AN ABSTRACT OF THE DISSERTATION OF

Christian E. Torgersen for the degree of Doctor of Philosophy in Fisheries Science presented on February 25, 2002.
Title: A Geographical Framework for Assessing Longitudinal Patterns in Stream Habitat and Fish Distribution.

Abstract approved _____

Hiram W. Li

New approaches are needed to quantify and understand spatial patterns of

stream fishes and their environment. Concepts in riverine ecology emphasize the

importance of thermal zones and gradual longitudinal changes in physical habitat and

biota, but little is known about spatial variability within the river continuum. I present

a conceptual framework for assessing patterns in streams that are difficult to detect

using standard site-based approaches to sampling. The ability to detect pattern is

defined as the scope, or the ratio of extent (the distance, area, or volume encompassing

all sample points) to grain size (the size of an individual sample unit). By increasing

the scope and continuity of sampling, I illustrate how greater sampling effort can

reveal new patterns and unexpected relationships between stream fishes and their

environment. Merging geography and stream ecology, I describe new approaches

including remote sensing, multiscale sampling, and extensive surveys for assessing

longitudinal patterns in stream habitat and fish distribution. Airborne thermal infrared

remote sensing was effective for quantifying spatially continuous patterns of water

temperature over a range of scales from channel units (10–50 m) to entire river sections (30–70 km). To examine factors influencing the spatial distribution of larval Pacific lamprey, a benthic fish species, I applied a nested sampling design and determined that stream habitat variables predicted patterns in larval abundance but played different roles at different spatial scales. Increases in the scope of data collection required adaptations in statistical analysis in order to accommodate larger and more complex ecological datasets. I evaluated multivariate ordination techniques with respect to their ability to describe fish community structure and found that non-parametric multivariate smoothing of presence–absence data was highly effective for detecting patterns in heterogeneous fish assemblage data. Spatially continuous analysis presented challenges in extracting patterns from noisy ecological data but provided the opportunity to evaluate distributional patterns over a range of spatial scales. I examined spatial variability of stream fish assemblages and observed that the relative influences of temperature and channel morphology on fish assemblage structure were dependent on the thermal context and the spatial scale of analysis.

A Geographical Framework for Assessing Longitudinal Patterns in Stream Habitat
and Fish Distribution

by

Christian E. Torgersen

A DISSERTATION

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<u>Doctor of Philosophy</u> dissertation of <u>Christian E. Torgersen</u> presented on <u>February 25, 2002</u>.

APPROVED:

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Major Professor, representing Fisheries Science

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Head of the Department of Fisheries and Wildlife

_____

Dean of the Graduate School

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.

_____

Christian E. Torgersen, Author

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CONTRIBUTION OF AUTHORS

Dr. Colden Baxter contributed to the ideas presented in Chapter 2 and assisted in the design and execution of analyses in Chapter 6. Mr. Russell Faux provided technical assistance and computer programming and helped develop the protocol for acquiring and interpreting thermal imagery in Chapter 3. Dr. Bruce McIntosh obtained funding and coordinated data collection for thermal remote sensing of stream temperature in Chapter 3 and provided input and field support for extensive fish surveys in Chapter 6. Dr. Nathan Poage helped design the system for analyzing spatially continuous patterns of stream temperature in Chapter 3. Project planning and organization for thermal remote sensing was provided by Mr. Douglas Norton through the U.S. Environmental Protection Agency, Advanced Monitoring Initiative. Mr. David Close assisted in study design, field sampling, and data interpretation in Chapter 4.

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Dedicated to Andy Moldenke for teaching me how much I don't know and encouraging me to continually ask new questions.

A Geographical Framework for Assessing Longitudinal Patterns in Stream Habitat
and Fish Distribution

CHAPTER 1

INTRODUCTION

New perspectives in riverine ecology stress the importance of viewing rivers

and streams as landscapes themselves, emphasizing discontinuities and heterogeneity

in the river continuum (Ward 1998a, Fausch et al., in press, Poole, in press). While

stream ecologists have been aware of the importance of landscape context for many

years (Hynes 1975), the need to understand spatial heterogeneity and scale in stream

ecosystems has been addressed only recently (Palmer et al. 1997, Cooper et al. 1998).

The dominant conceptual model for understanding large-scale longitudinal patterns in

lotic environments is the river continuum concept, which describes longitudinal

patterns in streams as continuous gradients in physical habitat and associated biotic

response from headwaters to downstream reaches (Vannote et al. 1980). Although not

stated directly, the implication of the river continuum concept is that longitudinal

patterns and processes are gradual. Therefore, other concepts have been proposed that

stress the importance of spatial and temporal variability in longitudinal processes

(Montgomery 1999, Rice et al. 2001). However, in theory, the river continuum

concept incorporates heterogeneity because longitudinal changes in abiotic and biotic

factors need not be gradual to be continuous (i.e., connected through an aqueous

medium). Differences between upstream and downstream reaches and boundaries

between geomorphic segments, reaches, channel units, and microhabitats may appear gradual or heterogeneous depending on the scale of observation (Frissell et al. 1986, Ward 1998b). Thus, our understanding of rivers and streams is largely a function of the manner in which we perceive them, i.e., how they are sampled (see Sale 1988). Typically, studies describe longitudinal patterns in streams as gradual because their sampling approaches are too coarse to quantify heterogeneity at finer scales (e.g., Rahel and Hubert 1991, Ward et al. 1994, Grubaugh et al. 1996).

Stream ecologists have recognized the importance of heterogeneity and scale in freshwater ecosystems but have not yet developed the sampling techniques necessary for assessing spatial variability in stream habitat and the distribution of aquatic organisms. Quantitative methods exist for identifying spatial variance and autocorrelation (Cooper et al. 1997), but there are few established procedures for collecting spatially continuous data in streams. The lack of spatial data on stream organisms is due, in part, to sampling difficulties. Aquatic environments are difficult to sample due to limitations in visibility and accessibility that are compounded by the high mobility of aquatic organisms (Giller et al. 1994). However, the logistical difficulties of sampling streams are minor compared to those encountered in marine research (Schneider 1994a). Thus, stream ecologists can benefit from applying methods already developed in oceanography and limnology to study longitudinal patterns in lotic environments (Ellis and Woitowich 1989, Hynes 1989, Kracker 1999).

Geospatial technology and remote sensing are easily transferable to the study of watersheds and stream networks but must be adapted to meet the needs and objectives of longitudinal analysis. From an aerial perspective, rivers and streams are much longer than they are wide and are quickly reduced to one-dimensional lines during the process of scaling up. The problem with representing a three-dimensional environment with a one-dimensional line is that fine-scale stream features cannot be easily depicted within the broader context of the landscape (Fausch et al., in press). However, when geographical methods are developed specifically for rivers and streams, remote sensing and geospatial technology can be highly effective for collecting and analyzing data over areas that are too large or too remote to sample efficiently on the ground (Isaak and Hubert 1997, Johnson and Gage 1997, Radko 1997). Remote sensing offers ecologists the opportunity to assess synoptic, high-resolution data over large areas but requires openness to new technology and a willingness to change study design (Roughgarden et al. 1991). More interdisciplinary research between remote sensing and stream ecology is needed in order to identify applications and develop methods that specifically address the questions and challenges of ecological studies (Matson and Ustin 1991).

Broad-scale patterns in stream habitat and channel morphology can be measured with aerial surveys, but assessing spatial patterns below the water surface is considerably more difficult. Spatially continuous surveys of stream fishes may require substantial changes in sampling methodology, with tradeoffs in precision for accuracy (Rahel 1990). The logistical challenge of quantifying longitudinal patterns in stream

habitat and fish distribution involves increasing the extent and resolution of sampling while minimizing the costs of data collection and the impacts on local fish populations. Electrofishing provides relatively precise estimates of fish abundance and community composition but is labor-intensive and costly to conduct continuously over long distances (Cowx 1990, Reynolds 1996). In streams with resident threatened and endangered species, it also may be necessary to minimize impacts on fish populations by using low-impact survey methods and limiting disturbance to short time periods (e.g., depletion electrofishing is often not permitted in streams with endangered salmonids).

The most feasible approach to surveying fish assemblages in long, continuous stream reaches involves a combination of underwater visual surveys and electrofishing at point locations to calibrate visual estimates of fish abundance (Roper and Scarnecchia 1994, Thurow and Schill 1996). In some cases, validation of visual survey data with electrofishing methods may not be possible due to management restrictions or limited access in roadless areas and private lands. Moreover, electrofishing methods are difficult to implement in 4th–5th-order streams that are often too shallow to sample from a boat and yet too deep for backpack electrofishing, potentially creating a gap in our understanding of stream fish assemblages in a large portion of the riverscape (Fausch et al., in press). Thus, the development of new approaches to sampling streams may result in significant payoffs in the additional knowledge gained by collecting data that can be analyzed across spatial scales,

providing a more complete picture of the links between ecological pattern and process in streams (Levin 1992, Wiens et al. 1993).

The following six chapters provide a geographical framework for assessing longitudinal patterns in stream habitat and fish distribution and illustrate the importance of quantifying spatial heterogeneity for understanding the ecology of stream fishes. Chapter 2 presents a conceptual framework (based on scaling theory) for using scientific methods and technology in a manner similar to innate pattern detection in humans to discern complex patterns in rivers and streams. Chapter 3 introduces a new method for assessing spatially continuous patterns in stream temperature using airborne thermal infrared remote sensing and describes the radiative and reflective thermal properties of flowing waters. Chapter 4 examines the influences of habitat heterogeneity on the spatial distribution of larval Pacific lamprey (*Lampetra tridentata*) in a mountain stream and describes a multiscale approach to sampling benthic fishes. Chapter 5 evaluates multivariate statistical analysis as a method for detecting community structure in spatially heterogeneous stream fish assemblages. Chapter 6 describes spatial variability in the distribution and habitat relationships of warm- and coldwater fishes with respect to patterns of stream temperature and channel morphology in three mountain streams with different thermal environments.

CHAPTER 2

PATTERN DETECTION, SCOPE, AND SAMPLING IN STREAMS

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ABSTRACT

New approaches are needed to detect ecological patterns that are too complex to evaluate using traditional sampling methods in streams. In this paper, we present a conceptual framework (based on scaling theory) for using scientific methods and technology in a manner similar to innate pattern detection in humans to discern complex patterns in rivers and streams. Standard scientific methods in stream ecology have typically approached pattern detection by inferring associations and relationships from a selection of representative sites. We propose that in order to detect complex, scale- and context-dependent patterns in streams we have to start looking for patterns in science the way we look for patterns with our eyes. Rivers and streams are especially difficult to visualize and sample in an extensive and spatially continuous fashion because aquatic organisms and the physical properties of flowing waters are essentially "invisible" and constantly in motion relative to the terrestrial observer. However, recent interest in ecological heterogeneity and scale has motivated stream ecologists to develop innovative approaches to sampling streams and has led to significant breakthroughs in our understanding of lotic environments. The ability to detect pattern in space or time, whether through our eyes or scientific methods, is defined as the *scope*, or the ratio of extent (the distance, area, or volume encompassing all sample points) to grain size (the size of an individual sample unit). By increasing both the scope and continuity of sampling, stream ecologists are filling in the gaps in a previously site-based methodology and providing a more spatially and temporally continuous picture of streams that complements existing methods of sampling and

analysis. We describe these new approaches, such as synoptic field sampling, extensive surveys, and remote sensing, and illustrate how increasing the scope of research can lead to discovery and new ecological understanding.

INTRODUCTION

The observation of patterns in nature and the development of general concepts for understanding and predicting natural phenomena is the essence of science (Levin 1992). Not surprisingly, the fascination with patterns and scientific explanation is inextricably linked to what we do as living organisms—consciously and unconsciously perceiving and responding to the patterns around us with speed, precision, and creativity. Our sensory systems are highly evolved for pattern detection, but because our most important sensing abilities tend to be automatic, they are either taken for granted or poorly understood. Therefore, much can be gained from evaluating the process of pattern detection in living organisms as a potential model for data collection and analysis in scientific research (Sale 1988). Pattern theory (originally described by psychologists) is now a major focus in computer science, information technology, and cybernetics, providing a context for applying the concepts of pattern detection in ecology (Watanabe 1985, Grenander 1996).

Investigation into the deceptively simple concept of pattern recognition yields interesting insights about a highly developed process in humans which is not fully understood. Patterns derive from order and structure and range, for example, from a random sequence of numbers (i.e., no pattern) to the completely regular crystalline

structure of a snowflake. Along the continuum between these two extremes, patterns can be described in terms of their complexity (Grenander 1996). The complexity of a pattern is determined by two factors: randomness, which tends to mask underlying structure and make a pattern difficult to replicate, and intricacy, defined as the number of interrelating parts or elements (e.g., the vertices in a crystalline structure or the number of terms in an algebraic equation). Some patterns appear complex but can be simply described and represented, such as fractals and natural laws in physics. However, many patterns in nature are both highly random and intricate and, therefore, not only appear complex but *are* complex (Grenander 1996). In ecology, patterns are complex because: (1) they are contingent on the organisms involved and their environment and (2) they cannot be reduced to basic principles and expressed mathematically as universal laws (Lawton 1999). Thus, the detection of patterns in ecology requires an approach that does not abstract patterns and processes from the context that gives them meaning. In the search for new patterns in ecology, we can use our own highly evolved sensory abilities (i.e., visual perception) as a model for detecting complex patterns in streams.

The goal of this paper is to pique the interest of ecologists, specifically stream ecologists, in the detection of patterns that are too complex to evaluate using reductionist approaches of measurement and analysis. We bring attention to the exceptional pattern detecting abilities of human vision and present a conceptual framework based on scaling theory (sensu Schneider 1994) for applying similar approaches in the study streams to facilitate our perception of new patterns worth

explaining (see Lawton 1996). Current trends in the study of rivers and streams indicate that stream ecologists are beginning to use creative approaches to fill in the gaps in a previously site-based methodology in order to provide a more spatially and temporally continuous picture of streams. We describe these new approaches and highlight how searching for patterns gives us new understanding of novel intellectual problems and provides a context for evaluating human impacts on aquatic ecosystems.

VISUALIZING PATTERNS IN STREAMS

Aquatic ecologists face the challenges of studying an environment in which a fluid, often opaque layer separates the terrestrial observer from the biotic and abiotic patterns of interest (Giller et al. 1994). While rivers and streams have certain advantages over terrestrial environments in terms of ecological analysis (e.g., relatively defined spatial boundaries and short response times), patterns in flowing waters are difficult to see and measure and are constantly in motion relative to the aquatic and terrestrial landscapes in which they are embedded. Moreover, in scaling up to obtain a broader perspective, the mosaic two-dimensional structure of streams at the scale of meters quickly becomes condensed into a one-dimensional line (or network of lines) at the scale of kilometers. The complexities of rivers and streams have fascinated ecologists for decades, but ecological theory is still dominated by the ideas of terrestrial ecology, in large part because riverine environments are so difficult to perceive and experimentally manipulate (Reynolds 1998). Fortunately, this leaves

stream ecologists creative enough to apply a wider range of methodological and epistemological approaches with much to discover (Fisher 1997).

Stream ecology has a rich background in spatially oriented concepts that are based on an intuitive understanding that comes from walking, floating, or driving along rivers and streams. As a testament to the highly developed pattern-detecting abilities of stream ecologists, many if not all of these concepts (see review by Lorenz et al. 1997) are based on limited data (Galat and Zweimueller 2001). Having never actually quantified spatially continuous patterns in streams, we still recognize at least in a general sense that (1) streams are composed of relatively continuous gradients in physical conditions and biological responses from headwaters to downstream reaches (Vannote et al. 1980), (2) a series of dams, or other physical disturbances, disrupt the continuity of downstream change in the riverine environment (Ward and Stanford 1983), and (3) lateral transport of nutrients and food between the river and floodplain links aquatic and terrestrial processes in riparian ecosystems (Junk et al. 1989, Gregory et al. 1991, Bayley 1995). In emphasizing a holistic, spatio-temporal perspective in four dimensions (Ward 1989), stream ecologists have embraced concepts derived from spatially continuous analyses of terrestrial environments, such as patch dynamics (Pringle et al. 1988), ecotones and connectivity (Bretschko 1995, Ward 1998b), and ecological heterogeneity and scale (Palmer et al. 1997, Cooper et al. 1998), and often sought to apply them in a spatially limited, site-based context.

A site-based sampling approach is an efficient and economical way to evaluate relationships that are simple enough to represent mathematically and test statistically.

However, a design in which the sampled area is small and sites are widely dispersed constrains one's natural abilities to detect complex patterns. The use of standard sampling approaches is not a matter of practicality or optimization for a given set of circumstances and objectives; in fact, sampling methods "are often based on tradition rather than on optimizing the data obtained per unit effort" (Norris et al. 1992). The recognition that one can *never* sample everything may even become a justification for not trying. Eventually, as in the story of the *Country of the Blind* by H. G. Wells (1913), the mode of perception influences the manner of thinking to the extent that a clearer picture of reality may no longer seem necessary or appealing. Thus, site-based measurement can lead to site-based thinking which in turn requires increasingly sophisticated statistical procedures in order to make up for limited data. It has been suggested that stream ecology may benefit from an infusion of geographical and spatial analysis methods already employed successfully in oceanography and fisheries research (Ellis and Woitowich 1989, Hynes 1989, Raffaelli et al. 1994). Still, it is important to recognize that techniques developed for mapping patterns in landscapes and large water bodies (Johnson and Gage 1997, Kracker 1999) require significant adaptation in order to resolve important instream features, not to mention biota (Fisher 1994). The change from a site-based towards a more spatially continuous view of streams requires not just a transfer of technology or an incorporation of readily available terrestrial GIS layers and spatial metrics into site-based statistical analyses but also a change in perspective that will lead to new ways of visualizing rivers and streams.

GRAIN, EXTENT, AND PATTERN DETECTION

Pattern is typically visualized as a two-dimensional design with recognizable structure or meaning (e.g., tartan plaid, or a human face). While this kind of pattern is actually quite complex compared to the one-dimensional equation of a line or the three-dimensional equation of a sphere, it is easy to imagine because one deals with a continuous stream of such visual patterns over the course of a lifetime. Therefore, for the purpose of illustration we focus on two-dimensional spatial pattern, but the principles discussed also apply in one, three, or four dimensions because all patterns have two basic components: *grain* and *extent* (Carpenter 1983, Wiens 1989). Grain is the size (distance, area, or volume) represented by an individual measurement or sample, whereas the extent is the distance, area, or volume encompassing all individual measurements or samples. Thus, the ability to *detect* a pattern is a function of both the grain and the extent of our perception (Wiens 1989). A particular pattern may be observed across a range of grain sizes and extents but is usually most apparent at a specific scale. A characteristic of ecological phenomena is that different patterns emerge at different scales. Therefore, determining the appropriate scale of an investigation may be less important than maximizing one's ability to detect patterns across a range of scales, particularly in poorly understood or traditionally undersampled aquatic environments (Sale 1998).

In scaling theory, the capacity to detect patterns at multiple scales is called the *scope*, or the ratio of extent to grain size (Schneider 2001). The concept of scope

proves especially useful in comparing the scaling qualities of natural phenomena, scientific instruments, experiments, and surveys (Schneider 1994). For example, the spatial scopes of a Landsat satellite image (30-m resolution) and the visual systems of a human (20/20 vision) and an eagle (Reymond 1985, Martin and Katzir 1999) are 3.8 x 10^7, 9.7 x 10^7, and 1.7 x 10^9, respectively. An eagle's ability to detect visual patterns is two orders of magnitude better than ours! Scope is actually more relevant ecologically than typical calculations of visual acuity—for example, resolving a small prey item may be important, but being able to *find* one in a complex environment is a different matter. Because scope is costly in a bioenergetic sense, the highly evolved visual systems of humans and raptors incorporate a two-stage, or foveal, design that simulates high-scope vision by interactively using high- and low-resolution portions of the retina to provide the detail (grain) and context (extent) necessary for pattern detection.

Scope ranges from one (i.e., no ability to detect patterns) to infinity and increases linearly or logarithmically with respect to changes in extent and grain size (Figures 2.1A and 2.1B, respectively). Simultaneous increases in extent and decreases in grain size lead to substantial improvements in scope compared to changes in only one or the other, particularly at extents greater than twice the grain size and at grain sizes between 20 and 40 percent of the extent (Figures 2.1A and 2.1B). Calculations of the scope of stream surveys can be made in one or two dimensions, but at the scale of kilometers it is often useful to condense two-dimensional survey data into a one-dimensional longitudinal profile. For linear features, the grain size is defined as the
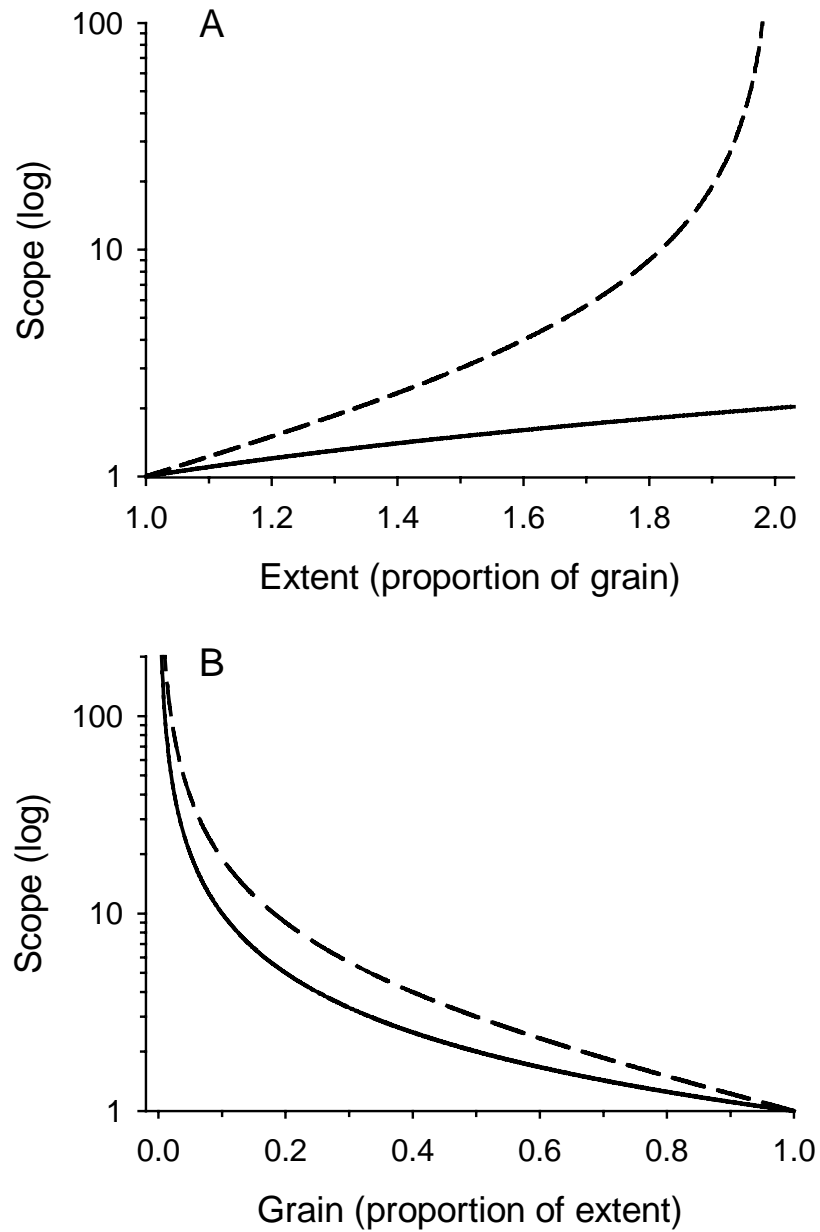
Figure 2.1. Changes in scope as a function of extent and grain. Horizontal axes indicate extent as a proportion of grain size (A) and grain size as a proportion of extent (B). Gradual changes in scope occur when one factor (extent or grain) is increased while the other is held constant (solid line). Simultaneous increases in extent and decreases in grain size lead to substantial improvements in scope (dashed line).

length of a sample unit, whereas the extent is the length of the surveyed reach (Figure

2.2A). When sample units are not contiguous, as in site-based sampling, one must

also consider the inferred component of the survey, i.e., the uncertainty that arises

from incomplete sampling (Figure 2.2B). Schneider (1994) describes this inferred

component as the *magnification factor*, which is the inverse of the ratio of the number

of samples, relative to the scope or potential number of samples. For example, in

Figure 2.2 the scopes of spatially continuous versus site-based sampling are 22 and 16,

respectively, and the magnification factor of site-based sampling is four times that of

the spatially continuous design. Partitioning the scope into measured and inferred

components is particularly useful for comparing complex research designs in which

the tradeoffs in scope are not intuitively apparent due to varying extents, grain sizes,

and sampling fractions (for more examples see Schneider 1994).

In evaluating new patterns or determining the range of scales over which

ecological processes operate, it is helpful to maximize the scope. However,

underlying structures typically emerge at specific scales beyond which further

increases in scope contribute little relevant information. Thus, the challenge for

ecologists is to detect these thresholds and design subsequent studies and experiments

accordingly. Changes in scope as a function of grain and extent are best illustrated

with visual examples (Figures 2.3 and 2.4). Depending upon the structure or question

of interest, relatively small changes in scope can have large impacts on one's ability to

detect pattern. For example, the golden stonefly nymph (*Hesperoperla pacifica*) in

Figure 2.3 is unrecognizable at a scope of 117 (Figure 2.3A) but after a twenty-five-
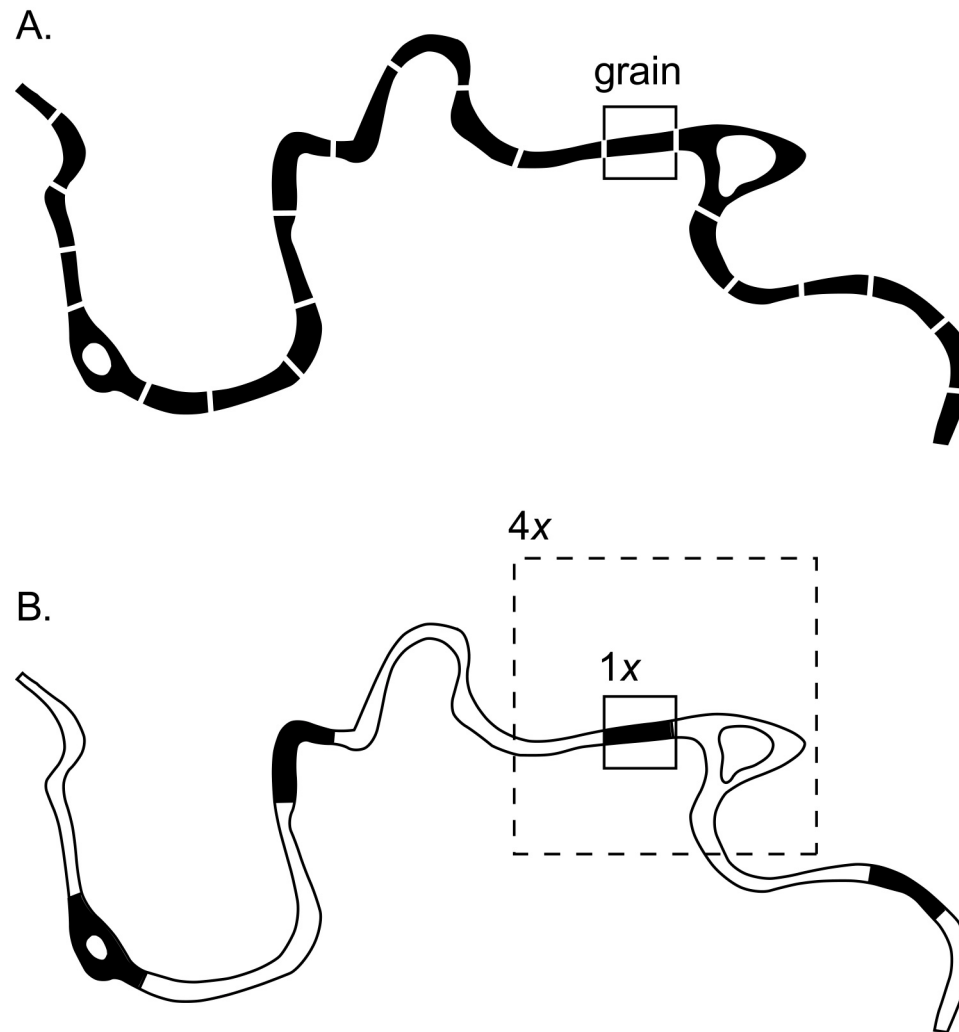
Figure 2.2. Grain and extent in spatially continuous (A) versus site-based (B) sampling in a conceptualized stream section. The grain (solid box) is defined as the length (x) of a sample unit (filled in black), and extent is the length of the surveyed stream section from the first to the last sample unit inclusive (e.g., $22x$ and $16x$ for Figures 2.2A and 2.2B, respectively). The magnification factor (dashed box) for site-based sampling (B) is four times that of the spatially continuous design (A).

A.

B.

C.

S = 117

S = 260

S = 726

D.

E.

F.

S = 2,904

S = 11,616

S = 289,956
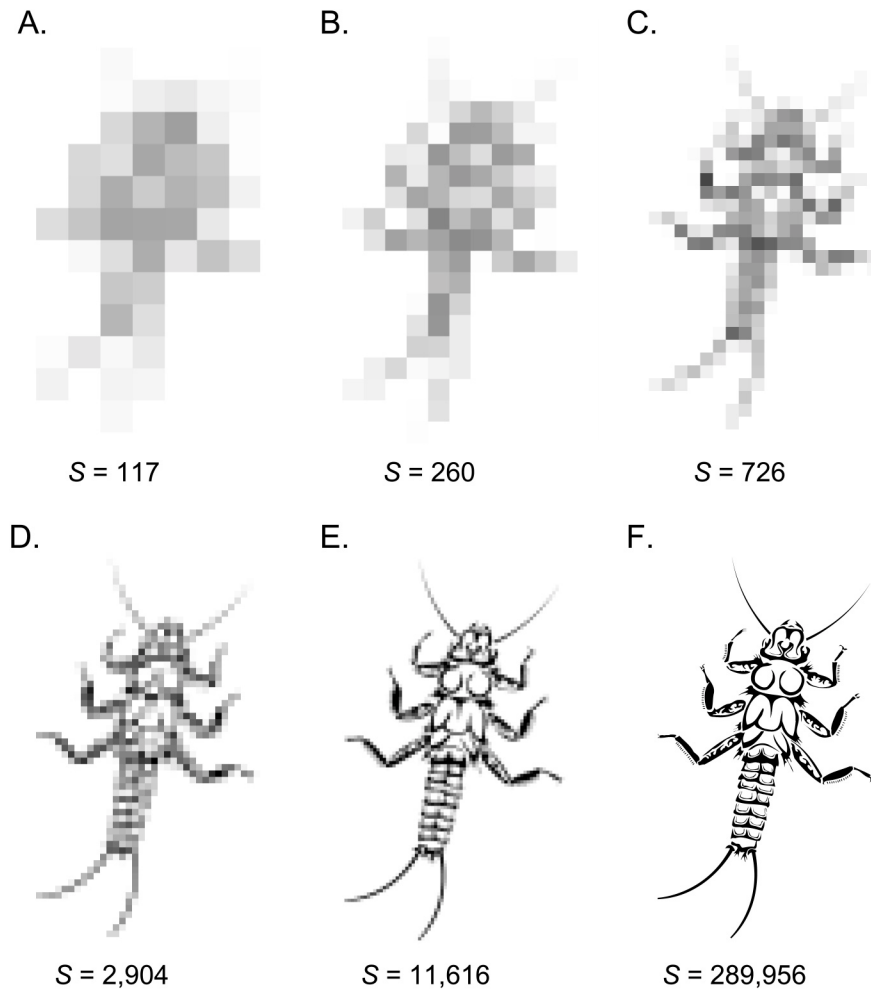
Figure 2.3. Detection of two-dimensional pattern at varying grain sizes. Scope (S) calculations are based on grain sizes of $(2,478x)^2$ (A), $(1,115x)^2$ (B), $(399x)^2$ (C), $(100x)^2$ (D), $(25x)^2$ (E), and $(1x)^2$ (F). To simulate a more natural image it may be helpful to smooth the pixel transitions by viewing the images through slightly squinted eyes. Golden stonefly nymph (*Hesperoperla pacifica*) illustration by J. Giersch.

A.   B.   C.

$S = 144$ $S = 209$ $S = 250$

D.   E.   F.

$S = 28$ $S = 390$ $S = 9,880$
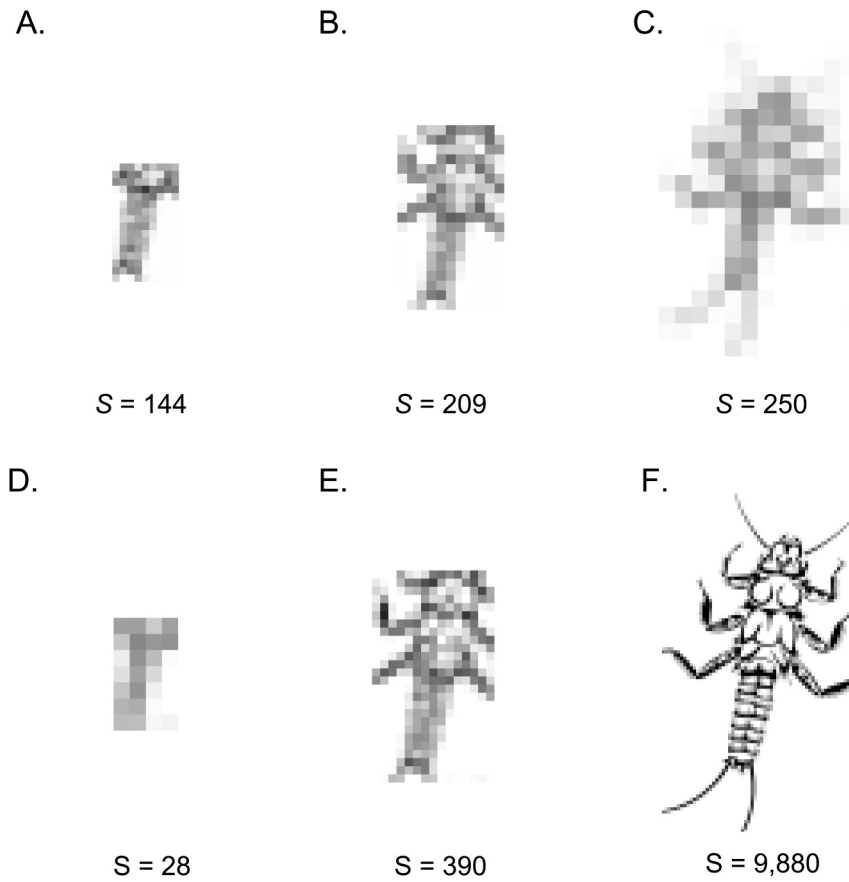
Figure 2.4. Effects of varying extent and scope on the detection of two-dimensional pattern. Enlargement of extent accompanied by relatively small improvements in scope contribute little new information but may confirm the presence of known patterns at larger scales (A, B, C). In contrast, simultaneous increases in extent and scope maximize one's ability to detect new patterns at multiple scales (D, E, F).

fold increase in scope the dominant pattern emerges (Figure 2.3D). After the

appropriate scale is identified, further increases in scope by two orders of magnitude

contribute little additional information on the pattern of interest (e.g., taxonomic

classification to genus or species levels). In more complex subjects, such as a

preserved specimen, new patterns continue to emerge with increasing scope.

As scientists, we are used to thinking that increases in extent necessitate

increases in grain size due to logistical constraints (Wiens 1989). This is due in part to

the way our eyes and other optical instruments function (e.g., zooming in with a

microscope or telescope). However, as logistical constraints themselves are defined

by researchers, it is ultimately psychological factors that constrain the scope of

ecological research—if scientists wanted to increase spatial and temporal scope they

would do so. In site-based studies, the process of "scaling up" usually refers to an

increase in extent with minimal or no increases in scope (i.e., increasing the number of

sites) often accompanied by large increases in magnification factor (Figures 2.4A–

2.4C). Increases in extent without significant changes in scope give the impression of

increased ability to detect pattern, but only because one knows what to look for

(Figure 2.4C). While such an approach is useful for detecting the presence of known

physical geographic gradients (e.g., temperature, precipitation, soil type, etc.), studies

of this type are unlikely to detect human impacts or identify new ecological patterns at

intermediate scales. For example, the general outline of the stonefly nymph in Figure

2.4C becomes more apparent at larger extents but reveals no additional information at

intermediate scales without simultaneous increases in scope (Figure 2.4F). If the

scaling properties of a system are poorly understood and the objective is to develop

rather than confirm existing ecological models, the added costs of increasing both

resolution (i.e., the inverse of grain size) and extent may be justified by the dramatic

improvements in scope that result from additional sampling effort (Figures 2.4D–

2.4F). In most cases, new technology and possibly less precise approaches to data

collection will be required in order to significantly increase the scope of ecological

research in rivers and streams (Townsend 1996).

Scope, Perception, and Lotic Environments

Ecologists retain a strong connection to the innate pattern-detecting abilities

that have proven so useful in recognizing complex patterns. In fact, the concept of

scope and its association with new discoveries is implicit in the natural sciences. This

is clearly evident in biogeography, demonstrated first by Darwin (1859)—who used

technology (a sailing ship) and the geological record to expand the extent of his

observations and detect patterns at scales vastly exceeding his own life span—and

later by MacArthur and Wilson (1967) in developing the theory of island

biogeography. The complementary skills of both scientists, R. H. MacArthur the

mathematician, and E. O. Wilson the taxonomist and zoogeographer, led to a

serendipitous merging of both kinds of pattern seeking and contributed substantially to

ecological theory. New discoveries often result from increasing the extent and

resolution of our perception. In mapping the large-scale structure of the universe,

Geller and Huchra (1989) decided to examine a dark region where nothing could be seen, and instead of mapping just a thousand galaxies as had been done before, they mapped many thousands. The patterns of the famous "stickman" structure that emerged brought about a change of perspective in astronomy and opened the door to new explanations for the origin of structure in the universe (see synopsis by Jablow 2001). While a simple increase in the scope of stream research may not have such profound implications for our understanding of the universe, there is equal potential for scientific discovery in traditionally undersampled aquatic environments (Giller et al. 1994).

New approaches for sampling lotic environments

The scale of resolution chosen by ecologists is probably the most important decision made in a research program because the number of samples influences financial decisions and methodology as well as the inferences that may be drawn from a study (Dayton and Tegner 1984). Thus, in designing field surveys effectively "a choice has to be made between a traditional measurement method, with known characteristics, and a newer method with greater capacity but less well known performance" (Schneider 1994). Depending on the environment (in this case streams), certain abiotic and biotic variables lend themselves more easily to high-resolution, spatially continuous sampling than others. For example, the degree to which a variable changes over time and the ease with which it can be measured determine the method of data collection (Figure 2.5). Variables that are transitory or difficult to
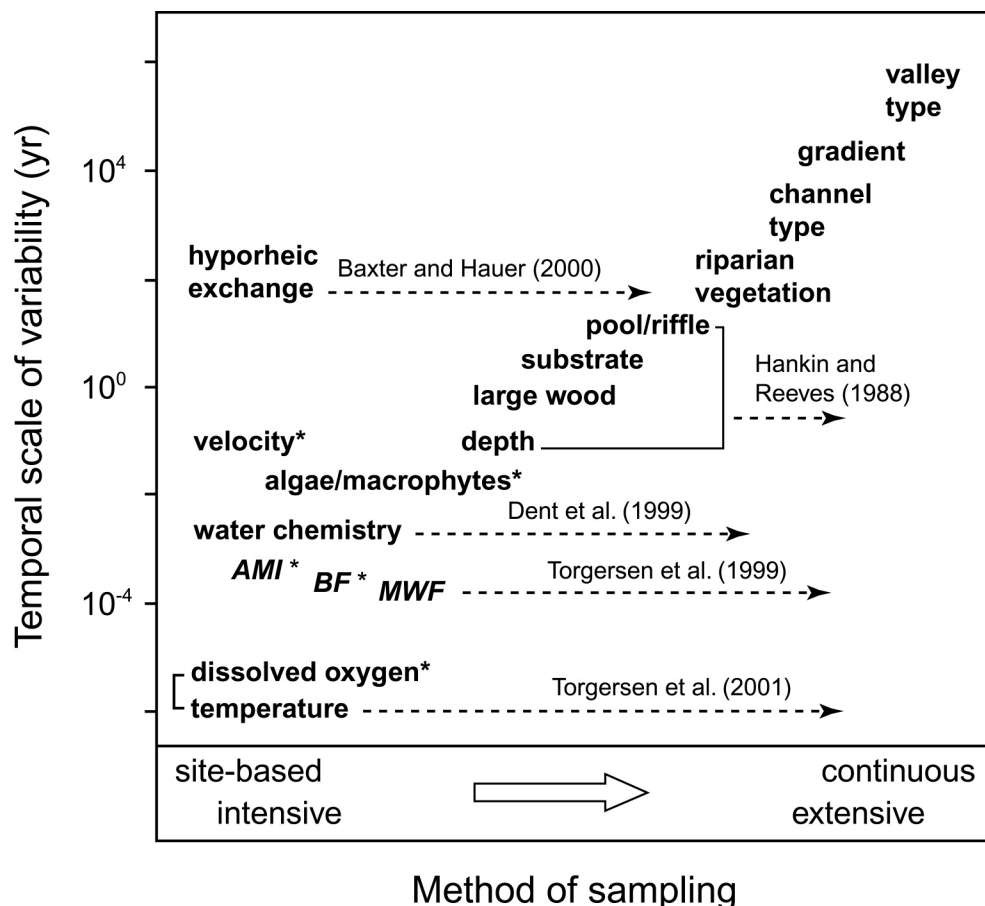
Figure 2.5. Sampling methods and temporal variability of biotic and abiotic variables commonly measured in streams. The position of measured factors with respect to the horizontal axis indicates the sampling method typically applied in data collection. Position with respect to the vertical axis indicates the transitory nature of measured factors and the relative ease of obtaining synoptic samples. Mobile organisms (bold italics), including aquatic macroinvertebrates (AMI), benthic fishes (BF), and mid-water fishes (MWF), and abiotic factors (e.g., discharge, substrate, large wood, etc.) vary over a range of temporal scales; thus, their position with respect to the temporal axis represents an average sufficient for general comparison. By applying more extensive methods, such as visual estimation and aerial mapping, or employing large numbers of field technicians, researchers have come closer to spatially continuous analysis for certain biotic and abiotic variables (dashed arrows). Variables that change rapidly over short time scales or are difficult to measure extensively require new, as of yet undeveloped methods of data collection (*).

measure, such as water chemistry, hyporheic exchange, macrophytes, velocity, and temperature, are typically sampled using a site-based approach, whereas large-scale geomorphic variables such as valley form, river sinuosity, and bedform morphology change gradually over time and are easy to quantify continuously from maps and aerial photographs. Unfortunately, a site-based approach provides little flexibility for evaluating spatial dynamics at multiple scales, so it is not surprising that the scaling properties of many important biotic and abiotic factors in streams are poorly understood. However, recent interest in heterogeneity and scale has motivated stream ecologists to develop novel solutions to sampling streams and has led to significant breakthroughs in our understanding of lotic environments.

The measurement of patterns in water chemistry and nutrient concentration presents major methodological challenges in flowing waters. Large numbers of samples must be collected simultaneously over a large area and then analyzed (often in replicate) in the laboratory within a relatively short period of time. In spite of these difficulties, there are ways to solve the sampling problem in streams. For example, by increasing the number of field technicians and by taking advantage of recent technological developments in analytical chemistry, it is possible to dramatically increase the scope of stream water analysis. In probably the most exhaustive study of spatial and temporal dynamics of nutrient concentrations ever conducted in streams, Dent et al. (1999) employed 10–14 people to collect near-simultaneous water samples every 25 m over a 10-km stream segment (a spatial scope of 10,000 with a magnification factor of 25). Not only did this approach provide a relatively

continuous longitudinal profile of nutrient concentration over time (multiple surveys were conducted), but it also provided the flexibility to analyze spatial variability in nutrient concentration using a sliding scale of grain sizes (Dent et al. 2001). In another equally groundbreaking study of turbidity and specific conductance in a glacial floodplain stream, researchers were able to evaluate shifting patterns in the physico-chemical riverscape over time (Malard et al. 2000).

In studies that incorporate spatial and temporal components, the overall capacity of each design to detect pattern can be evaluated by comparing respective scopes and magnification factors. For example, Dent et al. (1999) conducted 3 surveys (3 hours each) over a period of 665 days (a temporal scope of 5,320 with a magnification factor of 1,773). For comparison, the temporal scope of the study by Malard et al. (2000) is 4,393 with a magnification factor of 258 and the spatial scope and magnification factor are 20,000 and 154, respectively. While Dent et al. (1999) had a greater ability to detect spatial patterns, Malard et al. (2000) provided a better temporal perspective. Compared to studies of similar geographic extent, the scopes and magnification factors of both studies are exceptionally high and low, respectively, for stream research, and thus have high potential for detecting new, as of yet undiscovered patterns at multiple scales.

Remote sensing provides a solution to the sampling problem in streams by providing synoptic, spatially continuous data at resolutions typically unattainable through direct on-site measurement (Roughgarden et al. 1991). Imagery collected at various spatial and temporal resolutions and extents places physical and biological

processes in streams within a larger context in which patterns and relationships can be evaluated more effectively (Ellis and Woitowich 1989, Johnson and Gage 1997). While aerial photography and satellite imaging have been used by ecologists for decades, primarily as cartographic tools, more interdisciplinary research between remote sensing and ecology is needed in order to identify applications and develop methods that specifically address the questions and challenges of ecological studies (Matson and Ustin 1991). The advantages of remote sensing over traditional, on-site data collection methods are that (1) scope is maximized by collecting high-resolution data over a large area at relatively low cost (compared to field sampling), (2) patterns and relationships may be easily analyzed at multiple spatial scales, and (3) a photographic record is produced that facilitates objective assessment of environmental change over time. In recent years, there has been a dramatic increase in the use of remote sensing in ecological studies of large rivers and streams (Mertes, in review). In large part, this is due to the development of airborne digital sensors that provide the spatial resolutions (≤ 1 m) necessary for quantifying fine-scale instream features. Moreover, with the availability of low-cost digital cameras, video camcorders, and photo editing software there has also been a general increase in the recognition that continuous data collection is feasible. For example, even wadable streams and small rivers can benefit from innovative sampling approaches such as portable underwater and shore-based video mapping techniques that link videography to a global positioning system (GPS) and allow rapid evaluation of spatially continuous ecological datasets (Stohlgren et al. 2000). With the proliferation of emerging, as of

yet untested new technologies, it will also be important to conduct studies that identify the accuracy and limitations of remote sensing approaches (Edwards et al. 1998).

Airborne multispectral remote sensing and videography have been used effectively to quantify fine-scale geomorphic and riparian land cover changes (Bryant and Gilvear 1999) and evaluate hydrogeomorphic features such as pools, riffles, large wood, and bar formation (Crowther et al. 1995, Wright et al. 2000). By developing procedures to measure and classify stream characteristics directly from aerial imagery, researchers not only avoid the problems associated with observer bias (see Poole et al. 1997) but also dramatically increase the potential for describing and predicting the spatiotemporal dynamics of fluvial processes. In a recent paper on channel morphology in a glacial stream, Zah et al. (2000) used color infrared stereo aerial photography to create a digital elevation model of channel slope and bank inclination (2-m horizontal resolution; spatial scope = 14,000), which provided the physical template for analyses of riparian vegetation density and inputs of allochthonous organic matter. Similar techniques for evaluating three-dimensional structure in streams and riparian areas have even been developed using airborne light detection and ranging (LIDAR), which incorporates laser technology and a highly accurate GPS to map fine-scale topographic features (Fleece 2000).

Remote sensing technology also gives ecologists the ability to map wavelengths of light and sound that are invisible or difficult to detect with our own biological sensory systems. For example, airborne thermal infrared remote sensing provides a "picture" of stream temperature that cannot be obtained through visual

observation or direct measurement (Torgersen et al. 2001). Increases in the scope of

temperature measurement (0.1-m spatial resolution, scope = 500,000) have been

particularly effective in evaluating the response of stream fishes to thermal

heterogeneity (Torgersen et al. 1999) and in developing a conceptual model for

understanding temperature dynamics and the mechanisms of human-caused thermal

degradation in streams (Poole and Berman 2001). Standard photometric remote

sensing methods do have limitations in aquatic environments because water is semi-

transparent or opaque in large portions of the electromagnetic spectrum. However,

hydroacoustic remote sensing offers aquatic ecologists the opportunity to "see"

spatially continuous patterns beneath the water surface. Because our understanding of

large- and even medium-sized rivers is limited in large part by ineffective sampling

methods (Hynes 1989, Galat and Zweimueller 2001), hydroacoustic methods (e.g.,

side-scan sonar, underwater videography, and acoustic Doppler current profiling) can

provide invaluable information on bottom topography, benthic community structure,

substrate composition, water velocity, and patchiness in fish distributions in large river

systems (Duncan and Kubecka 1996, Edsall et al. 1997).

Riverscape perspectives of stream organisms and habitat

Spatial context, patchiness, and continuity in stream organisms and

environmental factors are recognized as key components of an emerging perspective

of the riverscape—a riverine mosaic of physical and biological patterns unfolding

through time (Townsend 1996, Ward 1998a, Fausch et al., in press, Poole, in press).

The idea of the riverscape holds promise for developing a more complete picture of stream ecosystems; however, a problem with applying the concept in the study of aquatic organisms is that spatially continuous measurements of stream biota are extremely difficult to obtain. This is due primarily to the time-consuming and labor-intensive processes of electrofishing and benthic invertebrate sampling, not to mention the processing of samples in the laboratory. However, in spite of the inherent difficulties of sampling organisms that are both difficult to see and often highly mobile, stream ecologists have made significant advances in the last few years towards describing and understanding riverscape patterns and processes.

Fish ecologists have the advantage that their study organisms are large enough to identify and count visually in the field and often can be evaluated indirectly through the presence of spawning redds. In fact, given the interest—and inclination towards the physical exertion of walking, snorkeling, or crawling along many kilometers of stream—spatially continuous data collection in fisheries research is actually quite feasible in low-turbidity systems. In a study on thermal refugia and chinook salmon (*Oncorhynchus tshawytscha*) in mid-order streams, Torgersen et al. (1999) used a combination of snorkeling, thermal remote sensing, and habitat surveys to map the distribution and abundance of adult salmon with respect to spatial patterns in water temperature and stream habitat in over 120 km of stream (a spatial scope of 12,000 with a magnification factor of 1). Stream habitat surveys now commonly conducted in fisheries research (see Hankin and Reeves 1988) incorporate visual estimation techniques with statistical correction of observer bias to collect high-resolution, low-

precision habitat data (e.g., channel unit type and dimensions, substrate composition, and large wood) over hundreds of river kilometers and have proven effective for assessing spatial and temporal trends in fish habitat (McIntosh 1995, for a cautionary note see Poole et al. 1997). Other ecological studies have used spatially continuous and multiscale approaches to explain the relationships between salmonid spawning behavior, hyporheic exchange, and geomorphology (Baxter and Hauer 2000, Fukushima 2001). The high cost of spatially extensive field research typically precludes the collection of data over time; thus, a temporal perspective is often lacking in spatially explicit fisheries research. However, by choosing a smaller study area and shortening the temporal extent it is possible to balance spatial and temporal scopes and thereby retain the capacity to detect patterns at multiple scales. For example, in an investigation of spatial and temporal dynamics in a population of Arkansas darters (*Etheostoma cragini*), Labbe and Fausch (2000) sampled darters and pool habitat over time (a temporal scope of 1,100 with a magnification factor of 183) in a 15-km reach (a spatial scope of 1,500 and a magnification factor of 1). In maximizing the scope of biological surveys, it may be necessary also to collect data less intensively (e.g., visual estimation, presence–absence, or relative abundance) or use a less rigorous technique in which greater sampling density may account for the reduced precision of individual sample units (Vadas and Orth 1993).

Visualizing patterns in stream invertebrate distribution is especially difficult because extensive sampling techniques commonly applied in fisheries are not easily transferable to benthic research. However, recent work on spatial variation in stream

invertebrate community structure indicates that ecologists are developing innovative study designs and sampling approaches to meet these challenges (Palmer et al. 2000, Rice et al. 2001). Recognizing the importance of habitat heterogeneity in the streambed landscape, Palmer et al. (2000) applied a nested design of four sample grids (20 x 6 m, with contiguous 1-m^2 cells) to evaluate the effects of patchiness and the spatial arrangement of sand and leaf substrates on colonization patterns and the abundance of stream invertebrates. While the spatial extent of the actual "landscape" was quite small, the continuity of measurement resulted in significant improvements in spatial scope (4,500) and magnification factor (9) over previous work in stream invertebrate ecology. In another study on longitudinal patterns in fluvial geomorphology and the spatial distribution of macroinvertebrates, Rice et al. (2001) collected 430 kick samples along a 25-km reach (a spatial scope of 25,000 and a magnification factor of 58) and were able to relate macroinvertebrate community structure to geographic patterns in sediment source dynamics and the distribution of tributary junctions.

Once the underlying structure of a given ecosystem has been described using high-scope methods, it is useful to design studies that incorporate sampling and experimentation at several predefined scales. Multiscale designs enable the researcher to match the scale of observation to the scale of the ecological phenomena in question and thereby identify not only how large-scale processes constrain small-scale results but also how small-scale processes integrate to produce large-scale patterns (Cooper et al. 1998). The number of studies that apply such an approach has increased

dramatically in recent years and is a testament to the power of multiscale models for

explaining spatial relationships in fishes (Fausch et al. 1994, Poizat and Pont 1996,

Thompson et al. 2001a), benthic communities (Azovsky et al. 2000, Li et al. 2001),

riparian vegetation (Johnson and Covich 1997), and riverine floodplain diversity

(Arscott and Ward 2000). Still, it is important to stress that a multiscale design is

most effective if it is preceded by surveys of sufficient resolution and extent to detect

underlying ecological patterns. These methods need not be sophisticated to provide

the necessary scope for pattern detection; for example, walking, snorkeling, or floating

along the length of a stream is a high-scope technique that provides significant insights

into the important ecological patterns and processes operating in a given system (for

an extraordinary example see Quammen 2000).

Extensive and intensive sampling for monitoring ecological change

Collecting spatially extensive, high-resolution biological datasets in streams is

time-consuming and costly, but once completed, spatially extensive surveys provide

the context for selecting a smaller number sites for intensive study. Extensive

sampling surveys tend to be coarse in spatial and temporal grain because the resources

and time required to collect data over large areas are limited, whereas intensive

surveys are typically finer in spatiotemporal grain and focus on temporal trends and

small-scale processes (Conquest and Ralph 1998) (Figure 2.6). In this respect,
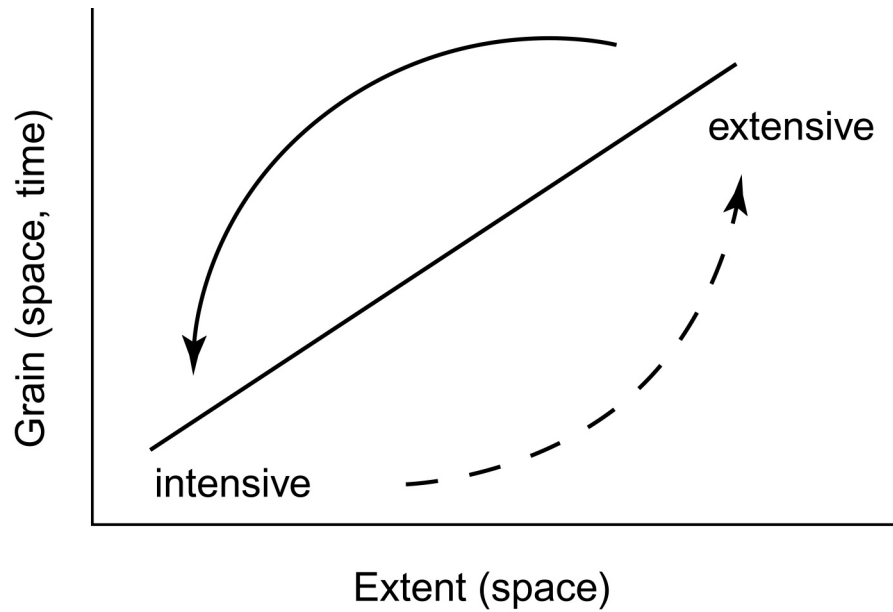
Figure 2.6. The relationship between spatiotemporal grain and the spatial extent of sampling and the complementary nature of extensive and intensive surveys. Increases in spatial extent typically require increases in the spatiotemporal grain of surveys because intensive data collection is costly and time consuming. A combination of extensive and intensive sampling approaches provides an effective alternative to collecting high-resolution spatial and temporal data over long distances and time periods. Extensive surveys provide a spatial context for selecting intensive monitoring sites (solid curved arrow), whereas intensive studies provide the information required to interpret the temporal context of extensive surveys (dashed curved arrow).

extensive and intensive methods are complementary. Extensive surveys provide a spatial context for selecting intensive monitoring sites, whereas intensive, site-based studies provide the information required to interpret the temporal context of spatially extensive surveys (see conceptual diagram in Figure 2.6). A recent example of extensive and intensive sampling approaches applied in water quality monitoring is the use of spatially extensive airborne thermal remote sensing combined with temporally intensive instream thermographs to monitor stream temperature (Faux et al. 2001).

Ecological data collected in surveys are often used to evaluate human impacts on ecosystems and monitor environmental change. However, ecological data may be gathered at specific, and usually small, spatial scales without the intent of representing a larger area. Thus, the challenge of monitoring programs is to detect ecologically relevant change beyond merely tracking the status and trends of individual sites (Bradshaw 1998). Some researchers have suggested that the solution to the problem of sample representativeness lies in monitoring environmental quality at larger "landscape" scales (O'Neill et al. 1997). However, as discussed earlier, an increase in extent only gives the impression of a greater capacity to detect pattern, whereas simultaneous increases in both resolution *and* extent provide the context and scaling flexibility necessary for detecting important but subtle ecological changes (Ralph and Poole, in press).

Ecosystem science and long-term ecological research offer perhaps the most integrated approach to assessing complex patterns by explicitly defining the importance of context and the limitations of site-based thinking. For example,

Gregory et al. (1991) state that "perspectives based on isolated components are ecologically incomplete" and Swanson and Sparks (1990) stress that "the significance of research results is difficult to interpret if a site's context in space [and time] is not understood." Still, in the ecological literature, particularly in stream ecology, the practical aspects of sample representativeness and pattern detection are rarely discussed and usually emphasize the importance of an informed selection of sites and scales (Wiens 1981, Rabeni et al. 1999, Poole, in press). Unfortunately, the level of sampling required to make such an informed selection is rarely attained, so sample locations are usually selected based on tradition, convenience or, at best, on stratified random design (Peterson et al. 1999). As the need increases to monitor ecological change and evaluate human impacts on aquatic systems, questions are also being raised about the problems of site-based analysis techniques for sorting out variation in ecological versus geographical factors (Dunham and Vinyard 1997, Ham and Pearsons 2000, Van Sickle and Hughes 2000, Ralph and Poole, in press). Although probability-based sampling and standard methods of statistical analysis still have much to contribute to ecology and resource management, a broadening of approaches is needed to better quantify complex patterns and advance ecological understanding.

THE SEARCH FOR PATTERNS IN ECOLOGY

Progress in ecology often results from integration or merging of different perspectives (Fisher 1997). In fact, by virtue of coincidence or juxtaposition, contrasting and even conflicting perspectives often lead to serendipitous findings and

ecological breakthroughs (Olson and Gosz 1999). Renewed interest in patterns and

complexity in ecological relationships (Lawton 1996, Lawton 1999) reflects an

emerging view of ecology that "deals in novel discoveries, establishes new contexts

for existing information, and integrates both into established knowledge" (Pickett et al.

1994). Ecologists have again recognized the need to search for new patterns worth

explaining after three decades of applying statistically rigorous experimental and

reductionist methods in an attempt to make ecology a more "predictive" science

(Smallwood 1993). Certain analytical approaches have taken such precedence in

science (e.g., sampling theory and the falsification method of hypothesis testing) that

an incorporation of other epistemological perspectives is needed. For example, the

"new" philosophy of science as outlined by Pickett et al. (1994) considers multiple

model disciplines beyond classical physics and maintains a pluralistic view of science

that is especially applicable to the complexity of pattern and causality in natural

systems.

Elucidation of the causal mechanisms underlying observed patterns in ecology

is clearly a daunting task. However, by developing ways to evaluate how scales of

information affect our understanding of complex processes, we can begin to sort out

the problems of perception and pattern in determining cause and effect (Sale 1988,

Poole, in press). Ecological topology—recently identified as a frontier of ecology—

provides precisely this kind of understanding by applying the concepts of scope and

context to characterize the spatial and temporal bounds of ecological patterns

(Thompson et al. 2001b). We now have the tools, technology (e.g., remote sensing

and geographic information science), and conceptual framework to describe and understand interactions among ecological phenomena across scales (Levin 1992). However, as ecology is "a science of contingent generalizations, where future trends depend on past history and on the environmental and biological setting" (May 1986), considerable increases in the scope of ecological sampling is still needed to untangle the many factors influencing the distribution and abundance of organisms (Thomson et al. 1996) and, perhaps most importantly, to provide a catalogue of interesting patterns that will be invaluable to ecologists of the future.

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CHAPTER 3

AIRBORNE THERMAL REMOTE SENSING FOR WATER TEMPERATURE ASSESSMENT IN RIVERS AND STREAMS

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ABSTRACT

Airborne remote sensing methods are needed to assess spatial patterns of stream temperature at scales relevant to issues in water quality and fisheries management. In this study, we developed an airborne remote sensing method to measure spatially continuous patterns of stream temperature and evaluated the physical factors that influence the accuracy of thermal remote sensing of flowing waters. The airborne thermal infrared system incorporated an internally calibrated thermal imager (8–12 μm) aligned with a visible band camera in a vertically mounted, gimbaled pod attached to the underside of a helicopter. High-resolution imagery (0.2–0.4 m) covering the entire channel and adjacent floodplains was recorded digitally and georeferenced in-flight along 50- to 60-km river sections ranging from 2 to 110 m in width. Radiant water temperature corresponded to kinetic water temperature (5–27°C) in a range of stream environments within ±0.5°C. Longitudinal profiles of radiant water temperature from downstream to headwater reaches provided a spatial context for assessing large-scale patterns of thermal heterogeneity and fine-scale thermal features such as tributaries and groundwater inputs. Potential sources of error in remote measurements of stream temperature included reflected longwave radiation, thermal boundary layer effects at the water surface, and vertical thermal stratification. After taking into account the radiative properties of the surrounding environment and the physical qualities of the stream, thermal remote sensing proved highly effective for examining spatial patterns of stream temperature at a resolution and extent previously

unattainable through conventional methods of stream temperature measurement using in-stream data recorders.

INTRODUCTION

Water temperature in rivers and streams has been identified as a critical element in the restoration of freshwater aquatic ecosystems and the recovery of salmon in the Pacific Northwest region of the United States (Nehlsen et al. 1991, NRC 1992, Naiman et al. 1995, McCullough 1997). As an index of water quality, stream temperature reflects watershed and stream corridor conditions and directly influences the biology of aquatic organisms (Beschta et al. 1987). To promote improvements in water quality and protect threatened and endangered aquatic biota, Section 303d of the Clean Water Act (United States Congress 1977) requires states and the U.S. Environmental Protection Agency to maintain a list of stream segments that do not meet water quality standards. In response to federal requirements, some states have established specific stream temperature standards to identify rivers and streams in which water temperature exceeds the thermal tolerances of native species of salmon and trout (Boyd and Sturdevant 1997). Stream temperature monitoring presents challenges for water resource managers charged with the task of administering many kilometers of streams that flow through public and private lands. Conventional methods of stream temperature measurement using in-stream data recorders provide information that is temporally continuous but spatially limited. Spatial data are

needed to map sources of thermal heterogeneity at the watershed scale and identify

biologically important areas such as thermal refugia (Torgersen et al. 1999).

Remote sensing methods for monitoring stream temperature can alleviate

problems of access to private lands and provide a spatial context for evaluating

relationships between land use and water quality. Stream temperature patterns are

influenced by multiple land-use practices that remove riparian vegetation and alter

channel morphology and streamflow (Holtby 1988, LeBlanc et al. 1997, Johnson and

Jones 2000). The response of stream temperature to landscape change is difficult to

predict, and as a consequence, considerable debate exists about the relative influence

of various land management practices on stream temperature (Larson and Larson

1996, Beschta 1997, Zwieniecki and Newton 1999). However, integration of spatial

data in stream temperature models will be useful for validating models and

understanding the effects of land management practices on stream temperature

(Norton et al. 1996, Chen et al. 1998a, Chen et al. 1998b).

Applications of TIR remote sensing have been important in obtaining sea

surface temperature measurements for oceanographic and meteorological applications

(Smith et al. 1996, Jessup et al. 1997). In addition, freshwater applications of TIR

remote sensing have been conducted to map surface temperature and circulation

patterns in lakes (LeDrew and Franklin 1985, Lathrop and Lillesand 1987, Anderson

et al. 1995, Garrett and Hayes 1997), model heat dispersion in thermal effluent plumes

(Schott 1979, Jensen et al. 1988, Davies et al. 1997), and identify subsurface springs

(Roxburgh 1985). However, few studies have been conducted with the explicit

purpose of mapping patterns of water temperature in riverine environments because

concerns about elevated stream temperatures and the implications for coldwater fishes

have only recently been raised (Atwell et al. 1971, Belknap and Naiman 1998,

Torgersen et al. 1999).

Airborne thermal infrared (TIR) remote sensing has potential for addressing

current needs in water resources science for spatial assessment and monitoring of

stream temperature. The application of remote temperature measurement in rivers and

streams is a relatively recent development and has proven effective for assessing

stream temperature patterns in relation to habitat use by salmon (Belknap and Naiman

1998, Torgersen et al. 1999). However, in spite of the applicability of remote sensing

technology to stream temperature measurement there has been no comprehensive

description of either a method or the physical factors that influence remote sensing of

flowing waters since the development of airborne digital thermal imagers (Atwell et

al. 1971). In this study, our objectives were to: (1) develop an airborne thermal

remote sensing method to measure spatially continuous patterns of water temperature

in rivers and streams, (2) assess the temperature accuracy of aerial thermography in

varied riverine environments and identify the sources of error in thermal imagery of

flowing waters, and (3) evaluate the potential of airborne thermal remote sensing for

assessing spatial heterogeneity in stream temperature at multiple scales ranging from

high-resolution imagery of tributary confluences and groundwater inputs (0.2–0.4 m)

to longitudinal profiles of entire river sections (50–60 km).

METHODS

Thermal remote sensing of water temperature

Remote measurements of water temperature are made with a sensor that detects thermal radiation (3–5 μm and 8–14 μm wavebands) emitted from the upper 0.1 mm of the water surface (Atwell et al. 1971, Anderson and Wilson 1984, Robinson et al. 1984). We define the temperature of the water surface measured remotely with a thermal sensor as the radiant water temperature (T_r) as opposed to the kinetic water temperature (T_k) measured 10 cm below the surface with a thermometer. Radiant water temperature measurements are representative of T_k when the water column is sufficiently mixed and thermal gradients have not formed as a function of depth.

The factors that influence measurements of T_r are emissivity, atmospheric absorption, TIR reflection, and surface characteristics (Smith et al. 1996). Emissivity describes the actual absorption and emission properties of the water surface and is expressed as a ratio of the emittance from the water surface at a given temperature to that from a black body at the same temperature (Avery and Berlin 1992). Because water has an emissivity very close to 1.0 and a high thermal inertia, it is relatively easy to obtain measurements of T_r compared to land surfaces. Atmospheric effects can be corrected based on water vapor content and transmission along the target sensor path, but TIR reflections can complicate precise temperature measurement because a thermal sensor measures longwave radiation that is both emitted and reflected from the water surface (Anderson and Wilson 1984, Schott 1994). Thus, emitted radiation

transmits temperature information from the water surface itself as well as reflected radiation from the surrounding environment (Figure 3.1).

Airborne TIR system

Thermal imagery in the 8–12 μm wave band was collected with a Thermovision 1000 forward-looking infrared (FLIR) system (FLIR Systems). The scanning array thermal imager used built-in blackbody temperature references to continuously calibrate the HgCdTe multi-element detectors. The FLIR thermal imaging system incorporated 12-bit signal processing and was capable of detecting noise-equivalent temperature differences of ±0.2°C.

Visible spectral band imagery (0.4–0.7 μm) was collected with a VX-1000 digital video camera (Sony Electronics) with a 3-chip charge-coupled device (CCD) imaging system. Thermal and visible cameras covered the same ground area with a 20° x 13° field-of-view and an image size of 600 x 400 pixels. The two sensors were aligned for vertical view in a gyro-stabilized, gimbaled pod attached to the underside of a Bell 206B-3 helicopter. Thermal images were collected digitally and recorded directly from the sensor to an on-board computer at a rate of 1 frame/s. At this rate, the FLIR system stored digital imagery at a rate of 2.5 gigabytes/h. Digital image files represented the full 12-bit dynamic range of the sensor and were tagged with acquisition time and differentially corrected geographic position data provided by a Trimble aeronautical global positioning system (GPS). Visible band imagery and acquisition time were recorded to an on-board digital video recorder at a rate of 30
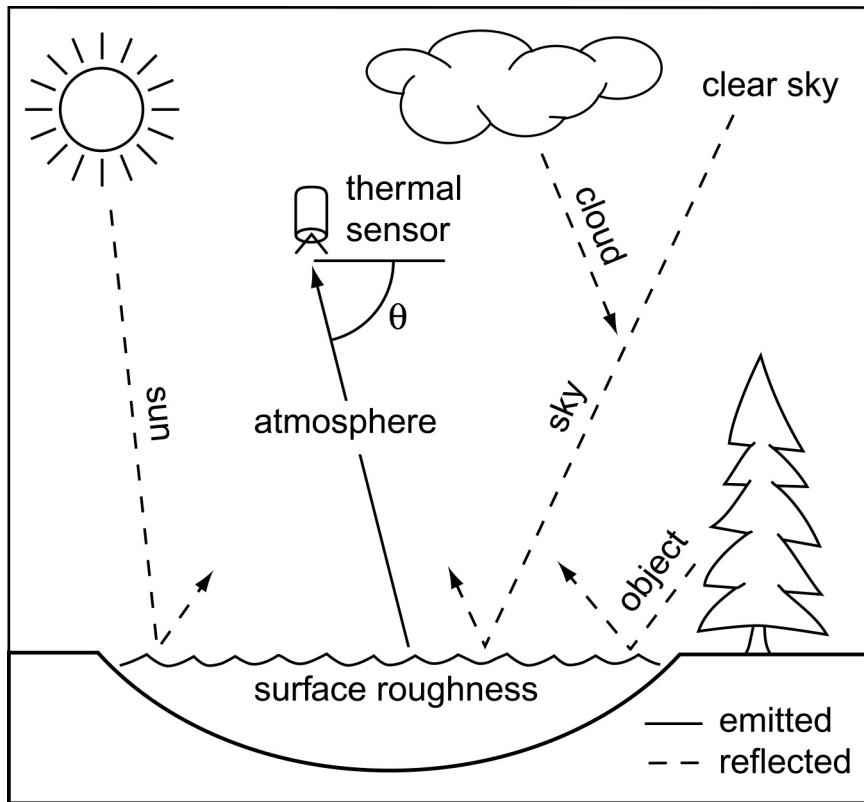
Figure 3.1. Sources of emitted and reflected TIR radiation in thermal remote sensing of rivers and streams.

frames/s. Downlinks of Greenwich Mean Time (GMT) from the GPS synchronized data collection to the nearest second and provided a means of correlating thermal and visible band imagery during post-flight image processing.

TIR data collection

The objective of aerial thermography was to examine patterns of T_r during summer low streamflow conditions. We conducted thermal overflights on cloudless days in late July through early September at times that coincided with maximum daily stream temperatures. Peak daily stream temperatures occurred at 14:00–18:00 in the afternoon, approximately halfway between land-water thermal crossover periods (Fagerlund et al. 1970). Meteorological data on air temperature, relative humidity, cloud cover, and surface winds were collected at local airports before, during, and after overflights and from U.S. National Weather Service remote automated weather stations distributed throughout the survey area.

Airborne thermal remote sensing at low altitudes required coordination between the helicopter pilot, navigator, and FLIR operator. Real-time GPS positioning and flight plan software provided map information necessary for locating start and end points of stream survey sections. Fine-scale adjustments of the flight path and altitude were made visually by the pilot in cooperation with the FLIR operator and navigator. Aerial surveys were conducted in an upstream direction. Flight altitude and speed varied depending on stream width, sinuosity, and valley configuration. Low-altitude aerial surveys along the streams required constant

compensation for land surface elevation change as a function of stream gradient. Radar altimetry was essential for maintaining, adjusting, and recording sensor height above ground level (AGL). Typical flight altitudes of 300–700 m AGL provided imagery with ground resolutions of 0.2–0.4 m sufficient for measuring T_r in streams and side channels 2–110 m in width. Ground speeds were maintained at 50 km/h over narrow, sinuous streams and increased to 90 km/hr over wide, straight rivers. Speeds in this range ensured approximately 40–60% overlap between image frames stored at a rate of 1 frame/s. To avoid image blur in the CCD digital video imagery, the speed of the aircraft was reduced at very low sensor heights.

Images from the thermal sensor were stored digitally with each pixel containing the radiance value measured by the detector. Thermal radiance values were converted to temperatures using Planck's radiation law and sensor calibration curves (Atwell et al. 1971). Radiant water temperatures were adjusted for the emissivity of natural water (0.96) and corrected for atmospheric transmissivity and ambient reflections using the LOWTRAN-7 atmospheric simulation model with inputs of air temperature, relative humidity, and path length (Kneizys et al. 1988, Schott 1994). The converted images were ultimately stored in a format in which each pixel contained a temperature value rounded to the nearest $0.1^{\circ}C$. Thermal imagery was color-coded to visually enhance temperature differences and facilitate interpretation of thermal patterns.

Study areas and field measurements

Field data used in this study were collected in watersheds representing a wide range of riverine environments in western and eastern Oregon (44–46° N, 117–123° W). Rivers and streams selected for thermal survey included the upper McKenzie River (western Oregon), the Middle and North forks of the John Day River, the North Fork of the Malheur River, and the Wenaha River (all in eastern Oregon). We surveyed moderate- to fast-flowing mountain streams (0.3–1.1 m/s average velocity) in canyons and alluvial valleys that ranged in elevation from 300 to 2000 m and had gradients of 0.4–2.0% (Table 3.1). Surveyed stream sections contained straight, meandering, braided, and anastomosing channel types that averaged ≈ 0.5 m in depth in all streams except for the McKenzie River, which was significantly wider and deeper than all other streams (Table 3.1). Canopy cover from conifer and broadleaf riparian vegetation ranged from completely closed (i.e., no measurements of T_r could be made) to wide open and was variable in extent and composition within and among the streams surveyed. Differences in regional climate, relative humidity (15–30%), and canopy cover type and extent among streams provided varied environments in which to assess the effectiveness of airborne TIR remote sensing for stream temperature assessment.

Ground-truth measurements were collected simultaneously with thermal overflights to compare T_k to T_r recorded in the imagery. Ground-truth measurements of T_k were made with submersible digital temperature recorders (Onset, accuracy ±0.2°C) programmed to sample T_k once every minute and positioned in the well-

Table 3.1. Physical characteristics of streams surveyed with airborne thermal remote sensing.

Stream	Section characteristics				Channel characteristics		
	Valley type [a]	Length (km)	Elevation (m)	Gradient (%)	Channel type [b]	Width (m)	Depth (m)
McKenzie River	cc, ac	45	300 – 650	0.8	s, m	15 – 110	0.2 – 6.0
Middle Fork John Day River	ac, av	70	1000 – 1300	0.4	s, m, a	3 – 15	0.1 – 3.0
North Fork John Day River	cc, ac	70	850 – 1750	1.3	s, m	5 – 30	0.2 – 4.0
North Fork Malheur River	cc, av	55	1000 – 2000	2.0	s, m	2 – 10	0.1 – 2.0
Wenaha River	cc, ac	45	500 – 850	0.8	s, m, b	4 – 30	0.2 – 4.0

[a] Valley types in survey streams included colluvial canyons (cc), alluviated canyons (ac), and alluvial valleys (aw) (Frissell 1992).
[b] Channel types observed are classified as straight (s), meandering (m), braided (b), or anastomosing (a) after Selby (1985).

mixed portion of the stream water column. Post-flight measurements of thermal

stratification were collected in deep pools and spring-fed side channels 10 cm below

the surface and 10 cm above the stream bottom with calibrated digital thermometers

(Atkins) and an immersible, stainless steel thermocouple (VWR Scientific) accurate to

$\pm 0.1°C$.

To evaluate variations in T_k as a function of water depth, thermal stratification

measurements were collected during the following year under similar seasonal and

diurnal conditions as thermal overflights. We identified areas of potential thermal

stratification in the thermal imagery and measured surface and bottom T_k in 1 x 1 m

grids across the water surface at a total of 5 sites in the Middle Fork John Day River,

Granite Creek (a tributary of the North Fork John Day River), and the Wenaha River.

To assess the temporal dynamics of thermal stratification, we sampled thermal

transects in the morning and afternoon on several different dates under both clear and

cloudy weather conditions.

TIR data analysis

Point pattern maps of thermal surveys were constructed in a geographical

information system (GIS) to provide a template for sampling and displaying

longitudinal T_r patterns in each stream section. A computer program was used to scan

sequential thermal image files and extract time and geographic coordinate information

to create a map of image collection points. Thermal and visible image pairs were

linked to points and sampled directly within the GIS environment. In producing

spatially continuous profiles of T_r, thermal image frames were analyzed individually

as opposed to image composites or mosaics. Values of T_r were sampled manually

from each thermal image in the main stream channel at 10 points in each image.

Sample points were selected in each image by evaluating fluvial characteristics to

identify areas of main stream flow and avoid partially submerged rocks and large

woody debris. Sample median of T_r (T_{rs}) for each image was automatically calculated

from the 10 sample points and updated in the GIS spatial database. Digital

hydrography data (1:100,000 scale) provided the map template for longitudinal

analysis of T_{rs} patterns in the study streams. The route-measure or river km system

was employed to record the locations of thermal image collection points along the

longitudinal stream profile. Route-measure coordinates of image collection points

were expressed as cumulative distance upstream from the river mouth.

Analysis of thermal image sequences at multiple spatial scales required the

integration of longitudinal profiles of T_{rs}, maps of image collection points, and

individual image frames. Coarse-scale sources of thermal heterogeneity were

identified in longitudinal profiles and located on point pattern maps of aerial surveys.

Individual image points were then queried to visually inspect thermal imagery and

locate sources of cold- or warm-water inputs. Fine-scale temperature patterns in

thermal image frames were examined and compared with hydrologic features and

channel morphology in visible spectral band imagery.

Values of T_{rs} were compared with ground-truth measurements to assess the

relationship between airborne TIR measurements and T_k. We calculated the average

absolute difference and standard error between measurements of T_k and T_{rs} collected during each overflight for four survey years. Linear regression was used to assess the statistical relationship between T_k and T_{rs}. To examine the relationship between the frequency distribution of temperature pixels within the stream channel and ground-truth measurements, we computed histograms of pixel frequency versus T_r in streams of different width and compared population median radiant water temperature (T_{rp}) and T_{rs} to measurements of T_k.

We assessed thermal stratification and its potential for introducing error in remote sensing of water temperature by comparing bottom and surface T_k at 5 sites during the years following thermal overflights. Bottom-surface temperature differences were calculated for each 1 x 1 m sampling grid. Thermal stratification was then estimated by comparing the proportion of temperature differences $\geq 0.2°C$ among sites under different environmental conditions. Plots depicting the spatial distribution of bottom-surface temperature differences were constructed to compare the patterns of T_k with thermal imagery collected the previous year.

RESULTS

Spatial patterns of radiant water temperature

Profiles of T_{rs} versus distance upstream provided a spatially continuous representation of longitudinal patterns in stream temperature in the McKenzie River and the Middle Fork John Day River (Figure 3.2). Tributary confluence T_{rs} plotted where the tributaries enter the main stream channel indicated where and to what extent
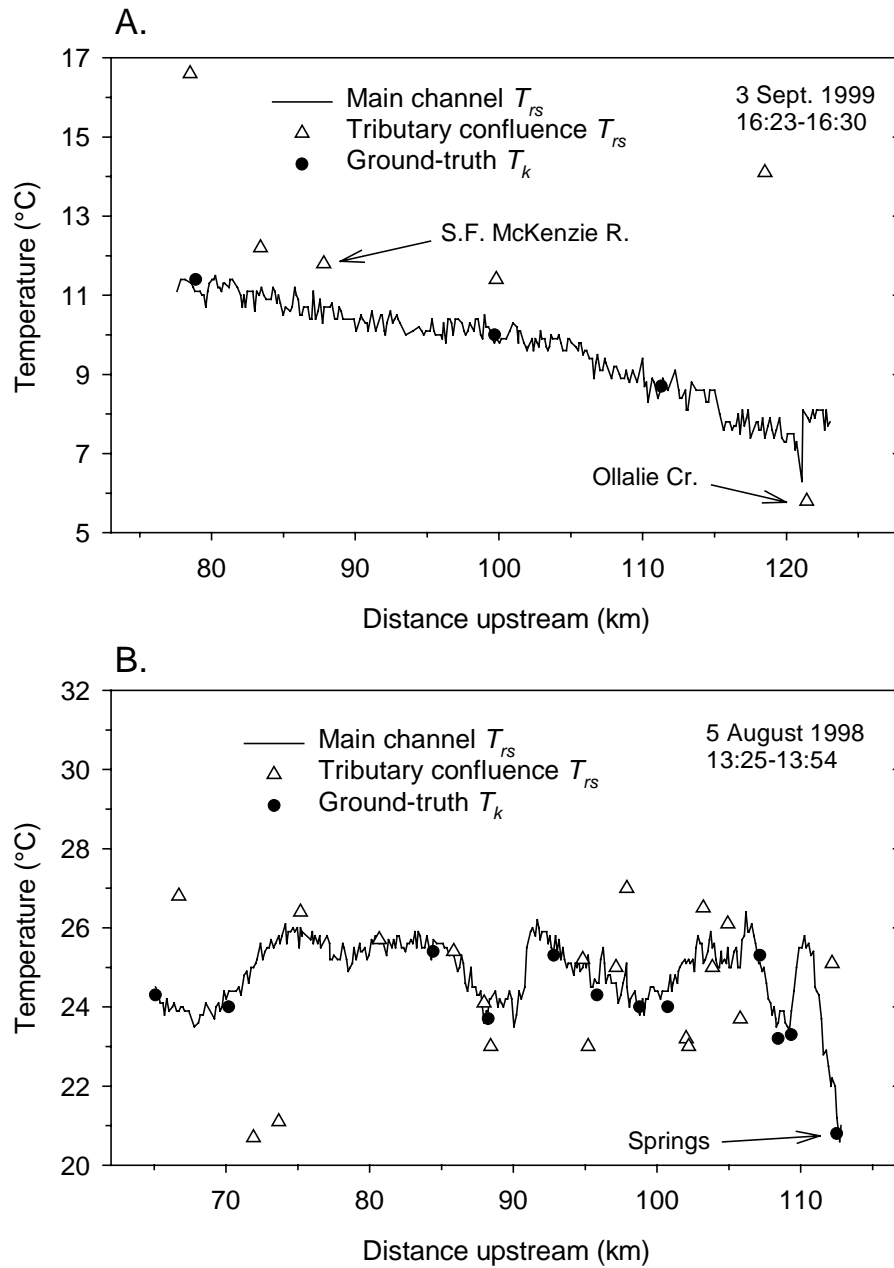
Figure 3.2. Longitudinal profiles of sample median radiant water temperature (T_{rs}) and ground-truth measurements of kinetic water temperature (T_k) in the McKenzie River (A) and the Middle Fork John Day River (B). Measurements of tributary confluence T_{rs} are plotted where the tributaries enter the main stream channel.

surface water inputs influence mainstem temperature. For example, Ollalie Creek, which has high volumetric flow relative to the main stream channel, caused decreases of 1–2°C in mainstem temperature where it entered the McKenzie River (Figure 3.2A). Values of T_{rs} from the thermal imagery corresponded well to ground-truth measurements of T_k over the wide range of temperatures in both study streams.

Remotely sensed thermal profiles in the study streams revealed patterns of spatial variability in T_{rs} and provided a means of characterizing the thermal signature of individual streams or rivers. The temperature of the Middle Fork John Day River increased 3.5°C over 50 km and displayed a dramatic series of peaks and troughs in a downstream direction (Figure 3.2B). In contrast to the Middle Fork, McKenzie River temperatures increased rapidly (5.0°C) over a similar distance and were much more homogeneous (Figure 3.2A). Peaks and troughs in temperature that occured over short distances in the longitudinal stream profile typically indicated tributary inputs (Figure 3.2A; Ollalie Creek), whereas large-scale patterns, such as gradual warming trends and large troughs covering 5–10 km, reflected physical geomorphic, riparian, and hydrologic processes occurring at the watershed scale (Figure 3.2B).

Longitudinal profiles of T_{rs} provided a watershed context for analyzing thermal patterns and hydrologic features depicted in individual thermal and visible band images. High spatial resolution imagery of the stream channel was useful for identifying and evaluating the influence of thermal inputs to the main stream channel such as tributaries (Figure 3.3A) and groundwater-surface water exchange in (Figure 3.3B). Visible band imagery facilitated differentiation between land and water
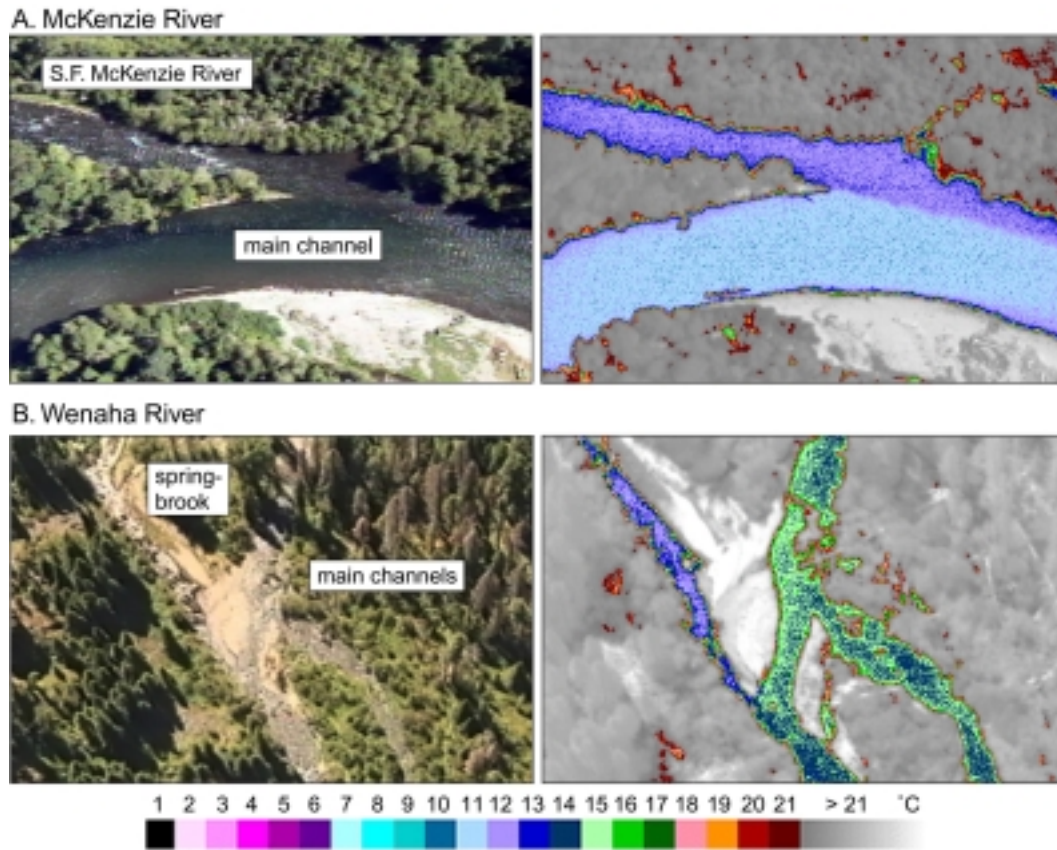
Figure 3.3. Hydrologic features and channel morphology in paired TIR and visible band images of the McKenzie River (A) and the Wenaha River (B). Colors in the thermal images represent radiant water temperature (T_r) in °C. Image frames for the McKenzie River and the Wenaha River represent ground areas of 216 x 144 m and 261 x 174 m, respectively.

surfaces in thermal images and classification of hydrologic features and channel morphology. Mosaics of thermal and visible band imagery were useful for qualitative assessment and presentation purposes but not for quantitative analysis because the imagery was not photogrammetrically rectified.

Temperature accuracy of TIR remote sensing

Values of T_{rs} were consistently within ±0.5°C of ground-truth measurements of T_k over four survey years in five different streams (Table 3.2). The average absolute temperature difference between T_{rs} and T_k for all four survey years was 0.3°C. Of the five streams surveyed, the streams with the narrowest stream channels (Middle Fork John Day River, North Fork Malheur River) had the greatest average absolute temperature differences (Tables 3.1 and 3.2). For all years and streams combined, T_{rs} measurements predicted T_k in a near perfect 1:1 relationship ($r^2 = 0.99$) with slightly increased error occurring at warmer temperatures (Figure 3.4).

Histograms of pixels in the stream channel provided information on the distribution of T_r in the thermal imagery (Figure 3.5). Values of T_{rs} were generally within ±0.5°C of T_{rp} and T_k, and T_{rs} was equivalent to T_{rp} when the distribution of T_r was not skewed (Figures 3.5A and 3.5C). However, when the distribution of T_r in the stream channel was slightly or severely skewed (Figures 3.5B and 3.5D, respectively), T_{rs} provided a more accurate estimate of T_k than T_{rp}. The primary cause for skewness in histograms of T_r was narrow stream width (i.e., < 9 pixels). Values of T_{rp} in the

Table 3.2. Average absolute temperature differences between sample median radiant water temperature (T_{rs}) and ground-truth measurements of kinetic water temperature (T_k).

Stream and year [a]	Number of ground-truth points	Average absolute temperature difference (°C) [b]	Standard error
McKenzie River			
1999	6	0.20	0.05
Middle Fork John Day River			
1994	9	0.4	0.1
1996	13	0.5	0.1
1998	14	0.30	0.05
North Fork John Day River			
1994	4	0.30	0.05
1998	8	0.20	0.05
North Fork Malheur River			
1998	3	0.40	0.03
Wenaha River			
1998	10	0.30	0.05

[a] Aerial thermal surveys conducted before 1998 used different FLIR systems described by Poage et al. (1996) and Torgersen et al. (1999).
[b] Average absolute temperature differences were calculated from comparisons between T_{rs} and T_k collected during thermal overflights at specific points along the spatial extent of the survey reach.
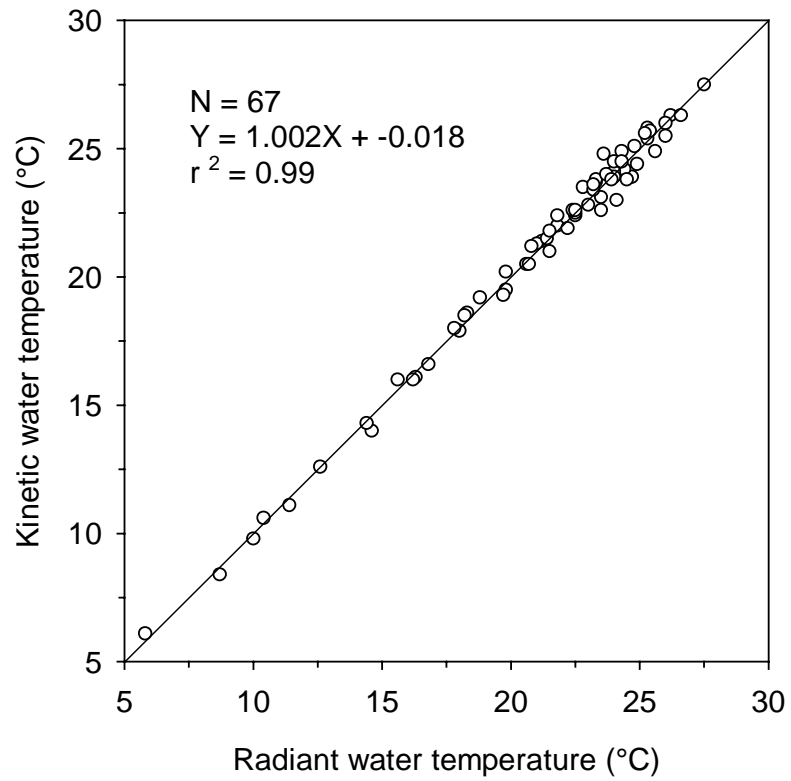
Figure 3.4. Linear regression analysis of ground-truth kinetic water temperature (T_k) versus sample median radiant water temperature (T_{rs}) for four survey years in five different streams (see Table 3.2).
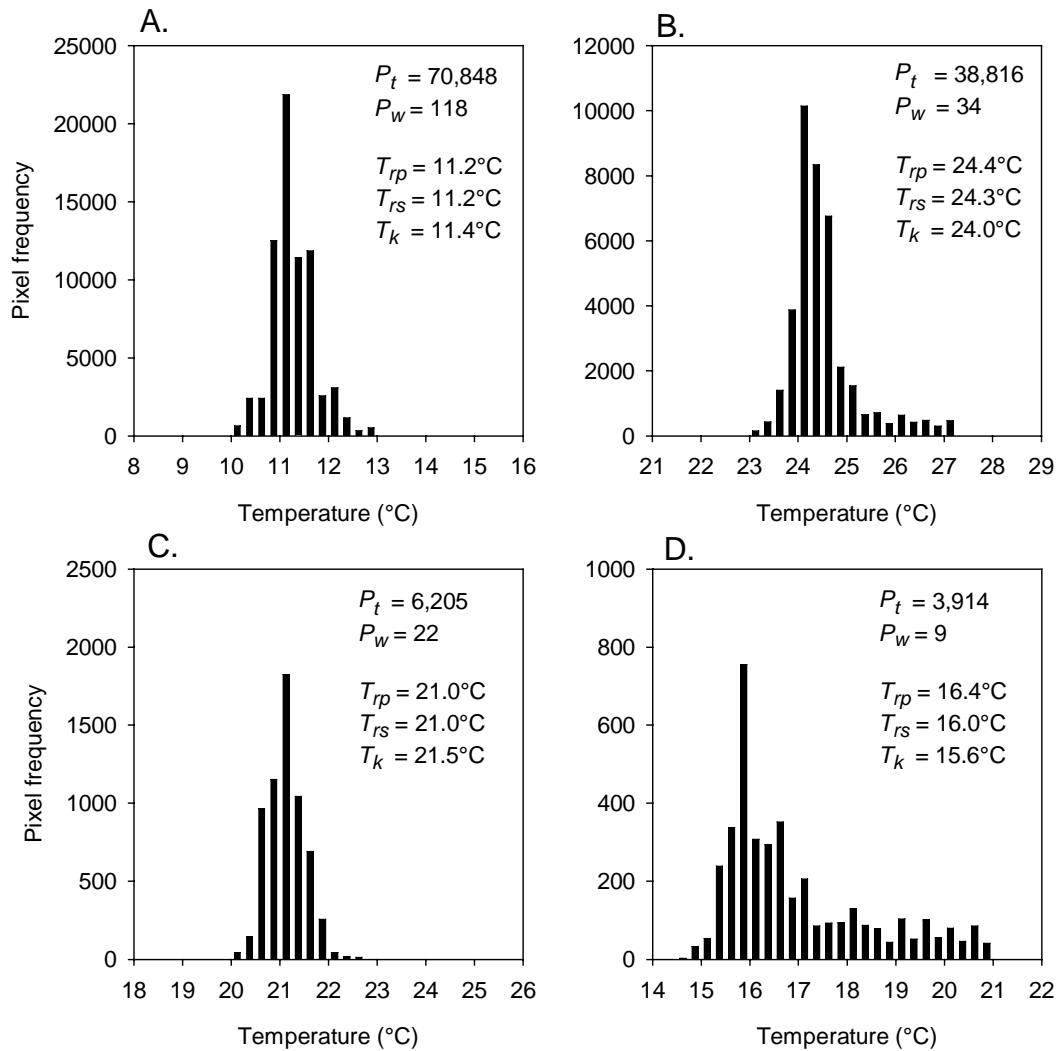
Figure 3.5. Histograms of radiant water temperature (T_r) in images of stream channels in the McKenzie River (A), the Middle Fork John Day River (B), and the North Fork Malheur River (C and D). Statistics for each histogram include total number of pixels (P_t), stream width measured in pixels (P_w), population median radiant water temperature (T_{rp}), sample median radiant water temperature (T_{rs}), and kinetic water temperature (T_k).

narrowest stream were skewed towards higher temperatures as indicated by a difference of 0.8°C between T_{rp} and T_k (Figure 3.5D). When the stream was narrow relative to the ground cell resolution, relatively few pixels in the stream channel contained only water surfaces. Thus, T_{rp} in narrow streams was skewed towards higher temperatures due to the large proportion of hybrid pixels that encompassed both land and water surfaces at the stream margins. In addition to land-water averaging in narrow streams, skewness in T_{rp} towards higher values also occurred in wide streams where the characteristics of the water surface changed from smooth to rough within a single image frame (Figure 3.5B).

Thermal stratification measurements

Study sites in the Middle Fork John Day River, Granite Creek (North Fork John Day River), and Wenaha River varied widely in physical characteristics and provided a setting for *in situ* evaluation of thermal stratification in main- and side-channel stream environments (Table 3.3). Study site GC4 in Granite Creek contained the deepest pool with a maximum depth of 3.20 m, and study site WEN1, a spring-fed alcove in the Wenaha River, had the second deepest pool at 1.31 m. Temperature differences in the water column were considered significant if bottom-surface temperature differences exceeded the ±0.1°C accuracy of the digital thermometer with which T_k measurements were made. Granite Creek (GC4) and WEN1 were the only sites that exhibited thermal stratification (Table 3.4). Thermal stratification was most

Table 3.3. Physical characteristics of thermal stratification study sites in the Middle Fork John Day River (MFJD), Granite Creek (GC4), and the Wenaha River (WEN1).

Study site	Length (m)	Width (m)	Maximum depth (m)	Mean depth (m)	Channel type [a]	Number of sample points
MFJD1	33	9	1.11	0.43	PR	40
MFJD2	31	11	0.93	0.38	PR	50
MFJD3	28	8	0.86	0.36	PR	32
GC4	28	25	3.20	1.24	PO	89
WEN1	50	3	1.31	0.64	PO	18

[a] Pool-riffle study sites (PR) contained one pool bounded by two riffles. Pool study sites (PO) contained one large pool.

Table 3.4. Proportions of bottom–surface kinetic water temperature (T_k) differences (Δ) in thermal stratification study sites under different meteorological conditions.

Study site	N [a]	Clear/sunny conditions Δ Temperature (°C) 0 ± 0.1	≥ 0.2	≤ -0.2	N	Cloudy/rainy conditions Δ Temperature (°C) 0 ± 0.1	≥ 0.2	≤ -0.2
MFJD1	129	1.00	–	–	73	1.00	–	–
MFJD2	177	0.98	0.01	0.01	92	1.00	–	–
MFJD3	120	0.98	0.01	0.01	61	0.98	–	0.02
GC4	243	0.93	0.00	0.07	126	1.00	–	–
WEN1	18	0.61	0.10	0.33	NA	NA	NA	NA

[a] Total number of bottom–surface comparisons in each site. The degree of thermal stratification is represented by the proportion of comparisons within a specified temperature range.

pronounced during clear/sunny conditions when solar heating at the water surface occurred faster than vertical mixing caused by stream flow. Under these environmental conditions, surface T_k was warmer than bottom T_k unless turbulent mixing brought cold water to the surface. Temperature measurements in WEN1 were collected only under clear/sunny conditions because cold groundwater inputs and limited vertical mixing at this site resulted in a constant stratified thermal profile during all weather conditions.

Thermal stratification in GC4 and WEN1 was minimal, even under environmental conditions in which we expected to find pronounced stratification (Figure 3.6). Comparisons of bottom and surface T_k in the deep pool in GC4 revealed only minimal stratification, and surface T_k patterns reflected cooler subsurface temperatures towards the deepest section of the pool (Figures 3.6A and 3.6B). Thermal stratification in WEN1, the groundwater-influenced site, was more pronounced than in GC4 (Figure 3.6D). The degree of stratification in this site increased with depth along the longitudinal transect to $\approx 1°C$. Surface T_k in WEN1 also increased along the longitudinal transect from the spring outflows to the main river channel (Figure 3.6C).

Patterns of T_r sampled from imagery corresponded with surface T_k measurements collected during the following year. Absolute values of T_r and T_k were different because daily maximum air temperature differed between years. However, the relative spatial patterns of T_r and T_k were similar because the physical characteristics and hydrologic properties of the two pools had not changed noticeably
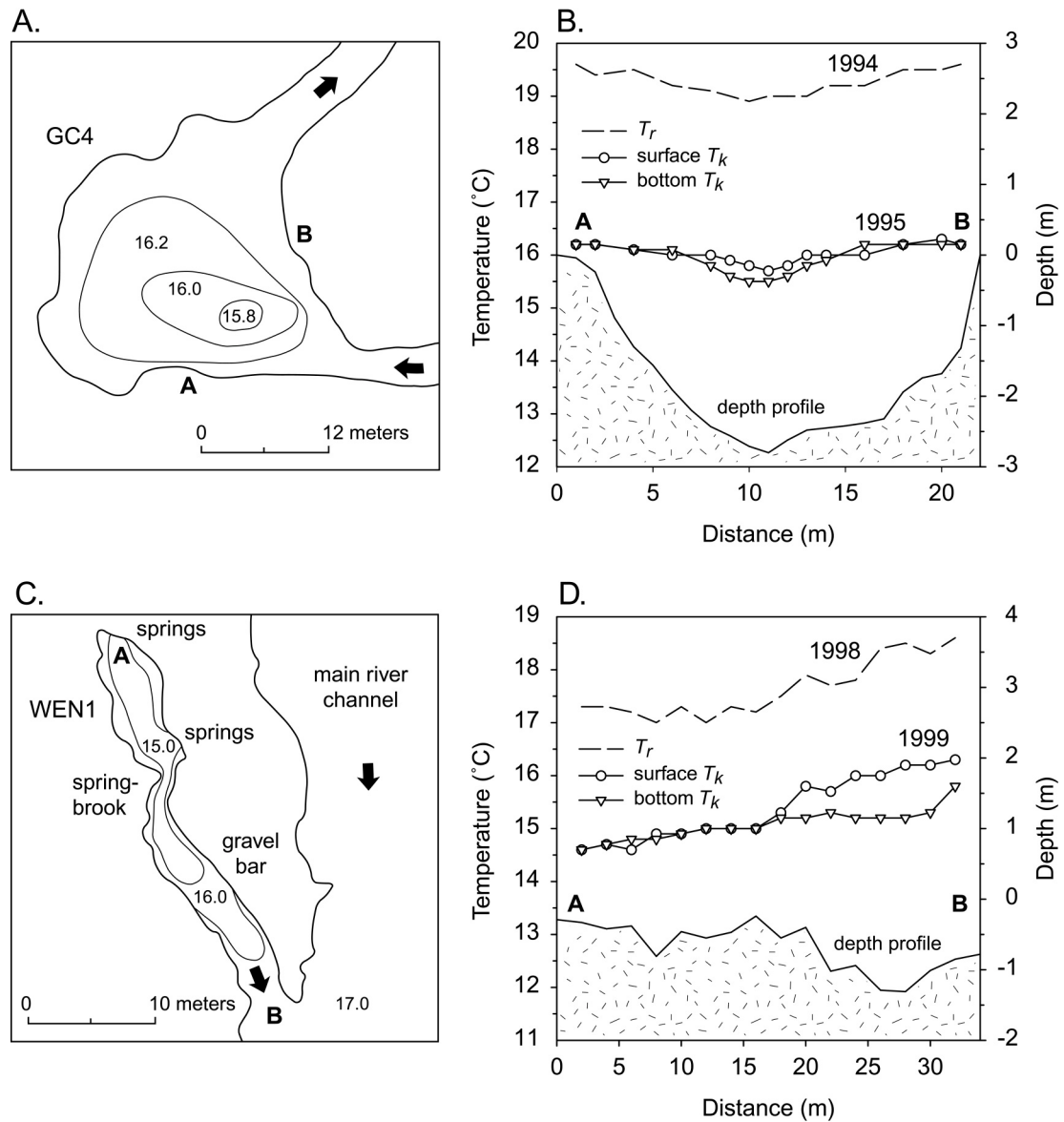
Figure 3.6. Spatial patterns of radiant and kinetic water temperatures (T_r and T_k, respectively) and depth in thermally stratified pools in study sites GC4 in Granite Creek (A and B) and WEN1 in the Wenaha River (C and D). Kinetic water temperatures (°C) and the location of thermal transects A and B are plotted on schematics of each pool (A and C). Thermal stratification measurements of T_k were collected during the year following remote sensing overflights in order to compare spatial patterns (not absolute values) of T_k and T_r.

since the thermal overflight. Patterns of T_r in GC4 paralleled T_k such that both T_k and T_r were slightly cooler towards the center of the pool (Figure 3.6B). In WEN1, the spring-fed alcove, patterns in T_r matched both the trend and the magnitude of T_k measurements collected during the following year (Figure 3.6D).

DISCUSSION

Airborne TIR Remote sensing system

Remote sensing of water temperature in rivers and streams is an exclusively airborne application that requires high-resolution imagery for mapping thermal patterns in streams with widths as narrow as 2 m. Sensor height is determined by stream width as opposed to stream length, and temperature measurement requires a linear survey method fundamentally different from remote sensing conducted from high-altitude platforms. Airborne remote sensing of streams shares methodological similarities with transect approaches such as airborne laser altimetry (Ritchie et al. 1993, Ritchie et al. 1994). However, surveys of a stream or river surface must follow a sinuous path, as opposed to a straight line, and simultaneously adjust for changes in ground elevation as a function of stream gradient. The specific requirements of thermal remote sensing of streams necessitate the use of helicopter rather than fixed-wing platforms in thermal surveys. Helicopters are costly to operate and have a restricted altitudinal and horizontal operating range, but they enable sensor height adjustments over short ground distances and thereby ensure maximum pixel coverage within the stream channel necessary for water temperature measurement. Analysis of

pixel frequency distributions in thermal imagery of narrow stream channels indicates

that temperature accuracy is compromised at stream widths less than 10 pixels (Figure

3.5D). Thus, it is necessary to maintain a sensor height low enough for resolving the

stream surface in as many pixels as possible. In thermal surveys of small streams, in-

flight estimations of stream width in pixels provide the pilot with a visual, scaled

reference on which to base altitude adjustments.

The TIR system for measuring T_r requires specialized data collection,

preparation, and sampling procedures in order to provide stream temperature data in a

format that is accessible and usable in water resources applications. Internally

calibrated thermal imagers measure stream temperature accurately and facilitate

immediate analysis with minimal post-flight calibration requirements. Sensors that

measure thermal radiance in either longwave or midwave thermal regions (8–12 μm

and 3–5 μm, respectively) both provide adequate measurements of T_r (Anderson and

Wilson 1984). However, the bulk of emitted radiation from natural water bodies (0–

30°C) is in the longwave region of the spectrum, and longwave systems are less

sensitive to solar reflections than systems operating in the midwave region. Midwave

systems can be filtered to reduce solar reflections and are typically more sensitive

radiometrically than longwave systems, but for *in situ* measurements of T_r where

environmental factors alone account for errors of ±0.5°C, the added sensitivity of

midwave systems may be unnecessary.

Thermal image collection and processing is an important practical

consideration in thermal remote sensing of streams. Image acquisition in digital

format directly from the sensor is recommended over video recording. Thermal

imagery can be recorded to SVHS videotape, digitized, and processed post-flight to

extract pixel values if sensor settings are locked in a specific temperature range (e.g.,

5–55°C) and displayed as 8-bit images with 256 gray-levels (Poage et al. 1996).

Video recording of imagery on SVHS tape alleviates the problems of digital data

storage but results in more data processing time and reduced temperature sensitivity

and accuracy. In addition, imagery recorded on SVHS tape has a fixed 8-bit

temperature range compared to digital imagery, which retains the full dynamic range

of the thermal sensor.

Digital data collection also facilitates the process of correcting thermal

imagery for atmospheric conditions because correction parameters can be applied to

raw imagery post-flight. Internally calibrated thermal imagers typically provide built-

in methods to correct for atmospheric transmission with user-defined parameters of

sensor-target distance, relative humidity, and ambient air temperature. It is necessary

to correct for atmospheric conditions in thermal remote sensing of stream temperature

because atmospheric transmission and absorption of longwave radiation by water

vapor between the sensor and the stream surface influences remote measurements of

water temperature. Temperature measurement error due to atmospheric conditions can

be further reduced if thermal surveys are conducted from early to mid afternoon when

relative humidity is low and relatively constant. Additional error due to spatial

variations in relative humidity can be reduced if atmospheric correction parameters are

recorded during thermal overflights at remote automated weather stations throughout

the survey area. Atmospheric radiation affects T_r and must be taken into account, but slight variations in atmospheric conditions (e.g., relative humidity differences between downstream and headwater reaches) have relatively little influence on T_r (Feijt and Kohsiek 1995).

Thermal imagery of flowing waters

The physical variables that influence remote measurements of water temperature in rivers and streams are similar to those encountered in remote observations of sea surface temperature from high-altitude and satellite platforms. Recent and extensive studies of TIR radiative properties of the ocean provide a basis for developing similar concepts in stream environments. Theoretical investigations into the factors that influence remote measurement of sea surface temperature have shown that the emissivity of the water surface varies with view angle, surface roughness (Sidran 1981, Masuda et al. 1988), turbidity, and salinity (Liu et al. 1987). Roughened water surfaces have lower emissivities and appear slightly warmer ($< 0.1°$) than placid water surfaces of the same temperature (Masuda et al. 1988, Rees and James 1992). Emissivity differences of 1% correspond to temperature differences of up to 0.5°C in satellite measurements of sea surface temperature (Feijt and Kohsiek 1995). Effects of emissivity variation on T_r in natural stream surfaces have not been quantified, but evidence from marine environments suggests that thermal imagery of riffles, rapids, and pools contains information on surface roughness in addition to water temperature, particularly at low viewing angles. This means that slight

variations in T_r (i.e., < 0.5°C) may occur across smooth and rough water surfaces in a single thermal image even though T_k is constant.

Reflected and emitted TIR radiation.—Interpretation of thermal imagery for water temperature assessment in rivers and streams requires an understanding of thermal radiative properties specific to the riverine environment (Figure 3.1). Because the thermal sensor does not differentiate between reflected and emitted thermal radiation, temperatures in thermal imagery are a combination of both sources. Thus, it is necessary for the interpreter to determine visually which pixels most likely represent T_k. Thermal reflections from the sun are minimal in the 8–12 μm region, but reflections from clouds and surrounding terrestrial objects are visible in thermal imagery of stream surfaces, often in pronounced contrast with cold reflections from clear sky radiation (Svendsen et al. 1990).

Reflection of thermal radiation from the sky and the surrounding terrestrial environment is dependent on view angle and water surface state. Reflectivity of thermal radiation on a smooth water surface in a controlled environment is low and constant at view angles ≤ 45° from normal but increases dramatically at view angles > 50° (Wolfe and Zissis 1985). On roughened water surfaces, reflectivity of thermal radiation increases considerably at view angles ≥ 25° from normal (Sidran 1981). Surface roughness determines whether thermal radiation is reflected specularly or diffusely. Specular reflections of cold sky radiation can be intense on smooth, mirror-like water surfaces. In contrast, diffuse reflections occur when radiation is scattered

by multiple wave surfaces, thus creating the low intensity glitter of water bodies characteristic of reflections in the visible spectral region (Cox and Munk 1954).

In thermal imagery of rivers and streams, pool surfaces were often observed to have a 0.4°C cooler temperature than adjacent riffles. The apparent difference was attributed to differences in reflective characteristics between pools and riffle surfaces in which cold sky reflections were scattered by the roughened water surface. We identified specular reflections in thermal imagery of stream surfaces by comparing thermal images with visible spectrum imagery in which surface roughness could be evaluated directly. As a consequence of the specular sky reflection effect, riffles provide more accurate sampling areas for T_r. Additionally, to minimize problems with reflections in thermal remote sensing of rivers and streams, particular care should be given to maintaining vertical view angles during aerial surveys.

Thermal boundary layer effects and stratification.—Physical processes at the stream surface and turbulent mixing in the water column determine whether T_r is representative of T_k. Thermal stratification occurs at two different spatial scales: the micro level (mm) and the macro level (m) (Schluessel et al. 1990). In the top few millimeters of the water surface, energy exchange between air and water results in evaporative heat loss from the top thin layer of the water surface and creates an aqueous thermal boundary layer 0.1–0.5°C cooler than underlying water (Robinson et al. 1984). The formation and persistence of the thermal boundary layer is dependent on heat flux, wind, and current stresses that disrupt the water surface.

A thermal imager is sensitive to water surface processes because the optical depth of the radiation detected is less than the thickness of the thermal boundary layer. This has proved useful in studies of energy flux and wave breaking in the ocean (Jessup et al. 1997). However, thermal boundary layer effects can also introduce average errors of 0.1–0.2°C in remote measurements of water temperature (Schluessel et al. 1990). In rivers and streams, thermal boundary layer effects are probably limited by streamflow in all but the most placid pool surfaces on which the thermal boundary layer has sufficient time to form. Research on temperature errors of this type in stream environments has not been conducted, but empirical work such as this is needed in order to further develop the application of TIR remote sensing in riverine environments.

Thermal stratification at the macro level can influence whether surface T_k is representative of T_k at depth. Below the thermal boundary layer, water is heated by shortwave radiation from the sun to a depth of 1 m (Schluessel et al. 1990). In the absence of turbulent mixing, water temperatures at depth are colder than surface temperatures, particularly when solar radiation reaches its peak in mid afternoon. As a result, errors in water temperature measurement can occur in remote sensing of thermally stratified environments if the stratified condition is not recognized. Several factors determine whether the flow of water in a channel is turbulent or laminar. The Reynolds number, R_e, describes the relationship of these factors and is defined as

$$R_e = \frac{\rho v r}{\mu}$$

where ρ is the fluid density (kg/m^3), v is the discharge velocity (m/s), r is the hydraulic

radius (m) (the ratio of cross-sectional area to wetted perimeter in the stream channel),

and μ is the water viscosity (kg/s·m) (Fetter 1994). The transition from laminar to

turbulent flow occurs when R_e exceeds a value of 2000. Simple calculations of R_e

provide a means to predict where remote temperature measurements may be

influenced by thermal stratification. Where velocity data are unavailable for the

calculation of R_e, water velocity can be estimated using the Manning equation and

stream gradient data from digital elevation models (Brooks et al. 1991).

Fluid dynamics theory suggests that turbulent flow is more common than

laminar flow in rivers and streams (Selby 1985, Narigasawa et al. 1988). Thus,

thermal stratification is relatively uncommon in rivers and streams in which turbulent

flow is sufficient to facilitate vertical mixing in the water column. In the reaches

selected for studies of thermal stratification, field measurements of surface and bottom

temperature verified R_e predictions of turbulent flow at water velocities of 0.07–0.20

m/s. For the pool in GC4 with an average depth of 2 m, a minimum velocity of

0.0015 m/s would be required to cause turbulent flow and vertical mixing in the water

column (Figure 3.6A). Measurements of T_k (bottom–surface) do show minimal

stratification in the deepest part of the pool (Figure 3.6B). However, these

measurements indicate that cool water from the bottom of the pool is being circulated,

as predicted by R_e, to the surface where it can be detected by remote sensing.

While laminar flow is uncommon in natural stream environments, thermal

stratification can still occur if cold water enters the stream channel at a point where

water velocity is very slow (Matthews et al. 1994). Side channels and floodplain

ponds with subsurface coldwater inputs present problems for remote measurement of

stream temperature unless the springs can be detected as lateral inputs (Figure 3.6C).

Thermal remote sensing of stream environments requires at least some streamflow to

provide accurate estimates of temperature in the water column. Thus, temperature

measurements of isolated pools during low flow conditions will be strongly biased by

warm surface water even though groundwater flow through the streambed may be

cold. For these reasons, isolated groundwater inputs to the stream channel are best

identified during winter months when groundwater is relatively warm and rises to the

water surface.

Spatial and temporal analysis of stream temperature patterns

Airborne thermal remote sensing provides a method for assessing spatially

continuous patterns of T_r in an entire river over a short period of time. The spatio-

temporal tradeoff of high-resolution thermal imagery is that stream temperatures

change over the course of an aerial survey. True synoptic surveys of stream

temperature cannot be acquired using a low-altitude remote sensing platform because

image data are collected sequentially in an upstream direction as opposed to areally in

a single image. However, there are methods that minimize the spatio-temporal

tradeoffs of longitudinal data collection. The upstream direction of the survey

compensates for stream temperature change over the duration of the flight because

rates of temperature change are generally slower in downstream reaches than in the

headwaters (Vannote et al. 1980). In addition, in-stream temperature recorders programmed to sample water temperature once every minute provide a temporally continuous context for temporally limited thermal imagery. During mid afternoon surveys in July and August in eastern and western Oregon, water temperature changed at rates of 0–1°C per hour within individual 50-km stream sections. By using in-stream temperature data, it is possible to correct spatially continuous thermal survey data for diurnal variations in stream temperature, but this requires assumptions to be made about temperature change in reaches without data recorders.

Stream temperatures change at different rates throughout a watershed depending on topography, riparian canopy structure, stream channel characteristics, water velocity, flow volume, and the relative influence of groundwater inputs (Brown 1983). An advantage of thermal remote sensing is that it provides high-resolution information on spatial patterns of heating and cooling that result from these physical processes. Spatially continuous data on stream temperature patterns have only recently become available through technological improvements in thermal sensors and computerized geographic analysis. Thus, many questions remain about the actual causes of stream temperature patterns made visible for the first time through thermal remote sensing. Although thermal remote sensing of streams provides limited information on the hydrologic processes and mechanisms that influence stream temperature, it will be a highly effective tool for evaluating the patterns that emerge from these processes.

CONCLUSIONS

Airborne thermal remote sensing provides an effective means of mapping spatially continuous patterns of water temperature in rivers and streams. The concept of remote water temperature measurement has been applied successfully in ocean and lake environments using standard high-altitude platforms, but aerial methods for stream temperature assessment and analysis require a remote sensing system specifically designed for high-resolution, linear surveys of stream networks. Interpretation of water temperature data from thermal imagery requires an understanding of TIR properties specific to the riverine environment because the radiative properties of flowing waters are influenced by multiple environmental factors and by the physical characteristics of the stream surface. In this article, we have presented a method for examining stream temperature at a resolution and extent previously unattainable through current methods of direct in-stream measurement; however, thermal imagery represents only one point in time and is most effective when used in conjunction with temperature data from in-stream monitoring stations. Spatially continuous temperature information from thermal remote sensing can be combined with temporally continuous data from in-stream temperature recorders and used to address current issues in water resources management and habitat conservation for aquatic organisms.

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CHAPTER 4

HABITAT HETEROGENEITY AND THE SPATIAL DISTRIBUTION OF
LARVAL PACIFIC LAMPREY (*LAMPETRA TRIDENTATA*) IN AN
OREGON STREAM

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ABSTRACT

Habitat heterogeneity at fine and coarse scales influences the detection of patterns in the abundance and habitat relationships of larval Pacific lamprey, *Lampetra tridentata*. In a 55-km section of the Middle Fork John Day River, a fourth- to fifth-order stream in northeastern Oregon, we used a nested sampling design and multiple logistic regression to evaluate heterogeneity in larval abundance and habitat within and among sites. Stream habitat variables predicted patterns in larval abundance but played different roles at different spatial scales. The spatial distribution of larvae at large scales (5–10 km) was positively associated with water depth and open riparian canopy (likelihood ratio χ^2 test, $P < 0.001$). Patchiness in larval occurrence at small scales (< 50 m) corresponded positively with low water velocity, pool habitats, and the availability of suitable burrowing habitat ($P < 0.001$). We determined that habitat variables explain a significant proportion of variation in larval abundance at large and small scales, but locational factors, such as longitudinal position in the stream section and sample location within the channel unit, explain additional variation that might otherwise be discounted as noise.

INTRODUCTION

The Pacific lamprey, *Lampetra tridentata*, is an anadromous parasitic lamprey that completes the freshwater phase of its life cycle in streams and rivers from Baja California, Mexico along the northern Pacific Rim to Hokkaido, Japan (Ruiz-Campos and Gonzalez-Guzman 1996). A highly migratory species, the Pacific lamprey

spawns in low-gradient streams, often hundreds of kilometers inland in the upper

drainages of large rivers in Oregon, Washington, Idaho, and British Columbia

(Hammond 1979, Beamish 1980, Richards 1980). Pacific lamprey spend more than

half of their 6–10-year life span as filter-feeding larvae burrowed in fine sediments of

streams and are susceptible, like other species of larval lampreys, to habitat alteration

by channelization and flow regulation (Kirchhofer 1995). While most efforts in the

United States and Canada have been directed at controlling invasive sea lamprey

(*Petromyzon marinus*) populations in the Great Lakes, recent concerns have been

raised for the conservation of lampreys in the Northern Hemisphere (Renaud 1997),

specifically in the Columbia River Basin (Pacific Northwest) where hydroelectric

facilities have impeded migrations of Pacific lamprey (Ocker et al. 2001, Vella et al.

2001). The construction of migration barriers has occurred concurrently with

modification of larval rearing habitats in headwater streams; thus, a need exists to

establish lamprey conservation and restoration programs to evaluate the habitat

requirements of larval Pacific lamprey and develop methods for monitoring status and

trends in larval abundance.

The response of larval lampreys to environmental heterogeneity is not well

understood, but recent work on stream macroinvertebrates has shown that the spatial

arrangement of habitat patches at large and small scales influences the distribution and

abundance of benthic organisms (Palmer et al. 2000, Li et al. 2001). Previous work on

the habitat ecology of larval lampreys has either been qualitative (Baxter 1957,

Pletcher 1963, Hammond 1979) or has focused on larval habitat relationships at one

scale only (Malmqvist 1980, Potter et al. 1986, Beamish and Jebbink 1994, Beamish and Lowartz 1996). Although studies of larval habitat have been useful for developing a general understanding of the biology of larval lampreys, conservation and management of lamprey populations require quantitative approaches for evaluating and predicting spatial patterns in larval abundance with respect to management actions. With the increased availability of geographic information systems (GIS) and the development of spatial analysis techniques, statistical models are now being used to predict the distribution of stream fishes at fine (m) and coarse (km) spatial scales (Knapp and Preisler 1999, Torgersen et al. 1999). Similar approaches can be used for lampreys to evaluate the suitability and effectiveness of larval restoration programs and to increase the precision of efforts to control lampreys where they are invasive species (Fodale et al., in review). However, spatially explicit larval habitat models will require extensive field data of sufficient resolution to define the scales at which habitat variables influence patterns of larval abundance.

Our goal was to evaluate spatial patterns and habitat relationships of larval Pacific lamprey at two different spatial scales. We hypothesized that (1) habitat heterogeneity at fine and coarse scales influences the measurement and detection of patterns in larval abundance, and (2) stream habitat variables predict patterns in larval abundance but play different roles at different spatial scales. We show that patterns in larval abundance are closely linked to habitat variation at two different scales and that locational factors, such as longitudinal position in the stream section and sample location within the channel unit, explain additional variation in larval abundance that

might otherwise be discounted as noise. In addition, we demonstrate that a nested sampling design is effective for evaluating patterns and habitat relationships of larval lampreys in heterogeneous stream environments.

METHODS

Study area and site selection

Larval Pacific lamprey were collected during August 2000 in the upper 55 km of the Middle Fork John Day River, a fourth- to fifth-order stream in northeastern Oregon (Figure 4.1). The upper Middle Fork John Day River ranges in elevation from 1000 to 1300 m and flows through semi-arid rangelands in alluvial valleys and alluviated canyons vegetated on the upslopes with mixed conifer forest (*Pinus ponderosa* and *Abies grandis*). The basin has been influenced by a number of land-use practices including mining, timber harvest, channelization, and grazing which have nearly eliminated deciduous riparian vegetation (*Populus trichocarpa*, *Crataegus douglasii*, and *Alnus rubra*) in unconstrained alluvial valley reaches (see Torgersen et al. 1999 for a detailed description of the study area).

GIS maps of stream habitat (channel unit type and dimensions) and channel gradient provided a high-resolution, spatially continuous context for selecting larval sampling sites in the Middle Fork John Day River study section. Longitudinal profiles of water depth and channel gradient derived from habitat surveys (conducted in 1996) and a 10-m digital elevation model (DEM) were georeferenced to 1:5,000-scale hydrography and compared with respect to river km (rkm), defined as the distance
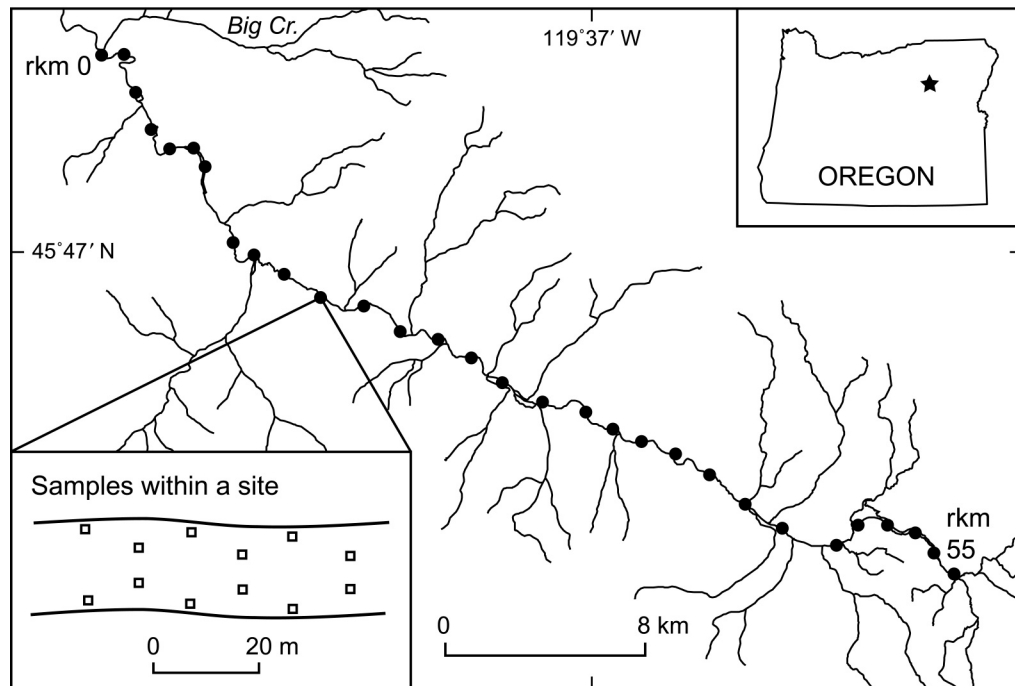
Figure 4.1. Study area and sampling design for the survey of larval Pacific lamprey in the upper 55 km of the Middle Fork John Day River, Oregon. Solid circles indicate the locations of larval sampling sites.

upstream from the lower boundary of the survey section (see Torgersen et al. 1999 for

a description of habitat surveys and GIS methods). Thirty sites were distributed along

the survey section and stratified with respect to longitudinal patterns in water depth

and channel gradient (Figure 4.2). Sampling sites were located in the field with a

hand-held global positioning system (GPS) to within 50 m.

Larval sampling

We used a nested sampling design to evaluate heterogeneity in larval

abundance and habitat at two different spatial scales—both within and among sites.

Sampling locations (1 x 1-m quadrats, $n = 12$) within a site were distributed in the mid

channel and along stream margins in 6 transects spaced every 10 m (Figure 4.1).

Larvae were collected at each sampling location in two 90-s passes with a backpack

model AbP-2 larval lamprey electrofishing unit (Engineering Technical Services,

University of Wisconsin, Madison, Wisconsin). The electrofishing unit delivered 3

pulses·s^{-1} (125 volts DC) at a 25% duty cycle, with a 3:1 burst pulse train (three pulses

on, one pulse off) to draw larvae from the substrate (Weisser and Klar 1990). Once in

the water column, larvae were stunned with 30 pulses·s^{-1} to facilitate capture (Hintz

1993, Weisser 1994). After collection, larvae were anesthetized in buffered MS-222

(tricaine methanesulfonate at 250 mg·L^{-1}), identified on the basis of caudal

pigmentation patterns (Richards et al. 1982), and measured for total length (±1 mm)

before they were returned to the stream. Depletion estimates for two-pass removal

were calculated and converted to larval densities per sample (number·m^{-2}) with the
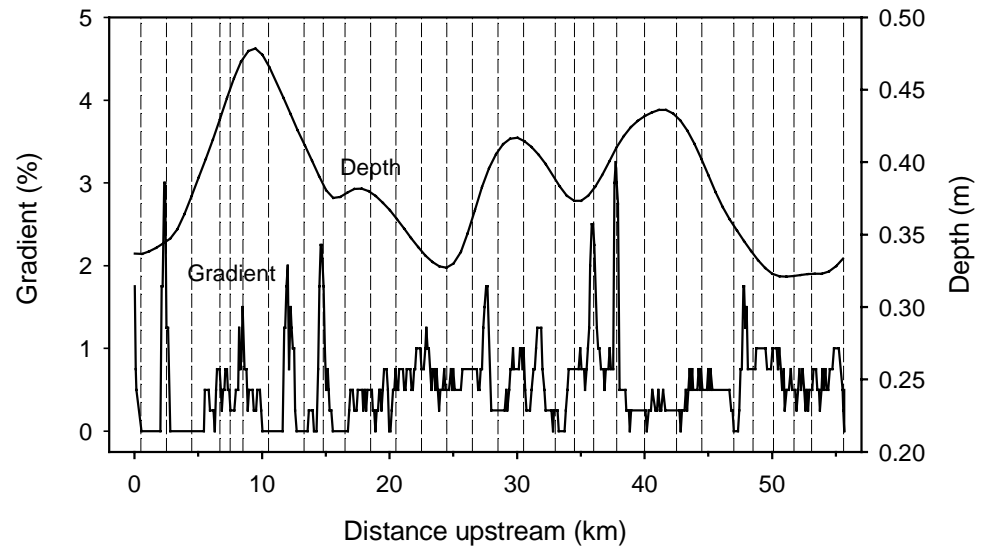
Figure 4.2. Spatially continuous longitudinal profiles of channel gradient and water depth in the upper 55 km of the Middle Fork John Day River. The longitudinal profile of channel gradient was generated from a 10-m digital elevation model (DEM) with a 500-m moving window for slope calculations. Locally weighted scatterplot smoothing (LOWESS) was used to evaluate spatial patterns in water depth. Dashed vertical lines indicate the positions of larval sampling sites.

Capture software program (Zippin 1958, White et al. 1982). Larval abundance,

defined as the sum of larval densities per site, was uncorrected for gear efficiency and

larval length.

Habitat description

Assessment of larval habitat was conducted at the sample or site level

depending upon the nature of stream habitat variables (Table 4.1). Measurements of

water velocity at 60% depth (Model 201D flowmeter, Marsh-McBirney, Inc.) and total

water depth were taken once per sample, and dominant substrate and larval habitat

type were estimated visually within each 1 x 1-m sampling quadrat. The following

definitions were used to classify larval habitat: type I—preferred larval habitat with a

mixture of soft sediment particles including silt, clay, fine organic matter, and some

sand; type II—suitable habitat similar to type I habitat but with a larger component of

sand; type III—unsuitable habitat for burrowing, composed of bedrock, hard clay,

cobble, or coarse gravel substrates (Fodale 1999).

At the site level, habitat characteristics were expressed either as a proportion of

samples within each habitat category (channel unit, substrate, and larval habitat types)

or as site means (channel dimensions and water velocity) (Table 4.1). Measurements

of channel gradient (Model RL-HB rotating laser, Topcon Corp.), pH, and

conductivity (pH/Con 10, Oakton Instruments) were taken once per site. Percent

canopy closure was assessed with a concave spherical densiometer at three equally

Table 4.1. Explanatory variables evaluated for associations with the relative abundance of larval Pacific lamprey.

Variable	Units/ category	Data type	Description
Depth	m	continuous	water depth
Organic depth	cm	continuous	depth of organic debris overlying substrate
Velocity [a]	m·s^{-1}	categorical	design variable based on percentiles
0–0.11			1st to 33rd percentile
0.12–0.23			33rd to 66th percentile
0.24–1.00			66th to 100th percentile
Unit type		binary	channel unit type
Pool	1		
Riffle	0		
Substrate		categorical	dominant substrate type in sample area
Organics	1		organic debris
Silt	2		< 0.1 mm
Sand	3		0.1–3 mm
Small gravel	4		3–10 mm
Large gravel	5		11–100 mm
Cobble	6		101–300 mm
Boulder	7		> 300 mm
Bedrock	8		
Habitat type		categorical	larval habitat classification
Type I	1		preferred
Type II	2		suitable
Type III	3		unsuitable
Position		binary	location of sample in stream channel
Margin	1		stream margin
Mid channel	0		middle of channel
Wetted width [b]	m	continuous	measured at three equally spaced transects
Canopy closure	percent	continuous	measured at three equally spaced transects
pH		continuous	measured once in the middle of each site
Conductivity [b]	μmhos·cm^{-1}	continuous	measurement taken with pH
Gradient	percent	continuous	channel slope calculated for 50-m site
Temperature	°C	continuous	measured with remote sensing
River km	km	continuous	distance upstream from lower boundary of survey section

Notes: All variables were measured at the sample level except for wetted width and canopy closure (transect level) and pH, conductivity, gradient, temperature, and river km (site level).
[a] Velocity was measured as a continuous variable but exhibited a nonlinear relationship with the logit and was therefore modeled as a categorical design variable.
[b] Wetted width and conductivity exhibited a significant ($P \le 0.05$) linear relationship with river rkm and were detrended with linear regression.

spaced transects along the length of the site (Platts et al. 1987). Spatially continuous

profiles of channel gradient and water depth were generated in a GIS and analyzed

longitudinally with a 400-m moving window for gradient calculations and with locally

weighted scatterplot smoothing (LOWESS) to identify trends in depth (Trexler and

Travis 1993, SPSS 2001).

Statistical analysis

We used multiple logistic regression to describe the relationship between larval

abundance and habitat variables within and among sites. Logistic regression has been

applied effectively to predict fish–habitat relationships at a variety of scales (Dunham

and Rieman 1999, Knapp and Preisler 1999, Torgersen et al. 1999) and was

particularly appropriate for modeling larval response to habitat heterogeneity because

it requires no assumptions regarding normality or homoscedasticity (Hosmer and

Lemeshow 1989, Trexler and Travis 1993). The logistic model uses maximum

likelihood estimation and the logit transformation of a binary response variable to

predict the probability of occurrence in relation to binary, categorical, or continuous

explanatory variables. To evaluate larval habitat relationships within sites (i.e., among

samples), we modeled larval occurrence (binary response) with respect to continuous

and categorical habitat variables measured at sample and transect levels (Table 4.1).

To assess larval habitat relationships among sites, we compared the spatial

correspondence of peaks and troughs in larval abundance with longitudinal profiles of

stream habitat. We created a binary response variable (i.e., peaks and troughs in larval

abundance) by relativizing larval abundance with respect to the median. Site-level

explanatory variables were also analyzed as binary variables relativized with respect to

either the median or the residuals from linear regression if variables exhibited a

significant ($P \leq 0.05$) linear relationship with river km (e.g., wetted width and

conductivity).

Logistic regression is robust to heterogeneity and non-normality inherent in

ecological data, but it is sensitive to multicollinearity among predictor variables and to

nonlinear relationships between continuous explanatory variables and the linear

predictor (i.e., the logit transform of the fitted response) (Tabachnick and Fidell 2001).

We assessed correlations between habitat variables for multicollinearity and

graphically evaluated relationships between continuous explanatory variables and the

linear predictor. Only one continuous variable, velocity (sample-level), exhibited a

nonlinear relationship with the linear predictor and was converted to a categorical

design variable based on percentiles. To incorporate spatial structure into the logistic

model and account for spatial dependence, we included locational predictors (i.e., river

km and sample position in the stream channel) in both site- and sample-level models

(Knapp and Preisler 1999). Habitat variables were evaluated individually for

significant associations with larval abundance (likelihood ratio χ^2 test, $P \leq 0.05$);

variables and combinations of variables were then selected manually and included in

the final multivariate model if they contributed to a significant drop in deviance

(Ramsey and Schafer 1997). To determine whether the logistic function adequately

fitted the observed data, we used the Hosmer–Lemeshow χ^2 test, in which small

probability values indicate a significant lack of fit (Hosmer and Lemeshow 1989).

The relative explanatory power of respective logistic models was measured with the

Nagalkerke coefficient of determination (R^2) (Nagelkerke 1991). Logistic regression

and all other statistical analyses were performed with Statgraphics Plus statistical

software (Statistical Graphics 1999).

RESULTS

Spatial distribution of larval lamprey

Larval lamprey occurred throughout the 55-km survey section of the Middle

Fork John Day River. A total of 1,414 larvae were collected, and larval abundance for

the sampled area (360 m^2) was estimated at 1,609 larvae. Variation in larval

occurrence was low among sites and high within sites, with larvae present in 28 of the

30 sites but in only 111 of the 360 samples. Maximum larval density (number·m^{-2}) in

a 1-m^2 sample ($n = 118$) was approximately 50% of the maximum number of larvae

found in a 12-m^2 site ($n = 232$).

Identification of larvae at the time of capture indicated that the Pacific lamprey

(*L. tridentata*) was the only species of lamprey present in the upper Middle Fork John

Day River. Total length of the larvae ranged between 20 and 160 mm and differed

significantly both longitudinally and laterally in the stream channel (Mann-Whitney

Wilcoxon test, $P < 0.01$). Median larval length was greater in the upper 27 km of the

survey section (76 mm) compared to downstream sites (59 mm). Within sites, median

larval length was greater in the mid channel (70 mm) than along stream margins (61 mm).

Larval abundance was patchy at large scales (5–10 km) and peaked at rkm 9, 26, and 43 (Figure 4.3A). Reaches with multiple consecutive sites exceeding median larval abundance occurred at rkm 7–18 and 40–45 and were identified as major larval rearing areas. Although larvae were present throughout the survey section, they were 3.4 times more abundant in the lower 27 km of the stream. Peaks in larval abundance among sites corresponded with longitudinal patterns of maximum larval density within sites (Figures 4.3A and 4.3B). Variation in larval density within high-density sites was large, indicating that the number of larvae per site was strongly influenced by relatively few samples containing large numbers of larvae (Figure 4.3B).

The proportion of samples containing larvae within individual sites was low throughout the survey section, even in sites where larvae were abundant (Figure 4.3C). In 73% of the sites, larvae were present in fewer than 50% of the samples. We evaluated the linear relationship between the proportion of samples containing larvae versus larval density per site and determined that the resolution of the sampling grid adequately captured variation in larval abundance in each 50-m site. Larval density was significantly correlated with the proportion of samples containing larvae and explained 55% of the variation in larval occurrence among samples (positive relationship, $P < 0.01$).
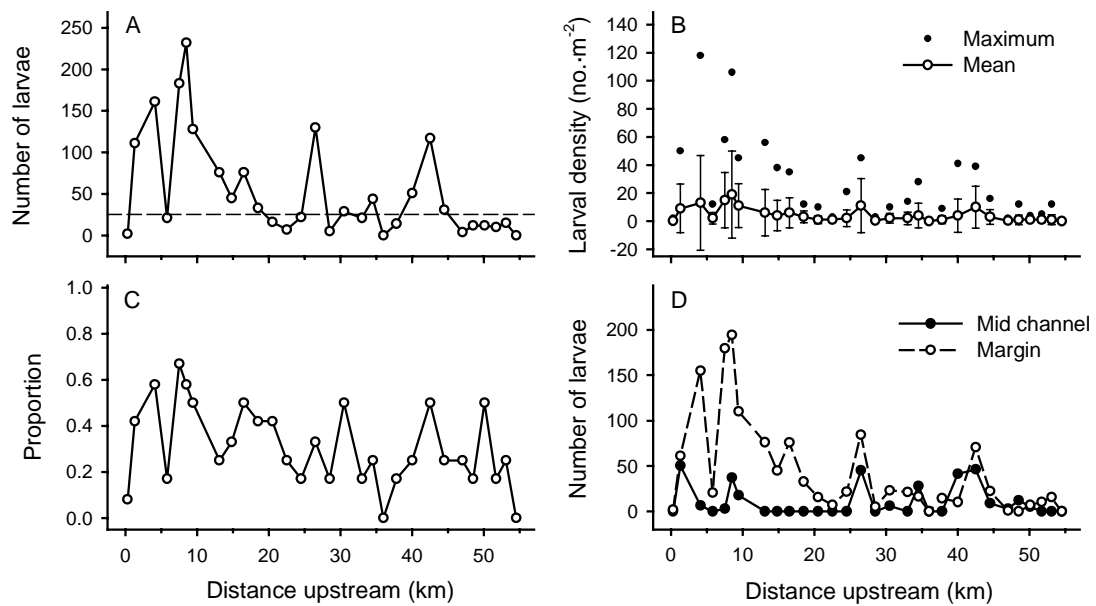
Figure 4.3. Longitudinal variation in larval abundance within and among sites. Patterns in mean (open circles) (± SD) and maximum (solid circles) larval larval density are plotted versus river km, the distance upstream from the lower boundary of the survey section: (A) larval abundance (dashed horizontal line indicates the median), (B) variation in larval density within sites, (C) the proportion of samples containing larvae within individual sites, and (D) the distribution of larvae in mid-channel versus stream margin sampling locations.

Spatial patterns of larval abundance within sites were heterogeneous, particularly laterally across the stream channel. Over 80% of the larvae were found along stream margins, and the difference in larval abundance between stream margin versus mid-channel habitats was most pronounced in downstream reaches (Figure 4.3D). Peaks in mid-channel larval abundance at rkm 2, 8, 27, and 40–43 corresponded with peaks in larval abundance in stream margins. Within high-density sites, larval abundance was greatest in channel margins and was generally skewed towards the left or right stream margin (Figures 4.4A, 4.4B, and 4.4C). In both high- and low-density sites, more than 40% of the larvae in each site were concentrated in one or two neighboring samples (see Figure 4.4 for representative sites).

Habitat heterogeneity at multiple scales

Spatially continuous longitudinal patterns in channel gradient and water depth revealed the complex geomorphic structure of the Middle Fork John Day River survey section (Figure 4.2). Peaks in LOWESS-smoothed water depth at rkm 10, 30, and 42 indicated the presence of reaches with high frequencies of deepwater habitats (e.g., pools and glides). Reaches with high channel gradient (2–3%) and low water depth (0.3–0.4 m) occurred at rkm 2, 15, and 36 and were identified as riffle reaches. A cascade reach characterized by a gradient of > 3% and a depth of 0.4 m was located at rkm 38. The longest contiguous low-gradient reaches of the survey section coincided with the highest peaks in water depth at rkm 5–12 and 40–43 (Figure 4.2).
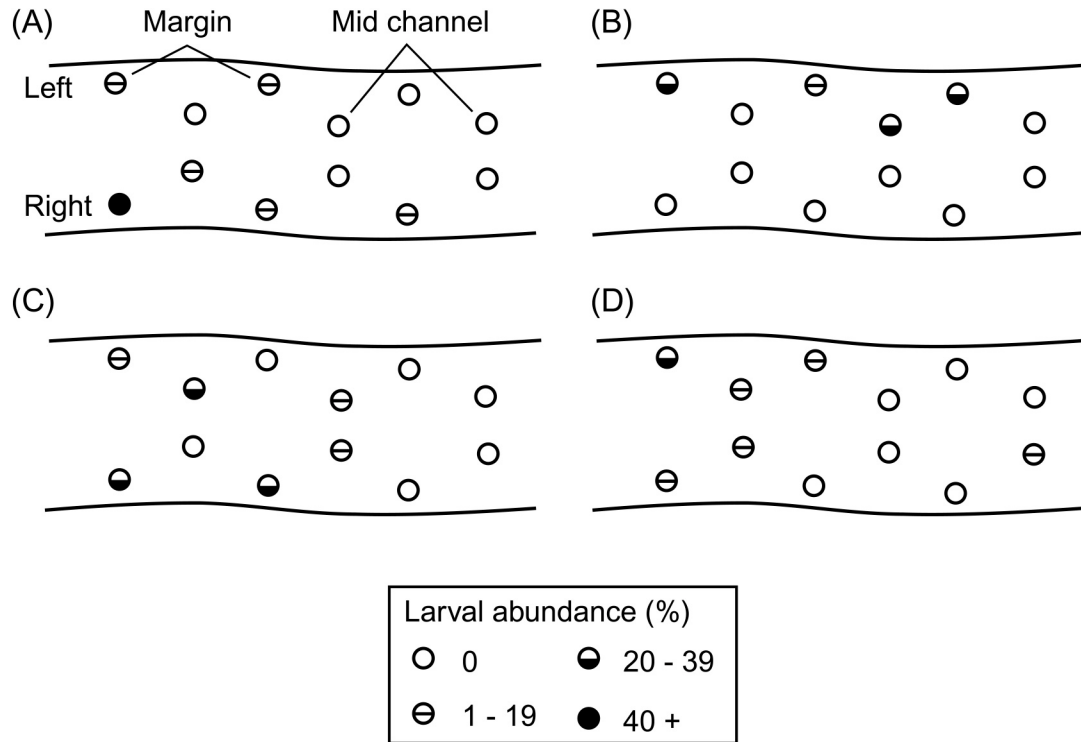
Figure 4.4. Spatial distribution and percent abundance of larval lamprey in mid-channel and stream margin sampling locations within sites. Sites represent high- and low-density reaches in the longitudinal distribution of larval lamprey: (A) rkm 8.5, $n = 232$, (B) rkm 26.5, $n = 130$, (C) rkm 42.5, $n = 117$, and (D) rkm 50.1, $n = 12$.

Physical characteristics of survey sites reflected spatial trends and heterogeneity in stream habitat in the Middle Fork John Day River study section (Figure 4.5). Wetted width and conductivity were the only two habitat variables that exhibited linear longitudinal trends (Figures 4.5A and 4.5B). Average distance between peaks in longitudinal habitat profiles provided a rough indicator of the varying scales at which habitat heterogeneity was expressed. Longitudinal profiles of water depth, canopy closure, velocity, and channel gradient reflected stream valley and geomorphic processes occurring over relatively long distances (15–20 km) (Figures 4.5C–4.5F), whereas wetted width and conductivity varied over shorter distances (5–10 km) (Figures 4.5A and 4.5B). Patterns of substrate composition also reflected the influences of fluvial and depositional processes occurring over long (e.g., sand, silt, type I habitat, and organic debris) and short distances (e.g., cobble/large gravel and type II habitat) (Figure 4.6).

Spatial heterogeneity in larval habitat was particularly apparent at small spatial scales within and among adjacent channel units (< 50 m). Cobble and large gravel substrate types dominated the survey sites and typically composed over 60% of the sampled area per site (Figure 4.6A). Sand, silt, and organic debris made up very small proportions (< 0.40) of the sampled area (Figures 4.6B, 4.6C, and 4.6F). The proportion of suitable burrowing habitat (types I and II) within a given site was rarely greater than 0.60 (Figures 4.6D and 4.6E). Mean within-site variability (coefficient of variation) in wetted width was low (0.14) compared to water depth (0.51) and water
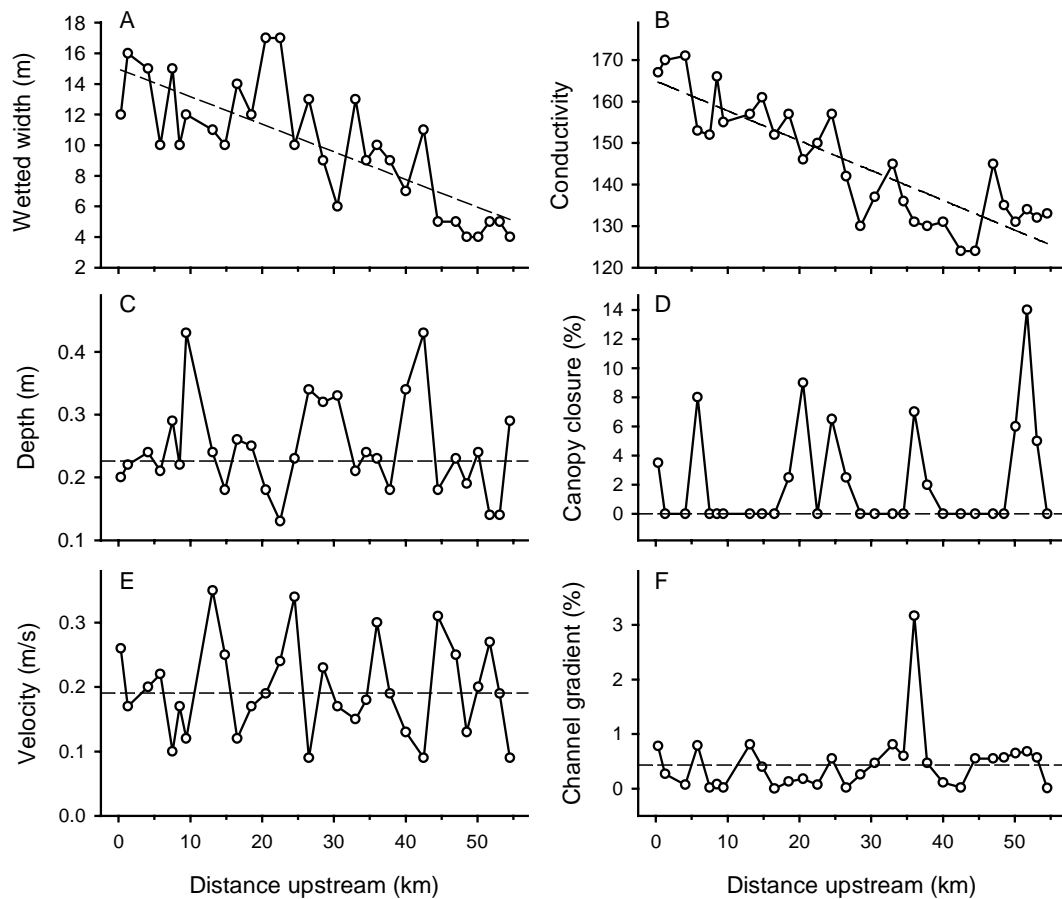
Figure 4.5. Longitudinal variation in channel morphology and stream habitat among sites. Longitudinal habitat patterns are plotted versus river km, the distance upstream from the lower boundary of the survey section: (A) wetted width, (B) conductivity, (C) water depth, (D) canopy closure, (E) water velocity, and (F) channel gradient. Dashed lines define peaks and troughs with respect to the median (horizontal line) or the residuals from linear regression (trend line).
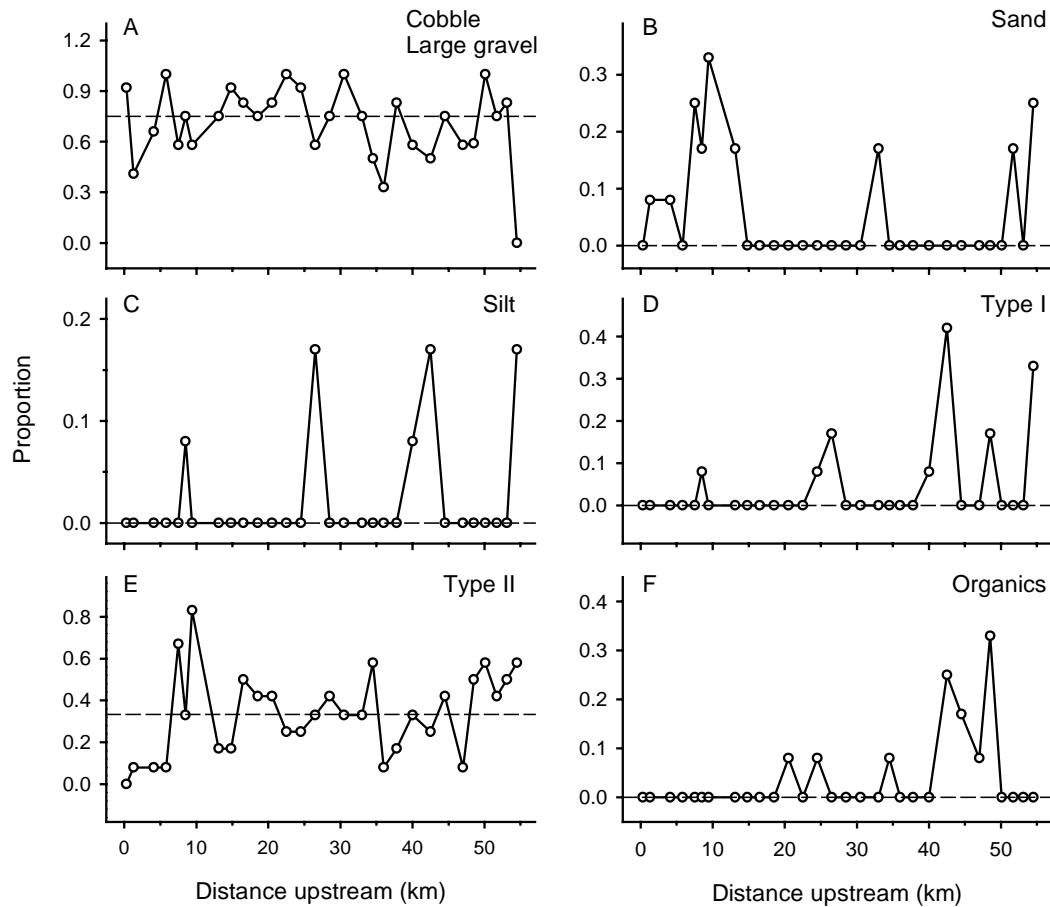
Figure 4.6. Longitudinal variation in substrate composition among sites. Substrate composition is expressed as the proportion of samples within in each substrate category. Longitudinal patterns are plotted versus river km, the distance upstream from the lower boundary of the survey section: (A) cobble and large gravel, (B) sand, (C) silt, (D) type I burrowing habitat, (E) type II burrowing habitat, and (F) organic debris. Dashed horizontal lines define peaks and troughs with respect to the median.

velocity (0.78). Differences in wetted width, water depth, and water velocity within sites ranged 0.4–7.8 m, 0.2–0.8 m, and 0.2–1.0 m·s^{-1}, respectively.

Multivariate analysis: Habitat associations of larval lamprey

Spatial associations between larvae and stream habitat variables varied depending on the scale of statistical analysis. Individual habitat variables explained 14–35% of the variation in the relative abundance of larvae among sites and 2–29% of the variation in larval occurrence among samples (Table 4.2). Depth, canopy closure, and gradient were the most important predictors of larval abundance at the site level, whereas velocity, burrowing habitat type, and sample position in the channel were the strongest predictors of larval occurrence at the sample level. Velocity and river km were significantly associated ($P \le 0.05$) with patterns of larval abundance at both sample and site levels; however, variables that were strong predictors at one scale were generally weak predictors at the other scale (e.g., depth, river km, and larval habitat type).

After accounting for other site-level explanatory variables, water depth and canopy closure were the only habitat variables that significantly predicted the relative abundance of larval lamprey among sites (likelihood ratio χ^2 test, $P \le 0.05$) (Table 4.3). Peaks in water depth and troughs in canopy closure corresponded with peaks in larval abundance and explained 49% of the variation in the relative abundance of larvae. The relative explanatory contribution of each variable, defined as the change in coefficient of determination that resulted from removing the variable from the

Table 4.2. Coefficients of determination from bivariate logistic regression of site- and sample-level variables explaining the abundance of larval lamprey. The coefficient of determination (Nagelkerke R^2) indicates the relative explanatory power of variables positively (+) or negatively (−) associated with larval abundance ($P \leq 0.10$).

Variable [a]	Site level	Sample level
Depth (+)	0.35 **	−
Organic depth (+)	0.14	0.03 **
Velocity (−)	0.20 *	0.29 ***
Unit type		
Pool	−	0.06 ***
Substrate		
Organics, silt, and sand	−	0.07 ***
Habitat type		
Type I and II	−	0.26 ***
Position		
Margin	n/a	0.20 ***
Wetted width (+)	−	0.02 *
Canopy closure (−)	0.29 **	n/a
Gradient (−)	0.27 **	n/a
River km (−)	0.21 *	0.03 **

* The asterisk symbol indicates the significance level of explanatory variables: $P \leq 0.05$ (*), $P \leq 0.01$ (**), and $P \leq 0.001$ (***).
[a] Position (margin), canopy closure, and gradient were modeled only at the levels at which they were collected.

Table 4.3. Model selection results from multiple logistic regression of site-level habitat variables explaining the relative abundance of larval lamprey among sites.

Variable	Estimated coefficient	Standard error	Likelihood ratio χ^2 test		$R^{2\ a}$
			χ^2	P	
Intercept	2.00	1.30			
Depth	3.15	1.33	8.13	0.004	0.21
Canopy closure	-2.67	1.31	5.43	0.020	0.13
River km	-0.09	0.04	7.11	0.008	0.18

Notes: Regression statistics for the logistic model ($n = 30$) were deviance (-2 log L) = 42 (intercept only) and 21 (intercept and covariates); likelihood ratio χ^2 test (3 df), $P < 0.001$; $R^2 = 0.67$.
[a] The R^2 value shown for each variable represents the change in coefficient of determination that resulted from removing that variable from the model.

model, was greatest for depth (21%), followed by river km (18%), and canopy closure (13%). The site-level model, with river km added to account for spatial autocorrelation, produced a good fit of the factors influencing larval distribution in the Middle Fork John Day survey section ($R^2 = 0.67$). The model passed the goodness of fit test ($P = 0.11$) and correctly classified 90% of the observations at the 0.5 cutoff level.

Habitat variables associated with the occurrence of larval lamprey among samples differed from variables associated with the relative abundance of larvae among sites. Low water velocity, suitable burrowing habitat (types I and II), and pool habitats were the most important habitat variables explaining variation in larval occurrence at the sample level after accounting for other explanatory variables (Table 4.4). Locational variables, including sample position (margin) and river km, contributed to a significant drop in model deviance and explained 4–6% of the variation in the sample-level model. The full model correctly classified 79% of the observations, passed the χ^2 goodness of fit test ($P = 0.31$), and explained approximately half of the variation in larval occurrence among samples ($R^2 = 0.48$).

DISCUSSION

Patterns in larval abundance were closely linked to variation in habitat structure. Physical gradients in channel morphology established the geomorphic template for larval distribution among reaches and set the context for larval habitat associations at finer scales. Larvae were most abundant in reaches where the stream

Table 4.4. Model selection results from multiple logistic regression of sample-level habitat variables explaining the occurrence of larval lamprey within sites.

Variable	Estimated coefficient	Standard error	Likelihood ratio χ^2 tests		
			χ^2	P	R^2 [a]
Intercept	-2.91	0.50			
Velocity			13.51	0.001	0.04
0–0.11 m·s^{-1}	1.56	0.45			
0.12–0.23 m·s^{-1}	0.81	0.46			
Unit type			10.25	0.001	0.03
Pool	1.10	0.36			
Habitat type			24.76	< 0.001	0.07
Type I	1.60	0.69			
Type II	1.61	0.33			
Position			12.96	< 0.001	0.04
Margin	1.18	0.33			
River km	-0.04	0.01	20.72	< 0.001	0.06

Notes: Regression statistics for the logistic model ($n = 356$) were deviance (-2 log L) = 442 (intercept only) and 294 (intercept and covariates); likelihood ratio χ^2 test (7 df), $P < 0.001$; Nagelkerke $R^2 = 0.48$.
[a] The R^2 value shown for each variable represents the change in coefficient of determination that resulted from removing that variable from the model.

channel was relatively deep (0.4–0.5 m) and gradient was low (< 0.5%). More precise

estimates of larval abundance, however, required statistical analysis at progressively

smaller spatial scales because larval habitat relationships were scale-dependent. Water

depth was positively associated with larval abundance at large scales (5–10 km) but

was unrelated to patterns of larval occurrence at small scales (< 50 m). Conversely,

water velocity, suitable burrowing substrate, and pool habitat explained variation in

larval occurrence at small scales but were not important predictors of larval abundance

at large scales. Habitat variables alone explained a large proportion of variation in

larval abundance, but locational factors such as sample position and river km

explained additional variation that might otherwise be discounted as noise. The

complexities of larval habitat relationships and spatial heterogeneity in the stream

environment have important implications both for our understanding of the biology of

larval lampreys and for their management and conservation.

Habitat heterogeneity and larval distribution

A hierarchical model of habitat classification provides a framework for

evaluating heterogeneity in streams based on nested geomorphic features at section

(10–100 km), reach (0.1–10 km), unit (1–100 m), and subunit (0.01–10 m) levels

(Gregory et al. 1991). Environmental heterogeneity in streams can thus be described

as patches within patches at sequentially smaller spatial scales (Kotliar and Wiens

1990). Fishes may respond to habitat heterogeneity differently at each respective

scale, but patterns of distribution and abundance are products of the collective spatial

structure of the riverine environment (Montgomery et al. 1999, Baxter and Hauer 2000). Investigations of lamprey ecology in streams and rivers have addressed the interplay of macro- and microenvironmental factors and their influence on larval distribution (Baxter 1957, Hardisty and Potter 1971). However, quantitative analysis of such relationships requires sampling approaches that are specifically designed to characterize spatial variance structure at multiple scales (Li et al. 2001). By collecting data with a nested sampling design, we were able to separate the relative influences of habitat heterogeneity on larval abundance patterns at two different spatial scales.

We observed that habitat heterogeneity both within and among sites influences the measurement and perception of patterns in larval abundance and habitat use. Patterns of larval occurrence at the site level indicated that nearly the entire 55-km survey section was suitable for larval rearing, with 93% of the sites containing larvae. Similar analysis of larval occurrence at the sample level, however, revealed that suitable burrowing habitats were much more limited, with larvae present in only 31% of the samples. The perception that suitable rearing habitats were either common or uncommon was largely dependent on the scale of observation. This phenomenon of differences in spatial variance structure at small versus large scales indicates a nested structure in larval abundance patterns and a high degree of heterogeneity in habitat suitability at the channel unit level. Habitat heterogeneity also influenced spatial variation in larval density, which was high among sites and even higher among samples. Larvae were highly concentrated in small areas; single 1 x 1-m quadrats

represented less than 10% of the sampled area and yet often contained 40–50% of the

maximum number of larvae found in a site.

Detailed qualitative studies of the distribution of larval Pacific lamprey at

small scales confirm our quantitative observations that concentrations of larvae are

associated with patchy fluvial features such as stream margins, backwaters, eddies,

insides of bends, and downstream ends of sand bars (Pletcher 1963, Hammond 1979).

Highly structured larval distribution patterns at small scales are generated both

passively with respect to physical gradients and actively through larval movement.

Larvae often emerge from their burrows and actively disperse to locate more suitable

living and feeding conditions (Potter et al. 1970, Potter 1980). Feeding primarily on

suspended material (e.g., diatoms and desmids), larval lampreys have specific flow

requirements (Moore and Mallatt 1980). Water velocity over larval habitats must be

fast enough to provide a steady influx of food and yet slow enough to promote the

deposition of soft sediments needed for burrowing. Thus, in streams with sufficient

flow for filter feeding, suitable burrowing habitats may be more limited than is

immediately apparent from large-scale habitat patterns.

Spatial scale and larval habitat relationships

While many studies have investigated the influence of environmental variables

on patterns in larval lamprey abundance, relatively little is known about variation in

larval habitat relationships as a function of spatial scale. Broad-scale distribution

patterns of larval lamprey have been attributed to variation in channel gradient within

and among streams (Baxter 1957, Pletcher 1963, Young et al. 1990). We also observed that patterns in larval abundance follow longitudinal trends in channel gradient; however, the significance of these relationships very likely depends on the scale over which gradient measurements were taken. In our study of larval distribution in a fourth- to fifth-order stream, channel gradient corresponded with large-scale larval abundance patterns but was not a significant predictor of relative abundance after accounting for water depth and canopy closure. Based on our observations of larval distribution, we suspect that the relative influence of channel gradient as a predictor of larval abundance increases at larger spatial scales due to the nested structure of channel-reach morphology in mountain streams (Montgomery and Buffington 1997). At the unit scale, channel gradient is stepped rather than gradual and low-gradient units are often nested within high-gradient reaches. Sediment transport processes during high flow events are not conducive to fine-particulate deposition anywhere in high-gradient reaches, so it is unlikely that larvae moving through high-gradient reaches will find suitable burrowing habitat even though they may encounter relatively low-gradient, low-velocity units.

Larval associations with low water velocity, fine-particulate burrowing substrates, and pool habitats described for other species of lamprey (Malmqvist 1980, Potter et al. 1986, Beamish and Jebbink 1994, Beamish and Lowartz 1996) confirm our observations of habitat selection by larval Pacific lamprey (Pletcher 1963, Hammond 1979, Richards 1980). However, our findings differ substantially from published work on the habitat ecology of larval lampreys because we identified that

these habitat variables were only significant at small spatial scales. Moreover,

variables we identified as positively associated with larval abundance at large scales

(e.g., water depth and an open riparian canopy) were generally considered negative

correlates of larval abundance in the published literature (as cited in Potter et al.

1986). Water depth was not a significant predictor of larval occurrence among

samples but was highly significant at large scales. Larvae were more abundant in sites

with greater than median depth, but within sites larvae were located along stream

margins regardless of depth. At small spatial scales (< 50 m), larvae selected pools

over riffles because the morphology of pool margins was more conducive to sediment

deposition than riffle margins. The interaction between depth, water velocity, and

channel morphology provides a potential explanation for the differential responses of

larvae to depth among and within streams and in different seasons (Pletcher 1963,

Potter et al. 1986). Suitable burrowing sediments are deposited along stream margins

during high flow events, leaving deeper thalweg habitats washed clean of sediments

during summer low flow. Water depth at large spatial scales, however, was positively

associated with larval abundance patterns because deep reaches were structurally

complex and therefore likely to meet the specific velocity and substrate requirements

necessary for larval settlement.

The relationship between larval abundance and riparian vegetation may be

related more to spatial context and geomorphic factors than to larval behavior as has

been suggested in the literature. Potter et al. (1986) found that shade from riparian

vegetation was positively related with larval density at small scales and attributed the

association to photophobic behavior by larvae. We could not directly test the association between larval occurrence and riparian canopy at small scales because we did not measure canopy closure or shade at the appropriate scale (i.e., canopy closure was measured at the transect level). However, as sample positions near channel margins are more likely to be shaded than samples in the mid channel, there may be a strong interaction between shade and sample position in predicting larval density at small spatial scales. At the site level, we observed exceptionally high larval densities (> 100 larvae·m^{-2}) in the most exposed sites and found that an open canopy was an important predictor of larval abundance at large scales. No other quantitative studies of larval lamprey have analyzed large-scale associations with riparian cover, so it is difficult to evaluate this relationship in the context of previous research. However, qualitative observations of larval Pacific lamprey rearing in Oregon coastal streams confirm a negative association with riparian canopy closure and may indicate differences in habitat selection related to primary productivity and the availability of larval food sources (Kan 1975). In the Middle Fork John Day River, the effects of an open canopy on larval abundance patterns are difficult to separate from other large-scale habitat factors (e.g., channel gradient, stream order, temperature, and land use). Mining and grazing have eliminated riparian vegetation in all of the low-gradient, alluvial valleys where larvae are most abundant, so it will be impossible to evaluate the relationship between riparian canopy and larval abundance effectively until riparian areas are revegetated. Fortunately, conservation programs in the upper

Middle Fork John Day River are currently underway and will provide an excellent opportunity to monitor the response of larval lamprey to riparian restoration.

Larval abundance patterns are directly linked to environmental variables, but the spatial context of biological factors such as the spawning distribution of adults also plays an important role in larval distribution. Larvae were much more abundant in downstream versus upstream portions of the study stream even though upstream habitats had greater proportions of suitable burrowing habitat (Figures 4.6D and 4.6F). The disproportionate distribution of larvae in downstream reaches may be attributable to adult spawning patterns. Pletcher (1963) observed that larval rearing areas were often located within or adjacent to reaches where spawning occurred. It is important to consider the effects of spatial context in studies of distribution and abundance because standard statistical analyses (e.g., multiple linear regression, principle components analysis, and analysis of variance) are sensitive to non-normally distributed data (Ramsey and Schafer 1997). Multiple linear regression of larval density, as opposed to relativized abundance, does not account for spatial context, such as the effect of adult spawning patterns, in larval distribution patterns and may erroneously identify sites with the highest larval densities as optimal habitats. Statistical analyses can be designed to account for spatial context by relativizing the response variable with respect to the median, thereby creating a binary response variable that places peaks in larval abundance on equal footing (DeAngelo et al. 1995, Torgersen et al. 1999). Further incorporation of spatial structure in statistical analysis can be achieved by including locational variables, such as river km and sample

position in the stream channel, in the regression model (Knapp and Preisler 1999).

Direct inclusion of locational variables relaxes the assumption in regression analysis

that observations be spatially independent and may explain additional variation in the

regression model.

Management implications

The measurement of patterns in larval abundance and the detection of larval

habitat relationships are important components of lamprey monitoring programs.

Recent technical advancements in larval sampling and habitat assessment methods in

lentic environments have shown that high-resolution data can be collected over large

areas and provide direct information on variability in larval distribution over a range

of spatial scales (Bergstedt and Genovese 1994, Fodale 1999, Fodale et al., in

review). We found that larval habitat assessment methods in small streams can benefit

from spatially explicit as opposed to random sampling approaches. While a stratified

random sampling design may be effective for obtaining larval population estimates in

homogeneous stream habitats (Pajos and Weise 1994), extrapolation of larval

abundance in complex stream environments should be based on spatially continuous

habitat surveys (Hankin and Reeves 1988). A Hankin–Reeves survey approach has

yet to be applied for larval lamprey, but the information provided in this paper on

spatial variation in larval abundance will be useful in designing future studies with the

objective of obtaining larval population estimates.

The size, number, and arrangement of sample plots have effects on the detection of patterns in larval distribution and habitat relationships. Collecting multiple samples within sites increases precision in distinguishing between suitable and unsuitable habitats and achieves a higher level of reproducibility than by taking fewer large samples (Southwood and Henderson 2000). Given the high degree of heterogeneity in larval abundance patterns at small scales, we concluded that twelve 1-m^2 samples distributed over a 50 m reach of stream were more effective at capturing variability in larval abundance than a single 12-m^2 sample. Potter et al. (1986) also recommended that sampling area for a given electrofishing quadrat be small (< 1 m^2) and that samples be distributed due to the high degree of environmental heterogeneity likely to occur in large samples. In our review of the literature on larval habitat, we found that a nested approach for sampling larval lampreys is generally uncommon and could be applied more frequently in studies of this type, particularly when there has been no a priori assessment of habitat heterogeneity in the environments to be surveyed. Similar guidelines with respect to environmental heterogeneity apply in the selection of larval sampling sites. In choosing the appropriate distribution and number of sites, a systematic design is superior for detecting spatial pattern but is also more labor-intensive. However, spatially continuous stream habitat data and 10-m digital elevation models are often available through natural resource agencies and can be used to stratify site locations based on longitudinal habitat patterns. Once an initial assessment of larval distribution patterns has been completed, follow-up monitoring of

temporal trends in larval abundance can be conducted in a selection of representative sites.

Understanding the relationship between habitat heterogeneity and the spatial distribution of larval lamprey is important for establishing conservation and restoration plans and may also be useful in controlling lamprey where they are an invasive species. Simplification of stream habitats through channelization has been identified as a significant cause for the decline of lampreys in Europe (Bohl 1995, Kirchhofer 1995) because larval lampreys in headwaters and low-order streams depend on complex channel structures (e.g., meanders, bars, alcoves, backwaters, and large wood) to create environments suitable for burrowing and filter feeding. Suitable larval habitats may occur throughout an entire stream section but be relatively limited at smaller spatial scales. Lamprey conservation and restoration efforts in rivers and streams need to recognize the importance of habitat heterogeneity at multiple scales and focus on maintaining and promoting complexity in channel morphology and sediment composition. Increased understanding of habitat heterogeneity and larval abundance also has implications for lamprey management and control, both for the efficient application of lampricide and for the regulation of flow. While managing for habitat heterogeneity is likely to improve habitat conditions for declining lamprey populations in fast-flowing streams, it may actually aid in lamprey control in regulated rivers and reservoirs where channel simplification and flow regulation have decreased water velocities and promoted the homogeneous deposition of fine sediments suitable for larval settlement. In either capacity, for conservation or control, habitat

heterogeneity is an important component in the biology of larval lampreys and warrants further descriptive and experimental study.

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CHAPTER 5

ASSESSING PRESENCE–ABSENCE VERSUS RELATIVE ABUNDANCE DATA
IN MULTIVARIATE ANALYSIS OF STREAM FISH ASSEMBLAGES

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ABSTRACT

Multivariate analysis of presence–absence data provides a more statistically robust and ecologically interpretable assessment of gradients in fish community structure than relative abundance data. We compared different ordination methods and data transformations with respect to their ability to quantify community structure in a complex fish assemblage matrix. Non-parametric ordination and multivariate analysis techniques such as non-metric multidimensional scaling (NMS), multi-response permutation procedure (MRPP), and Beals smoothing made it possible to analyze heterogeneous presence–absence and categorical fish assemblage data without violating the normality assumptions that limit other ordination procedures (e.g., principal components analysis). We found that even the most robust method of non-parametric ordination (NMS) was incapable of extracting meaningful ecological gradients from a data matrix containing a large number of relative abundance estimates. Only after applying Beals smoothing, a multivariate smoothing function that uses presence–absence data to calculate probabilities of species occurrence, were we able to identify dominant trends in fish community structure associated with environmental gradients. The utility of presence-absence data in ordination analysis was greatly enhanced by Beals smoothing, which retained necessary assemblage information while filtering out the noise that might otherwise mask ecologically relevant species gradients. Multivariate methods that are capable of analyzing presence–absence data can facilitate more extensive data collection by freeing up

resources that would normally be expended in collecting estimates of relative

abundance and population density.

INTRODUCTION

A major problem with understanding stream fishes is the difficulty of obtaining

accurate estimates of fish population abundance and community composition (Bayley

and Dowling 1993, Angermeier and Smogor 1995). To assess longitudinal patterns

and discontinuities in stream fish community structure and determine the role of

small- and large-scale gradients in temperature and physical habitat, it may be

necessary to sample long reaches of stream (40–60 km) in a spatially continuous

manner. This poses a problem for traditional fish sampling methods that are

fundamentally site based such as electrofishing, which can only provide counts of

fishes in short reaches (1–300 m) (Cowx 1990). Restrictions of sampling time and

injury to fish, which may be subjected to repeated stress, render electrofishing

inappropriate for assessing spatially continuous fish assemblage patterns (Reynolds

1996). Snorkeling provides the means to sample long reaches in relatively short

periods of time while minimizing disturbance to fish (Thurow and Schill 1996,

Mullner et al. 1998). However, visual surveys such as snorkeling have the

disadvantage that exhaustive counts of fish can only be obtained with great effort and

expenditure of time. Relative abundance estimates and presence-absence, however,

are easily collected during snorkeling surveys. Many researchers collect total

abundance data when simple relative abundance estimates or presence–absence data

would have satisfied their research objectives (Rahel 1990). The objective of this short paper is to compare multivariate analyses of relative abundance and presence-absence data and demonstrate that fish assemblage analysis with presence-absence data may be more effective than with abundance data, especially when the analysis involves very heterogeneous data matrices composed of many small sample units.

METHODS

Description of data matrices

Fish assemblage data were collected during snorkeling surveys of the upper Middle Fork John Day River in northeastern Oregon during August 1996. Visual estimates of relative abundance of fishes (logarithmic category, i.e., dominant, common, and rare) and estimates of total abundance for dominant species were recorded in 293 sample units (pools and riffles) distributed throughout a 55-km stream section. Physical dimensions of each sample unit including channel width, depth, and geographic location were recorded in conjunction with fish species data.

The raw data sets used in multivariate analysis included two fish assemblage matrices and one environmental variable matrix. Each fish assemblage matrix had 293 rows and 12 columns (species). The elements in one fish assemblage matrix consisted of categorical values of relative abundance (0 = absent, 1 = rare, 2 = common, and 3 = dominant), and the elements in the other matrix contained extrapolated abundances

that were calculated from field-estimated abundance categories (0, 1, 2, and 3) and

estimates of the total abundance of dominant fish species in each sample unit:

$$A = A_d \bullet 1 \qquad \text{if } A_c = 3$$
$$A = A_d \bullet 0.5 \qquad \text{if } A_c = 2$$
$$A = A_d \bullet 0.1 \qquad \text{if } A_c = 1$$

where A is extrapolated abundance, A_d is the estimated abundance of dominant

species, and A_c is the field-estimated categorical abundance. As the total abundance of

species varied among sample units, each sample unit had a different adjustment. In

many sample units, no dominant species were recorded, so total abundances of

common species were estimated. Although there are obvious problems associated

with extrapolating abundance estimates, the data served the purpose of simulating a

large, heterogeneous data set containing real abundance values. The environmental

matrix was composed of 293 rows and 9 columns representing several habitat

characteristics described in Table 5.1 (see Chapter 6 for a description of field data

collection methods).

Data adjustments

Before calculating descriptive statistics for fish assemblage matrices, two

extremely rare species (longnose dace, *Rhinichthys cataractae*, and mountain sucker,

Catostomus platyrhynchus) were removed from the data (for recommendations on data

adjustments in multivariate analysis see Tabachnick and Fidell 2001). A third species,

Table 5.1. Descriptions of quantitative (Q) and categorical (C) variables in the enviromental data matrix.

Variable[a]	Data type	Description
Distance upstream	Q	Cumulative distance upstream represents position in the river continuum.
Habitat type	Q	Ranges from 1–4; represents a range of slow- to fast-water habitats, i.e., pool, glide, riffle.
Channel width	Q, C	Wetted width of channel; categories are binary w/respect to median.
Depth	Q, C	Maximum depth in sample unit; categories are binary w/respect to median.
Temperature	C	Position in longitudinal thermal profile; categories include peak, trough, or neither.
Habitat type	C	Channel unit type (pool or riffle).
Valley type	C	Unconstrained, partially constrained, or constrained.

[a] See Chapter 6 for a description of field data collection methods.

the torrent sculpin (*Cottus rhotheus*), was removed because it was difficult to detect by divers. Statistical analysis was conducted only on mid-water fishes (rainbow trout, *Oncorhynchus mykiss*; juvenile chinook salmon, *Oncorhynchus tshawytscha*; mountain whitefish, *Prosopium williamsoni*; largescale sucker, *Catostomus macrocheilus*; bridgelip sucker, *Catostomus columbianus*; redside shiner, *Richardsonius balteatus*; and Northern pikeminnow, *Ptychocheilus oregonensis*). In the total abundance matrix, average skewness and coefficient of variation (CV) of species totals were high, as was the CV of sample unit totals. As expected, average skewness and CV were low to moderate in row and column totals in the categorical abundance matrix. This is because the sample units were effectively relativized during

data collection into abundance classes. Beta diversity was low to moderate (2.4) in the community matrices. Several sample units had no fish and had to be removed prior to multivariate analysis. Following examination of descriptive statistics of both matrices, adult chinook salmon were removed from the analysis because they were rare and their distribution was highly skewed.

Data transformations and relativizations were necessary to prepare both fish assemblage matrices for ordination. Several different ecologically relevant transformations and relativizations were used to assess the response of ordination methods to contrasting data formats. The species abundance matrix was transformed in two different ways to produce two separate matrices (see Fshab4 and Fshab6 in Table 5.2). Other variations in data formats included simple quantitative and categorical versions of the categorical abundance matrices (see Fshrel5 and Fshrel6 in Table 5.2). Skewness and CV for species and sample unit totals after transformation were very low. The original species abundance matrix was also relativized by row totals to account for different sample areas and intensities in pool and riffle habitats. After relativization, species totals (columns) were still skewed.

Beals smoothing was selected for transforming the categorical abundance data set. Beals smoothing is a multivariate smoothing function offered in the software package PC-ORD and is well suited to analyzing heterogeneous data with a high percentage of zeros (McCune 1994, McCune and Mefford 1999). The smoothing function converts matrix cells to presence-absence data and then computes new cell values based on the probability of a particular species occurring in a particular sample

Table 5.2. Fish species matrix descriptions, data adjustments, and transformations.
All matrices contain assemblage data for 8 species.

Matrix	*n*	Data adustments	Average skewness		Coefficient of variation (%)	
			row	column	row	column
Fshab1	290	Raw total abundances.	1.56	4.82	123	95
Fshrel1	290	Raw abundance categories.	1.11	1.32	37	84
Fshab4 [a]	285	Log transform w/o outliers.	0.62	0.91	57	66
Fshab6 [a]	287	Relativized by rows w/o outliers.	1.37	2.71	0	95
Fshrel4 [b]	284	Beals smoothing w/o outliers.	0.06	1.04	5	53
Fshrel5 [b]	287	Quantitative (no Beals) w/o outliers.	0.91	0.93	36	75
Fshrel6 [b]	287	Categorical (no Beals) w/o outliers.	0.91	0.93	36	75

[a] Created from matrix containing species abundances (Fshab1).

[b] Created from matrix containing abundance categories (Fshrel1), i.e., 3 = dominant,
2 = common, 1 = rare, 0 = absent.

unit. The smoothing function is particularly useful when the data set consists of many small sample units and the data exhibit high levels of noise. Although small sample size and lack of zeros can cause problems with the Beals smoothing algorithm, this was not a problem with the large fish assemblage data sets which each consisted of 60% zeros.

All matrices were checked for multivariate outliers in rows and columns using Sorensen's distance measure in PC-ORD. A cutoff level of 2 standard deviations of the mean of average distances was used to flag outliers. All outliers exceeding 3

standard deviations were removed from analysis. The greatest number of outliers ($n =$ 6) was detected in the smoothed matrix (fshrel4). Skewness and CV in rows and columns ranged from low to moderate (CV > 100), but all matrices improved after transformation and relativization.

Ordinations

For comparison of different transformations, three different ordination methods were used to assess multivariate gradients of sample units in species space. The ordination techniques were performed using the software package PC-ORD. All ordination methods except principle components analysis used the quantitative version of the Sorensen coefficient as a distance measure (McCune 1994). Principle components analysis (PCA) was run using correlations in the cross-products matrix as distance measures. Bray-Curtis (BC) ordination was run in two dimensions with variance-regression, end-point selection, and Euclidean projection geometry (Beals 1984). Non-metric multidimensional scaling (NMS) was run on the relative abundance matrix because it is a more robust method, particularly when dealing with non-normal, heterogeneous data such as the fish assemblage data (Clarke 1993). NMS analysis required initial runs from six to one dimensions to assess reductions in stress associated with increasing dimensionality. Two hundred iterations were used for each NMS run, using random starting coordinates. Maximum reductions in stress occurred in the two-dimensional solution, and this was confirmed as statistically significant ($P = 0.05$) by 20 Monte Carlo runs. Stability of the final solutions in NMS was

assessed by examining reduction of stress relative to number of iterations (McCune

and Mefford 1999). After initial runs of NMS with Monte Carlo simulations

significantly determined the two-dimensional model as the best solution, all

subsequent NMS analyses were run with two dimensions only.

The effectiveness of each ordination method was evaluated by comparing

cumulative percent variation explained by each method for each data transformation

and by examining ordination plots with species overlays. Cumulative percent variance

explained, or coefficient of determination (r^2), is the correlation between distance in

ordination space and distance in the original *p*-dimensional space. Ordinations of

sample units in species space were assessed using overlays of species and

environmental matrices to identify fish species responses to ecologically relevant

multivariate gradients. Joint plots of environmental and species matrices on

ordinations were used to interpret the strength and direction of species responses with

respect to ordination axes (Jongman et al. 1995). The effectiveness of various

ordination methods at representing the underlying data structure in various data

formats, transformations, and relativizations was evaluated by graphically comparing

the relative degree of distortion and interpretability of each ordination.

Analysis of groups

Multi-response permutation procedure (MRPP) in PC-ORD was used to

analyze the differences in fish species assemblage pattern with respect to

environmental parameters such as valley segment type, spatial patterns of temperature,

and in-stream habitat (specific variables listed in Table 5.1) (Biondini et al. 1985).

MRPP results for both relative abundance and smoothed presence-absence data were

compared to determine the limitations or strengths of each data type. MRPP analysis

of the smoothed data was used for qualitative and comparative purposes only. Only

unsmoothed data were used for the purposes of statistical inference. As with the

ordination methods, the Sorensen coefficient was applied as a distance measure, and a

priori groups were weighted by group sums. Differences in fish species with respect

to group membership were evaluated with significance tests ($P \leq 0.05$) and chance-

corrected within-group agreement statistics.

RESULTS AND DISCUSSION

Transformations and relativizations had profound effects on the outcome and

interpretability of various ordination methods (Table 5.3). Beals smoothing and

relativization of total abundance by rows proved to be the most effective

transformation of the fish assemblage matrix. Log transformation of total fish

abundances was ineffective in the PCA ordination and only slightly improved the

more robust NMS method. In spite of reasonably good variance explained by both

methods, the trends in both ordinations were difficult to interpret. The untransformed,

field-estimated categorical abundance matrices (data types specified as quantities or

categories) caused severe stability problems in NMS analysis at greater than one

dimension, and both PCA and NMS were unable to explain more than 48% of the

variance on the ordination axes. Although it explained relatively little variation in

Table 5.3. Comparisons of NMS, PCA, and Bray-Curtis ordination methods with differing, ecologically relevant data adjustments and transformations. Ordination methods and transformations were evaluated by the coefficient of determination (r^2), which is the cumulative percent variance explained. Cumulative percent of variance explained is the correlation between distance in ordination space and distance in the original p-dimensional space.

Data adjustment	Ordination method [a]	Stability	r^2 Axis 1	r^2 Axis 2	Graphic evaluation
Log transform	NMS	fair	33	80	Trends unclear, zeros [b], separation.
	PCA	NA	55	71	Funnel-shaped, compression.
Relativized by rows *	NMS	good	45	83	Trends clear, zeros, separation.
	PCA	NA	37	70	Funnel-shaped, but trends clear.
Categorical (quantity)	NMS	poor	19	31	Distorted ordination, compressed.
	PCA	NA	21	35	Minor distortion, trends unclear.
Categorical (category)	NMS	poor	15	48	Distorted in circular pattern.
	PCA	NA	21	35	Trends fair, no major distortions.
Beals smoothing *	PCA	NA	72	85	Very good correlations, trends.
	Bray-Curtis	NA	62	88	Virtually the same as PCA.
	NMS	very good	74	93	Same as above.

* Indicates matrices selected for final analysis in two dimensions.

[a] NMS ordinations calculated for a two-dimensional solution.

[b] Large numbers of zeros in the data matrix made it difficult to interpret overall data trends in ordination plots due to pronounced data separation.

community structure, the two-dimensional solution in NMS did provide more reduction in stress than was expected by chance ($P \leq 0.05$). The matrix containing abundances relativized by rows was ordinated successfully by NMS (83% of variance explained), whereas the ordination produced by PCA for the same matrix was distorted in a funnel-shaped pattern. In contrast to other transformations, all of the ordinations of the smoothed data were interpretable and highly effective at explaining the variance on each axis. In summary, NMS was the most robust ordination method with respect to its ability to deal with noisy data. A disadvantage of NMS, however, was that computation time was slow especially if Monte Carlo simulations were calculated. PCA performed poorly except with the smoothed data. All three ordinations of the smoothed data produced virtually identical ordination plots, in which PCA was most similar to Bray-Curtis, and Bray-Curtis was most similar to NMS.

Fish species correlations with ordination axes varied both in direction and in correlation strength with respect to data transformation and ordination method (Table 5.4). The two matrices selected for correlation analysis were the smoothed data matrix and the matrix relativized by rows. Ordinations of both matrices resulted in greater than 80% of the variance explained by two axes. PCA, Bray-Curtis, and NMS detected the underlying species gradient of fastwater to slow-water fishes, i.e., rainbow trout, juvenile chinook, and mountain whitefish to suckers and pikeminnow. The direction of correlations among methods and data transformation was consistent

Table 5.4. Results of matrix overlay analysis of fish species correlations and ordination axes. Species correlations (Pearson's *r*) are presented for comparison of various ordination methods and transformations. Directions of correlations were standardized to account for differing axis assignments of ordination methods. Fish species are listed in order of placement on the fast- to slow-water environmental gradient.

| | Relativized by rows NMS method | | Beals smoothing NMS method | | Beals smoothing PCA method | | Beals smoothing Bray-Curtis method [a] | | | |
| | | | | | | | Axis 1 | | Axis 2 | |
Species	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	0°	40°	0°	40°
Rainbow trout	- 0.74	0.24	- 0.81	- 0.04	- 0.78	0.39	- 0.79	- 0.73	- 0.36	0.44
Juv. chinook	- 0.20	0.05	- 0.48	0.59	- 0.33	0.81	- 0.55	- 0.25	0.33	0.82
Mt. whitefish	- 0.05	0.18	- 0.18	0.44	- 0.09	0.42	- 0.33	- 0.07	0.37	0.64
Speckled dace	- 0.30	- 0.89	- 0.14	- 0.77	- 0.31	- 0.87	- 0.04	- 0.36	- 0.73	- 0.61
Redside shiner	0.53	0.67	0.77	0.22	0.82	0.01	0.76	0.77	0.49	- 0.31
Bridgelip sucker	0.63	0.03	0.92	0.43	0.94	0.06	0.87	0.97	0.74	- 0.19
N. pikeminnow	0.58	0.03	0.93	0.31	0.93	- 0.03	0.90	0.94	0.64	- 0.30
L. sucker	0.28	0.16	0.60	0.59	0.69	0.42	0.51	0.70	0.73	0.15

Notes: NMS ordinations calculated for a two-dimensional solution.
[a] For the Bray-Curtis ordination, correlations with ordination axes are reported for 0° and 40° ordination rotations. Graphic depictions of the 40° rotation are shown in Figures 5.1 and 5.2.

for species at the extremes of each axis, such as redside shiner, bridgelip sucker and

juvenile chinook, but varied only slightly for species such as rainbow trout and

pikeminnow, which may have been responding to both axes. Correlations varied from

0.20 to 0.50 among different transformations and ordination methods.

The fish assemblage responses to both Axis 1 and Axis 2 were most

interpretable in the NMS and Bray-Curtis ordinations of the smoothed data. Both

ordinations performed equally well; therefore, the simpler method, Bray-Curtis

ordination, was selected for depiction in Figures 5.1 and 5.2. In order to interpret each

ordination axis more easily, the ordination was rotated by 40° around the centroid.

This effectively removed the current velocity gradient from Axis 2 and allowed

juvenile chinook and mountain whitefish to align more clearly with Axis 2. Joint plots

of fish species and environmental variables of depth and habitat type (see Table 5.1)

demonstrated that the fish assemblage structure responded to field-measured

parameters (Figure 5.1). Fishes such as Northern pikeminnow and suckers that prefer

deep, slow water were separated along Axis 1, a current velocity gradient, from

fastwater species such as trout, juvenile chinook salmon, mountain whitefish, and

speckled dace (Figure 5.2). The fish species responding most strongly to Axis 2 also

correspond positively and negatively, respectively, with natural groups of coolwater

fishes (rainbow trout, juvenile chinook, and mountain whitefish) and warmwater

fishes (redside shiner, Northern pikeminnow, speckled dace, largescale sucker, and

bridgelip sucker) (Table 5.4). Further interpretation of Axis 2 required more detailed
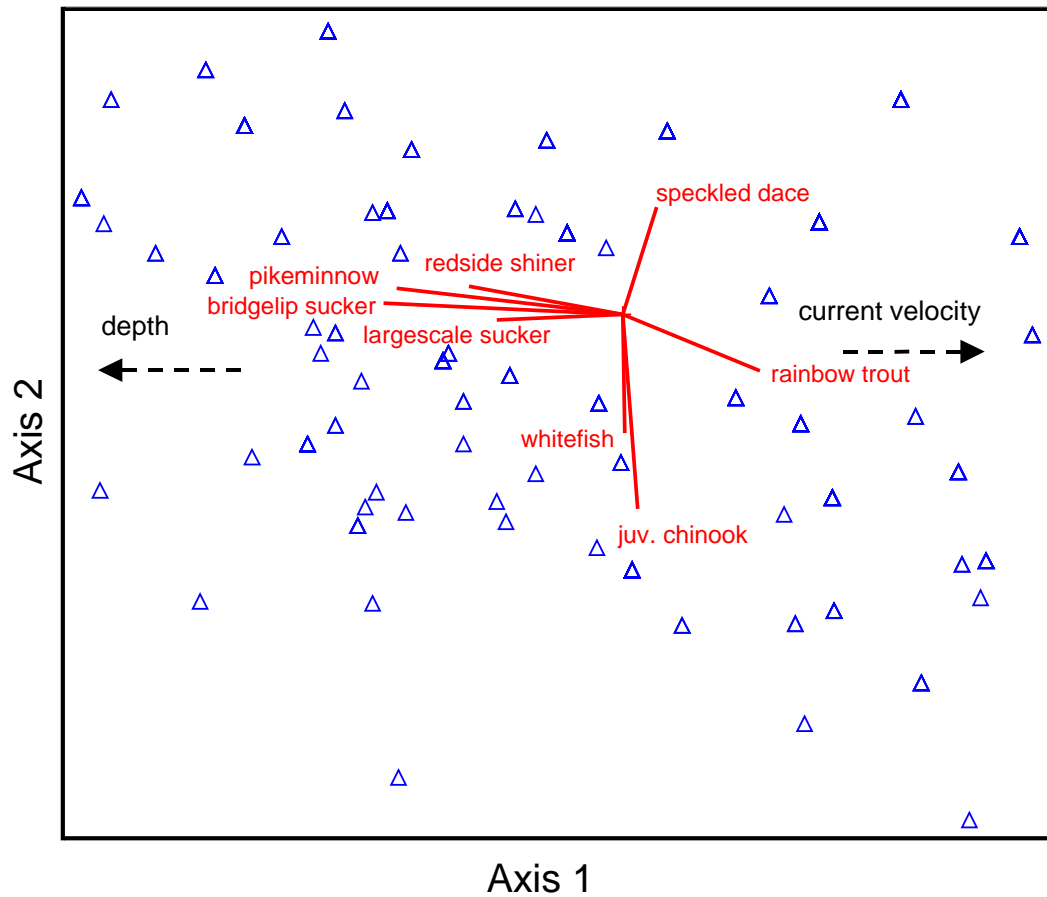
Figure 5.1. Bray-Curtis ordination of sample units in species space with joint plots of fish species and environmental variables. Species and environmental vectors are indicated by solid and dashed lines, respectively. Fishes that prefer deep, slow water (e.g., cyprinids and catostomids) are separated in the ordination from fastwater species such as trout, chinook salmon, mountain whitefish, and speckled dace. See Table 5.4 for species correlations.
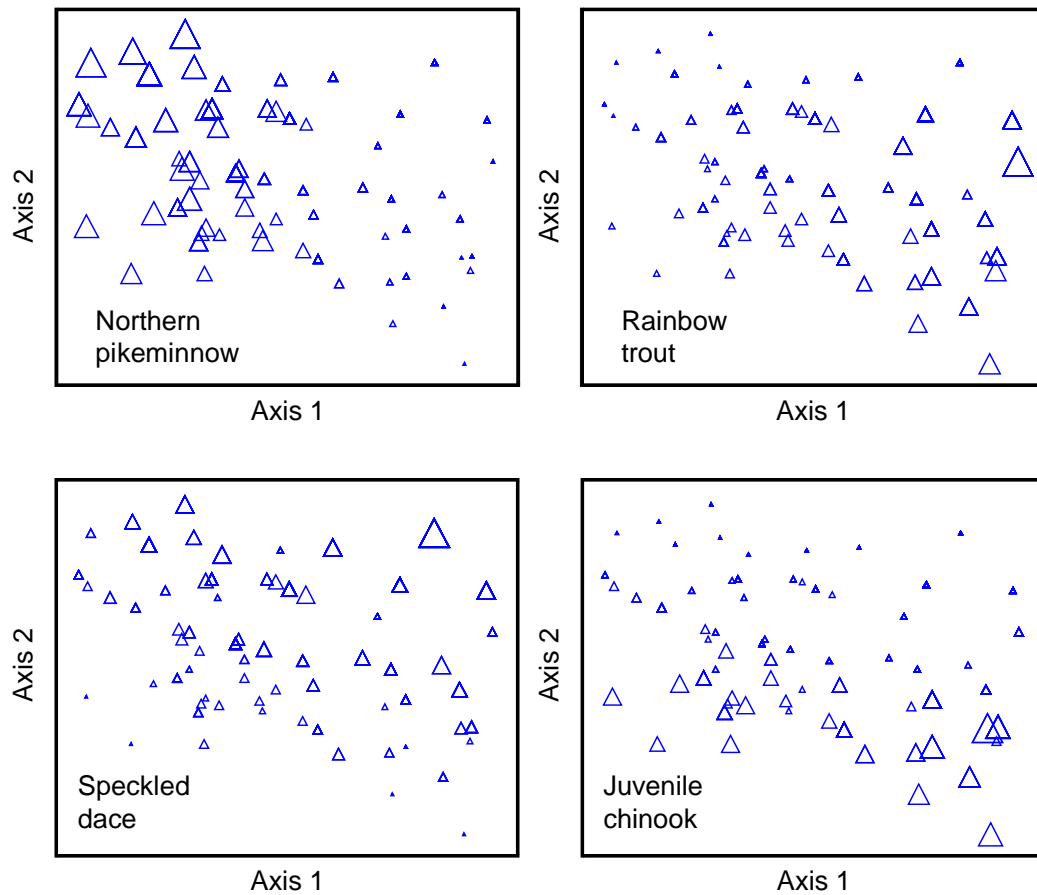
Figure 5.2. Bray-Curtis ordination of sample units in species space with fish species overlays depicting gradients in community structure. Fish species data in sample units were transformed using Beals smoothing. Axis 1 depicts a current velocity gradient (increasing from left to right). Slow-water species, such as Northern pikeminnow, are separated in ordination space from fastwater species, such as rainbow trout.

geographic analysis of environmental gradients in habitat and thermal patchiness and was beyond the scope of this paper (see Chapter 6).

Analysis of groups.—Data transformation had little or no effect on group analysis of fish assemblage and environmental groups in MRPP (Table 5.5). Fish assemblages differed significantly ($P < 0.01$) with respect to all measured environmental groups (i.e., habitat type, water temperature, water depth, and channel width) except valley type. Chance-corrected within-group agreement was highest for water depth and habitat type, thereby reinforcing the ordination results that depicted strong associations of fish assemblages with current velocity.

Multivariate analysis of a heterogeneous fish assemblage data set revealed that abundance data had no explanatory advantage over presence-absence data with respect to PCA and NMS ordination techniques. Transformation of presence-absence data with Beals smoothing improved the interpretability of overall gradients on ordination axes compared to ordinations of direct relative abundances calculated from total abundance data. When fish assemblage data are collected over large areas containing many small sample units, which is typically the case in extensive snorkeling surveys, it may not be necessary to obtain exhaustive counts or even relative abundances of fishes if ordination is the preferred mode of analysis. Categorical abundances and estimates of numbers of dominant species, however, may be helpful in subsequent geographic analyses in which overall estimates of fish numbers are needed. Advantages of presence–absence data are that they are easier and faster to collect and

Table 5.5. Chance-corrected within-group agreement from MRPP analysis of stream fish assemblage and habitat group variables.

	Chance-corrected within-group agreement	
Group variable	Relativized by rows (*n* = 287)	Beals smoothing (*n* = 284)
Valley type	**0.00**	**0.00**
Unconstrained	139	139
Partially constrained	62	60
Constrained	86	85
Temperature	**0.01 ***	**0.02 ***
Peak	55	55
Median	111	110
Trough	121	119
Habitat type	**0.06 ***	**0.04 ***
Pool	179	177
Riffle	108	107
Water depth	**0.04 ***	**0.03 ***
> Median	155	155
< Median	132	131
Channel width	**0.01 ***	**0.01 ***
> Median	197	193
< Median	90	91

Notes: Chance-corrected within-group agreement (bold) values for group variables and species matrices are presented with group size (regular).
* Statistically significant (P ≤ 0.05) group effect. Low p-values indicate that groups differ with respect to multivariate species data.

may be less sensitive to variation in sampling intensity and sample unit size.

Nevertheless, estimates of absence are still susceptible to sampling error an should be

evaluated carefully prior to ordination (Bayley and Dowling 1993). The utility of

presence–absence data in ordination analysis was greatly enhanced by Beals

smoothing, which retained necessary assemblage information while filtering the noise

that might have otherwise masked ecologically relevant species gradients.

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CHAPTER 6

SPATIAL VARIABILITY IN STREAM FISH–HABITAT RELATIONSHIPS:
INFLUENCES OF TEMPERATURE AND CHANNEL MORPHOLOGY

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ABSTRACT

Processes influencing fish assemblages at large and small spatial scales are well understood, but little is known about spatial variability in fish assemblage structure or how these patterns are linked with physical habitat and temperature across scales. The objective of this study was to investigate spatial variability in stream fish–habitat relationships and the influences of temperature and channel morphology on longitudinal patterns of stream fishes in northeastern Oregon. We conducted extensive airborne and underwater surveys (35–70 km) to map spatially continuous distributions of fishes and habitat in three 4–5th-order mountain streams with different thermal environments. To evaluate changes in fish community structure in relation to environmental gradients in temperature, depth, habitat type, and channel gradient, we used multivariate analyses including non-metric multidimensional scaling and Bray-Curtis ordination with Beals smoothing. Although we focused primarily on the distributional patterns of coldwater fishes, and specifically on juvenile chinook salmon (*Oncorhynchus tshawytscha*), we interpreted our results within the context of the entire freshwater fish assemblage. Spatial structuring of fish assemblages exhibited a generalized pattern of warm- and coldwater fish assemblage zones but was patchy within thermal zones, particularly in the warmest stream. Fish community relationships with channel gradient, depth, and water velocity changed with respect to thermal gradients and the spatial scale of analysis. At cold water temperatures, juvenile chinook were associated with a slow-water, pool-dwelling fish assemblage (Cyprinidae–Catostomidae), but at warmer temperatures they were associated with

fishes in fast-water, riffle habitats (rainbow trout, *Oncorhynchus mykiss*; mountain whitefish, *Prosopium williamsoni*; and speckled dace, *Rhinichthys cataractae*). The increased effort of collecting spatially continuous data on stream fishes and habitat effectively limited the precision of fish abundance estimates but revealed unexpected ecological patterns and provided a perspective on stream fishes that would be difficult to obtain using standard electrofishing methods.

INTRODUCTION

Stream temperature and physical habitat factors including channel gradient, depth, and current velocity change as a function of stream order and are frequently cited as major determinants of longitudinal patterns in stream fishes (Huet 1959, Sheldon 1968, Rahel and Hubert 1991). Distributional patterns of stream fishes are generally viewed as biotic zones consisting of cold- and warmwater assemblages in which species are added or replaced along continuous gradients in temperature and habitat from headwaters to downstream reaches (Li et al. 1987). Beyond the concepts of biotic zonation and species addition, however, there is little understanding of spatial variability in stream habitat and fish distribution within biotic zones or throughout the river continuum (Vannote et al. 1980, Fausch et al., in press). The perception that stream fish assemblages change gradually with respect to downstream gradients is largely a function of the scale (i.e., grain and extent) of data collection and analysis (Naiman et al. 1988, Wiens 1989, Poole et al., in press).

As a consequence of the discontinuous and spatially limited manner in which stream fishes are sampled, fundamental questions about the nature and extent of spatial variability in stream fish–habitat relationships still remain unanswered: How finely tuned are longitudinal patterns in fish assemblages to thermal heterogeneity and physical habitat? Is species addition and replacement across thermal transitions gradual or abrupt? Can the effects of temperature on stream fish assemblages be separated from the effects of channel morphology? We propose that these questions can be addressed only by adapting and changing the manner in which fish assemblage and habitat data are collected thus providing a more spatially continuous view of stream fishes and their environment.

Stream fish assemblages in montane regions with steep thermal gradients are strongly associated with temperature patterns over a range of spatial scales. At a regional level, temperature limits the distribution of coldwater fishes and is often discussed with respect to global warming (Meisner 1990b, Meisner 1990a, Rahel et al. 1996). Keleher and Rahel (1996) estimated that 1–5°C increases in mean July air temperature would cause 9–76% areal reductions in coldwater fish habitat in the North Platte River drainage of Wyoming. Other studies of salmonids in mountainous regions of Oregon have demonstrated the significance of coldwater reaches and thermal refugia in determining basin- and reach-level fish distributional patterns (Roper and Scarnecchia 1994, Torgersen et al. 1999, Ebersole et al. 2001). As a consequence of human activities in riverine landscapes and the impacts of land-use practices on stream temperature dynamics (Schlosser 1991, Johnson and Jones 2000,

Poole and Berman 2001), there is a management concern for the persistence of coldwater fish species in an increasingly thermally fragmented environment (Sedell et al. 1990, Rieman and McIntyre 1995). Therefore, understanding stream fish responses to thermal heterogeneity is important for evaluating the ecological effects of habitat degradation, particularly at intermediate scales (1–2 stream orders) where human impacts are most likely to occur (Fausch et al., in press).

The role of stream temperature in determining the distribution of stream fishes is usually considered in the context of other abiotic and biotic factors (Matthews 1987, Matthews 1998). Stream fishes are influenced by three fundamental environmental gradients: physical-chemical factors (e.g., temperature and dissolved oxygen), channel morphology, and current velocity (Schlosser 1990, Bayley and Li 1992). Extensive ecological study of stream fish assemblages in rivers has shown that longitudinal functions of stream order (i.e., channel gradient, depth, and substrate size) are important drivers of fish assemblage structure (Sheldon 1968, Hughes and Gammon 1987, Gelwick 1990, Paller 1994, Kruse et al. 1997), particularly in low-elevation European rivers with gradual thermal gradients (Penczak et al. 1991, Oberdorff et al. 1993, Belliard et al. 1997). Biotic components such as competition and predation influence stream fish assemblage structure at local scales. Interspecific interactions are recognized as key determinants of fish assemblages in both freshwater and marine systems (Larkin 1956, Noakes and Grant 1986, Hixon and Beets 1993), but investigations of localized thermal gradients and their effects on interspecific interactions are relatively rare in stream fish ecology (Baltz et al. 1982, Reeves et al.

1987). Different species of fishes have varying ranges of thermal tolerance and their

capacities to compete and avoid predators vary with water temperature (Schreck and

Li 1991). Thus, stream fishes are affected by thermal patterns both directly, due to

physiological limitations, and indirectly through the differential thermal tolerances of

competing species and predators.

Recent studies on fish distribution and habitat heterogeneity indicate that

spatially explicit, multiscale studies are required to describe the influences of multiple

factors in fish–habitat relationships (Poizat and Pont 1996, Torgersen et al. 1999,

Baxter and Hauer 2000). Moreover, integration of spatial variability and patch

dynamics in stream fish–habitat models provides an appropriate conceptual framework

for assessing longitudinal patterns in fish distribution (Pringle et al. 1988, Palmer et al.

1997). Rahel and Hubert (1991) present a model of stream fish assemblage

organization that stresses the importance of patchy riverine features, such as thermal

transitions and geomorphic discontinuities, and illustrates zonation in fish

communities in response to environmental transitions. In their study, Rahel and

Hubert (1991) observed that in conjunction with overall patterns of fish assemblage

zonation, downstream addition of species also occurred within fish community zones.

Thus, zonation in stream fish assemblage structure occurs on a broad spatial scale as a

result of stream temperature, but distributional patterns of fishes within these zones are

determined largely by variation in channel morphology and habitat structure at finer

scales. Unfortunately, many studies in stream fish ecology are limited in scope (sensu

Chapter 2) and provide little or no information on spatial variation in fish distribution

and physical habitat *between* sample points. Relatively short sampling reaches (< 500

m) spaced at wide intervals (> 10 km) along the longitudinal stream profile or

throughout a stream network may provide the information necessary to detect coarse

environmental gradients associated with temperature and stream order (Vannote et al.

1980). However, traditional site-based studies lack the scope necessary for detecting

patterns in fish–habitat relationships across a range of spatial scales.

The complexity of biotic and abiotic interactions in stream fish–habitat

relationships makes it particularly difficult to evaluate the effects of temperature on

fish assemblages independent of other factors. Temperature is usually discussed in

studies of longitudinal succession in stream fishes (Huet 1959, Hughes and Gammon

1987, Stewart et al. 1992, Belliard et al. 1997), but there still has been no critical

attempt to separate the effects of temperature from other biotic and abiotic factors (see

Sheldon 1968). We propose that a more spatially continuous perspective of stream

fish assemblages is needed in order to better understand and predict longitudinal

patterns in fish–habitat relationships. While several studies have described spatial

variation and scaling in stream fish–habitat relationships in short reaches (< 1 km) or

among disjunct sites along the longitudinal stream profile (Collares-Pereira et al. 1995,

Duncan and Kubecka 1996, Bult et al. 1998), few researchers have evaluated spatially

continuous data on fish assemblages over entire river sections (30–70 km). Our

objectives were to (1) characterize and compare spatially continuous longitudinal

patterns in stream fish assemblages in mountain streams with contrasting thermal

environments, (2) examine the response of fish assemblages to environmental

gradients and patchiness in the longitudinal stream profile, and (3) determine the

interaction between temperature and channel morphology in structuring fish

assemblages over a range of spatial scales.

METHODS

Study area

We selected three 4th–5th-order streams in the Blue Mountains of northeastern

Oregon and southeastern Washington in which to study stream fish assemblages. The

study streams included the Middle Fork John Day River (MFJD) (upper 55 km), the

North Fork John Day River (NFJD) (upper 70 km), and the Wenaha River (WEN)

(lower 35 km) (Figure 6.1). Study sections in each stream ranged in elevation from

500 m in the lower WEN to over 1600 m in the upper NFJD and shared a similar

geology of Columbia River basalt at lower elevations and folded metamorphosed

rocks partially overlain by volcanic tuff in headwater reaches (Orr et al. 1992).

Although the NFJD study section had the largest drainage area and the highest

elevations, the WEN received more annual precipitation and had higher summer base

flow (Table 6.1). Longitudinal gradients in elevation and annual precipitation were

steepest in the WEN, followed by the NFJD and the MFJD. Maximum summer water

temperature patterns reflected differences in streamflow among basins and represented

a range of warm, cool, and cold thermal environments (Figure 6.2).

Seasonal weather patterns throughout the study area are typical of high desert

climates with hot, dry summers, and cold, relatively wet winters (-15–38°C)
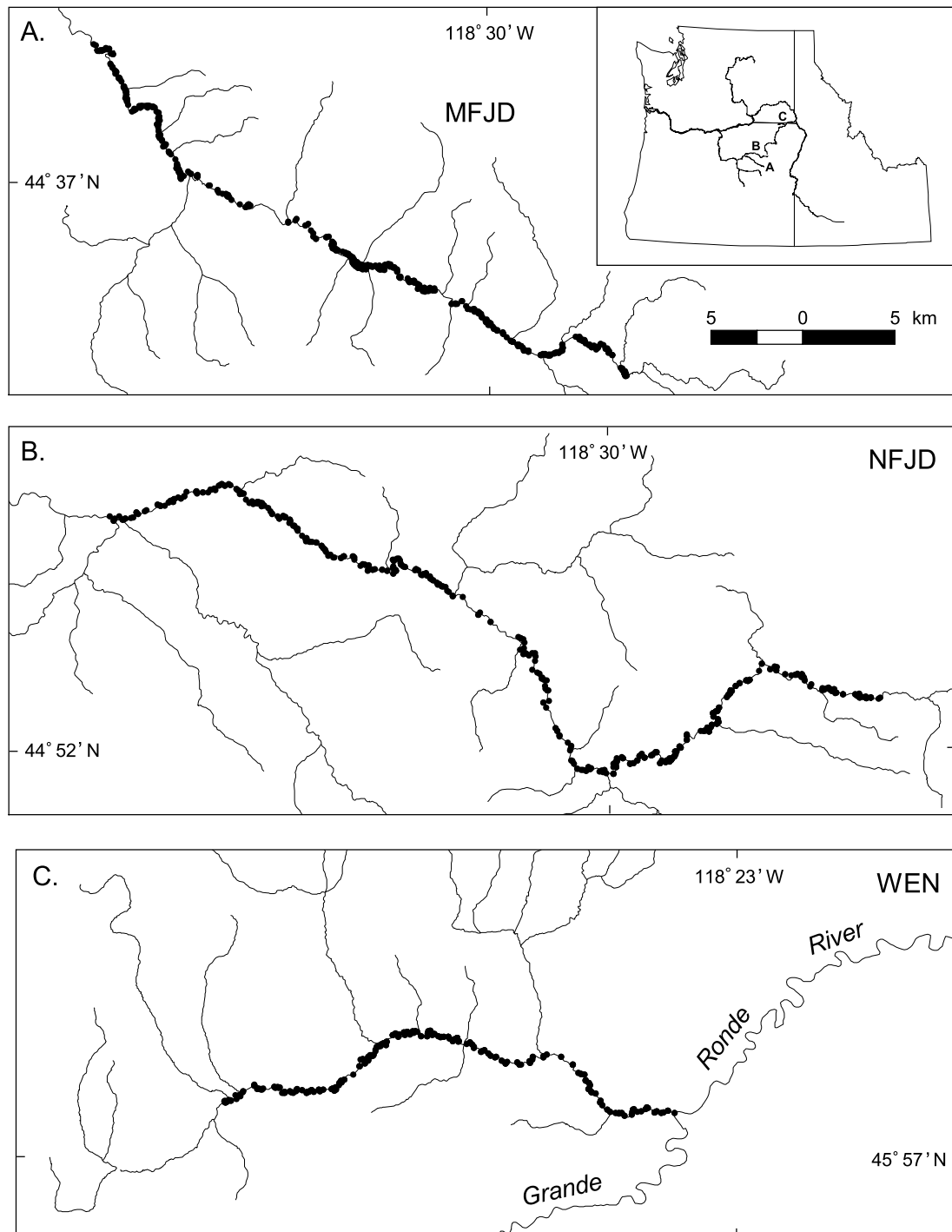
Figure 6.1. Study area and sections surveyed for fish assemblages in northeastern Oregon. Study streams include (A) the Middle Fork John Day River (MFJD), (B) the North Fork John Day River (NFJD), and (C) the Wenaha River (WEN). Black dots indicate the spatial extent and continuity of underwater visual surveys.
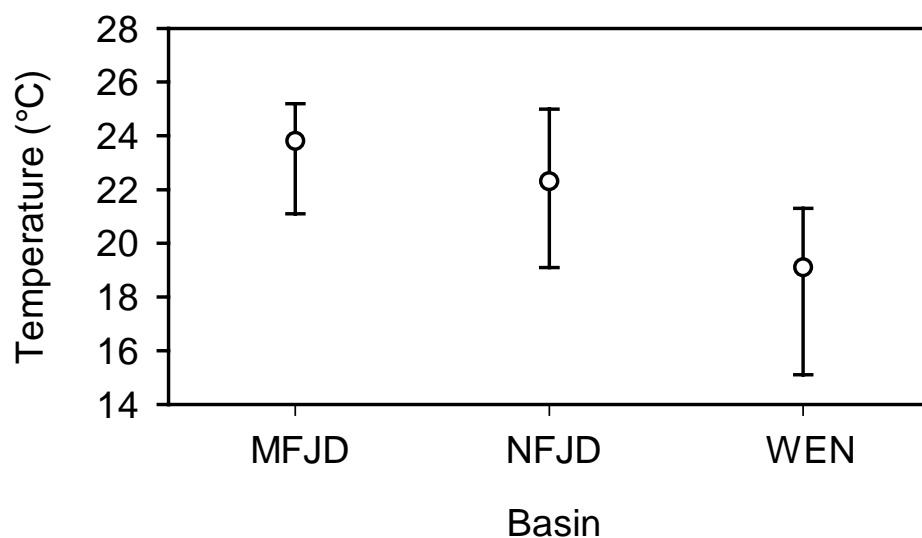
Figure 6.2. Mean maximum water temperatures in study sections of the Middle Fork John Day River (MFJD), the North Fork John Day River (NFJD), and the Wenaha River (WEN), August 1–7, 1998. Upper and lower horizontal bars indicate the mean maximum water temperatures at the lower and upper boundaries, respectively, of the study section. Midpoints represent the temperatures at the geographic center of each section.

Table 6.1. Physical characteristics of study sections in the Middle Fork John Day River (MFJD), the North Fork John Day River (NFJD), and the Wenaha River (WEN).

Stream	River kilometer (rkm)[a]	Drainage area (km^2)[b]	Elevation (m)	Precipitation (cm/yr)	Summer base flow (m^3/s)[c]
MFJD	62–117	1000	1000–1300	35–60	1.4
NFJD	95–165	1600	800–1700	50–90	2.8
WEN	0–35	750	500–1100	50–150	5.7

[a] Distance upstream from mouth.
[b] Drainage area upstream lower boundary of study section.
c Streamflow estimates are approximations of summer low-flow conditions based on field measurements in late August and September 1997–1999.

(Loy et al. 2001). The Blue Mountains ecoregion is characterized by contrasts in temperature, precipitation, and vegetation corresponding with steep elevation gradients (Clarke and Bryce 1997). Canyons and alluvial valleys in the Wenaha and John Day river basins are vegetated with mixed conifer forest (ponderosa pine, *Pinus ponderosa*; grand fir, *Abies grandis*; Douglas-fir, *Pseudotsuga menziesii*; western larch, *Larix occidentalis*; and lodgepole pine, *Pinus contorta*) on the upslope and broadleaf communities of black cottonwood (*Populous trichocarpa*), willow (*Salix* spp.), and red alder (*Alnus rubra*) in the valley bottom. Human activities in the study area include a range of public and private land management practices. The upper NFJD and the WEN are designated wild and scenic rivers situated within public wilderness areas, whereas the MFJD flows mainly through private lands managed for cattle grazing. Land-use impacts are minimal in the relatively pristine WEN compared to the NFJD and the MFJD, which have experienced extensive mining, grazing, and logging during the last century.

Fish assemblage

Stream fish assemblages in the Blue Mountains provided a unique opportunity to study the biology of coldwater fishes in a hot, semi-arid environment. Native fishes common in the study streams included four species of salmonids, three species of catostomids, four species of cyprinids, and two species of cottids. Two non-native fishes (brook trout, *Salvelinus fontinalis*, and smallmouth bass, *Micropterus dolomieui*) are known to occur in the study area but were extremely rare and therefore

not included in analysis. We selected a subset of species for community analysis based on their relative abundance and ease of identification underwater (Figure 6.3). Sculpins (*Cottus*, spp.), longnose dace (*Rhinichthys cataractae*), and mountain sucker (*Catostomus platyrhynchus*) were noted during surveys but not included in analysis because they were difficult to detect and identify underwater, as determined by comparisons of snorkeling and electrofishing in selected sections of the MFJD (H. Li, unpublished data).

Cold- and warmwater fish assemblage zones overlapped in each of the study streams and provided an excellent opportunity to evaluate patterns in community structure in relation to water temperature. Although we expected each fish species to have its own complex distributional patterns, it was beyond the scope of this paper to treat each species individually. Therefore, we focused on coldwater fishes, and specifically on juvenile chinook salmon (*Oncorhynchus tshawytscha*), within the context of the fish assemblage as a whole. Juvenile chinook salmon provided an excellent case study because they occurred in all three study streams and their physiology and thermal tolerances are well documented (Armour 1991, McCullough 1997). Moreover, understanding the habitat requirements of chinook salmon is important in the mid and upper Columbia River basin because the species is currently at risk of extinction (Nehlsen et al. 1991).

Figure 6.3. Stream fish assemblage surveyed in northeastern Oregon. Benthic fish species including longnose dace (*Rhinichthys cataractae*), mountain sucker (*Catostomus platyrhynchus*), torrent sculpin (*Cottus rhotheus*), and Paiute sculpin (*Cottus beldingi*), were noted during surveys but not included in analysis.

Longitudinal surveys of fish distribution and stream habitat

We conducted extensive underwater surveys to quantify longitudinal patterns in stream fish assemblages during summer low-flow conditions in July–August 1996 (MFJD), 1997 (NFJD), and 1998 (WEN). Underwater visual surveys provide accurate assessments of fish abundance in small streams and offer an alternative to electrofishing when sampling methods are restricted or when streams are either too remote or too large to sample with a backpack electrofishing unit (Thurow and Schill 1996, Mullner et al. 1998). We evaluated the distribution and abundance of stream fishes using a modified version of point abundance sampling (Persat and Copp 1990), in which numerous individual sample units (e.g., pools, riffles, and glides) compensate for the relatively low precision of visual estimates of abundance. The objective of modified point abundance sampling was to collect large numbers of closely spaced samples (< 100 m separation), providing a relatively continuous assessment of fish distribution (Figure 6.1). Underwater visual estimates of fish abundance were not calibrated empirically due to logistical constraints (e.g., stream size and accessibility) but nevertheless provided an accurate (though imprecise) assessment of fish distribution (H. Li and P. Bayley, unpublished data, see also White 2002). Gaps in extensive surveys of the MFJD and the NFJD occurred where access was denied to private lands or where steep canyons and rapids prevented sampling. Survey sections in the study streams were divided into reaches of equal length and sampled by two-person crews consisting of a diver and a data recorder walking along the shore. Divers counted fish in two or more passes in an upstream or downstream direction depending

upon stream depth and current velocity. Using this approach, a diver–recorder crew

was capable of surveying an average of 2–3 km per day.

Fish abundances were recorded in categories indicating whether a species was

dominant (> 50%), common (< 50%), or rare (< 10%) in relation to the total number

of fish observed in a sample unit. In all cases, divers were highly experienced in fish

identification and calibrated their estimates of fish abundance regularly through repeat

dives of the same channel unit by different divers. In addition to collecting data on

fish assemblages, field crews also collected information on channel morphology (e.g.,

side channel/main channel, depth, width, pool/riffle habitat, and water temperature)

and recorded geographic coordinates (±100 m) of individual sample units with a

handheld global positioning system (GPS). Pool/riffle habitats were evaluated in four

qualitative categories corresponding to current velocity and channel morphology: (1)

pools, (2) slow-moving glides, (3) fast-moving glides, and (4) riffles (Bisson et al.

1982). Qualitative estimates of current velocity and channel morphology (i.e., habitat

types 1–4) explained 68% of the variation in current velocity measured with a

flowmeter ($n = 33$, $P < 0.001$, $y = 0.39 + 0.26x + 0.08x^2$).

Geographical analysis and remote sensing

A geographical information system (GIS) was essential for mapping,

displaying, and analyzing the large number of sample points required to assess spatial

patterns in stream habitat and fish distribution (Figure 6.1). Sampled channel units

were mapped as individual points linked to a database containing information on fish

abundance and habitat characteristics. Longitudinal analysis was accomplished using route and dynamic segmentation procedures in ARC/INFO GIS (ESRI 1996, Radko 1997). Digital stream layers were derived from 1:5,000-scale aerial photographs (MFJD) and 1:100,000-scale topographic maps (NFJD and WEN). Route-measure coordinates, defined as the distance upstream from the mouth (i.e., river kilometer, rkm), were applied to each sample point and used as a common axis with which to compare longitudinal profiles of fish distribution and stream habitat. Channel gradient profiles were generated from a 10-m digital elevation model (DEM) sampled every 100 m along the stream channel; individual estimates of channel gradient were calculated using a 500-m moving window.

Spatially and temporally continuous patterns in stream temperature were assessed with airborne thermal infrared (TIR) remote sensing and automated instream thermographs (Torgersen et al. 2001). Aerial surveys were conducted on cloudless days on 4–9 August 1998 at 13:00–14:00. Thermographs served as ground-truth points for TIR remote sensing and provided temporal data necessary for comparing mean and maximum water temperatures within and among basins.

Statistical data analysis

We examined spatial patterns and habitat relationships of stream fish assemblages within and among three streams with different thermal environments. To evaluate spatial patterns and associations in fish distribution, channel morphology, and temperature, we compared peaks and troughs in fish abundance to longitudinal

profiles of stream temperature and habitat. Spatial trends in longitudinal profiles were

identified using locally weighted scatterplot smoothing (LOWESS), a robust,

nonparametric regression technique used to identify trends in heterogeneous

ecological data (Trexler and Travis 1993). Locally weighted regressions were

calculated with a second-degree polynomial smoothing function using SigmaPlot

statistical software (SPSS 2001).

Multivariate analysis was necessary to distinguish patterns in fish community

composition within and among streams. Multivariate methods (e.g., principal

components analysis and detrended correspondence analysis) are commonly applied in

studies of stream fishes because they reduce complex community data into two or

more dimensions, or axes, representing gradients in community structure (Hughes and

Gammon 1987, Rahel and Hubert 1991, Paller 1994, Taylor et al. 1996). We

computed multivariate ordinations using non-metric multidimensional scaling (NMS)

and Bray-Curtis ordination in PC-ORD, a multivariate analysis program specifically

designed for ecological data (McCune and Mefford 1999). Non-metric

multidimensional scaling is a non-parametric procedure that calculates axis scores

based on ranked distances and therefore alleviates the problems of zero truncation

caused by heterogeneous ecological data sets (Clarke 1993, Tabachnick and Fidell

2001). Disadvantages of NMS are that it is computationally intensive and may have

difficulties extracting gradients from unusually large and heterogeneous datasets.

When NMS was unable to find a suitable solution ($P > 0.05$), it was necessary to use a

combination of Beals smoothing and Bray-Curtis ordination (Chapter 5). Beals

smoothing is a multivariate transformation designed specifically for analyzing heterogeneous community matrices (McCune 1994). The smoothing function in PC-ORD first converts relative abundances in the community matrix to presence–absence data and then calculates the likelihood of finding each species in each sample based on joint occurrences of species throughout the dataset (McCune and Mefford 1999).

Two-dimensional solutions in NMS were calculated using the Sorensen distance measure and 15 runs of real data with 20 iterations to evaluate stability. Monte Carlo runs ($n = 30$) provided a means to evaluate the probability ($\alpha = 0.05$) that ordination axes explained more variation than would be expected by chance. Beals smoothing and Bray-Curtis ordination were required to analyze the MFJD community matrix, which was too large and heterogeneous for analysis with NMS (Chapter 5). To identify environmental gradients associated with ordination axes, we constructed joint plots (Jongman et al. 1995) of samples in species space and examined Pearson's correlations of physical habitat variables (mean depth, maximum depth, habitat type, and channel gradient) and temperature with axis scores. Ordinations were rotated in ordination space to separate the loadings of environmental factors among axes. We also plotted LOWESS-smoothed longitudinal profiles of ordination scores to assess spatial variation in fish community composition.

To evaluate the habitat relationships and community structure of stream fishes at different spatial extents, we performed multiple ordinations (Bray-Curtis with Beals smoothing) over different lengths of stream and compared gradients in community structure within and among streams. In the NFJD, the longest of the study streams (70

km), we analyzed upper and lower sections of the river separately to evaluate changes

in community structure with respect to spatial context and temperature. In all three

streams, we divided each study section into 10 reaches of different spatial extents

(e.g., rkm 0–70, rkm 0–65, rkm 0–60 km, etc.) and performed a separate ordination for

each reach. This process is essentially a scaling analysis that quantifies the effects of

spatial extent and geographic context on community composition (see Nekola and

Wagner 2001). By comparing Pearson's correlations of environmental variables (i.e.,

depth, habitat type, and temperature) with ordination axis scores along the longitudinal

stream profile, we were able to examine the combined effects of spatial extent (i.e.,

reach length) and geographic context on the relative influences of temperature and

channel morphology on stream fish assemblage structure.

RESULTS

Longitudinal patterns in fish distribution and stream habitat

Stream fish assemblages were highly variable among channel units and among

reaches throughout the longitudinal stream profile. The distribution of juvenile

chinook salmon illustrated the extent of spatial variability typical of stream fish

abundance patterns within and among basins (Figure 6.4). Juvenile chinook were

generally rare in the MFJD but increased in relative abundance in the NFJD and the

WEN. As juvenile chinook increased in relative abundance among basins, their

distribution also became less patchy within basins, particularly in the WEN where
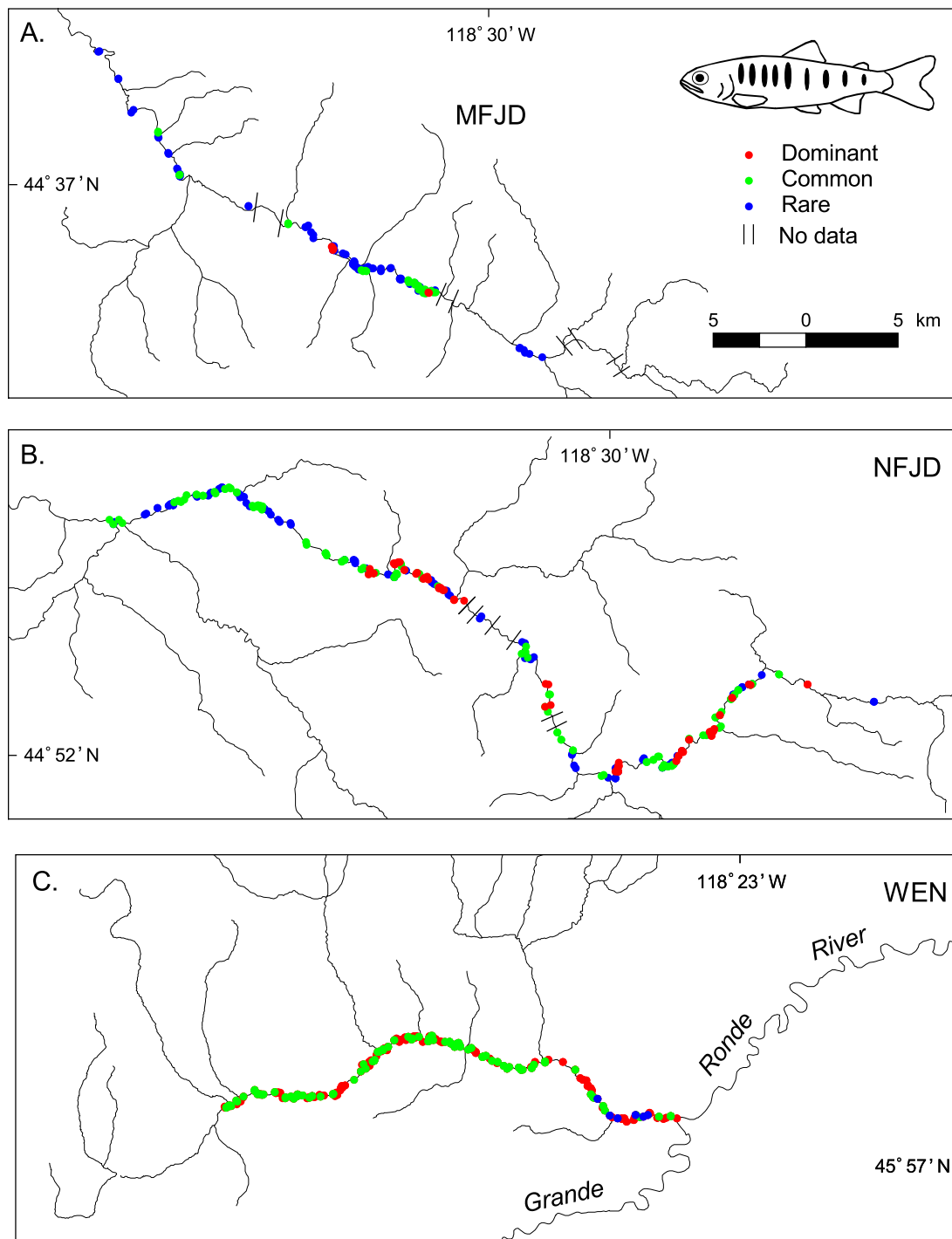
Figure 6.4. Spatial distribution and relative abundance of juvenile chinook salmon in (A) the Middle Fork John Day River (MFJD), (B) the North Fork John Day River (NFJD), and (C) the Wenaha River (WEN).

juvenile chinook were the must abundant species in the local fish assemblage and were common in nearly every pool surveyed (Figure 6.4).

Locally weighted regressions of fish abundance, channel morphology, and stream temperature were essential for detecting spatial trends and associations in fish distribution and physical habitat (Figures 6.5–6.7). In the MFJD, the distribution of juvenile chinook was patchy and limited largely to two distinct reaches centered at rkm 85 and 98 (Figure 6.5). The relative abundance of rainbow trout increased gradually in an upstream direction to a peak at rkm 92 and then declined rapidly, increasing again only after rkm 107. Juvenile chinook salmon and rainbow trout were rare between rkm 102 and 105 where channel gradient was low and maximum depth was high. Peaks in juvenile chinook abundance corresponded with peaks in channel gradient and troughs in maximum depth.

Spatial patterns of coldwater fishes in the NFJD were similar to the patterns observed in the MFJD (Figure 6.6). Juvenile chinook salmon exhibited a patchy distribution with 2–3 peaks in local abundance. Rainbow trout increased in abundance gradually in an upstream direction but were rare in the uppermost reaches of the NFJD. Bull trout, an additional coldwater species, increased in abundance gradually in an upstream direction from the lowermost occurrence at rkm 150. Reach-level associations between fish assemblage structure and channel morphology and temperature were not as pronounced in the NFJD as they were in the MFJD. Of the three coldwater fishes, juvenile chinook exhibited the most variable spatial

Figure 6.5. Longitudinal patterns of stream habitat and the distribution of coldwater fishes in the Middle Fork John Day River. Trend lines are smoothed values from locally-weighted scatterplot smoothing (LOWESS) of spatially continuous (channel gradient and temperature) and near-continuous survey data (fish abundance, maximum depth, and habitat type). Dashed horizontal bars below each trend line depict the spatial continuity of fish and habitat surveys and provide a relative indicator of the number of data points used to calculate LOWESS regressions. Dashed vertical lines provide a reference for peaks in the relative abundance of juvenile chinook salmon. Relative abundance values indicate the extent to which fish species were rare (1), common (2), dominant (3) in a given sample unit. Habitat type is a qualitative variable that represents a continuum of slow- to fastwater channel units (pool, glide, riffle) and ranges from 1 to 4, respectively. Mean daily water temperatures were recorded on the day of synoptic surveys (thermal infrared remote sensing).

Figure 6.5
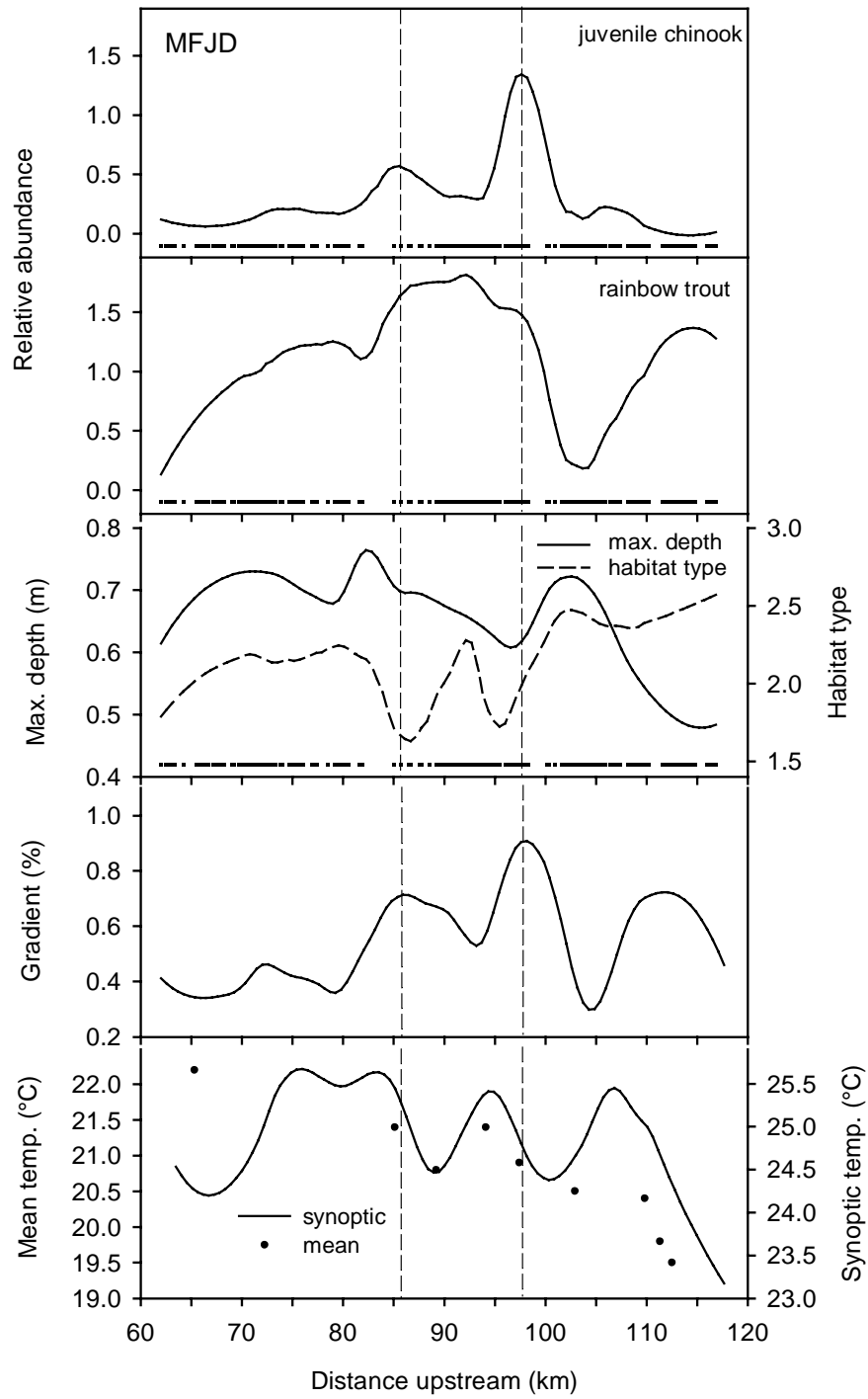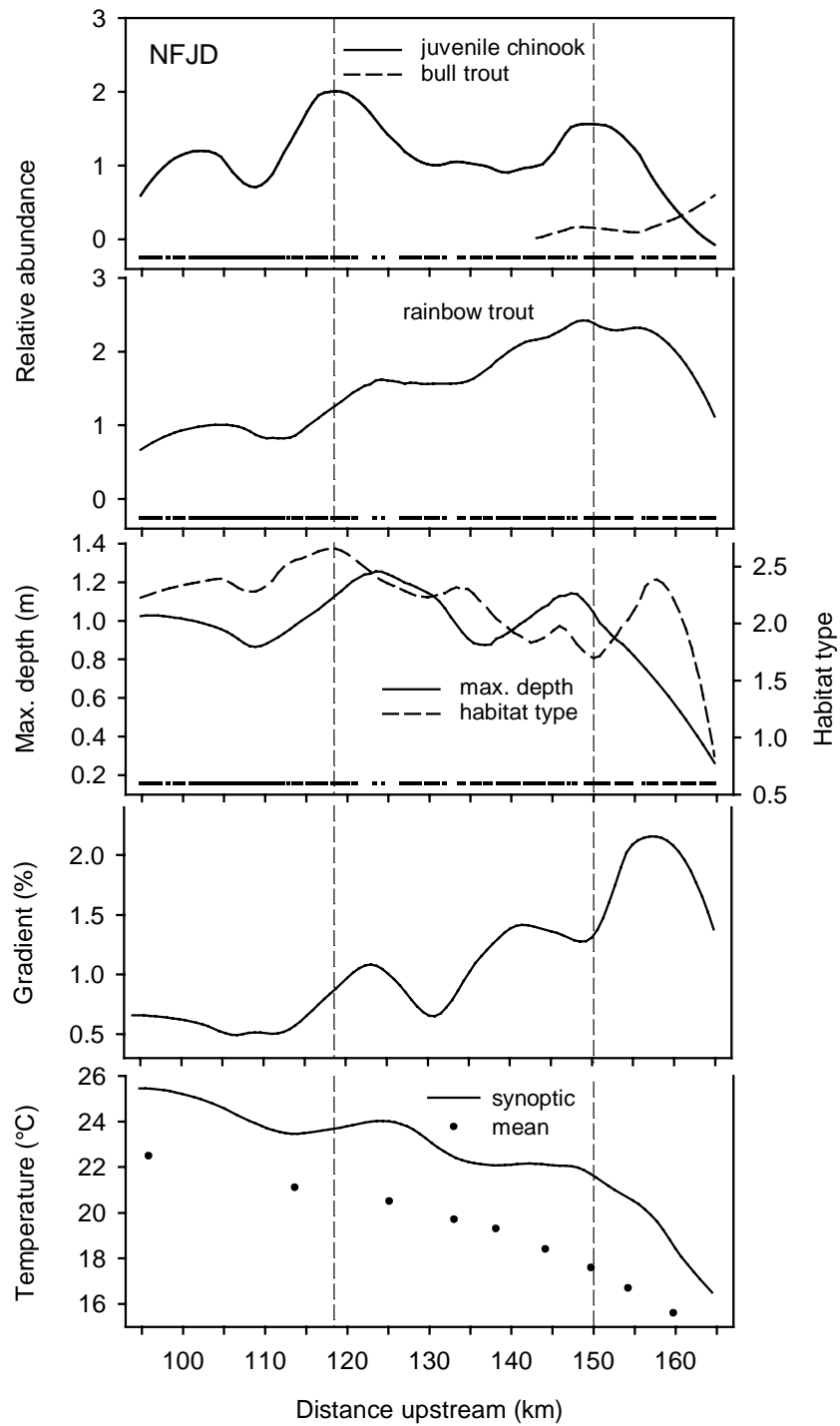
Figure 6.6. Longitudinal patterns of stream habitat and the distribution of coldwater fishes in the North Fork John Day River. See Figure 6.5 for a detailed description.
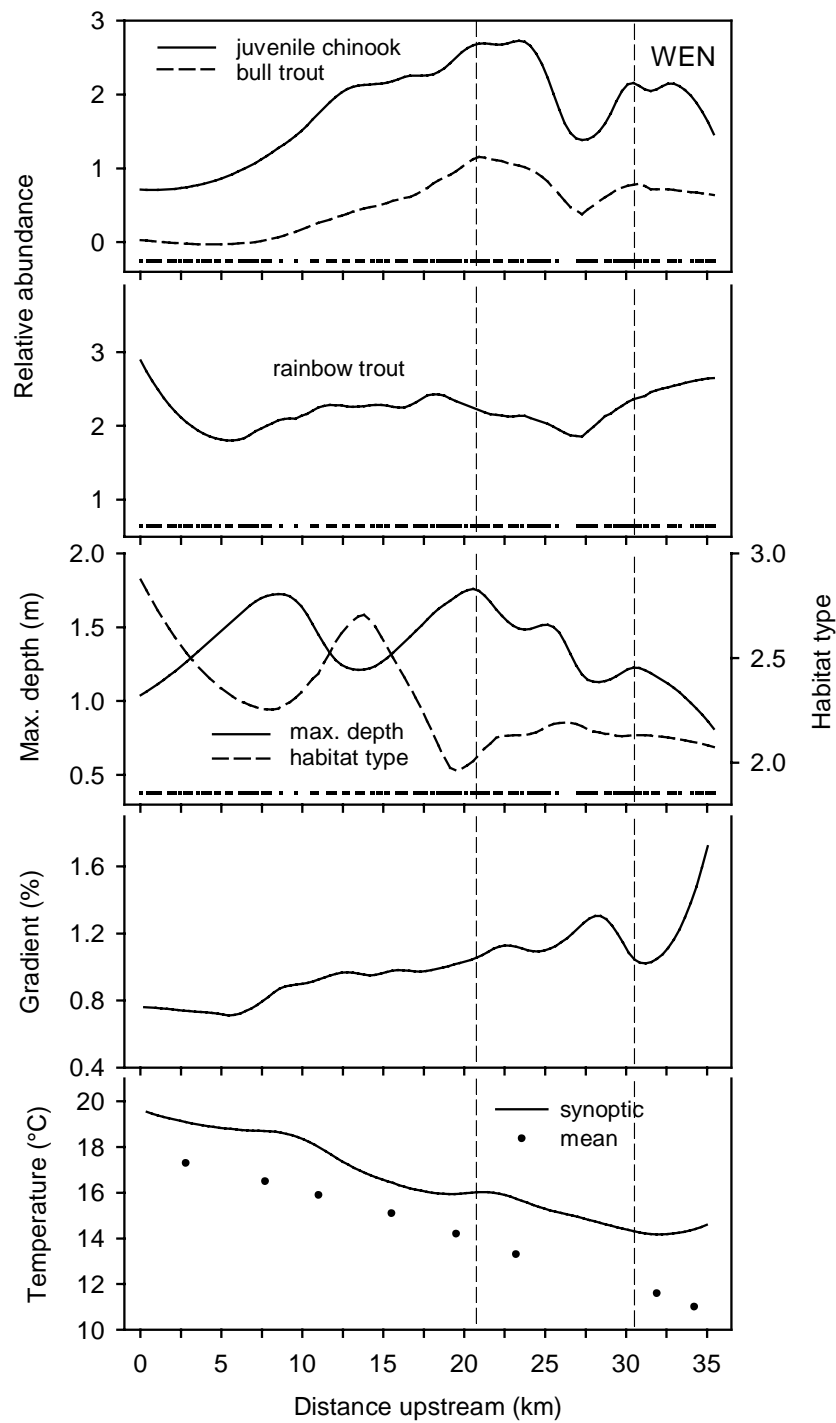
Figure 6.7. Longitudinal patterns of stream habitat and the distribution of coldwater fishes in the Wenaha River. See Figure 6.5 for a detailed description.

distribution, corresponding with peaks (downstream of rkm 135) and troughs (upstream of rkm 135) in habitat type and channel gradient.

Coldwater fishes composed the dominant fish assemblage in the WEN. Juvenile chinook and rainbow trout were equally abundant throughout the study section, but juvenile chinook were spatially more variable (Figure 6.7). Rainbow trout were common throughout the study section, increasing in relative abundance only in riffle-dominated downstream reaches (rkm 0–8) or in high-gradient reaches upstream (rkm 33–35). Relative abundances of bull trout and juvenile chinook increased gradually in an upstream direction and peaked at rkm 20–23, coinciding with a peak in maximum water depth, and a trough in habitat type (i.e., low current velocity). Troughs in the relative abundance of juvenile chinook, bull trout, and rainbow trout corresponded with a local trough in maximum water depth and a peak in channel gradient (rkm 28).

Multivariate analysis of community structure

Stream fishes exhibited distinct differences in community structure among study streams. In the MFJD, variation in fish assemblage composition among channel units corresponded with environmental gradients in depth, habitat type, and channel gradient (Figure 6.8). The primary ordination axis (depth and habitat type) explained 65% of the variation in fish assemblage structure. Fishes were strongly segregated among shallow riffles (rainbow trout, juvenile chinook, mountain whitefish, and speckled dace) and deep pools (redside shiner, bridgelip sucker, Northern

Figure 6.8. Bray-Curtis ordination of fish community structure in the Middle Fork John Day River. The location of each fish indicates its position with respect to environmental gradients in habitat type and depth (axis 1) and channel gradient (axis 2). Solid triangles indicate the distribution of sample units in ordination space. The amount of variation explained by each axis is shown in parentheses. See Figure 6.3 for key to the fishes.

pikeminnow, and largescale sucker). Fish species most strongly correlated with the primary axis (depth and habitat type) included bridgelip sucker, Northern pikeminnow, largescale sucker, redside shiner, and rainbow trout. Species associated with the second axis (channel gradient) included juvenile chinook, rainbow trout, and Northern pikeminnow (Table 6.2).

In the NFJD, stream fish assemblages were structured along gradients of temperature, channel slope, and depth (Figure 6.9). Temperature and channel gradient were strongly correlated with the primary axis (Table 6.2). Distribution of fish species with respect to the primary ordination axis (temperature and channel gradient) indicated a separation between warmwater fishes (redside shiner, largescale sucker, bridgelip sucker, Northern pike minnow, and speckled dace) and coldwater fishes (rainbow trout and bull trout). The primary axis also reflected differences in geographic distribution that were unrelated to temperature. For example, juvenile chinook salmon are a coldwater species but were relatively rare in the cold, headwater reaches of the NFJD (Figure 6.6). Fish species most strongly correlated with the primary axis included rainbow trout, speckled dace, and redside shiner (Table 6.2). The secondary axis explained only a small percentage of the variation in fish assemblage structure (26%) but was strongly associated with mean and maximum water depth (Table 6.2). With the exception of bull trout and rainbow trout, fishes in the NFJD were generally grouped into deepwater (mountain whitefish, largescale sucker, juvenile chinook, and Northern pikeminnow) and shallow-water (bridgelip sucker, speckled dace, and redside shiner) assemblages.

Table 6.2. Pearson correlation coefficients of species and habitat variables versus axis scores from ordinations of fish assemblage structure in entire survey reaches. The surveyed lengths in the Middle Fork John Day River, the North Fork John Day River, and the Wenaha River are 55, 70, and 35 km, respectively.

Variable	Middle Fork John Day River [a] (n = 286)		North Fork John Day River [b] (n = 244)		Wenaha River [b] (n = 179)	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Species						
Bull trout	—	—	0.30	-0.11	0.22	0.31
Juvenile chinook	-0.07	0.76	-0.24	0.29	0.50	0.76
Rainbow trout	-0.65	0.71	0.79	-0.18	0.24	-0.46
M. whitefish	-0.07	0.57	-0.29	0.71	-0.86	0.40
N. Pikeminnow	0.90	-0.61	-0.42	0.06	-0.29	0.31
Largescale sucker	0.74	-0.15	-0.44	0.09	-0.50	0.19
Bridgelip sucker	0.95	-0.56	-0.40	-0.30	—	—
Redside shiner	0.73	-0.52	-0.54	-0.23	—	—
Speckled dace	-0.52	-0.31	-0.78	-0.42	—	—
Habitat						
Temperature	0.25	-0.23	-0.76	0.00	0.65	-0.04
Channel gradient	-0.13	0.22	0.57	-0.02	0.35	-0.07
Maximum depth	0.40	-0.07	-0.22	0.30	-0.18	0.35
Mean depth	0.32	0.02	-0.18	0.28	-0.23	0.29
Habitat type [c]	-0.39	0.08	0.14	-0.22	0.11	-0.28

[a] Beals smoothing transformation and Bray-Curtis ordination (presence–absence).
[b] Non-metric multidimensional scaling (relative abundance).
[c] Habitat type is a qualitative variable that represents a continuum of slow- to fast-water channel units and ranges from 1 to 4.

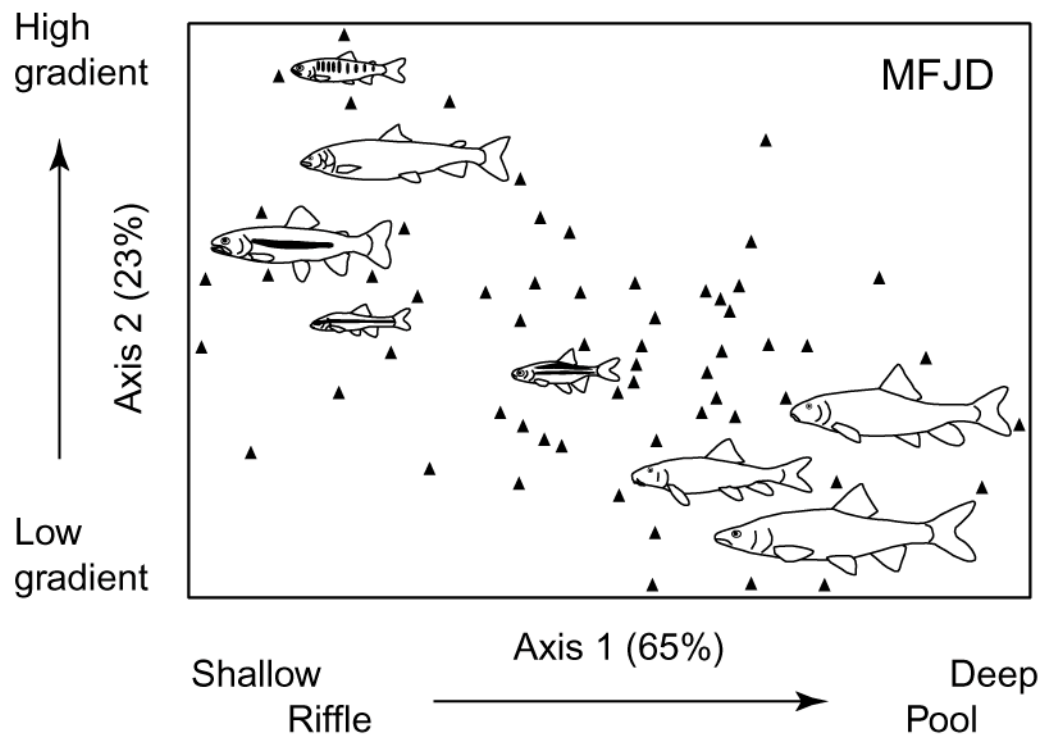Figure 6.9. Non-metric multidimensional scaling ordination of fish community structure in the North Fork John Day River. The location of each fish indicates its position with respect to environmental gradients in water temperature and channel gradient (axis 1) and depth (axis 2). See Figure 6.8 for a detailed description.

Fishes in the WEN responded to gradients in temperature, channel slope, depth, and habitat type (Figure 6.10, Table 6.2). Coldwater fishes (juvenile chinook, bull trout, and rainbow trout) were most abundant in upstream reaches, while warmwater fishes (Northern pikeminnow and largescale sucker) were most common downstream. Mountain whitefish, largescale sucker and juvenile chinook were strongly correlated with ordination scores on the primary axis (Table 6.2). On the secondary ordination axis, depth and habitat type explained 43% of the variation in fish assemblage structure. Fish species most strongly associated with the secondary axis included juvenile chinook, rainbow trout, and mountain whitefish (Table 6.2). Of the three coldwater fishes in the WEN, juvenile chinook exhibited the strongest positive association with the secondary ordination axis (water depth and slow-water habitats) (Table 6.2).

Spatial variation in community structure

Longitudinal patterns in fish assemblage structure were most variable in the MFJD compared to the NFJD and the WEN (Figure 6.11). Slow-water fishes in the MFJD (axis 1) were most common in lower (rkm 62–72) and upper reaches (rkm 107–112), whereas fast-water fishes (axis 2) were most common in middle reaches (rkm 86–89 and rkm 97–99). In comparison to the MFJD, spatial patterns of fish communities in the NFJD and WEN were gradual with respect to temperature (axis 1), depth, and habitat type (axis 2). In the NFJD and WEN, warmwater fishes gradually replaced coldwater fishes in a downstream direction.
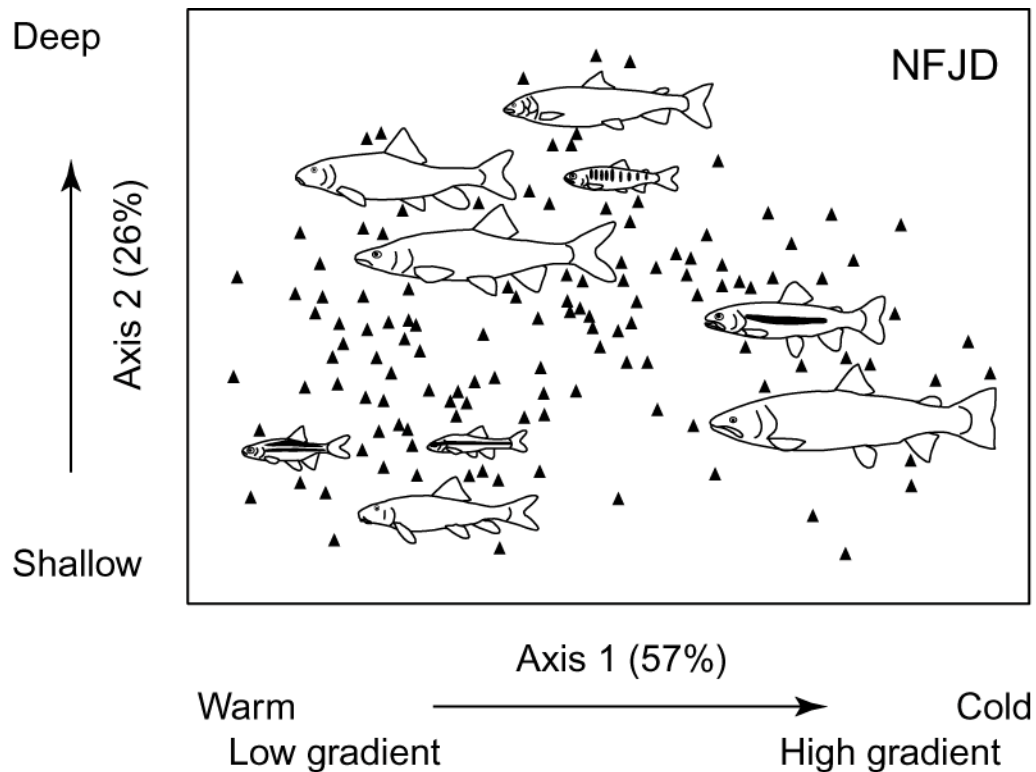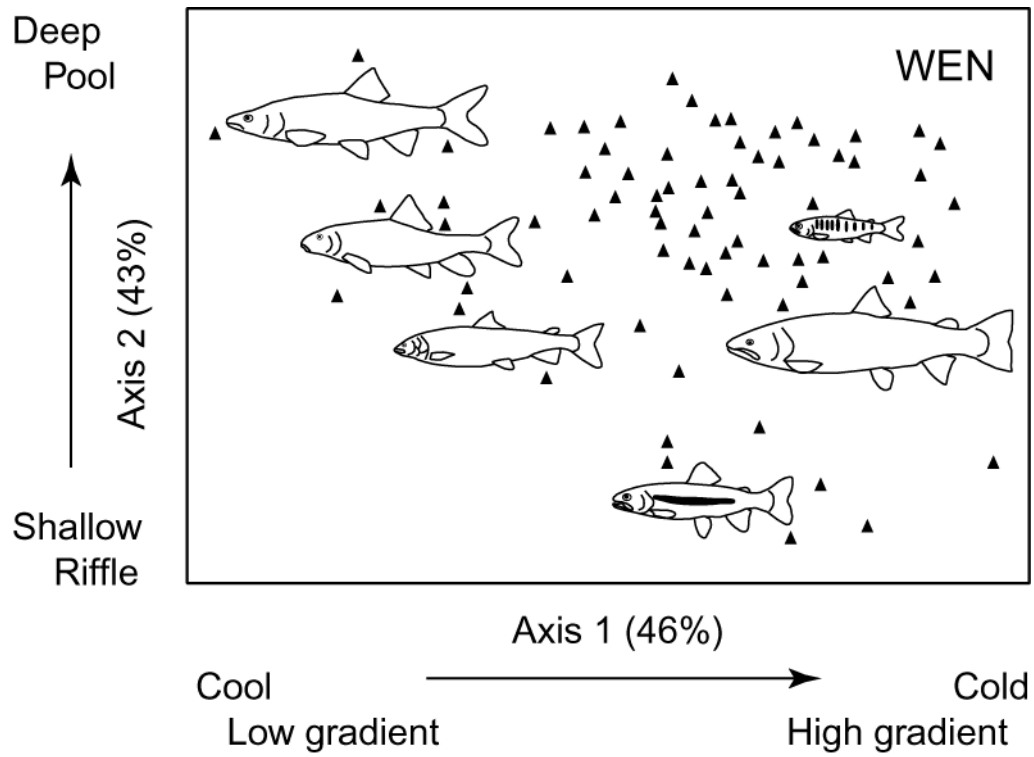
Figure 6.10. Non-metric multidimensional scaling ordination of fish community structure in the Wenaha River. The location of each fish indicates its position with respect to environmental gradients in water temperature and channel gradient (axis 1) and depth (axis 2). See Figure 6.8 for a detailed description.
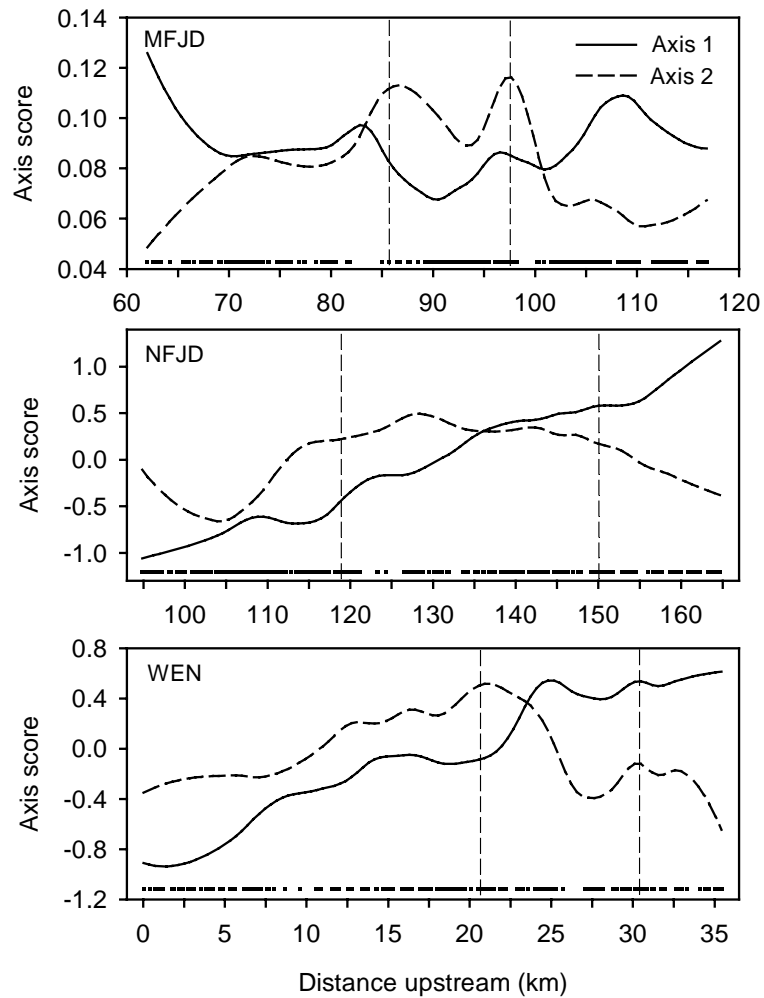
Figure 6.11. Longitudinal patterns in stream fish community structure in the Middle Fork John Day River (MFJD), the North Fork John Day River (NFJD), and the Wenaha River (WEN). Axis scores from the ordinations in Figures 6.8–6.10 are plotted versus distance upstream. Dashed vertical lines provide a reference for peaks in the relative abundance of juvenile chinook salmon.

Fish assemblage structure varied within streams with respect to the spatial extent and geographic context of multivariate analysis. Because the NFJD study section was 70 km in length, we were able to examine downstream and upstream fish communities separately. In the downstream (warm) subsection of the NFJD, stream fishes were structured much as they were throughout the entire study section (Figure 6.12). However, juvenile chinook in the lower NFJD were not associated with deepwater habitats as they were in the ordination of the whole stream (Table 6.3). In the ordination of the lower NFJD, juvenile chinook were more associated with the shallow/riffle assemblage (rainbow trout, speckled dace, and bridgelip sucker) than they were with the deep/pool fish assemblage (largescale sucker, mountain whitefish, Northern pikeminnow, and redside shiner) (Figure 6.12). In the upstream (cold) subsection of the NFJD, the primary axis shifted from temperature to habitat type and depth and explained 60% of the variation in community structure (Figure 6.13). In contrast to the lower reaches of the NFJD, juvenile chinook in the upper subsection were strongly associated with slow-moving, deepwater habitats (Table 6.3).

To further examine the effects of spatial extent and locational context on our perception of stream fish–habitat relationships, we analyzed a succession of stream reaches (e.g., rkm 0–70, rkm 0–65, rkm 0–60, etc.) and performed a separate ordination for each reach. Changes in the correlations of environmental variables with ordination axes with respect to spatial extent indicated that the relative influences of temperature and channel morphology (i.e., depth and habitat type) on fish assemblage

Figure 6.12. Non-metric multidimensional scaling ordination of fish community structure in the lower 40 km of the North Fork John Day River. The location of each fish indicates its position with respect to environmental gradients in water temperature and channel gradient (axis 1) and depth (axis 2). See Figure 6.8 for a detailed description.

Table 6.3. Pearson correlation coefficients of species and habitat variables versus axis scores from ordinations of fish assemblage structure in the upper and lower reaches of the North Fork John Day River. Ordination axis scores for both reaches were calculated with non-metric multidimensional scaling (relative abundance).

Variable	Lower reach ($n = 134$)		Upper reach ($n = 85$)	
	Axis 1	Axis 2	Axis 1	Axis 2
Species				
Bull trout	—	—	-0.02	0.09
Juvenile chinook	0.08	-0.02	0.86	0.25
Rainbow trout	0.44	-0.26	-0.74	0.15
M. whitefish	0.38	0.78	0.32	-0.91
N. Pikeminnow	-0.21	0.34	—	—
Largescale sucker	-0.26	0.39	—	—
Bridgelip sucker	-0.46	-0.11	—	—
Redside shiner	-0.65	0.16	—	—
Speckled dace	-0.81	-0.35	—	—
Habitat				
Temperature	-0.69	0.03	0.05	-0.27
Channel gradient	0.30	0.12	-0.18	0.19
Maximum depth	0.05	0.43	0.30	-0.25
Mean depth	0.16	0.38	0.29	-0.20
Habitat type [a]	0.12	-0.40	-0.40	0.10

Notes: Upper and lower reaches were defined with respect to the confluence of Granite Creek (rkm 138) and include rkm 95–137 (lower reach) and rkm 138–157 (upper reach).

[a] Habitat type is a qualitative variable that represents slow- to fast-water channel units and ranges from 1 to 4.
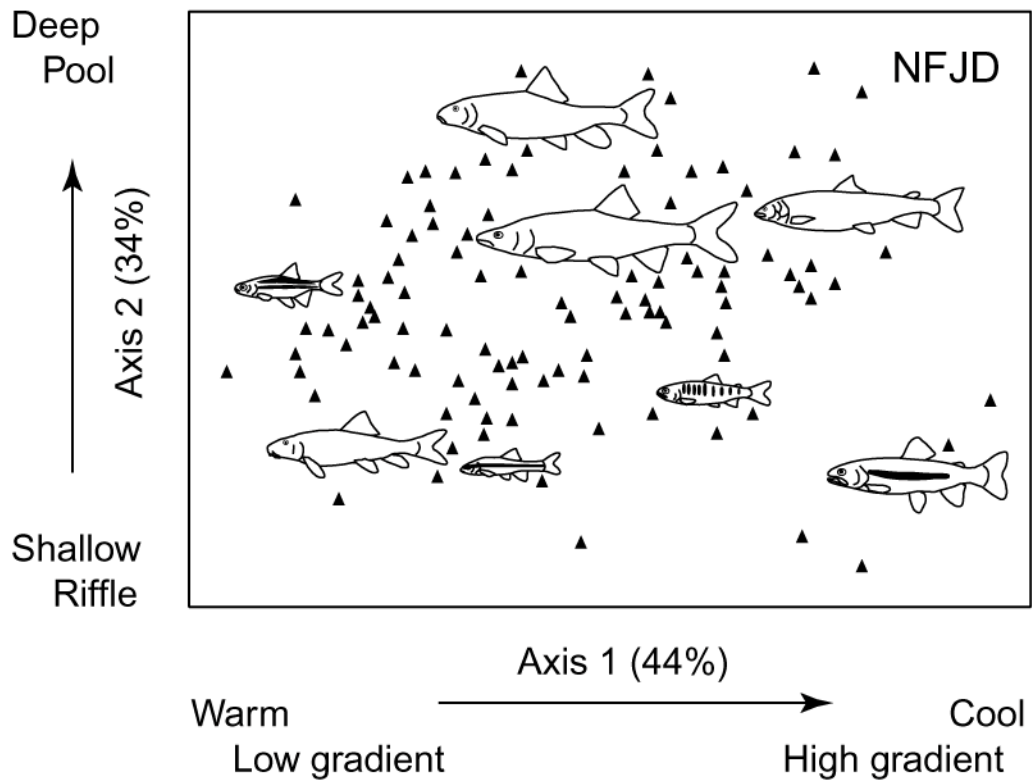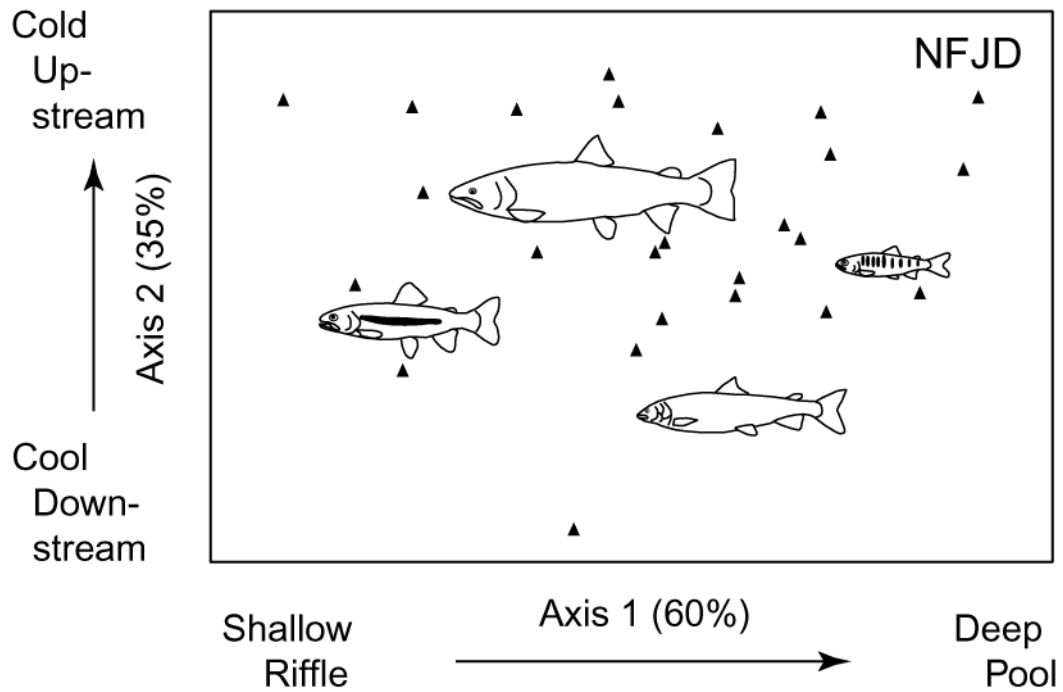
Figure 6.13. Non-metric multidimensional scaling ordination of fish community structure in the upper 40 km of the North Fork John Day River. The location of each fish indicates its position with respect to environmental gradients in depth and habitat type (axis 1) and temperature (axis 2). See Figure 6.8 for a detailed description.

structure were scale and context dependent. In the MFJD and the NFJD, the relative

influences of temperature and channel morphology increased and decreased,

respectively, at larger spatial extents (Figure 6.14). Crossover points, i.e., where

temperature and channel morphology explained approximately equal amounts of

variation in stream fish assemblage structure, indicated transitions between warm- and

coldwater fish assemblage zones (Figure 6.14). In the MFJD, the warmest of the

streams, a crossover point occurred in the upper portion of the basin (rkm 48), whereas

in the NFJD this transition occurred in the lower 20 km of the study section (rkm 115).

In the coldest stream, the WEN, the relative influence of channel morphology on

stream fish assemblage structure increased at larger spatial extents. There was no

strong trend in the relative influence of temperature on stream fish assemblage

structure in the WEN, indicating that the crossover point between warm- and

coldwater fish assemblage zones occurred farther downstream.

DISCUSSION

Longitudinal changes in stream fish assemblages were gradual or

heterogeneous depending upon the spatial scale and thermal context of analysis. At

the scale of entire river sections (30–70 km), longitudinal patterns of temperature and

channel gradient corresponded with a coldwater trout (Salmonidae) assemblage and a

warmwater minnow–sucker (Cyprinidae–Catostomidae) assemblage as predicted by

the river continuum concept and current models of stream fish distribution (Vannote et

al. 1980, Li et al. 1987, Rahel and Hubert 1991). However, imbedded within the

Figure 6.14. Scale-dependent effects of temperature and channel morphology on stream fish assemblage structure in the Middle Fork John Day River (MFJD), the North Fork John Day River (NFJD), and the Wenaha River (WEN). Pearson's correlation coefficients (r) indicate the relative influence of temperature and channel morphology on stream fish community structure over a range of spatial extents.

Figure 6.14
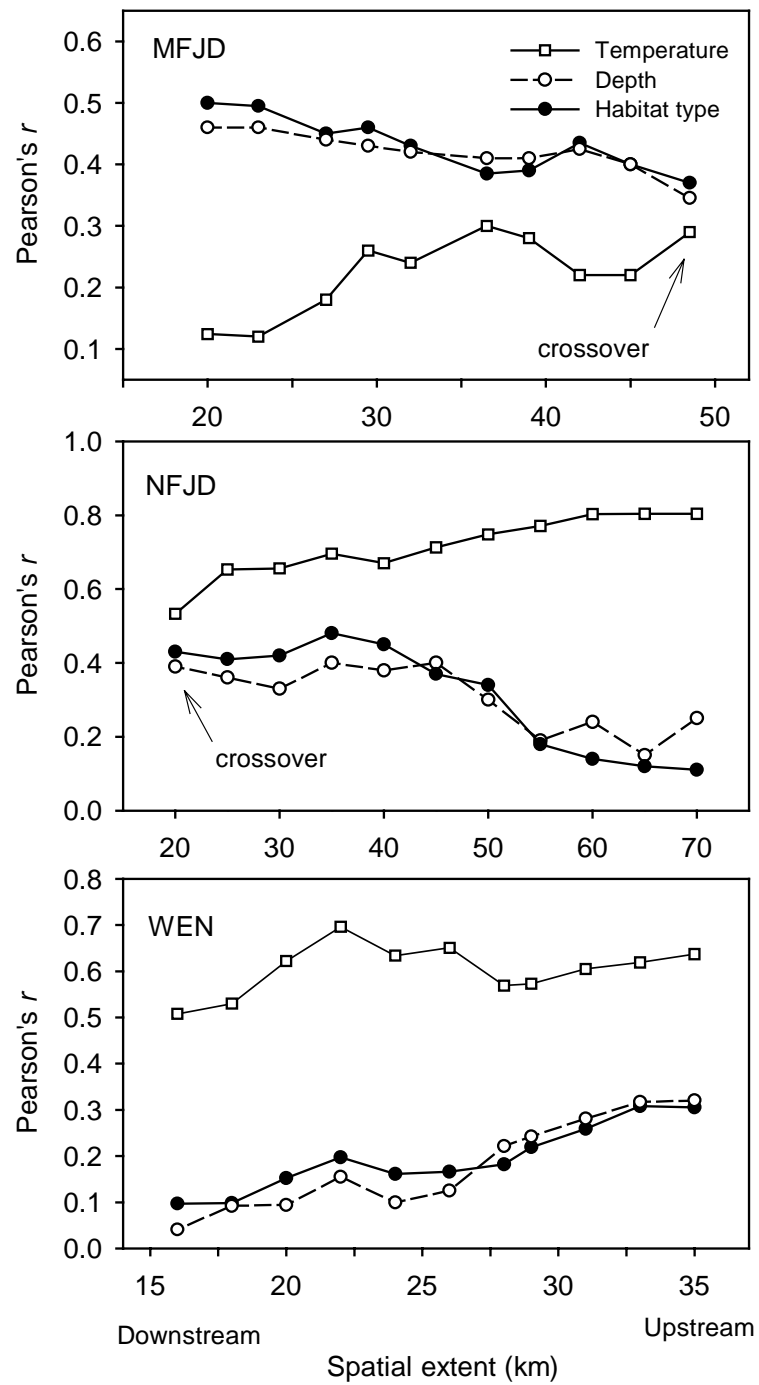
broad-scale template of warm- and coldwater fish assemblage zones, the distribution

of stream fishes was patchy and corresponded with reach and channel unit-scale

variation in channel morphology (i.e., depth and habitat type). Fish assemblages were

particularly variable in the MFJD where warm- and coldwater assemblages overlapped

and the longitudinal thermal gradient was not so pronounced. Our observations of

spatial variability in stream fish assemblages of the Blue Mountains confirmed that

fish assemblages differ as much or more within as between adjacent stream orders

(Stewart et al. 1992, Roper and Scarnecchia 1994).

Context dependency of fish–habitat relationships

Detailed studies of fish distribution within stream sections (20–100 km) are

important for evaluating fish–habitat relationships across scales (Fausch et al. 1994).

Stream fish responses to channel gradient provide a case in point. Trout are generally

associated with higher elevations and higher channel gradient than juvenile chinook

salmon (McMichael and Pearsons 1998, Montgomery et al. 1999); however, juvenile

chinook in the MFJD were strongly associated with the fish community in high-

gradient reaches and fastwater habitats. We suspect that species interactions (e.g.,

competition and predation) and the relative influence of channel gradient on the

abundance of juvenile chinook salmon were highly context dependent. Warmwater

fish species, such as redside shiner and Northern pikeminnow, had a physiological

advantage over coldwater fishes throughout the MFJD and most likely expressed this

advantage in the fish community through competition. Salmonids are usually

associated with higher channel gradients than warmwater fishes (Rahel and Hubert 1991), but this is usually because higher gradient reaches tend to be cooler in water temperature. The MFJD provided a unique opportunity to evaluate the response of juvenile chinook salmon to high-gradient reaches in a warmwater environment. Our data indicated that the association between channel gradient and the relative abundance of salmonids is dependent on thermal context and the spatial extent of analysis.

In mountain streams, elevation, channel gradient and cold water temperatures are often closely correlated (Isaak and Hubert 2001), so it is difficult to assess the influence of channel gradient on salmonid abundance (Isaak and Hubert 2000). In the NFJD and the WEN, for example, the relative abundance of juvenile chinook increased with elevation, channel gradient, and lower water temperatures. We found that large numbers of sample points collected over long distances provided the flexibility across scales that was necessary to evaluate the relative influences of temperature and channel gradient on the abundance of juvenile chinook salmon. At high water temperatures in the MFJD, juvenile chinook occupied relatively high-gradient reaches, whereas at low water temperatures in the NFJD and the WEN, juvenile chinook exhibited the opposite behavior. Without fine-scale information on spatial variation in juvenile chinook abundance and channel gradient, it might not have been apparent that juvenile chinook were associated with local low-gradient discontinuities in coldwater streams. Because the spatial patterns of stream fish communities are so poorly understood, considerable increases in sampling effort may

be needed in order to accurately characterize and understand stream fish communities (Angermeier and Smogor 1995). Moreover, temperature and gradient are only two out of many factors that influence the distribution of stream fishes, and large-scale evolutionary processes such as disturbance regime and dispersal barriers must also be considered in predicting fish occurrence across scales (Dunham and Rieman 1999).

Temperature and fish community structure

Temperature effects on stream fish interactions and habitat relationships are well documented at microhabitat and channel unit levels and over broad geographic scales. However, stream fish responses to thermal heterogeneity at intermediate scales are poorly understood (Fausch et al. 1994, Fausch et al., in press). In large part, this is due to the relative ease of either assessing large-scale patterns in fish distribution with respect to geographic variation in elevation and air temperature (Dunham et al. 1999, Rahel and Nibbelink 1999) or observing small-scale patterns in fish behavior in individual pool–riffle sequences and in the laboratory (Reeves et al. 1987, Taniguchi et al. 1998). In either approach, the number of samples required to evaluate statistical relationships is relatively small. The challenge in stream fish community ecology is to simultaneously evaluate the contribution of large-scale and local-scale processes to variation in community structure (Menge and Olson 1990, Dunham and Vinyard 1997). We suspect that this can be accomplished only by increasing the scope (sensu Chapter 2) of surveys of stream habitat and fish distribution.

We found that differences in temperature both among and within streams accounted for spatial variation in the habitat relationships of stream fishes. Comparisons between the MFJD and the WEN indicated that juvenile chinook shifted from a fastwater assemblage at warm temperatures to a slow-water assemblage at cold temperatures. We also observed a similar shift in the NFJD where juvenile chinook were associated with pools in the upper reaches and riffle–glides in the lower reaches. Warmwater fishes were most abundant species in deep, slow-water habitats in the MFJD and the lower NFJD and may have excluded juvenile chinook through competition with redside shiner (Reeves et al. 1987) or through predation by Northern pikeminnow (Isaak and Bjornn 1996). Increased riffle use by salmonids has been shown to occur in response to higher metabolic demands at warmer water temperatures (Smith and Li 1983). Faster current velocities provide higher invertebrate drift rates and may actually balance out the increased metabolic costs of maintaining a position in faster current.

At optimal temperatures, salmon and trout differ in habitat preferences in part due to differences in body form (Bisson et al. 1988). Juvenile chinook have a deep, laterally compressed body with large median and paired fins which are better adapted to slow-water habitats, whereas rainbow trout have a more cylindrical form and short median fins which are well adapted to holding a position in swift water. However, flexibility in behavior is an important survival strategy for salmonids in marginal habitats (Thorpe 1994), and both species are capable of occupying a range of fast- to slow-water habitats depending upon the availability of food. Shifts in habitat use from

slow to fast water may occur regardless of water temperature. Where juvenile chinook salmon and steelhead (*Oncorhynchus mykiss*) exist in sympatry, steelhead tend to select riffle habitats, whereas in upstream reaches where juvenile chinook are less abundant, steelhead avoid riffles in favor of slow-water habitats (Roper and Scarnecchia 1994). We also observed that rainbow trout were more adaptable than juvenile chinook and occupied a range of slow- and fastwater habitats depending upon what was immediately available.

Although individual fish species varied dramatically from one channel unit to the next, we observed that transitions between warm- and coldwater fish assemblages were not clearly defined. In the MFJD, the coldwater fish assemblage (rainbow trout and juvenile chinook) was restricted to high-gradient reaches in the middle portion of the study stream as opposed to colder reaches upstream. Warm- and coldwater fish assemblages overlapped considerably in all three study streams, and it was difficult to recognize the boundaries between warm- and coldwater fish assemblage zones. Identifying the transitions between warm- and coldwater fish assemblages is important for monitoring stream temperature and protecting sensitive coldwater fishes (Boyd and Sturdevant 1997). We suggest that the upper allowable limits for water temperature in streams be based, in part, on changes in fish community structure in addition to the distribution and physiological tolerances of individual species (Armour 1991). Crossover points in the relative influences of temperature and channel morphology on fish community structure reflect biologically relevant transitions between warm- and coldwater fish assemblages and may provide a useful index for assessing biological

potential in streams. In the MFJD and the NFJD, crossover points in community

structure occurred at 20–22°C (mean daily temperature during the hottest week of the

year). This temperature range corresponds with the highest average mean weekly

temperatures recommended for coldwater fish species cited by Armour (1991) and the

thermal transition zone recorded by Taniguchi et al. (1998) for trout and non-trout

assemblages in the Rocky Mountains.

New challenges to sampling stream fishes

Increasing the resolution and extent of sampling was necessary to assess spatial

variability in fish distribution but effectively decreased the precision of abundance

estimates. In order to make spatially continuous sampling more feasible, we collected

data on fish relative abundance as opposed to population density. In many instances,

relative abundance and presence–absence data are sufficient for identifying important

trends in stream fish assemblages (Rahel 1990); however, even estimates of relative

abundance and presence–absence can be unreliable if they are uncorrected for

sampling efficiency (Bayley and Dowling 1993). Nevertheless, many streams are too

large or inaccessible to sample with electrofishing methods, making it often difficult to

validate visual estimates of fish abundance. To compensate for the lack of precision in

snorkeling surveys, we used a modified version of point abundance sampling (Persat

and Copp 1990) and found that large numbers of visual estimates of fish abundance

were quite effective for quantifying spatial patterns in stream fish assemblages.

Although our estimates of relative abundance were uncorrected for efficiency and

observer bias, the patterns we detected were ecologically meaningful and provided a perspective on stream fishes that would be difficult to obtain using standard electrofishing methods. The statistical aspects of point abundance sampling have been described for monitoring bird populations (Barker and Sauer 1995) but are applicable to surveys of stream fishes and represent an area needing research in stream fish ecology.

Existing sampling techniques for stream fishes may need to be modified to detect and predict changes in fish communities in response to environmental change (Fausch et al., in press). Visual survey and electrofishing methods provide accurate estimates of salmonid abundance in small streams (Hankin and Reeves 1988, Thurow and Schill 1996, Mullner et al. 1998) but are often applied in a site-specific manner that makes it difficult to evaluate the spatial context of individual sites and determine whether the revealed patterns are real (see Wiens 1981). Standard sampling approaches and statistical techniques for estimating fish abundance are probably not sensitive enough to detect declines in fish populations in time to limit management impacts (Ham and Pearsons 2000). Given the difficulties of conducting large-scale experiments in streams and the limitations of species–habitat association studies (Wolff 1995), ecological modeling may be the most feasible method for predicting stream fish responses to environmental change. Spatially continuous data and new modeling approaches that are capable of quantifying context-dependent relationships hold great promise for predicting fish distributions in complex environments (D'Angelo et al. 1995, Rathert et al. 1999).

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CHAPTER 7

CONCLUSION

In the preceding chapters, I have described a geographic framework for assessing longitudinal patterns in stream temperature, habitat, and fish distribution. By increasing the scope of data collection in streams (sensu Chapter 2), I demonstrated how increased sampling effort (i.e., larger extent and smaller grain size) can reveal new patterns and unexpected relationships between stream fishes and their environment. Moreover, the merging of geography and stream ecology resulted in significant methodological contributions to both fields (see Fisher 1997) and provided new insights on how temperature and physical habitat influence fishes at multiple spatial scales.

Remote sensing of rivers and streams is an important new subdiscipline of geography with implications for stream ecology (Bryant and Gilvear 1999, Wright et al. 2000, Torgersen et al. 2001, Mertes, in review). I described the methodological considerations and physical aspects of airborne thermal infrared (TIR) remote sensing for assessing spatially continuous patterns of stream temperature (Chapter 3). Remote measurements of water temperature were accurate (±0.5°C) in a variety of stream environments and were highly effective for evaluating thermal heterogeneity both within and among reaches. However, interpretation of thermal imagery of streams presented challenges unique to flowing waters and required an understanding of the radiative and reflective properties of the water surface and the surrounding

environment. Spatially continuous data on stream temperature patterns have only recently become available, and many questions remain about the causes of stream temperature patterns made visible for the first time through thermal remote sensing. Therefore, more research is needed to investigate the physical and geomorphic factors affecting spatial variability in water temperature and its effects on stream ecosystems.

Understanding stream organisms requires an assessment of habitat heterogeneity at multiple spatial scales (Palmer and Poff 1997). Larval Pacific lamprey in the Middle Fork John Day River (MFJD) provided an opportunity to study spatial patterns and habitat relationships of a benthic fish species (Chapter 4). Spatially continuous sampling methods such as snorkeling are ineffective at surveying benthic fishes that are either too small or too cryptic to identify during underwater surveys. However, multiscale designs offer an effective alternative to spatially continuous data collection and have been applied successfully in studies of benthic invertebrates (Azovsky et al. 2000, Li et al. 2001). I found that a nested sampling design was necessary for predicting the relative abundance of larval lamprey among and within reaches because the effects of habitat variables (e.g., depth and riparian canopy) varied with spatial scale. Understanding large- and small-scale patterns in the distribution of larval lamprey was important because larval habitat relationships were context dependent. Upstream habitats were more suitable for larval settlement than downstream habitats, yet other factors, such as the spawning distribution of adult lamprey, limited the distribution of larvae to downstream reaches. Distributional data are difficult to analyze statistically because they are spatially autocorrelated and

dependent on spatial context (Knapp and Preisler 1999). However, by using non-traditional methods of regression (e.g., logistic regression and locally weighted scatterplot smoothing) and including spatial position as an explanatory variable, it is possible to evaluate the relative influence of location on fish–habitat relationships.

Increases in the scope of data collection often require adaptations in statistical analysis in order to accommodate larger and more complex ecological datasets (Schneider 1994b). A disadvantage of collecting spatially continuous data on stream fish assemblages is that individual observations of fish abundance are non-normally distributed and highly heterogeneous. Unfortunately, multivariate methods commonly used to assess community structure are particularly sensitive to heterogeneous ecological data (McCune 1997). I evaluated several parametric and nonparametric multivariate techniques (principal components analysis, non-metric multidimensional scaling, Bray-Curtis ordination, and Beals smoothing) with respect to their ability to describe community structure in a complex fish assemblage matrix (Chapter 5). I compared ordinations of relative abundance and presence–absence data and found that a combination of Bray-Curtis ordination and Beals smoothing of presence–absence data provided the most ecologically interpretable results. Robust non-parametric methods of multivariate analysis that are capable of extracting patterns from presence–absence data may allow researchers to collect higher-scope data due to tradeoffs in the effort required to obtain estimates of fish abundance.

An advantage of extensive underwater surveys of fish assemblages is that spatial variability in distributional patterns and habitat can be evaluated over a range

of scales as opposed to a set of predetermined levels (e.g., multiscale design). I examined longitudinal patterns in the distribution of stream fishes with the specific objective of quantifying spatial variability in fish assemblage structure (Chapter 6). In contrast to the general perception of stream fish distribution as a series of warm- and coldwater fish assemblage zones in which species are gradually added or replaced in a downstream direction (Rahel and Hubert 1991), I observed that species assemblages differed as much or more within as between thermal zones. Moreover, the factors influencing the distribution of fishes within and among streams were dependent on thermal context and the spatial extent of analysis. The relative importance of channel morphology in structuring fish assemblages increased at warmer temperatures and decreased with larger spatial extents. At warm water temperatures, coldwater fishes, such as juvenile chinook salmon (*Oncorhynchus tshawytscha*), generally occupied fastwater habitats but shifted to slow-water habitats at colder temperatures. The increased scope of underwater surveys made it possible to detect subtle spatial patterns and scale-dependent habitat relationships in stream fish assemblages. However, spatially continuous data collection effectively limited the precision of fish abundance estimates and provided only a snapshot of fish distribution during one part of the year.

In the preceding chapters, I have emphasized the importance of quantifying and explaining spatial patterns of stream fishes and their environment. However, longitudinal patterns of stream fishes are temporally dynamic and reflect changes in the riverine environment throughout the seasons (Baxter 2002). Therefore, it is important to interpret spatial patterns of stream fish assemblages within a temporal

context. While it may be impossible to evaluate spatially and temporally continuous patterns simultaneously, there are ways to combine spatial and temporal sampling to provide a temporal context for spatially continuous surveys (Chapter 2). Spatially extensive surveys (e.g., snorkeling, habitat surveys, and remote sensing) can be used initially to select a number of sites for temporal monitoring (i.e., intensive, site-based studies) which in turn afford the information necessary to place spatial patterns in a temporal context.

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APPENDICES

Appendix A. Description and field reference for visual habitat classification based on channel morphology and surface characteristics.

Habitat type	Field code	Channel morphology	Surface characteristics [a]
Pool	1	Defined lateral or mid-channel scour created by pool-forming agent (e.g., boulder, log, channel curvature); relatively high width-to-length ratio.	Placid, low turbulence, minimal or poorly defined directional flow.
Slow-moving glide	2	No defined scour, relatively uniform water depth laterally and longitudinally, relatively low width-to-length ratio.	Same as pool.
Fast-moving glide	3	Same as slow-moving glide.	Directional flow apparent, but with minimal or no wave formation and surface turbulence.
Riffle	4	Relatively uniform water depth, low width-to-length ratio, steeper slope than glide.	Visible directional flow with surface waves and/or turbulence.

[a] A surrogate for water velocity.
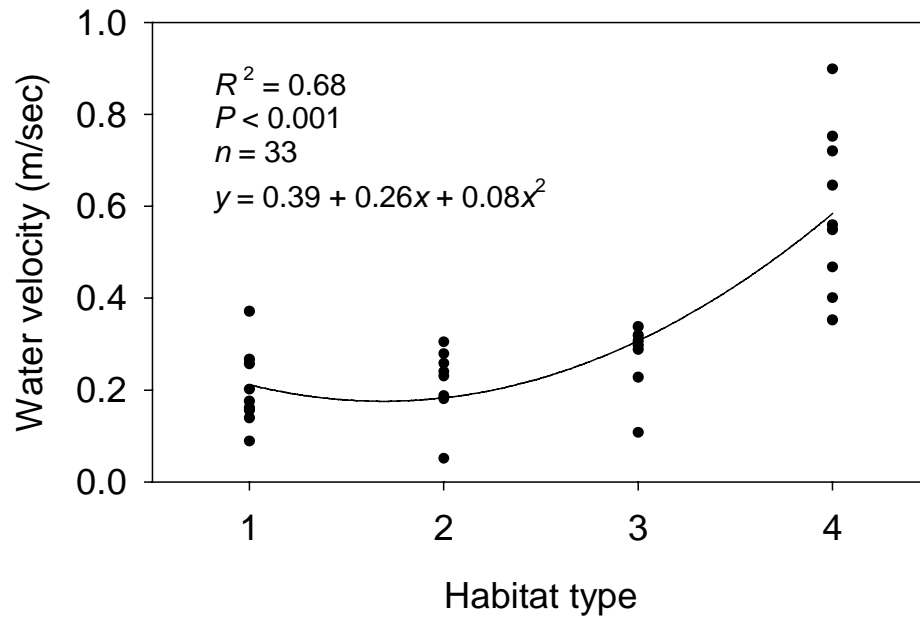
Appendix B. Field measurements of water velocity versus visual classification of habitat type. Visual classifications of habitat type explained 68% of the variation in water velocity. Water velocity measurements and habitat classifications were recorded at base flow (August 1998) in the Middle Fork John Day River. See Appendix 1 for descriptions of habitat type.