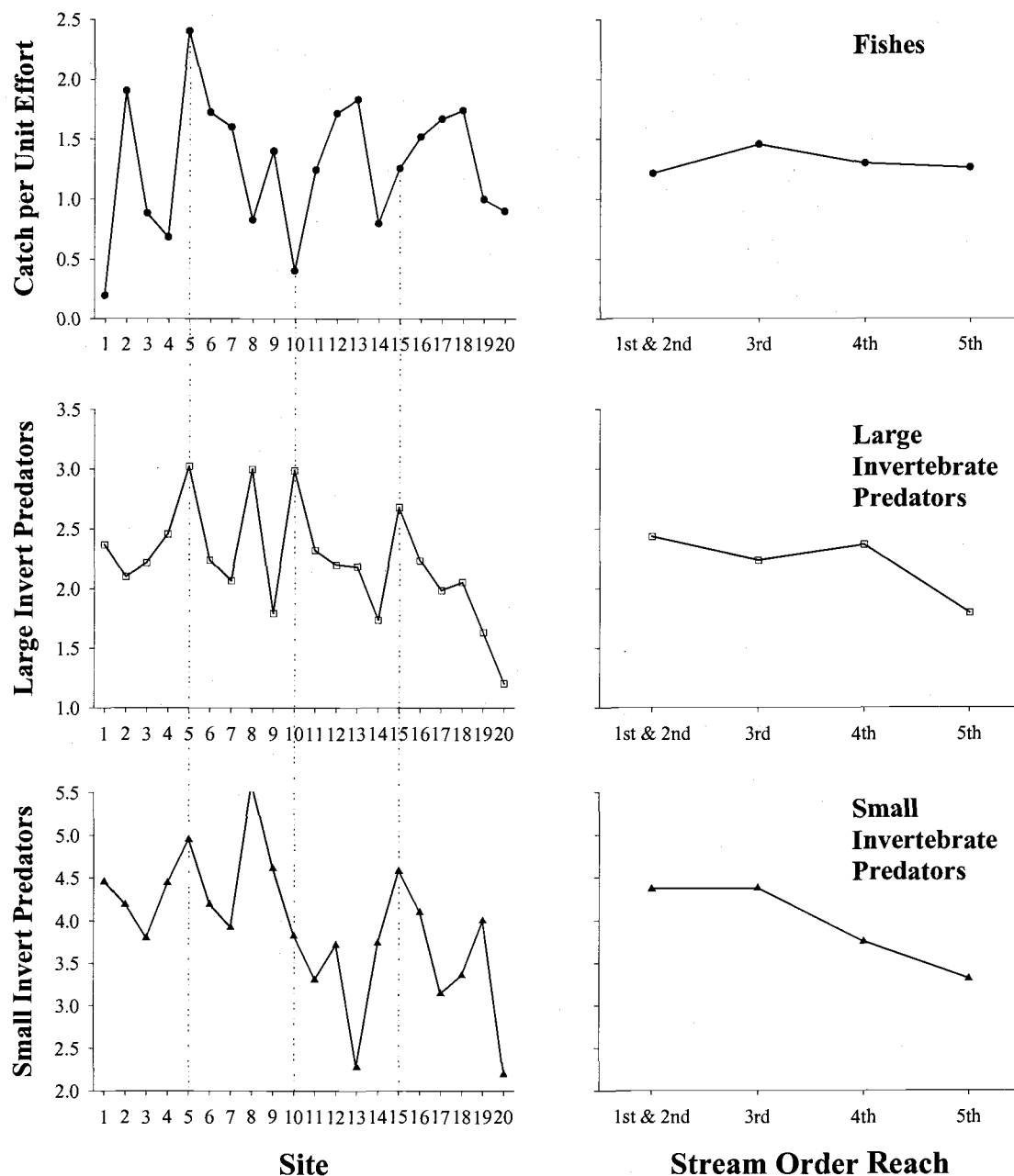
Figure 4.6. Site and reach scale trends in the mean values of fish caught per unit effort and densities of large (e.g. Perlid stoneflies and Odonates) and small (e.g. Tanypodinae midges) macroinvertebrate predators in the Middle Fork of the John Day River. Figures represent a 100km longitudinal gradient from headwaters down stream (left to right).
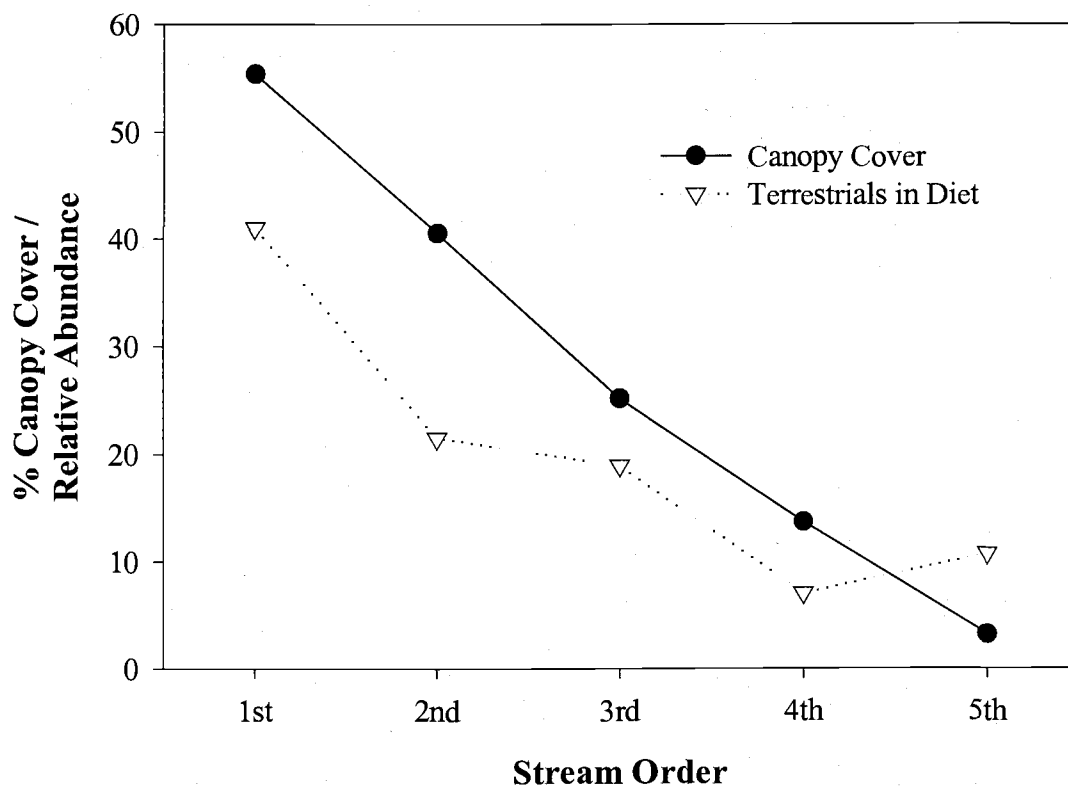
Figure 4.7. Relationship between the percent canopy cover and the relative abundance of terrestrial invertebrates in the diets of fishes at sites within 1st - 5th order stream segments of the MFJD. For canopy cover n = 18, 27, 36, 63, and 36 respectively, and for fish diets n = 12, 46, 107, 262, and 161 respectively.

For the fish-scraper-algae food chain (Figure 4.3), sites 1, 4, 10, 14, and 19 had relatively low fish numbers, high scraper densities, and low algal biomass, whereas sites 2, 5, and 13 had relatively high fish numbers, low scraper densities, and higher algal biomass. Only sites 3, 10, and 12 had trends of relatively high levels of solar input, algal biomass, and invertebrate scraper densities or vice versa (Figure 4.4). There was a relationship of relatively high canopy cover and high shredder densities at sites 1, 2, 4, 8, 12, and 15, while sites 14, 17, 19, and 20 had limited canopy cover and low shredder densities (Figure 4.5). The proportion of terrestrial invertebrates found in fish diets did decrease as the percent of canopy cover decreased along the MFJD (Figure 4.7). Just three sites, 2, 9, and 10, indicated a relationship between relatively high fish abundance, low large invertebrate predator densities, and high small invertebrate predator densities (Figure 4.6).

Discussion

It is possible that in open systems like streams, connectivity and the physical habitat template are such important drivers of community structure at large scales that the expression of trophic interactions is apparent only at small, local scales (i.e. site, unit, sub-unit, microhabitat). Indeed, localized, experimental evidence exists for trophic dynamics influencing stream communities (e.g. Jacoby 1987, Lamberti et al. 1987, Lamberti et al. 1995, Power 1990 & 1992, Walton et al. 1995, Wooton et al. 1996), and there is limited evidence for such processes influencing community structure over larger scales (i.e. reach, segment, and watershed). In an effort to explore this evidence, I considered the interactions of fish, macroinvertebrate, and algal communities from both site and stream order reach perspectives along the longitudinal profile of a stream in eastern Oregon. Although structures of fish and macroinvertebrate communities were correlated with distributions of potential predators and prey, I found only qualitative trends of bottom-up relationships at the reach scale and little evidence of consistent top-down controls among the communities at either reach or site scales in the MFJD.

Evidence of predatory regulation of benthic communities in stream systems has been highly variable (Allan 1982, 1983, Flecker 1984, Hemphill & Cooper 1984, Schofield et al. 1988, Wooster 1994, Englund & Evander 1999). In the MFJD, there was only suggestive evidence of top-down trophic control by fishes at 8 of the 20 individual sites where there were relatively high fish numbers, low macroinvertebrate scraper densities, and high algal biomass or vice versa. Fish in the MFJD consumed a wide range of macroinvertebrates but primarily foraged on prey which were most ubiquitous throughout any given reach. There was no indication of a preference for any of the macroinvertebrate functional feeding groups or large bodied invertebrate predators, and in most cases high electivities for individual taxa were associated with macroinvertebrates that had extremely limited availability. A potential factor limiting the expression of top-down processes at larger spatial scales in a stream (i.e. greater than unit) could be the high mobility and colonization potential of stream macroinvertebrates (see Resh & Rosenberg 1984) and connectivity among sites for fishes.

Based on an abundant and diverse macroinvertebrate community and the wide diet breadths of fishes in the MFJD, food was probably not a limited resource for fishes. However, the abundance of preferred prey items may have influenced the reach or local scale distribution of certain fish species. Macroinvertebrate ordination coordinates along the primary longitudinal gradient were strongly correlated with the relative abundance of two common fish predators in the MFJD, sculpins and rainbow trout. Although sculpin were present only in sites from 3rd through 5th order reaches, their diets were composed of macroinvertebrate taxa whose abundance generally increased downstream (primarily Baetid, Heptageniid, and Ephemerellid mayflies). Relative abundance of rainbow trout was highest in headwater sites and decreased dramatically downstream. Terrestrial invertebrates were the rainbows' primary diet item in the headwaters, whereas diets for trout in higher order, open-canopied reaches switched to Heptageniid mayflies and Hydropsychid caddisflies. In general, the relative abundance of rainbow trout and torrent sculpin was highest in reaches that had

high availability of prey, suggesting that availability of macroinvertebrates may have influenced the distribution of these fishes at sites along the MFJD.

Despite the lack of a significant relationship between canopy cover and shredder densities along the longitudinal profile of the MFJD, both canopy cover and shredders were generally most abundant in the 1st and 2nd order sites. However, I did observe one of the highest abundance of shredders in a 4th order site (# 12) that also had relatively higher canopy cover than other 4th order sites. Though riparian canopy was relatively open from 3rd order down stream, local patchiness in the riparian corridor appeared to be another factor influencing variability in macroinvertebrate community structure along the MFJD. While these observations suggest that available sources of particulate organic material were limited in higher order reaches, this study did not measure in-channel organic matter. As an important caveat, Johnson & Covich (1997) found that local measures of riparian vegetation were generally weaker indicators of a site's organic material than up-stream measures taken at much larger spatial scales. Within the limitations of the data, canopy cover provided a useful indicator of potential allochthonous or solar input effects on site-specific stream trophic dynamics.

A link between canopy cover and the stream trophic web that is often overlooked is the terrestrial invertebrate prey base (Wipfli 1997). Canopy cover was strongly correlated with axes 1 and 3 coordinates of the fish ordination, and terrestrial invertebrates were the most common prey item in 1st and 2nd order reaches where rainbow trout were the dominant fish species. Salmonids generally forage on drifting aquatic macroinvertebrate larvae and terrestrial adult insects entrapped on the water surface (e.g. Newman 1987, Angradi & Griffith 1990, Wipfli 1997). In systems with limited or patchy riparian vegetation, the input of terrestrials may be reduced, causing salmonids to expand their diet breadths (Wipfli 1997). Consequently, limited riparian canopy in down stream reaches (e.g. MFJD) may force salmonids to compete for aquatic macroinvertebrate resources with other fish species. In this study, diets of rainbow trout shifted from mainly terrestrials in the headwaters to benthic invertebrates in higher order reaches. Other fish species foraged primarily on benthic

invertebrates and were most abundant in higher order reaches, suggesting salmonids in the lower MFJD may face potential competition for food.

Based on both availability of solar input and levels of algal biomass, one can assume that food is not limited for many herbivorous macroinvertebrates in the MFJD (i.e. grazers, collectors, and filterers) (see also Tait et al. 1994). Although structure of the macroinvertebrate community along the longitudinal gradient was positively correlated with rates of gross primary production, there was no significant relationship between invertebrate scrapers and either gross primary production or algal biomass. There was only suggestive evidence of top-down trophic control of periphyton by scrapers at 8 of the 20 individual sites, and at the reach scale scraper abundance and algal biomass appeared to positively correlated (Figures 4.4 & 4.5). From a bottom-up perspective, algal biomass was not correlated with available solar input along the MFJD. This suggests that the patchy canopy cover throughout the MFJD not only limits allochthonous inputs and the terrestrial invertebrate prey base, but also allows for considerable autochthonous production to occur up into the headwaters. This would account for the high relative abundance of scrapers throughout the system.

Chapter 3 illustrated strong correlations between the different stream community ordinations and many of the physical habitat characteristics, whereas this chapter showed that community patterns also were correlated with the distribution of other aquatic organisms. Strong correlations between axis coordinates of one biological community ordination with the individuals from other trophic levels could indicate many things. For example, there are four potential hypotheses for a strong correlation between axis 1 coordinates from the macroinvertebrate taxa ordination and relative abundance of an individual fish species. First, the fish species responded to the same *physical* environmental gradients as the macroinvertebrate community; such that the fish species had a distribution either similar (positive *r*) or opposite (negative *r*) to the macroinvertebrate community distribution. In this scenario, the fish and macroinvertebrates are distributed along a gradient based solely on individual taxonomic responses to the physical template. The second hypothesis is a bottom-up approach where distribution of the fish species (predator) was a function of

availability of macroinvertebrate prey; the fish species was influenced less by the *physical* environmental gradients and more by the *biological* ones. For example, a fish species might have been abundant in areas where the macroinvertebrate community most closely resembled that species' diet. The third hypothesis is a top-down perspective where the macroinvertebrate community (prey) is a function of the distribution of the fish species (predator). In this case, the macroinvertebrate community was less influenced by the *physical* environmental gradients, and more influenced by the *biological* ones, primarily predation by fishes.

In all three hypotheses above, the physical template has some influence on the distribution of both fish and macroinvertebrates along the primary longitudinal gradient. However, in the second and third hypotheses this influence becomes indirect for one of the communities because of either bottom-up (#2) or top-down (#3) trophic interactions. The fourth hypothesis combines the previous hypotheses. Perhaps the structures of all biotic communities are functions of the physical template and bottom-up, top-down trophic interactions. In this case, variability in community structure along a gradient would depend on the varying degree to which individual communities are influenced by physical and/or biological interactions. Ultimately, if no such correlations existed there would be no evidence supporting any of the stated hypotheses. Because correlations *do* exist between and among physical and biological gradients in the MFJD, the fourth hypothesis appears the most probable. However, it is critical that the scale and context of these correlations are considered.

Structures of fish and macroinvertebrate communities along the MFJD were most strongly correlated with large-scale, physical habitat characteristics (Chapter 3). However, variability of the communities within this landscape-scale context suggested there were additional factors influencing community structure. Further correlations suggested local scale habitat variables (Chapter 3) and trophic interactions may influence among-site community variability along the longitudinal gradient. These findings illustrate that within the proper context, aspects of both the RCC and Geomorphic-Trophic Hypothesis are applicable to stream systems. From a large, segment or reach scale perspective, stream communities are structured through

bottom-up processes according to geomorphic gradients present throughout the landscape (sensu the RCC). As the scale of inference becomes smaller and more 'closed', local scale habitat variations and trophic interactions will have greater influence on the structure of communities in question (sensu the Geomorphic-Trophic Hypothesis).

Few studies have considered such a breadth of physical and biological components along such an extensive longitudinal profile of a stream. While I have certainly excluded numerous biotic and abiotic factors, this study provides a unique and expansive foundation for multivariate examinations of stream communities. Perhaps more than anything, this study illustrates both the importance of recognizing and the ability to integrate a complex suite of physical and biological factors influencing any community structure.

5. A SEARCH FOR LARGE SCALE HYPORHEIC UPWELLING IN THE MIDDLE FORK OF THE JOHN DAY RIVER

Introduction

The River Continuum Concept (RCC) is a conceptual model that predicts a continuous change in the physical and biological attributes of a river from headwaters down stream. The RCC is an effective heuristic tool because it allows researchers to question whether their study systems are continuous gradients. The RCC was based on reach/segment scale phenomena within pristine, temperate, mountain stream ecosystems, so studies conducted at different spatial scales (e.g. sites, reaches, or segments), in different ecotypes, or within managed landscapes may report discontinuous longitudinal patterns (e.g. Ward & Stanford 1983, Minshall et al. 1983, Brussock et al. 1985, Minshall et al. 1985, Statzner & Higler 1985, Brussock & Brown 1991, Stanford and Ward 1993, Townsend 1996).

In the glaciated and montane upper section of the Flathead River, Montana, reach-scale, subsurface water upwelling and down-welling is associated with large changes in valley constraint (Stanford & Ward 1993). These patterns suggest reach-scale discontinuities in hyporheic-stream interactions along the longitudinal gradient. Such changes in the geomorphology and hydrology of a stream directly or indirectly affect the biological communities within a stream, contributing to deviations from RCC predictions. Therefore, the scale and magnitude of hyporheic exchange within a stream may significantly affect longitudinal patterns of biological communities and physical habitat.

Subsurface water may interact with the stream via springs, seeps and zones of upwelling throughout a watershed. Although seepage areas of subsurface water into the stream may be highly variable, locations of potential upwelling zones may be predictable within some stream systems. Upwelling of subsurface water typically occurs as a result of either valley geomorphic constraint (Stanford & Ward 1993, Brunke & Gonser 1997) or changes in stream bed topography (Vaux 1968, Thibodeaux & Boyle 1987, Savant et al. 1987, Harvey & Bencala 1993). Stanford &

Ward (1993) proposed that as a river flows downstream from an open, alluvial floodplain reach into a constrained reach, the subsurface-water from the floodplain is constrained and forced laterally and upward into the stream channel.

These transitional points in the river are areas where the biotic community may show a strong response to upwelling. During summer low flows subsurface water generally has lower temperatures, reduced oxygen and is nutrient rich compared to stream water (Grimm & Fisher 1984, Valett et al. 1990, Hendricks & White 1991, Valett 1993, Triska et al. 1993 a & b, Brunke & Gonser 1997). Because temperature, oxygen and nutrients are key regulators of stream biota, the subsurface-stream connections are potentially fundamental determinants of stream communities (Boulton 1993). There is evidence that upwelling subsurface water enhances algal standing crop (Grimm et al. 1991, Valett et al. 1992, 1994) and influences egg survival (Cooper 1965) and adult distribution of salmonids (Keller & Kondolf 1990, Torgersen 1996). However, little is known about the influence of subsurface-stream connections on multiple trophic levels within a stream and, in systems that have experienced a series of historical and current land-use practices, such patterns may be altered.

The upper reaches of the Middle Fork of the John Day River (MFJD) in eastern Oregon are composed of a series of broad, unconstrained, alluvial floodplains and narrow, constrained valley segments. The stream channel and biota have been influenced by multiple land-use practices such as mining, timber harvest, grazing, and channelization. During the summer of 1997, I examined the potential of subsurface upwelling in this system by comparing multiple physical and biological variables at sites in both constrained and unconstrained reaches of the MFJD.

I hypothesized that the MFJD would follow the proposed scenario of Stanford & Ward (1993) in which there would be large-scale subsurface water upwelling at sites located in the downstream end of unconstrained reaches, but not at sites in constrained reaches. Consequently, sites within upwelling reaches would have greater rates of primary productivity and more algal biomass than sites in non-upwelling reaches, due to increased nutrients from subsurface waters. In addition, upwelling sites were predicted to have higher macroinvertebrate diversity and abundance, greater

benthic fish diversity, and fish with narrower diet breadths, than those areas without upwelling. Greater diversity of macroinvertebrates and fishes in upwelling sites would result from increased availability and productivity of algae and possible thermal refugia. A high diversity of macroinvertebrates would enable different fishes to specialize on their preferred prey, narrowing diet breadth.

Methods

Site Selection

We selected ten sites along a 52 km stretch of the MFJD that included 3rd through 5th order reaches; five sites were in areas of predicted upwelling and five were in areas where upwelling was not expected to occur (Figure 5.1). Sites were selected based on information from topographic maps, aerial photos (Figure 5.2), valley width profiles, and thermal imagery (Torgersen 1997). In general, potential upwelling sites were in transitional areas between unconstrained and constrained reaches. Potential non-upwelling sites were selected in non-transitional reaches of the river. Although non-upwelling areas might have riffle-pool exchange of hyporheic water, I assumed the influence of such a small-scale process would be overshadowed by larger scale upwelling of valley constraint. All sites were 50 meters in river length and composed of primarily riffle and run habitat. All sampling was done in late July - early August during low-flow conditions.

Physical Habitat

Measured abiotic variables ranged from large-scale landscape features such as valley slope and stream order, to small-scale site-specific characteristics like depth and substrate type. Stream velocity (m/s) and discharge (m³/s) were measured along 3 transects per site using a digital flow meter held at a depth of 1/8 of the water column. Available solar radiation and canopy cover (calculated using a Solar Pathfinder) were measured at 9 points within each site (3 at mid-channel width, 3 at 2 m out from each bank). Habitat type, substrate and depth (m) were recorded with each Surber sample
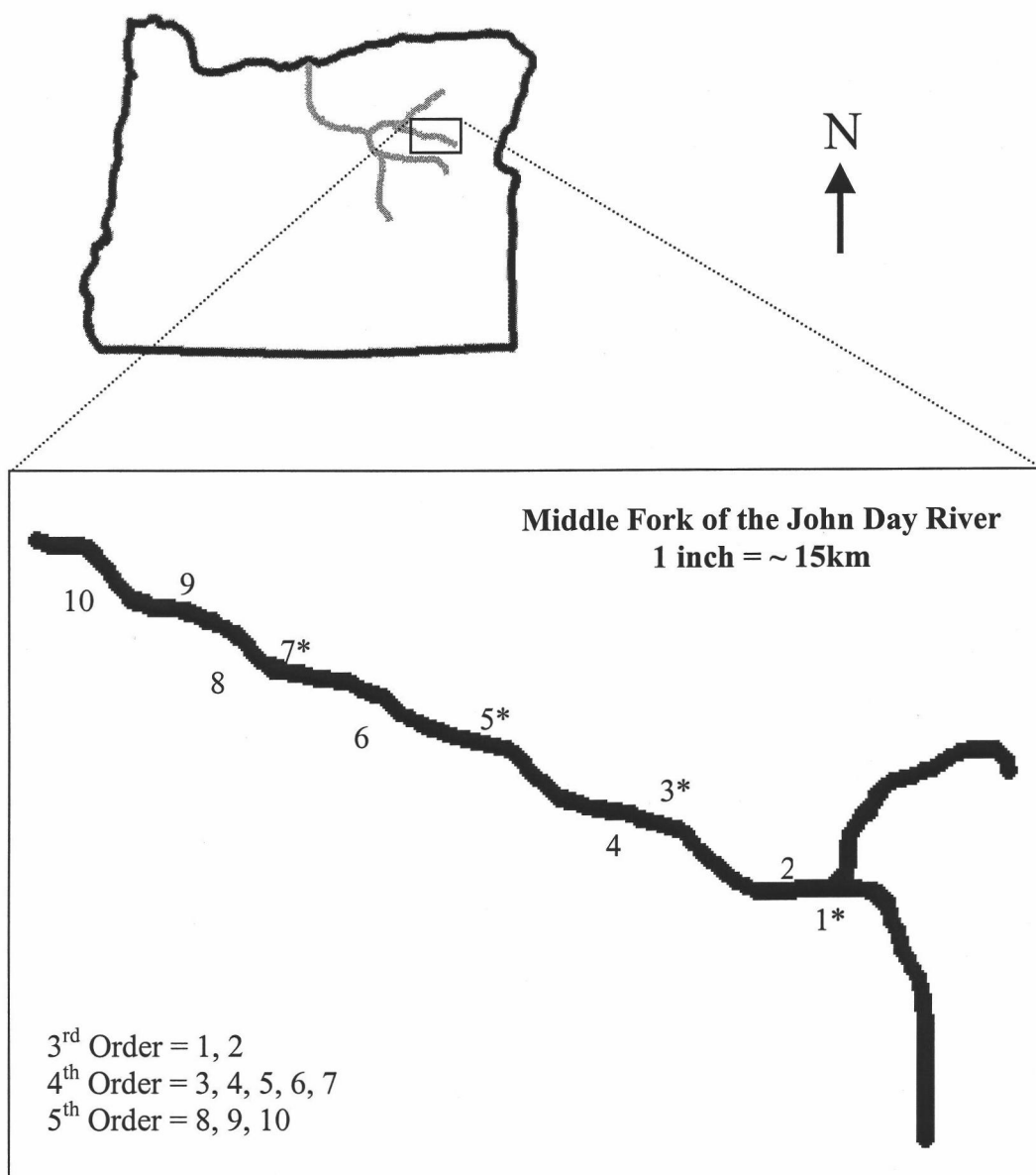
Figure 5.1. Map of the Middle Fork of the John Day River in eastern Oregon. Approximate locations of study sites are indicated on inset map. Asterix (*) indicates those sites located at the downstream end of large, alluvial valley segments, and that were predicted to experience subsurface upwelling.

Figure 5.2. An aerial photo with the location of study site 7 in the Middle Fork of the John Day River. Sites in predicted upwelling reaches (like site 7) were positioned at the downstream end of large alluvial valley segments. The stream is flowing toward the upper left corner. Note the extensive dry-channel network in the floodplain on the lower right portion of the photo.

and at 1 m intervals along 5 random transects spanning the wetted width at each site. Habitats were classified as riffle, glide(run), pool, backwater, and edge habitat. Edge habitat was defined as any location within 30 cm of a bank, gravel bar, or island. Substrates were classified as bedrock, large boulder, small boulder, cobble, gravel, sand and silt based on a modified Wentworth (1922) scale. At each site wetted channel widths were recorded at 10 m intervals and averaged. Channel gradient was measured using a clinometer, and aspect was determined from 3 compass measurements. Stream order (Strahler), valley slope, valley width, drainage area, and elevation were determined from 7.5 minute USGS topographic maps.

Stream temperature was measured using Thermal Data Loggers. Measurements were recorded at 15 minute intervals for a period of two weeks that included all sampling dates. Temperature data were represented as weekly mean, minimum, maximum, and the average amount of time each site exceeded 22°, 24° and 25° C in a 24 hr period.

To examine differences between subsurface and in-channel water quality, I defined subsurface water as that which is present at a depth of 20 cm into the substrate. In-stream water was defined as the water present at mid-depth of the water column. Temperature, dissolved oxygen, pH, and specific conductivity, were measured for both subsurface and in-stream water at three points within each site. Mid-channel sample points were located longitudinally at 0, 25 and 50 meters at each site. Subsurface water was extracted from a stainless-steel well, driven 20 cm into the substratum, by manually drawing water from 2 m long surgical tubing inserted into the well. Wells were purged immediately before each extraction. Sampled water (subsurface and stream) was collected in a 200 ml glass bottle and temperature, dissolved oxygen, pH, and conductivity were measured immediately using a Corning CheckMate probe.

Water levels in wells also were used to verify predicted upwelling signatures within the sites. The vertical direction and magnitude of subsurface-water flows are measured by calculating the vertical hydraulic gradient (VHG). VHG is the difference in water levels between the stream and within a well divided by the depth at which the

well penetrates the substrate (Lee & Cherry 1978). Because all wells in this study were driven to a depth of approximately 20 cm, a positive head in the well would indicate upwelling and a negative head indicate downwelling. Water levels were recorded at all wells using a resistance meter and a flexible probe with 0.5cm measurement markings (see Baxter 1997). Falling head tests also were conducted to estimate the rate of flow through the substrates and hydraulic conductivity (Lee & Cherry 1978). Falling head tests were done by pouring water into each well to the point of overflow, and then measuring the rate at which the water level dropped within the well.

Fish and fish diets

Fishes were sampled using a backpack electro-fisher, two dip nets and a 5 mm mesh, 2 m wide block net. For each pass, the block net was set 10 m downstream from the electro-fisher. Sampling progressed downstream toward the block net within a 2 m wide frame outlined by the block net. Substrates were disturbed along the pass to ensure burrowing fishes were dislodged. Fish were captured along the pass by dip nets and any missed fish were retained in the block net. Passes were made within a site until at least 15 of the two most common taxa were collected. All fish were counted and measured for total and fork length. Fishes were identified to species and also categorized according to thermal guilds (Hokanson 1977, Zaroban et al. 1998): (1) warm water fishes: redside shiners (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), and northern pike minnow (*Ptychocheilus oregonensis*); (2) cool water fishes: torrent sculpin (*Cottus rhotheus*), bridgelip and mountain suckers (*Catostomus columbianus* and *platyrhynchus*), Pacific lamprey (*Entosphenus tridentatus*), and longnose dace (*Rhinischthys cataractae*); and (3) cold water fishes: rainbow trout (*Oncorhynchus mykiss*) and chinook salmon (*Oncorhynchus tshawytscha*).

Stomach contents of all species were collected from anesthetized fish by flushing the stomachs with water into standard coffee filter papers. Fish were released upon recovery from the anesthetic. Stomach contents were stored in 95% ethanol until

laboratory examination was possible. Other fishes caught in the net and not used for diet analysis were immediately released after recovery in a separate holding bucket. Stomach contents were examined under a dissecting microscope (25 X); individual items were identified to the lowest possible taxonomic level and counted according to number of head capsules. Numbers of individuals and point volume estimates (Hynes 1950) were recorded for all taxa groups in each stomach.

Benthic Samples

Six randomly chosen benthic macroinvertebrate samples were taken at each site, using a (0.093 m^2) modified Surber sampler with a 250 μm mesh net. Substrates were disturbed for 30 seconds to a depth of 10 cm where possible, and material collected in the net sieved through a 250 μm screen, and preserved in 95% ethanol. Depth, habitat and substrate were also recorded with each sample. Each sample was counted individually using a 300 count sub-sampling method (Vinson & Hawkins 1996), and identified individual genera using a dissecting microscope. From the six samples at each site, mean site densities of total benthic macroinvertebrates, EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa, and Chironomid taxa were calculated, in addition to taxa richness and diversity indices.

In situ visual counts of large-bodied invertebrates were made using a 0.1 m water scope (Li 1990). Five transects perpendicular to shore, extending the wetted channel width, were randomly chosen, using a random number generator (Quattro Pro for Windows 5.0), within each of the sites. Counts were made at 1 meter intervals along each transect, resulting in no less than sixteen samples per site.

Periphyton

Chlorophyll *a* biomass samples were collected by randomly selecting 18 rocks (approximately 10 cm in diameter) from each site. Algae was brushed and/or scraped off a 3 cm^2 area of each rock. The 18 scrapings were composited into sets of 3, and each set was individually stored in water within a light-sealed bottle and frozen for transportation. In the laboratory, chlorophyll *a* biomass was extracted by filtering the

water from each bottle through glass fiber filters and then soaking the filters in 90% buffered acetone in the laboratory. The acetone solution was analyzed by spectrophotometry (Strickland & Parsons 1968). Surface area of the rocks was determined by wrapping the rocks in foil and trimming off any excess. The foils were then weighed, and a regression of foil weight to surface area was used to calculate the rock's surface area.

Algal primary production was measured using self-contained, circulating production chambers at each site. Chambers were constructed from pieces of clear plexiglass pipe 30 cm long and 12.5 cm in diameter. The chambers were sealed with modified, water-tight caps that had outlets with 6.25 mm surgical tubing which connected to Teal submersible pumps that recirculated water. At each site, three rocks of approximately 5 cm diameter were placed in each of six chambers. Three chambers were run for one hour in direct sunlight while three chambers were simultaneously run in complete darkness (provided by an opaque plastic container). Water was collected from each chamber after every run and dissolved oxygen was determined using a dissolved oxygen meter. Water temperature within and outside the chambers also was recorded to correct for any warming effect the pumps may have had. Net primary production was calculated as the average amount of oxygen production from photosynthesis minus the average amount of oxygen consumption of respiration. To account for any differences in algal biomass among the sites, calculations of production per unit biomass were determined for each site using chlorophyll a biomass measurements from the rocks in each chamber (see methods above).

Data Analysis

Sites in predicted upwelling reaches were compared to sites in predicted non-upwelling reaches, to examine the potential relationships between large-scale subsurface water upwelling and in-stream physical and biological parameters. With five sites in each group and at least 3 samples per site, we used either Single Factor Analysis of Variance (ANOVA) or, to account for physical habitat variables, Multiple Factor Analysis of Variance (MANOVA) to test for both physical and biological

differences between site groups. All analyses were performed using StatGraphics v. 3 statistical software. I relied on qualitative analyses, using graphics that displayed the sites in sequential positions from 3rd order reaches down stream, to look for discontinuities along the longitudinal profile of this 52 km stretch of the MFJD.

Results

There were no significant differences between the predicted upwelling and non-upwelling site groups based on any of the measured physical habitat variables (Table 5.1). All sites were in single channel reaches that had relatively open canopies, cobble and gravel substrates, and low ($< 1°$) stream gradients.

I found very little physical evidence of large-scale, subsurface water upwelling. The stream bed at all sites had an underlying layer of compacted, fine sediments (> 10 cm below substrate surface) and there was no significant difference in vertical hydraulic gradients (VHG) between the site groups after accounting for physical habitat variables (MANOVA p-value > 0.1, F-ratio $= 0.02$, df $= 29$) (Figure 5.3). The mean VHG for the predicted upwelling sites was 0.01 (± 0.04 SE) and the mean value for the non-upwelling sites was 0.01 (± 0.02 SE); the highest VHG reading from any well in the MFJD was 0.13. Falling-head tests suggested movement of water through the substrates was extremely slow among the sites; hydraulic conductivity averaged 0.004 cm/s (± 0.007 SE) in predicted upwelling sites and 0.005 cm/s (± 0.007 SE) in non-upwelling sites (Figure 5.3).

There were no significant differences between site groups regarding daily in-stream temperature means, maximums, or minimums after accounting for physical habitat variables (MANOVA p-values > 0.1, F-ratios < 1.0, df $= 9$) (Table 5.1, Figure 5.4). Subsurface water was consistently lower in dissolved oxygen and pH and higher in conductivity than the stream water (Figure 5.5). There were no significant differences between site groups regarding dissolved oxygen, pH, and conductivity after accounting for physical habitat variables (MANOVA p-values > 0.1, F-ratios < 0.05, df $= 29$). Dissolved oxygen showed the most variation among sites, whereas pH

Table 5.1. Mean values (± 1 SE) for measured physical parameters in the MFJD according to sites in predicted large-scale, upwelling reaches and predicted non-upwelling reaches.

	Site Groups			
	Predicted Upwelling	**SE**	**Non-upwelling**	**SE**
Elevation (m)	3726	338	3702	318
Wetted Width (m)	9.1	3.9	10.8	5.3
Valley Slope (%)	0.75	0.31	0.79	0.31
Stream Gradient (°)	0.65	0.30	0.60	0.34
Aspect (radians)	285	35	259	38
Time Sun Hits Stream per Day (h)	10.9	1.1	9.1	2.2
Available Solar Energy Reaching Stream (%)	96.4	2.0	79.1	18.3
Mean Depth (m)	0.29	0.04	0.29	0.09
Width : Depth	32	13	40	25
Percent Riffle Habitat	100	0	97	7
Percent Cobble/Gravel Substrate	97	7	87	12
Percent Fines Substrate	23	39	33	38
Percent Boulder Substrate	7	8	26	17
Percent Macrophyte Cover	10	20	3	7
Mean Daily Stream Temperature (C)	19.6	1.4	19.8	1.2
Maximun Daily Stream Temperature (C)	24.3	1.6	24.6	1.3
Minimum Daily Stream Temperature (C)	15.0	1.2	14.9	0.8
Daily Range of Stream Temperature (C)	9.3	1.2	9.7	0.8
Time over 22° per Day (h)	8.3	4.3	8.7	3.0
Time over 24° per Day (h)	5.4	2.7	5.4	2.7
Time over 25° per Day (h)	2.3	2.0	3.0	2.5
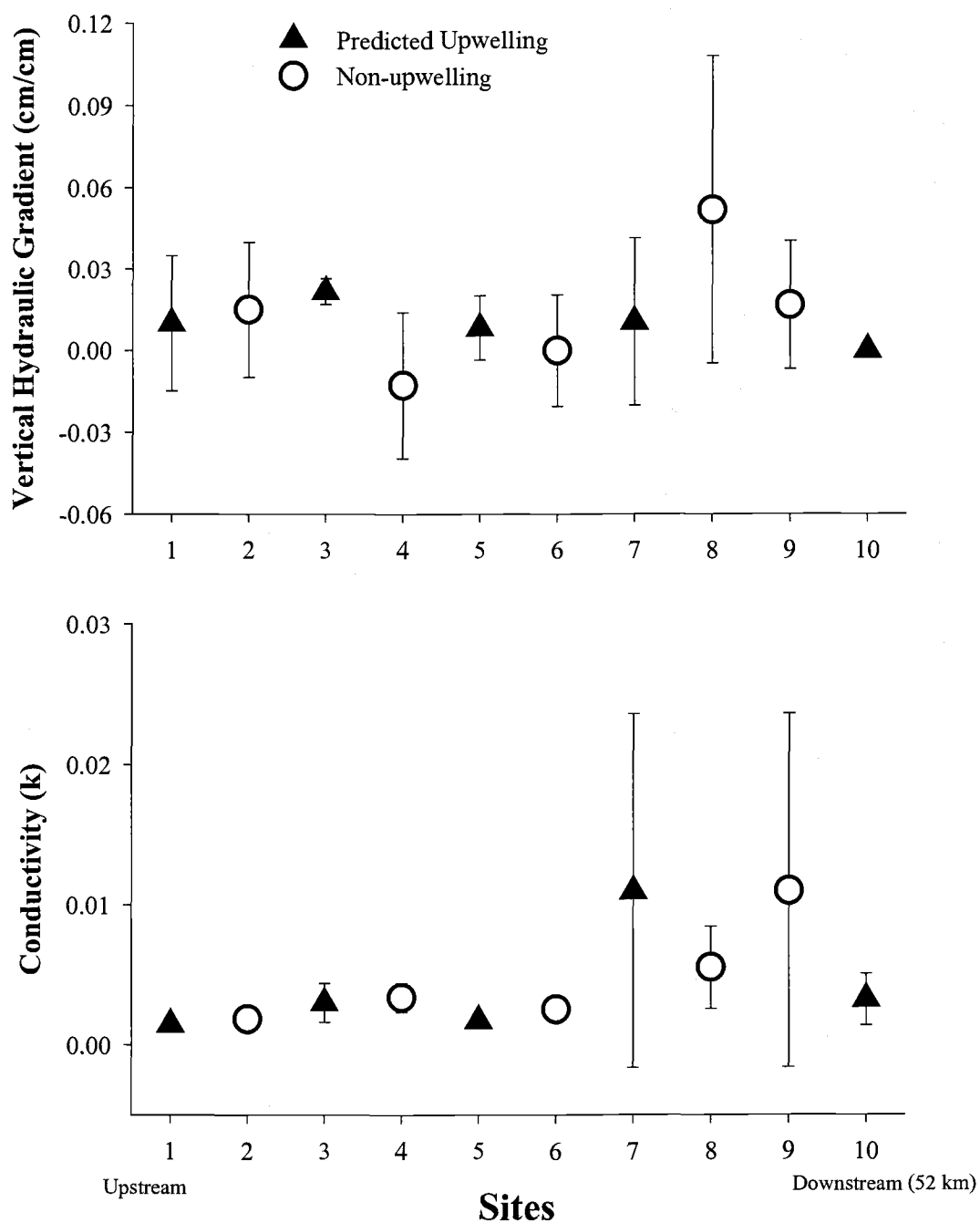
Figure 5.3. Longitudinal profiles of mean vertical hydraulic gradient (VHG) and hydraulic conductivity (± 1 SE) at 10 sites in the Middle Fork of the John Day River. Sites are grouped according to predicted large-scale, upwelling reaches associated with valley constraint and predicted non-upwelling reaches (*n* = 3 at each site).
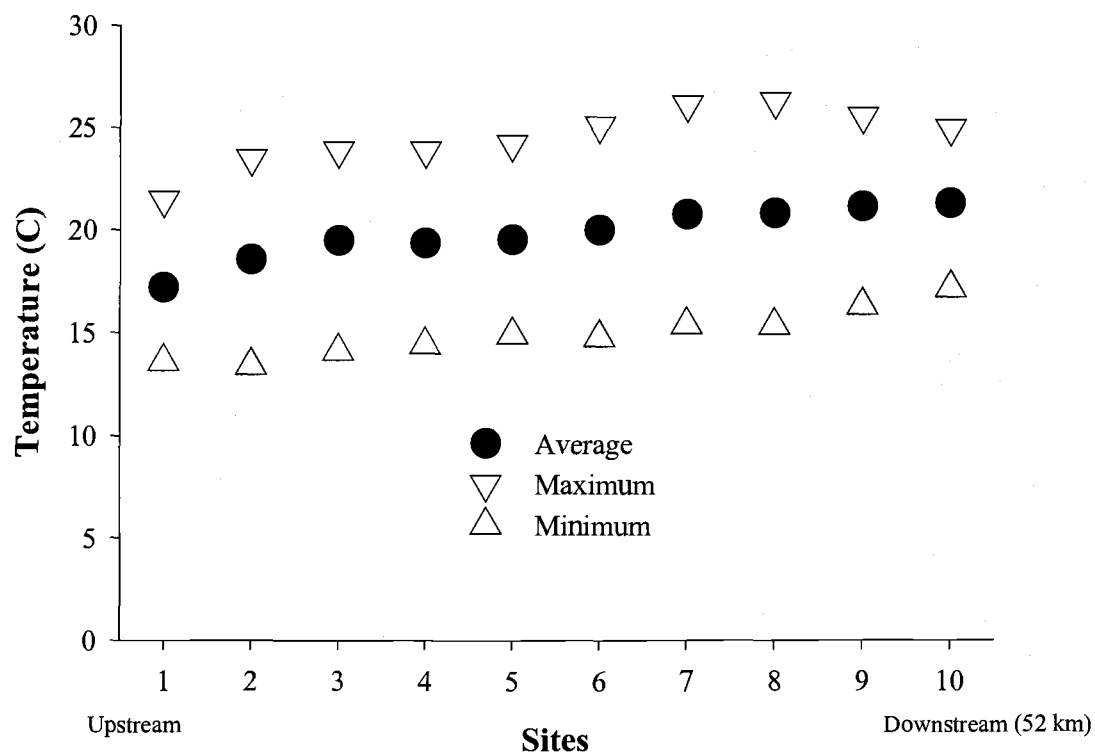
Figure 5.4. Longitudinal profiles of daily, in-stream temperature means, maximums, and minimums at 10 sites in the Middle Fork of the John Day River. Sites 1, 3, 5, 7, and 10 were in predicted large-scale, upwelling reaches associated with valley constraint and sites 2, 4, 6, 8, and 9 were in predicted non-upwelling reaches. Data were collected from a single data logger at each site and averaged across 7 consecutive days in early August.
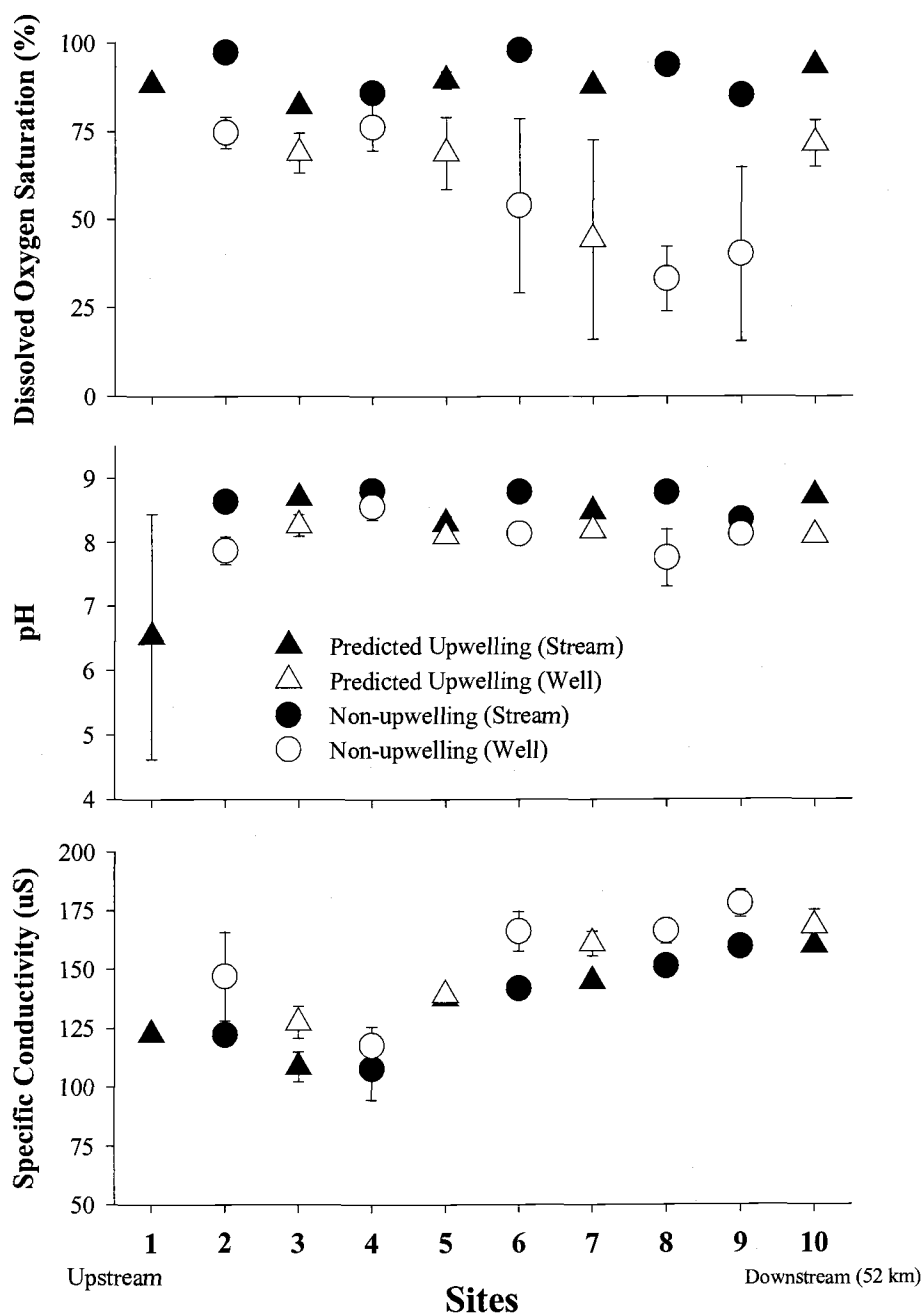
Figure 5.5. Longitudinal profiles of mean dissolved oxygen saturation, pH, and specific conductivity (± 1 SE) at 10 sites in the Middle Fork of the John Day River. Sites are grouped according to predicted large-scale, upwelling reaches associated with valley constraint (triangles) and predicted non-upwelling reaches (circles) ($n = 3$ at each site).

remained relatively consistent; there was a downstream trend of increasing specific conductivity among the sites (Figure 5.5).

Additional evidence for the lack of large-scale subsurface upwelling was provided by biological components. There were no significant differences between site groups with regard to: 1) chlorophyll a biomass, 2) primary production; 3) macroinvertebrate abundance and diversity, and 4) fish community diversity and thermal guild representation (ANOVA p-values > 0.07, F-ratios < 4.16, df = 29-59). Site 4, a non-upwelling site, had the highest levels of chlorophyll a biomass and rates of gross primary production among all sites (Figure 5.6). With the exception of site 4, there was a relatively steady, but not statistically significant, increase in chlorophyll a biomass along the longitudinal profile (Figure 5.6). Gross primary productivity was highly variable among all sites (Figure 5.6).

Macroinvertebrate community metrics were remarkably similar between the two site groups including total abundance (13,828 and 13,625 per m^2), average taxa richness, percent EPT taxa, and relative abundance of the dominant taxon (Table 5.2). Functional feeding group composition revealed a consistent dominance of collectors and scrapers among the sites (Figure 5.7). Relative abundance of collectors and scrapers ranged from 21% to 50% and 21% to 39% respectively among the sites (Figure 5.7). Although I did not directly sample macroinvertebrates in the hyporheic zone, I noted no macroinvertebrates entrained during the well-water collections.

Thermal guild composition of the fish community was relatively similar among all sites; however, there was a tendency toward relatively more abundant cold-water fishes upstream (Figure 5.8). Relative abundance of cold-water fishes was not higher in predicted upwelling reaches than in non-upwelling reaches. Taxa richness ranged from 5 to 8 fish species among all sites; sites in both predicted upwelling and non-upwelling reaches averaged 6 fish species. Although the relative abundance of long-nose dace in predicted upwelling sites was twice as high as in non-upwelling sites (4% and 2% respectively), the difference was not statistically significant (ANOVA p-value = 0.45, F-ratio = 0.62, df = 29). Diet breadth also was not

Figure 5.6. Longitudinal profiles of mean chlorophyll a biomass and gross primary productivity (± 1 SE) at 10 sites in the Middle Fork of the John Day River. Sites are grouped according to predicted large-scale, upwelling reaches associated with valley constraint and predicted non-upwelling reaches ($n = 18$ rocks for biomass and 3 chambers for production at each site).

Table 5.2. Mean values (± 1 SE) for macroinvertebrate community metrics in the MFJD according to sites in predicted large-scale, upwelling reaches and predicted non-upwelling reaches.

	Site Groups			
	Predicted Upwelling	SE	Non-Upwelling	SE
Taxa Richness	50	3	49	5
EPT Taxa Richness	29	5	28	6
Ephemeroptera Genera	12	2	11	2
Plecoptera Genera	8	2	7	3
Trichoptera Genera	9	2	10	3
Non-Insect Genera	6	1	5	1
Abundance (no./m^2)	714	103	703	116
EPT Abundance (no./m^2)	279	68	279	96
Ephemeroptera Abundance (no./m^2)	178	54	162	42
Plecoptera Abundance (no./m^2)	24	13	30	22
Trichoptera Abundance (no./m^2)	77	50	87	70
Chironomidae Abundance (no./m^2)	172	43	165	76
Percent EPT Taxa	39	5	39	10
Percent Ephemeroptera Taxa	25	6	23	4
Percent Plecoptera Taxa	3	2	4	3
Percent Trichoptera Taxa	10	6	12	8
Percent Chironomidae	24	3	23	8
Relative Abundance of Dominant Taxon	17	4	16	4
Percent of Non-Insect Taxa	10	6	8	3
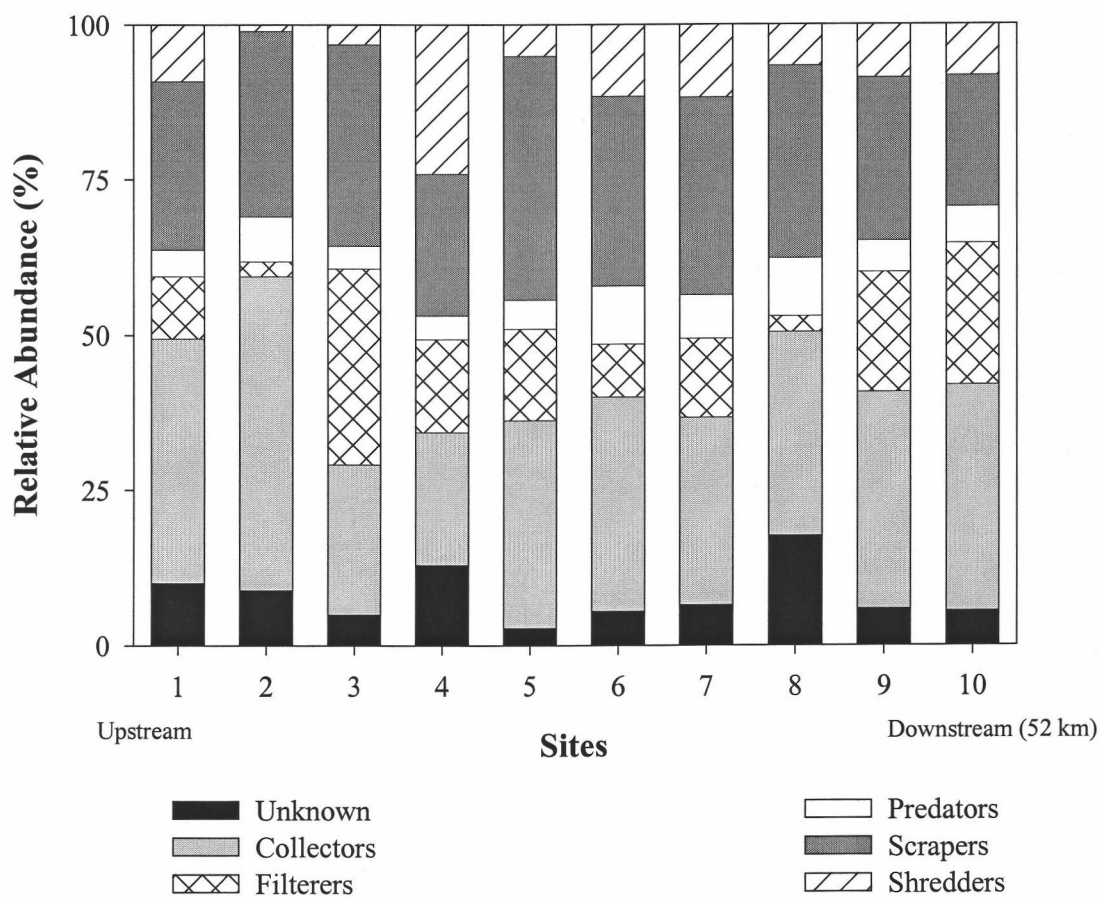
Figure 5.7. Relative abundance of macroinvertebrate functional feeding groups at 10 sites in the Middle Fork of the John Day River. Sites 1, 3, 5, 7, and 10 were in predicted large-scale, upwelling reaches associated with valley constraint and sites 2, 4, 6, 8, and 9 were in predicted non-upwelling reaches ($n = 6$ at each site).
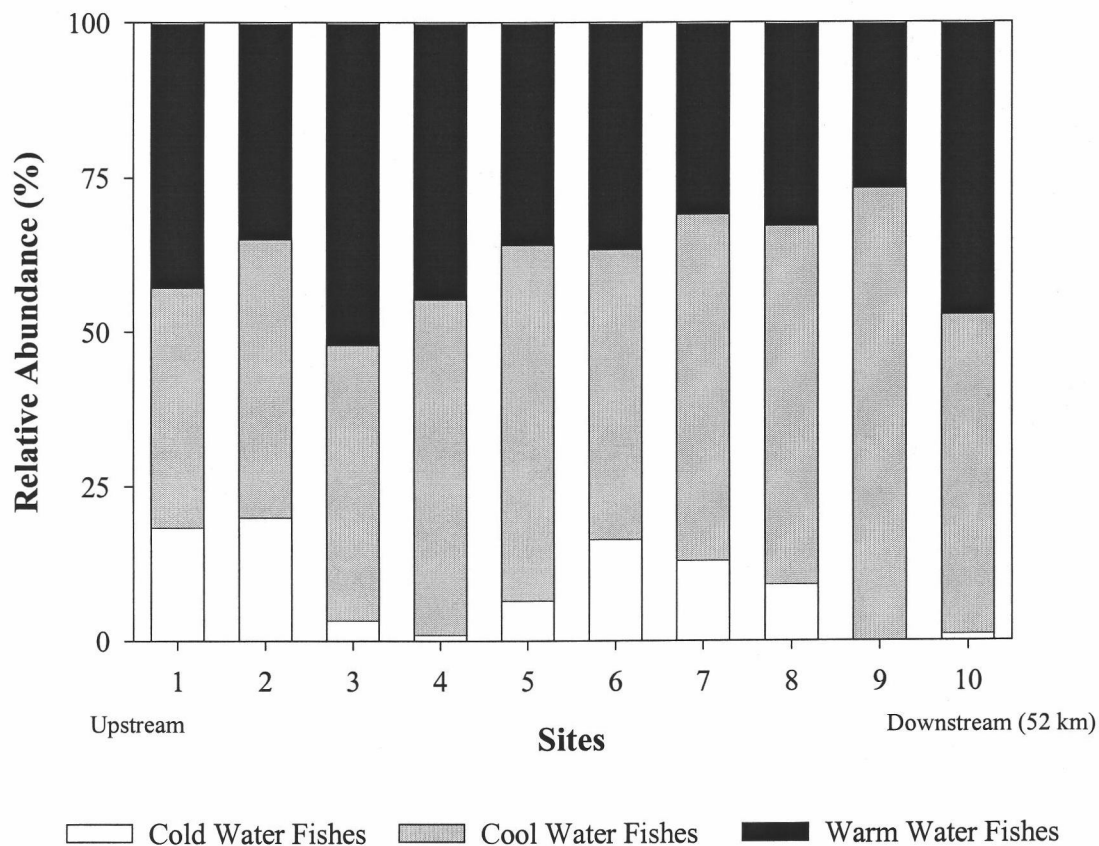
Figure 5.8. Relative abundance of cold, cool, and warm water fishes at 10 sites in the Middle Fork of the John Day River. Sites 1, 3, 5, 7, and 10 were in predicted large-scale, upwelling reaches associated with valley constraint and sites 2, 4, 6, 8, and 9 were in predicted non-upwelling reaches ($n = 4$-8 sample passes at each site).

significantly different between the site groups; fish consumed an average of 21.2 (±

1.11 SE) macroinvertebrate taxa in predicted upwelling reaches and 21.8 (± 1.11 SE)

taxa in non-upwelling reaches. Ephemeroptera and Diptera species comprised the

majority of fish diet items among all sites, however the relative abundance of these

taxa groups in fish diets differed between site groups (Figure 5.9). Species of Baeitid

mayflies were the most common diet items (representing approximately 20-50% of all

items consumed) in all sites except non-upwelling site 9 where Simulid black fly

larvae comprised approximately 65% of all items consumed.

Discussion

Unlike observations of Stanford & Ward (1993) in the Flathead River,

Montana, I found very little evidence of reach-scale, subsurface water upwelling

associated with valley constriction in the MFJD. There were no physical or biological

discontinuities in the longitudinal profiles associated with predicted upwelling sites.

In short, I found no support for any of my initial hypotheses regarding hyporheic

exchange in the MFJD. In addition to a lack of upwelling signatures in the MFJD,

there were few discontinuities in general associated with physical and biological

variables along the longitudinal profile. While some variables reflected a downstream

gradient, many were relatively consistent from 3rd order sites down through 5th order

sites. Although there are some obvious changes simply due to stream size, the

substrate, physical habitat, and biota are remarkably similar throughout the section. In

addition, this entire section of stream has been influenced by similar land-use practices

and has limited riparian canopy cover. These observations support the idea that the

3rd-5th order segment of the MFJD is relatively homogenous from an in-stream, reach-

scale perspective (sensu Chapter 3).

In the MFJD, I believe it is a combination of different factors that limit the

expression of large-scale upwelling and contribute to the reach-scale similarities in

habitat and biota. The MFJD is a relatively low-gradient mountain stream that: (1)

drains a basin without any glacial history and, (2) has floodplains primarily composed
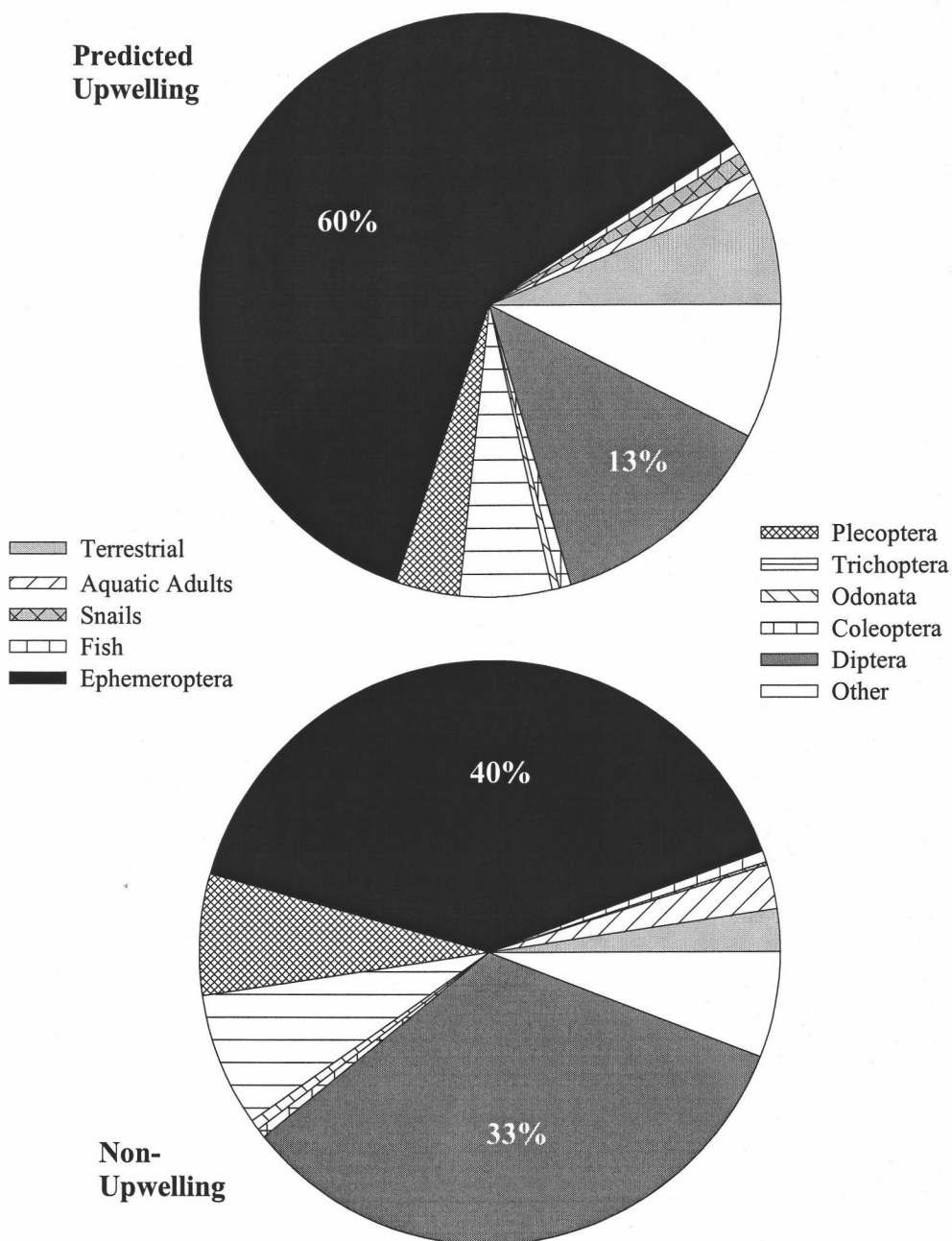
Figure 5.9. Relative abundance of stomach contents from fishes in the Middle Fork of the John Day River (based on item counts). Five sites were in predicted large-scale, upwelling reaches associated with valley constraint and five sites were in predicted non-upwelling reaches (*n* > 50 for each site group). All ten fish species collected were included in the analysis.

of fine textured soils and gravels. The MFJD also has been subjected to multiple land-use practices over the past century including mining, timber harvest, cattle grazing, and channelization, all of which may influence the extent of hyporheic exchange by increasing the input of fine sediments and lowering water table elevations (sensu Brunke & Gonser 1997). Finally, within the stream channel itself, there was a compacted layer of fines below approximately 10 cm depth.

One limitation of this study was the small number of wells at each site. However considering: (1) there was relatively little variability in the measurements from all 30 wells in the MFJD, (2) overall ranges of both VHG and hydraulic conductivity among all sites were relatively low compared to other stream systems (e.g. Valett 1993, Valett et al. 1994, Hendricks & White 1995, Baxter 1997), and (3) there was a lack of any biological signatures, it is unlikely that the addition of more wells would have changed the overall conclusions. There was no evidence to suggest that large-scale hyporheic exchange is occuring in the MFJD during summer low flows.

Although this study did not find any evidence of large-scale upwelling, local or small scale hyporheic processes may occur in the MFJD; to appropriately examine local hyporheic characteristics would require more than 3 wells per site. There also may be considerable lateral exchange in the MFJD, particularly during spring snow-melt, but this study was not designed to address this potential. However, based on observations from this study and Hopson (1998), I would expect most exchange rates in the MFJD to be quite slow.

Despite the apparent reach-scale similarities in the 3rd-5th order segment of the MFJD, some individual sites were anomalous. This illustrates the inherent variability along a gradient at the local-scale within any given system. For example, fish diets in site 9 were primarily composed of Simulid black-fly larvae, whereas Baetid mayflies were the most common diet item at all other sites. Site 9 was located in a channelized reach that runs through old mine tailings. I suggest that larger substrates and higher flow velocities may have influenced both the macroinvertebrate and fish communities within this site, such that Simulidae larvae were readily abundant and the fishes were

adapted for primarily bottom or drift feeding. This site-specific phenomena at site 9 would also account for the larger proportion of Diptera in diets from fish in non-upwelling sites (Figure 5.9). The mining history and substrates at site 9 also may have contributed to the relatively large range in hyporheic conductivities at this predicted non-upwelling site (Figure 5.3).

One of the many implications of slow or absent hyporheic exchange in an Interior Pacific Northwest stream is the loss of a potential mechanism to buffer stream temperatures. In this region, stream temperature has received much attention by management and researchers because of dwindling salmonid populations that depend on cold water (sensu Li et al. 1994). A lack of hyporheic influence on stream temperature places greater importance on the role of riparian vegetation and channel morphology to control solar input and limit heating. However, many streams in the Interior Pacific Northwest, like the MFJD, have relatively open riparian canopies resulting from both natural and anthropogenic factors. Whether or not the lack of hyporheic exchange and riparian cover are consequences of land-use practices, it is crucial managers recognize that thermal refugia will be limited for fishes in these streams.

Based on the scope of this project, large-scale hyporheic upwelling due to valley constraint appears to be limited in the middle reaches of the MFJD during summer low flows. This study emphasizes the importance of context and variability in the study of hyporheic processes within stream ecosystems. The findings of this study do not mean hyporheic processes do not occur in the MFJD, but it does suggest that the extent and influence of hyporheic exchange will vary from one ecosystem to another. Systems that: 1) are not in glaciated regions, 2) have compacted or fine-textured valley fill, 3) flow through low gradient areas, or 4) have been influenced by land-use practices may reflect variations from the hyporheic corridor concept developed in the Northern Rocky Mountains.

6. SUMMARY

The structure of any community is a function of both independent and interacting physical and biological factors. These factors also influence community structure at multiple temporal and spatial scales. This study was a multi-trophic level, multivariate examination of stream community structure along a longitudinal gradient. I examined the physical template and structure of fish, benthic macroinvertebrate, and algal communities along a 1st through 5th stream order gradient of the Middle Fork of the John Day River (MFJD) in semi-arid eastern Oregon. I developed a new approach to examine community patterns along an environmental gradient using non-parametric, multivariate ordination (Chapter 2). This approach was used to examine longitudinal gradients and relationships of physical habitat and in-stream communities (Chapter 3), and the potential influence of top-down and bottom-up trophic interactions on community structure along the longitudinal gradient of the MFJD (Chapter 4). Finally, the evidence for large-scale hyporheic exchange and its potential influence on longitudinal patterns of community structure were explored in Chapter 5.

Multivariate techniques are popular with ecologists because they depend on numerous variables and incorporate the inherent variation within community data. One concern with multivariate analyses in ecology is that for any given analysis there may be numerous possible interpretations due to the lack of any *a priori* hypotheses (sensu Austin 1985). Chapter 2 describes a conceptual framework and methodological approach for examining community patterns using multivariate ordination techniques that: (1) provides a set of qualitative, *a priori* hypotheses regarding community structure, (2) can be used for both biotic and abiotic gradients over multiple scales, (3) utilizes numerous taxa and variables, and (4) is generally applicable to any ecosystem or community. The conceptual framework provides three *a priori* qualitative, null hypotheses of ordination patterns: 1) an ideal continuum, 2) a highly variable distribution, and 3) discrete patches (Figure 2.2). This conceptual framework can be used to describe community patterns along a gradient regardless of system or spatial scale. By asking, "How much do ordinations of actual communities vary from the

proposed conceptual models?" and "*Why* do ordinations of actual communities vary from the proposed conceptual models?", we begin to integrate factors influencing community structure and the spatial scales at which they operate. The methodological component of this approach is directly linked to multivariate, non-parametric, ordination techniques and the rotation of the ordination space to a consistent set of variables. Data from the MFJD were used to illustrate how this approach could be used to compare patterns of physical and biological variables along a stream gradient from both reach and site scale perspectives simultaneously. Despite potential limitations with sampling error, limited number of variables, and nonlinear relationships, the possible applications or adaptations of this approach are many. While this proposed approach could provide a much needed tool for multivariate examinations in community ecology, it is recognized as a starting place rather than a conclusion.

The River Continuum Concept (Vannote et al. 1980) set the stage for considering how in-stream community structure may be influenced by geomorphic, hydrologic, and other physical factors. The RCC predicted how continuous longitudinal gradients in stream size directly or indirectly influence the primary sources of available energy (i.e. allochthonous vs. autochthonous) and the structure of in-stream communities. However, particular ecotypes, patchy or discontinuous geomorphic features, and anthropogenic influences may cause variations from the RCC predictions (Ward & Stanford 1983, Minshall et al. 1983, 1985, & 1992, Brussock et al. 1985, Statzner & Higler 1985, Huryn & Wallace 1987, Brussock & Brown 1991, Lugthart & Wallace 1992, Stanford and Ward 1993, Grubaugh et al. 1996, Townsend et al. 1997, Delong & Brusven 1998).

The MFJD is located in semi-arid eastern Oregon. The upper reaches of the MFJD are a series of broad, unconstrained, alluvial floodplains and narrow, constrained valley segments. Within the last century, the MFJD also has been influenced by multiple land-use practices such as mining, timber harvest, grazing, and channelization; grazing and timber harvest are the only land-uses currently practiced. The purpose of Chapter 3 was to examine the applicability of the RCC in a high-desert

stream subjected to these multiple physical and anthropogenic constraints. It was hypothesized that physical habitat characteristics, structures of fish and macroinvertebrate communities, and algal abundance would not reflect continuous longitudinal gradients from headwaters to downstream reaches. Results from NMS ordinations suggested there was sufficient variability among the study sites such that the MFJD does not follow the RCC for some parameters. However, there were longitudinal gradients expressed by both physical and biological elements in the MFJD. Fish and macroinvertebrate community structures along the MFJD were more strongly correlated with landscape scale, longitudinal gradients that than site scale variability; algal abundance and productivity were highly variable throughout the MFJD. When considered individually, most physical and biological variables measured along the MFJD were discontinuous or patchy gradients from a site scale perspective and more continuous from a reach scale perspective. Results from Chapter 3 suggested that interpretations of longitudinal gradients are dependent on the type of community in question and the scale of observation used to determine those gradients.

While the RCC provided a template for considering how longitudinal patterns of in-stream community structure may be influenced by geomorphic, hydrologic, and other physical factors, little work has been done on the influence of trophic interactions affecting longitudinal trends in stream community structure. Chapter 4 examined potential bottom-up and top-down trophic relationships between the fish, macroinvertebrate, and algal communities along the longitudinal profile of the MFJD. In particular, this chapter focused on the relationships among: 1) fishes, macroinvertebrate scrapers, and algal biomass, 2) solar input, algal biomass, and macroinvertebrate scrapers, 3) canopy cover and macroinvertebrate shredders, and 4) fishes and macroinvertebrate predators. In addition, I explored how the interpretations of these potential trophic relationships would change according to different spatial scale perspectives. Although structures of fish and macroinvertebrate communities were correlated with distributions of potential predators and prey, there was only suggestive evidence of bottom-up relationships at the reach scale and little evidence of

consistent top-down controls among the communities at either reach or site scales in the MFJD. Trophic interactions may influence community structure in the MFJD at the within-site and micro-habitat scales, but it is suggested that at larger scales (i.e. site and reach) connectivity among communities prevents the expression of trophic controls along the longitudinal gradient.

Lastly, Chapter 5 explored large-scale hyporheic exchange in the MFJD, and the potential influence that it may have on longitudinal patterns of community structure. Stanford & Ward (1993) proposed that as a river flows downstream from an open, alluvial floodplain reach into a constrained reach, the subsurface-water from the floodplain is constrained and forced laterally and upward into the stream channel. These transitional points in the river are areas where the biotic community may show a strong response to upwelling. It was hypothesized that the MFJD would follow the proposed scenario of Stanford & Ward (1993) in which there would be large-scale subsurface water upwelling at sites located in the downstream end of unconstrained reaches, but not at sites in constrained reaches. In predicted upwelling sites greater rates of primary productivity, more algal biomass, higher macroinvertebrate diversity and abundance, greater benthic fish diversity, and fish with narrower diet breadths were expected than in non-upwelling reaches. Unlike observations of Stanford & Ward (1993), there was very little evidence of reach-scale, subsurface water upwelling associated with valley constriction in the MFJD, and there were no physical or biological discontinuities in the longitudinal profiles.

Few studies have considered this breadth of physical and biological components along such an extensive longitudinal profile of a stream. This study provides a unique and expansive foundation for multivariate examinations of stream communities. In addition, the approach developed in this study may be used to examine community structure in any ecosystem at multiple spatial scales. The spatial scope and breadth of measures in my study revealed how perceptions of stream gradients absolutely depend upon the spatial extent of our observations. This study illustrates that continuous and patchy aspects of both physical and biological parameters occur together in stream systems and are not mutually exclusive.

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APPENDICES

Appendix 1. Total number of each fish species collected at all sites in the Middle Fork John Day. Sites sampled more than one year are indicted by lower case letters (a = 1996, b = 1997, c = 1998). Number of passes refers to the number of 10m electro-fishing passes made within each site. Fish species are abbreviated such that RBT = rainbow trout (*Oncorhynchus mykiss*), CNS = chinook salmon (*Oncorhynchus tshawytscha*), TS = torrent sculpin (*Cottus rhotheus*), LND = longnose dace (*Rhinischthys cataractae*), MTS = mountain suckers (*Catostomus columbianus*), BLS = bridgelip suckers (*Catostomus platyrhynchus*), LAM = Pacific lamprey (*Entosphenus tridentatus*), SPD = speckled dace (*Rhinichthys osculus*), RSS = redside shiners (*Richardsonius balteatus*), and NPM = northern pike minnow (*Ptychocheilus oregonensis*).

		Fish Species									
Site	No. Passes	RBT	CNS	TS	LND	MTS	BLS	LAM	SPD	RSS	NPM
1	7	4	0	0	0	0	0	0	0	0	0
2	5	19	0	0	0	0	0	0	0	0	0
3	5	21	0	0	0	0	1	0	1	0	0
4	5	12	0	0	0	0	0	0	5	0	0
5	4	7	0	0	0	0	7	0	28	13	0
6a	4	9	7	18	0	4	2	0	17	6	0
6b	4	9	4	27	0	9	0	1	24	5	0
6c	3	8	9	9	0	0	3	0	10	7	0
7a	3	8	5	18	0	0	1	1	18	4	0
7b	3	7	2	18	0	0	1	0	21	0	0

Appendix 1. (cont.)

Site	No. Passes	RBT	CNS	TS	LND	MTS	BLS	LAM	SPD	RSS	NPM
8	4	5	4	9	0	0	1	2	14	1	0
9	4	5	8	19	0	0	0	0	18	6	0
10	4	1	0	2	0	0	0	0	13	0	0
11a	4	6	4	35	2	0	1	0	25	2	1
11b	9	4	9	51	5	0	0	0	28	3	0
11c	4	9	0	19	0	0	3	0	22	2	3
12a	4	4	2	16	4	0	0	0	10	1	0
12b	6	9	15	51	0	0	0	3	42	0	0
12c	4	2	3	37	3	0	0	0	14	0	0
13	6	5	9	56	0	0	0	1	34	55	0
14	10	4	9	80	3	0	0	0	47	0	0
15a	6	1	2	27	1	0	0	3	41	1	0
15b	7	1	2	35	1	0	0	4	46	1	0
15c	5	2	3	20	2	0	0	2	37	0	0
16	6	0	0	62	3	0	1	5	26	0	0

Appendix 1. (cont.)

Site	No. Passes	RBT	CNS	TS	LND	MTS	BLS	LAM	SPD	RSS	NPM
17a	4	0	0	14	2	0	0	0	24	1	0
17b	6	0	1	52	0	0	2	3	31	16	0
18a	8	2	2	50	5	0	0	0	37	9	0
18b	8	4	5	72	8	0	0	0	44	6	0
19a	9	1	0	29	2	0	6	12	30	12	3
19b	5	0	0	18	2	0	0	3	21	11	5
20	4	2	0	21	2	0	1	0	10	1	0

Appendix 2. Mean densities (no./m^2) of benthic macroinvertebrates collected at 20 sites in the Middle Fork of the John Day River during summer, low flow conditions 1996-98. Densities were averaged from 6 Surber samples taken at each site per sample date.

Site	1	2	3	4	5	6	6	6	7	7	8	9	10	11	11	11
Sample Year	1998	1998	1998	1998	1998	1996	1997	1998	1996	1997	1996	1996	1996	1996	1997	1998
Non-insect Taxa																
Juga	0	0	0	0	0	1671	456	745	405	386	0	0	0	0	0	0
Lymnaeidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physiidae sp.	0	0	13	18	140	866	346	109	5	29	206	20	8	11	11	222
Planorbidae sp.	0	29	0	0	840	193	0	2	0	0	25	5	327	51	45	440
Limpet sp.	0	0	0	0	27	112	0	0	4	0	38	16	50	11	0	11
Sphaeriidae sp.	131	99	5	619	513	409	47	16	22	25	144	20	14	2	11	32
Ostracods	1982	300	41	41	1573	191	63	197	9	13	536	97	54	0	0	36
Amphipods	122	61	25	276	47	169	25	57	104	9	474	400	0	9	0	0
Annelid sp.	7	0	7	13	0	0	4	0	0	0	0	0	0	0	48	39
Oligochaetes	127	79	13	314	1415	488	508	178	421	572	947	127	120	33	68	761
Hirudinoidea sp.	0	0	0	25	22	32	0	7	0	0	0	0	0	0	0	0
Mite sp.	538	388	100	267	533	1046	61	328	210	115	501	77	78	13	84	169
Ephemeroptera sp.	1184	533	258	239	151	3	395	190	0	282	0	355	118	82	108	45
Ameletus	59	2	5	7	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae sp.	588	542	457	474	798	12	1146	1733	592	651	1177	886	183	415	721	152
Acentrella	0	0	20	2	0	70	0	27	55	0	20	0	11	13	43	43
Diphetor	59	167	59	136	574	36	531	1222	126	578	156	219	379	145	447	183
Labiobaetis	167	18	108	65	97	156	393	314	223	99	276	588	208	200	486	111
Procloeon	16	41	14	23	63	0	0	0	0	0	0	0	0	0	0	9
Ephemerellidae sp.	273	181	18	11	36	7	2	0	0	5	0	16	34	72	154	34
Attenella	0	0	0	0	0	0	0	0	0	0	48	5	11	2	20	23
Ephemerella	0	4	0	0	0	0	0	18	0	0	0	0	0	0	34	0
Drunella	11	0	0	0	4	0	0	0	0	0	0	0	0	0	27	0
Serratella	61	18	0	22	43	0	0	0	0	0	0	0	0	0	0	0
Timpanoga	0	0	16	18	0	0	0	0	0	0	0	0	0	0	0	2
Heptageniidae sp.	50	79	54	88	13	61	34	0	16	83	0	22	62	34	178	2

Site	1	2	3	4	5	6	6	6	7	7	8	9	10	11	11	11
Sample Year	1998	1998	1998	1998	1998	1996	1997	1998	1996	1997	1996	1996	1996	1996	1997	1998
Cinygmula	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epeorus	0	0	14	22	0	0	0	14	7	11	4	0	77	12	179	99
Leucrocuta	0	2	45	25	0	4	4	11	0	0	0	4	9	20	38	22
Paraleptophlebia	43	502	59	102	461	48	154	84	34	278	34	97	72	11	5	13
Trichorythodes	0	0	0	0	0	170	90	314	42	161	187	208	63	7	0	79
Hexagenia	0	0	0	0	0	0	0	0	0	0	23	0	0	0	0	0
Plecoptera sp.	38	30	14	38	0	0	0	0	0	0	0	0	0	0	97	0
Capniidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chloroperlidae sp.	48	7	0	20	0	0	0	0	0	14	0	0	0	3	0	0
Suwallia	0	14	0	0	0	0	0	0	0	0	0	0	12	0	0	0
Sweltsa	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltoperlidae sp.	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yoraperla	0	126	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perlodidae sp.	41	7	29	11	0	65	4	0	0	0	0	0	102	4	34	13
Perlinodes	0	0	4	0	0	0	0	16	0	0	0	0	0	0	0	5
Setvena	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Skwala	0	0	0	11	0	36	34	39	5	25	0	5	127	39	97	14
Perlidae sp.	0	0	0	0	0	0	0	0	0	5	0	0	9	16	20	4
Acroneuria	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Calineuria	5	0	2	0	0	0	0	0	0	0	0	0	13	4	16	0
Claassenia	0	0	0	0	0	0	0	0	0	0	0	0	0	2	52	4
Hesperoperla	0	4	4	34	0	0	0	0	0	0	0	0	0	0	5	0
Nemouridae sp.	172	398	233	260	0	0	0	4	0	0	0	0	0	0	91	41
Malenka	0	303	25	72	52	0	5	0	0	0	0	0	0	0	0	0
Pteronarcys	0	0	0	0	0	0	2	4	2	0	0	0	2	0	11	2
Trichoptera sp.	4	5	9	0	0	0	0	0	0	0	0	0	0	0	0	2
Dicosmoecus	0	0	2	0	0	2	0	4	0	2	0	0	0	0	11	2
Glossosoma	0	0	0	0	0	4	48	23	0	39	0	14	163	31	217	38
Helicopsyche	0	0	0	0	0	0	0	0	0	0	0	7	0	0	32	9

Appendix 2 (cont.)

Site	1	2	3	4	5	6	6	6	7	7	8	9	10	11	11	11
Sample Year	1998	1998	1998	1998	1998	1996	1997	1998	1996	1997	1996	1996	1996	1996	1997	1998
Hydroptillidae sp.	0	0	0	0	43	54	4	11	294	65	1200	303	45	70	0	18
Hydroptilla	0	0	0	0	136	0	7	7	0	0	0	269	0	0	16	59
Leucotrichia	0	0	0	0	0	0	5	56	0	77	0	0	4	4	0	30
Hydropsychidae sp.	0	0	0	34	0	0	11	0	0	22	0	183	91	152	39	41
Cheumatopsyche	0	0	0	0	0	4	0	0	0	5	0	5	22	30	5	0
Hydropsyche	0	0	13	4	0	0	0	0	102	0	144	0	18	27	457	77
Brachycentrus	0	0	0	0	0	0	0	0	5	0	0	5	0	0	0	4
Micrasema	350	325	54	388	41	0	41	7	0	0	0	0	10	0	0	0
Psychoglypha	38	0	2	25	39	0	0	0	0	0	0	0	0	0	0	0
Rhyacophila	50	45	43	20	0	0	0	4	13	0	11	0	0	0	0	0
Philopotomadae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	75
Wormaldia	0	0	9	0	0	0	0	0	0	0	0	0	27	72	752	97
Polycentropidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polycentropus	4	2	48	5	0	0	0	0	0	0	0	0	0	0	0	0
Leptoceridae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostoma	52	29	113	83	66	0	11	0	0	0	11	39	205	167	29	138
Lepidoptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petrophila	0	0	2	0	0	0	0	0	0	0	13	0	64	6	0	4
Megaloptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sialis	0	2	9	4	22	11	20	5	10	16	0	0	0	0	0	0
Hemiptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corixidae sp.	0	0	0	0	285	10	25	20	0	0	0	5	0	0	0	0
Veliidae sp.	0	7	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Odonata sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
Cordulegaster	0	0	0	2	7	0	0	0	0	0	0	0	0	0	0	0
Gomphidae sp.	0	0	0	0	0	0	7	14	0	13	0	0	0	2	4	4
Ophiogomphus	0	0	0	0	0	26	9	7	18	5	32	5	0	2	0	9
Argia	0	0	0	0	0	0	13	7	7	22	160	43	5	2	0	22
Aeshnidae sp.	0	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0

Appendix 2 (cont.)

Site	1	2	3	4	5	6	6	6	7	7	8	9	10	11	11	11
Sample Year	1998	1998	1998	1998	1998	1996	1997	1998	1996	1997	1996	1996	1996	1996	1997	1998
Coenagrionidae sp.	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0
Coleopetera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brychius	0	0	0	0	0	21	5	0	0	0	65	0	0	0	0	0
Haliplus	0	18	5	4	0	4	0	0	0	0	0	0	0	0	0	0
Dytiscidae sp.	0	0	30	0	93	0	0	0	0	0	0	0	0	0	0	2
Hydrophilidae sp.	0	2	0	0	22	0	0	0	0	0	0	0	0	0	0	0
Hydraena	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elmid sp.	32	266	142	637	54	738	452	127	783	553	935	1285	691	433	570	61
Cleptelmis	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
Dubiraphia	0	0	0	0	0	44	0	5	0	0	0	0	0	0	0	0
Heterlimnius	11	0	0	0	0	6	11	0	0	11	0	5	9	8	22	0
Optioservus	5	106	165	416	66	369	447	608	224	1014	217	321	487	179	637	188
Heter/Optio (adult)	0	5	13	126	0	19	41	52	30	95	66	32	346	83	124	5
Zaitzevia	0	56	7	163	7	128	160	75	7	84	88	407	255	145	479	131
Ordobrevia	0	38	11	108	0	0	0	120	0	0	0	0	0	0	0	0
Lara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pshenididae sp.	0	0	0	0	0	0	0	0	2	0	0	0	38	17	18	14
Diptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antocha	0	7	50	63	5	0	0	20	16	56	11	5	53	36	83	113
Atherix	0	0	0	13	0	0	124	88	32	359	2	32	27	30	106	7
Ceratopogoninae sp.	25	16	4	34	39	2	0	7	7	9	0	0	0	0	0	5
Culicidae sp.	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixa	0	0	0	5	0	0	0	9	0	0	0	0	0	0	0	0
Empididae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Setacera	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Ptychoptera	0	0	0	79	0	0	0	0	0	0	0	0	0	0	0	0
Tabanidae sp.	0	0	0	43	30	0	0	0	0	0	0	0	0	0	0	0
Chrysops	0	0	0	0	0	10	0	0	0	0	0	0	5	0	0	0
Tipulidae sp.	11	0	4	2	0	0	0	0	0	11	0	0	0	0	0	0

Appendix 2 (cont.)

Site	1	2	3	4	5	6	6	6	7	7	8	9	10	11	11	11
Sample Year	1998	1998	1998	1998	1998	1996	1997	1998	1996	1997	1996	1996	1996	1996	1997	1998
Hexatoma	0	0	0	0	0	0	0	0	0	0	2	0	33	11	0	0
Chironomidae sp.	75	88	0	0	106	0	0	52	0	0	0	0	0	0	0	18
Chironominae	1645	305	170	296	1528	323	1270	757	199	1839	2415	775	238	20	57	93
Orthocladinae	1265	605	572	737	1787	1371	431	350	521	705	2971	1353	926	309	2097	509
Tanypodinae	314	260	327	535	465	107	262	102	95	337	2411	687	269	74	169	192
Tanytarsini	88	163	13	14	117	27	113	38	66	104	1037	102	127	17	18	9
Silvius	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0
Simulium	350	127	99	47	0	20	244	145	47	20	553	307	14	4	187	18
Total	10073	6433	3558	7135	12432	9154	8062	8351	4768	8801	17138	9361	6318	3143	9264	4603

Site	12	12	12	13	14	15	15	15	16	17	17	18	18	19	19	20
Sample Year	1996	1997	1998	1996	1997	1996	1997	1998	1997	1996	1997	1996	1997	1997	1998	1996
Non-insect Taxa																
Juga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lymnaeidae sp.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Physiidae sp.	36	27	0	14	0	43	0	12	0	4	0	0	0	0	0	0
Planorbidae sp.	41	16	20	89	0	65	4	0	0	13	0	0	0	5	4	0
Limpet sp.	7	27	14	2	0	27	0	0	0	0	0	0	0	0	0	0
Sphaeriidae sp.	18	0	22	5	0	151	23	45	7	5	0	0	5	5	7	0
Ostracods	13	29	70	0	120	106	83	105	11	13	25	0	4	25	7	0
Amphipods	0	0	0	0	2	0	0	4	0	0	0	0	0	0	2	0
Annelid sp.	7	0	0	7	0	0	0	4	0	0	0	0	0	0	0	0
Oligochaetes	39	262	834	256	160	3504	459	2107	91	203	104	54	83	739	352	11
Hirudinoidea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mite sp.	91	77	371	5	95	1033	120	244	362	43	382	57	222	474	277	5
Ephemeroptera sp.	341	605	133	19	75	22	90	153	86	111	396	160	13	115	95	100
Ameletus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae sp.	719	597	646	199	246	1015	389	251	296	176	181	484	244	190	149	167
Acentrella	70	43	149	2	57	334	50	44	48	5	27	156	84	38	28	41
Diphetor	257	508	623	143	99	1202	219	334	99	88	65	124	152	158	100	118
Labiobaetis	178	129	269	43	142	373	66	80	161	59	83	108	192	131	116	113
Procloeon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephemerellidae sp.	22	99	9	0	396	167	231	32	450	0	359	25	176	196	35	0
Attenella	0	5	11	0	0	13	0	49	0	5	0	0	0	0	30	7
Ephemerella	0	0	13	0	176	81	244	19	115	0	135	4	59	161	25	0
Drunella	0	22	0	0	93	7	20	0	27	0	0	0	0	5	0	0
Serratella	0	0	11	4	43	32	43	4	5	0	0	2	4	0	0	0
Timpanoga	0	0	0	0	5	0	4	0	0	0	0	0	0	0	0	0
Heptageniidae sp.	43	226	111	9	72	50	152	22	79	45	72	56	106	52	135	13
Cinygmula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epeorus	100	22	127	13	124	83	145	63	56	2	5	20	50	86	32	9

Appendix 2 (cont).

Site	12	12	12	13	14	15	15	15	16	17	17	18	18	19	19	20
Sample Year	1996	1997	1998	1996	1997	1996	1997	1998	1997	1996	1997	1996	1997	1997	1998	1996
Leucrocuta	7	0	48	16	99	48	30	18	11	20	70	7	4	27	13	5
Paraleptophlebia	5	39	22	39	88	43	109	89	11	154	7	11	0	61	39	2
Trichorythodes	0	0	39	75	0	129	0	17	0	179	0	23	0	0	22	13
Hexagenia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plecoptera sp.	14	38	65	0	13	0	109	110	91	0	4	0	25	47	22	0
Capniidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chloroperlidae sp.	0	5	0	3	16	0	14	4	11	7	63	0	4	5	2	0
Suwallia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sweltsa	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0
Peltoperlidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yoraperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perlodidae sp.	38	27	41	4	30	93	364	4	59	0	61	68	178	63	13	7
Perlinodes	0	0	43	0	0	111	0	4	56	0	32	0	56	29	2	0
Setvena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Skwala	41	111	36	46	11	100	50	18	59	29	30	52	39	39	4	11
Perlidae sp.	4	16	14	0	9	7	135	13	5	7	0	0	13	16	13	11
Acroneuria	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0
Calineuria	0	5	0	5	2	34	7	22	14	0	0	9	11	2	2	2
Claassenia	4	5	25	0	9	2	0	0	0	0	0	0	14	5	7	0
Hesperoperla	0	11	0	0	0	9	0	0	0	0	0	0	0	0	0	0
Nemouridae sp.	30	23	54	7	142	18	61	4	104	0	0	2	59	0	4	0
Malenka	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteronarcys	7	5	0	2	0	11	4	0	7	0	0	0	5	2	0	0
Trichoptera sp.	203	0	11	0	0	11	0	0	27	0	25	0	174	72	0	0
Dicosmoecus	2	7	0	5	16	11	13	9	14	14	14	7	0	5	2	2
Glossosoma	165	152	187	10	90	56	77	113	135	2	7	0	126	45	18	9
Helicopsyche	0	11	18	14	48	0	90	111	0	2	56	0	61	27	2	0
Hydroptillidae sp.	18	5	83	5	0	0	0	0	0	5	4	30	11	5	32	144
Hydroptilla	0	11	52	0	25	0	66	33	22	0	4	0	25	11	5	0

Site	12	12	12	13	14	15	15	15	16	17	17	18	18	19	19	20
Sample Year	1996	1997	1998	1996	1997	1996	1997	1998	1997	1996	1997	1996	1997	1997	1998	1996
Leucotrichia	23	109	258	0	0	29	0	4	0	0	0	0	0	0	4	0
Hydropsychidae sp.	269	316	84	33	36	2295	29	66	11	23	2	335	39	628	336	289
Cheumatopsyche	97	5	0	2	0	0	0	0	0	2	0	0	0	0	0	83
Hydropsyche	199	156	154	9	111	789	63	38	38	0	4	111	161	66	53	5
Brachycentrus	126	16	4	0	22	445	14	4	95	2	13	176	79	100	33	1037
Micrasema	2	4	0	0	0	11	0	4	0	0	0	0	0	0	2	0
Psychoglypha	0	5	4	0	0	2	0	0	0	5	0	0	0	5	0	0
Rhyacophila	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0
Philopotomadae sp.	0	0	43	0	0	0	0	4	0	0	0	0	0	0	13	0
Wormaldia	142	149	174	7	102	45	61	4	27	0	0	7	108	27	27	0
Polycentropidae sp.	0	0	0	0	0	·0	0	0	0	0	0	0	0	0	0	0
Polycentropus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptoceridae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostoma	355	1333	1270	535	32	2103	420	651	260	61	149	61	294	361	107	79
Lepidoptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petrophila	16	34	7	13	0	0	0	4	0	0	0	0	0	0	0	27
Megaloptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sialis	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0
Hemiptera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corixidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veliidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odonata sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordulegaster	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gomphidae sp.	2	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0
Ophiogomphus	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0
Argia	0	9	0	2	0	0	0	0	0	0	0	2	0	0	0	0
Aeshnidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coenagrionidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleopetera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2 (cont).

Site	12	12	12	13	14	15	15	15	16	17	17	18	18	19	19	20
Sample Year	1996	1997	1998	1996	1997	1996	1997	1998	1997	1996	1997	1996	1997	1997	1998	1996
Brychius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Dytiscidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elmid sp.	470	538	310	223	280	2881	545	214	705	337	578	425	475	592	239	117
Cleptelmis	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0
Dubiraphia	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Heterlimnius	2	48	16	2	100	0	152	4	47	39	52	7	38	34	11	4
Optioservus	226	563	465	363	662	784	906	416	624	142	621	27	373	339	351	52
Heter/Optio (adult)	32	91	111	63	109	235	90	45	57	25	54	108	109	57	29	43
Zaitzevia	106	443	685	48	838	576	518	424	484	213	364	133	694	797	499	115
Ordobrevia	0	0	0	0	0	0	0	4	0	0	0	0	0	11	13	0
Lara	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Pshenididae sp.	25	4	65	2	0	84	18	100	0	14	0	5	20	23	53	27
Diptera sp.	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0
Antocha	84	118	217	26	88	447	93	135	65	11	154	22	39	30	64	29
Atherix	50	70	70	19	43	346	170	132	0	9	22	9	14	4	34	0
Ceratopogoninae sp.	2	0	0	0	16	81	45	9	48	2	36	0	32	25	7	0
Culicidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empididae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Setacera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptychoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tabanidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0
Chrysops	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae sp.	0	11	14	0	5	11	7	13	63	4	50	0	29	47	22	0
Hexatoma	0	0	0	0	0	41	0	0	0	4	0	2	0	0	0	2
Chironomidae sp.	0	0	100	0	0	147	0	40	0	0	0	0	0	0	40	0

Appendix 2 (cont).

Site	12	12	12	13	14	15	15	15	16	17	17	18	18	19	19	20
Sample Year	1996	1997	1998	1996	1997	1996	1997	1998	1997	1996	1997	1996	1997	1997	1998	1996
Chironominae	29	183	495	62	212	190	405	256	384	126	364	29	1563	1491	132	36
Orthocladinae	456	908	1313	500	958	1055	370	831	587	75	386	152	823	486	524	962
Tanypodinae	74	282	86	67	231	239	169	206	90	25	147	20	43	160	91	74
Tanytarsini	25	38	59	23	145	380	104	91	34	2	61	13	70	66	11	22
Silvius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simulium	36	11	57	5	27	140	7	4	174	2	16	104	276	38	0	2
Total	5368	8611	10237	3071	6530	22463	7660	7847	6317	2316	5282	3208	7485	8229	4297	3791