AN ABSTRACT OF THE DISSERTATION OF

Colden V. Baxter for the degree of Doctor of Philosophy in Fisheries Science presented on January 23, 2002.  Title: Fish Movement and Assemblage Dynamics in a Pacific Northwest Riverscape.

Abstract approved:___

Signature redacted for privacy.

Hiram W. Li

Signature redacted for privacy.

Bruce A. McIntosh

This study examined fish movements and assemblage dynamics in the Wenaha, Grande Ronde, Snake river system of northeast Oregon and southeast Washington.  I investigated the role of fish movement in the dynamics of stream fish assemblages and evaluated relationships between species movement, assemblage structure, and the heterogeneity of habitat at multiple scales within the river network.  In doing so, I employed a landscape approach, visualizing the heterogeneity and dynamics of the system as a "riverscape" that sets the stage for the ecology of stream fishes.  I quantified fish assemblage dynamics, characterized the nature and extent of movement by representative fish species, and assessed spatial and temporal heterogeneity of stream habitat within the river network.  I applied multiple methods, including underwater fish surveys and radio telemetry, and used multiple sampling approaches that allowed me to detect patterns at nested spatial and temporal scales.

I found that spatial patterns in fish assemblage structure were highly dynamic over seasonal to diel temporal scales.  Seasonal changes in fish assemblage patterns along the length of the river system were primarily driven by the migration of native fishes such as mountain whitefish, bull trout, and largescale suckers.  These highly migratory species exhibited a diverse array of movement strategies and often had annual ranges of hundreds of kilometers.  The movement of fishes at smaller spatial scales influenced diel dynamics of fish assemblage patterns.  Important habitat features at stream, valley

segment and channel unit scales were separated spatially, and fish species exhibited a variety of migratory strategies that reflected the complementary use of habitats distributed throughout the riverscape. The importance of fish migration and the dynamic nature of stream fish assemblages and fish habitat relationships should be taken into account in research and conservation of stream fishes. Current conceptual frameworks for stream fish assemblages do not fully reflect the temporal complexity of stream fish life histories or the spatial heterogeneity of stream habitat. I introduce an alternative framework by integrating fish movement into a dynamic perspective of assemblages set within the context of the riverscape, and raise questions regarding the nature of ecological communities.

# FISH MOVEMENT AND ASSEMBLAGE DYNAMICS IN A
# PACIFIC NORTHWEST RIVERSCAPE

by

Colden V. Baxter

A DISSERTATION

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed January 23, 2002
Commencement June, 2002

Doctor of Philosophy dissertation of <u>Colden V. Baxter</u> presented on <u>January 23, 2002</u>

APPROVED:

Signature redacted for privacy.

Co-Major Professor, representing Fisheries Science

Signature redacted for privacy.

Co-Major Professor, representing Fisheries Science

Signature redacted for privacy.

Head of Department of Fisheries and Wildlife

Signature redacted for privacy.

Dean of the Graduate School

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

Signature redacted for privacy.

Colden V. Baxter, Author

# ACKNOWLEDGEMENTS

# TABLE OF CONTENTS

TABLE OF CONTENTS, CONTINUED

# LIST OF FIGURES

# LIST OF FIGURES, CONTINUED

# LIST OF TABLES

# DEDICATION

This dissertation is dedicated to the fish of the Wenaha, Grande Ronde, Snake River system, and especially to those individuals that were drafted into service as radio-tagged representatives of their kind.

# FISH MOVEMENT AND ASSEMBLAGE DYNAMICS IN A PACIFIC

# NORTHWEST RIVERSCAPE

## CHAPTER 1: INTRODUCTION

## *1.1    General Ecological Background and Rationale*

Ecologists have long recognized that the abundance and distribution of organisms is a complex function of interactions between organisms and the physical environment, as well as among organisms. The movement of organisms is a factor that both reflects these interactions and influences them, yet in some respects its role in the expression of ecological phenomena has been under-appreciated. For example, introductory texts (e.g., Begon et al. 1986, Postlethwait & Hopson 1989) have treated movement sparsely and done so primarily in the context of behavioral ecology, with less attention given to its role in the structure and dynamics of populations and communities. Ecological phenomena are expressed within the context of evolution and occur at different levels of biological organization, from individuals, populations, and species, to assemblages, communities and ecosystems. Organism migration and dispersal play a critical role at all of these levels. There is a special need, however, for a better understanding of movement in the context of communities and species assemblages.

What is a community? Marston Bates (1960) wrote, "At the community level we have difficulty even in definition, both in defining the general concept and in defining particular communities." A typical definition is given by Begon et al. (1986), who vaguely define a community as "an assemblage of species populations which occur together in space and time." Yet ecologists have conceived that communities are 'real' entities, that populations do not exist in isolation but rather as a part of a complex web involving many direct and indirect relations with the environment and other organisms. Since Stephen Forbes (1887) wrote of "the lake as a microcosm," a basic tenet of community ecology has been that understanding populations requires understanding their connections within communities and ecosystems. However, since the beginnings of the science of ecology, there has also been debate over the nature of the community. Are communities groups of co-evolved populations closely-knit by strong biotic interactions? Or, are they loosely associated populations of species whose shared distribution is

primarily driven by the physiological constraints of the environment? Though these perspectives are no longer viewed as mutually exclusive but rather as endpoints in a continuum, the question of where particular communities exist along this continuum remains essential, and in most cases, largely unanswered. Part of the reason for this, I will argue, is that for many communities we lack a fundamental understanding of the spatial and temporal heterogeneity of the system, both in terms of environmental heterogeneity and with respect to the dynamics of species associations. Better understanding of the former requires more thorough description of physical and biological heterogeneity at larger scales than typically addressed by community ecologists, while insight into the latter requires a more comprehensive focus on the movements of organisms.

Despite the recognition of habitat as the templet or stage, *sensu* Southwood (1977), upon which ecological dramas are played out, decades of research have not fully embraced the importance of environmental heterogeneity. However, in recent years and partly as a result of advances in the field of landscape ecology, there has been growing recognition that heterogeneity in the habitat templet is important in and of itself (e.g., Turner 1989, Pickett & Cadenasso 1995). At the same time, ecologists attempting to understand the processes that affect populations and communities in complex landscapes have increasingly recognized the importance of organism movement, the spatial arrangement of landscape features, and habitat relationships that occur across multiple scales (Dunning et al. 1992, Taylor et al. 1993). However, there have been relatively few studies that have empirically assessed these landscape-level phenomena, and those that have attempted to do so have typically focused on single populations.

Through this study I describe the movement of fishes and the expression of fish life histories in the context of stream habitat heterogeneity, and I investigate the interactive effects of movement and habitat heterogeneity on local fish assemblage dynamics. In doing so, it was my goal to advance understanding and raise questions regarding not only fish assemblages and stream communities, but also ecological communities in general.

### 1.2  *Stream and Stream Fish Ecology Background and Rationale*

Researchers have long sought to understand the mechanisms responsible for observed patterns in fish assemblages along the length of river systems. However, many studies of stream fish assemblages result in a summer-time snapshot of the distribution and abundance of species along a river section. Investigations of the seasonal dynamics of longitudinal assemblage patterns have been relatively rare (Matthews 1998). The supposition that assemblage patterns are largely static through the seasons has often been implicit in researchers' interpretations of species-habitat associations as well as the outcome of field experiments designed to elucidate factors governing stream community structure and function. As such, this static perception may be method-driven by the ease of study during summer months as opposed to being a true reflection of stream fish assemblages.

There has also been a long-standing assumption that many resident (i.e., non-anadromous) stream fish exhibit restricted movement (Gerking 1959, Gatz & Adams 1994, Rodriguez 2002), an idea that has circularly contributed to the assumption that longitudinal assemblage patterns are static in time. This "restricted movement paradigm" has been called into question in recent years, and researchers have come to recognize that many stream fishes require habitat at much larger scales than previously thought to complete their life cycles (Gowan et al. 1994, Fausch & Young 1995).

Through this study, I asked the questions, "Are stream fish assemblage patterns seasonally dynamic?" and if they are, "What is the role of fish movement in influencing these dynamics?" To address these questions, we felt it was important to take a somewhat different approach than has been traditional in many studies of streams and stream fish. Often for logistical reasons, most studies involve collection of data that are highly discontinuous in space and/or time. We feel that this approach may result in an incomplete view, much as though one were trying to visualize a painting through holes in a curtain draping it, or attempting to piece together the plot of a movie by viewing only

small portions of the film. In this study, we endeavored to gain a more spatially and temporally continuous perspective of physical and biological heterogeneity within the riverine landscape, or, as we have termed it in a recent paper (Fausch et al. in press), the "riverscape." Subsequently, this perspective set the stage for my research as well as future investigations of stream fish and community ecology within the Pacific Northwest riverscape I studied.

Through this "riverscape" approach (see also Torgersen 2002), this study was able to address two critical "big picture" questions that serve as themes in this dissertation: 1) "What is the character of fish-habitat relationships?" and 2) "What is the nature of a fish assemblage or a stream community?" With a more continuous perspective on stream fish and their habitat, I was able to assess processes that depend on the spatial arrangement and composition of habitat features within the riverscape, and that are closely linked to fish movement. The integration of perspectives gained from the field of landscape ecology (Dunning et al. 1992, Taylor et al. 1993) has led to increased awareness of these processes. These factors may be especially relevant to the ecology of mobile organisms such as fishes, thus it was a goal of this study to explore their importance to stream fish in the riverscape (Figure 1). For example, the ecology and movements of fish in an area can be influenced by the spatial arrangement and extent of non-substitutable (habitat complementation) or substitutable (habitat supplementation) habitat resources. In addition, the demographics and ecology of a species in an area can be influenced by the proximity of other source and/or sink areas for that species. Neighborhood effects and connectivity can also influence the ecology and movements of fish in an area. For example, some boundaries for a species in the riverscape may be permeable, while others may be only semi-permeable or impermeable. Applying these concepts, Schlosser (1995) describes a dynamic landscape model of stream fish life history (Figure 2) in which fish movement plays an important role in transporting different life stages across landscape scales to occupy patches of critical habitat required to complete their life cycles. One of the aims of this study was to evaluate the applicability of Schlosser's conceptual model to stream fish in a river system of the Pacific Northwest.

Figure 1. Habitat relationships that could influence fish at landscape scales. I.
*Landscape complementation.* A species requires non-substitutable resources found in
two different habitats (shaded and open). Regions of the landscape where both habitats
are relatively close may support more individuals (area A) than regions where one habitat
is relatively rare (area B). II. *Landscape supplementation.* A species requires resources
found in the shaded habitat patches. Patches A and B are too small to support
populations on their own. However, patch A may support a population if individuals can
supplement their resources from nearby patches within an accessible portion of the local
landscape (oval). III. *Sources and sinks.* Species occupies two habitat types: a rich type
capable of producing excess individuals (sources: open patches), and a poor type which
can not produce enough individuals to maintain a population without dispersers (arrows)
from nearby sources. IV. *Neighborhood effects.* Boundary effects are one type of
neighborhood effect. Dispersers (arrows) from central patch of habitat type A move into
neighboring habitats if boundaries are permeable (Habitat A), or semi-permeable (Habitat
B). Dispersers are unable to colonize Habitat C, with an impermeable boundary. Figure
adapted from Dunning et al. (1992), following Schlosser (1995).
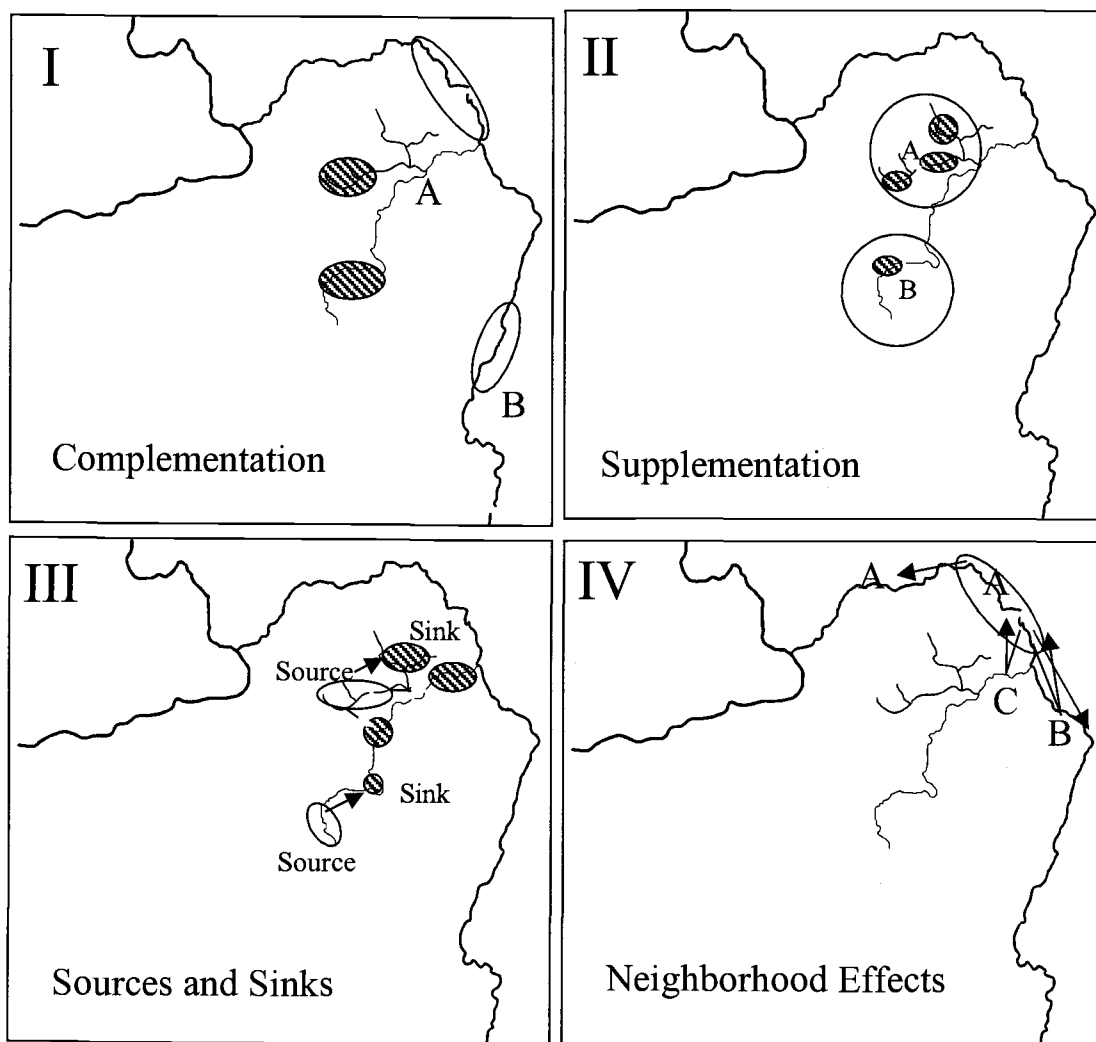
Figure 2. Schematic depicting Schlosser's (1995) dynamic landscape conceptual model of stream fish life history. A key feature of this model is the movement of fish at different life stages among spatially separated habitats. From Schlosser (1995).
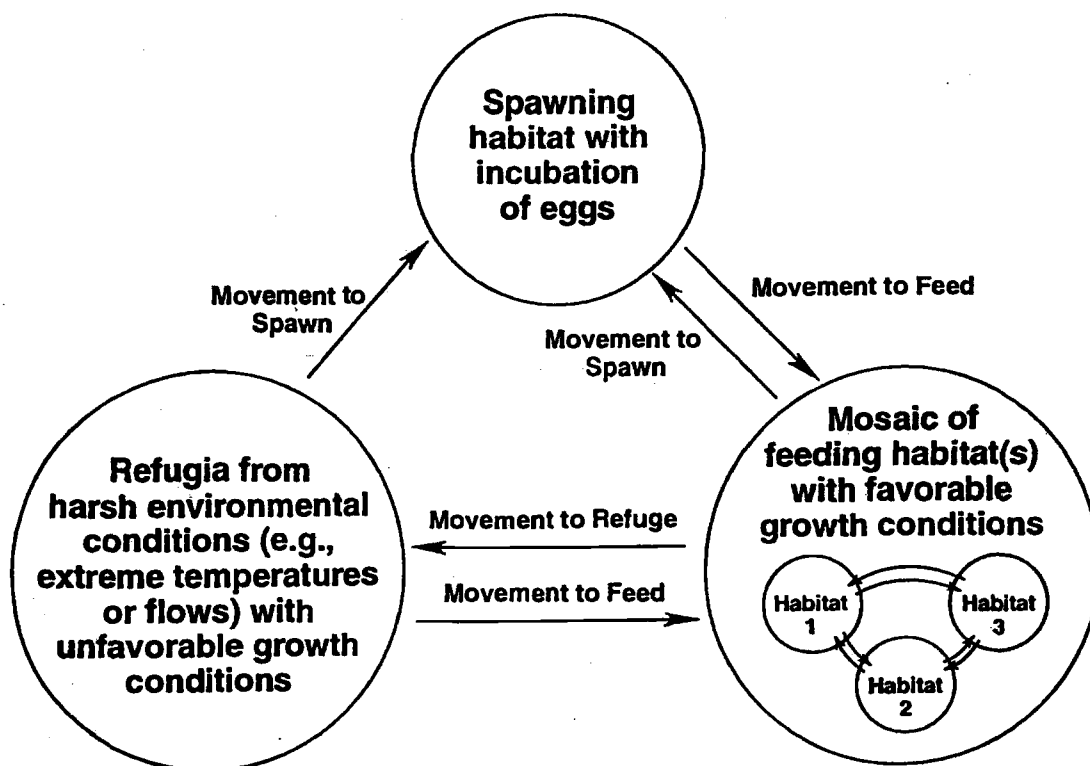
What is the nature of fish assemblages or stream communities? Despite criticism of the restricted movement paradigm, little is known about how fish movements may influence seasonal changes in assemblage (i.e., including only fish species) and stream community (i.e., including species other than fish) structure. One reason for this may be that, even amongst the relatively species-poor fish assemblages in rivers of the Pacific Northwest, there is deficient understanding of the nature and extent of movement or migratory life histories of non-anadromous fishes (particularly non-game fishes). In general, conceptual frameworks that describe "rules" governing assemblage (e.g., Matthews 1998) and community (e.g., Vannote et al. 1980) structure in streams do not take into account the migratory behavior of many stream fish species or the resulting transitory nature of community associations. Consequently, there are conspicuous gaps in our perspectives and understanding of the dynamics of stream communities.

## 1.3    Study Objectives

My purpose in this study was to address some of the gaps in understanding of stream fish assemblages within the context of a Pacific Northwest river system. I hypothesized that large-scale seasonal migrations by several species were responsible for dramatic dynamics of fish assemblage patterns, that movement by fishes would be associated with the composition and spatial arrangement of habitat resources at multiple scales, and that the expression of life history strategies would reflect the heterogeneity of the habitat in the riverscape. The broad objectives of this study were to 1) assess spatial and temporal patterns of potentially important aspects of fish habitat within the riverscape, 2) quantify fish assemblage dynamics, 3) characterize the nature and extent of movement by representative fish species in the assemblage, and 4) evaluate fish assemblage dynamics and the expression of fish behaviors and life histories in the context of the riverscape.

**CHAPTER 2:  STUDY AREA AND METHODS**

## 2.1   Study Area

The area where this study took place was the Wenaha, Grande Ronde, Snake River network in northeast Oregon and southeast Washington (Figure 3). The study area is geologically and topographically complex, encompassing a transition from the Blue Mountains physiographic province (including most of the study area except reaches of the Snake River) and the Walla Walla Plateau province (Fenneman & Johnson 1946). The Grande Ronde basalts, a member of the Late-Cenozoic Columbia River basalt group, are the primary formation underlying the area. However, the basalt lithology differs between the Wenaha drainage and the lower Grande Ronde, and Mesozoic metamorphic rocks of the Wallowa accreted terrane are exposed in the Snake River canyon (Ross 1980, Camp & Hooper 1981, Swanson & Wright 1983, Orr et al. 1992). There is also a structural transition in the study area, with the Wenaha drainage being closer to the axis of the Blue Mountains Uplift than the lower Grande Ronde and Snake portions of the study area (Ross 1980, Camp & Hooper 1981, Swanson & Wright 1983). These geologic patterns have consequences for the expression of stream habitat in the study area.

My research lead across a range of stream size, from 1st-5th order reaches in the Wenaha-Tucannon wilderness area to 7th-9th order habitat of the lower Grande Ronde and Snake rivers (Figure 4). The Wenaha is a low gradient (mainstem average 1.7%), low elevation (450-1200 m), 5th order (760 km$^2$) drainage that flows west to east to join the Grande Ronde River near the small town of Troy, Oregon. Typical summer base flow for the Wenaha is 200-250 cfs (Thompson & Haas 1960; Baxter, C., unpublished data) while average summer base flow for the 7th order (8482 km$^2$) Grande Ronde River at Troy is 875 cfs (USGS gauging station data). The Grande Ronde flows northeast to meet the Snake River at the downstream end of Hell's Canyon. Stream courses throughout the study area generally follow alluviated troughs (there has been no glaciation in the study area), and channels sharply dissect the basalt terrain into a mosaic of finger ridges and steep canyons. The Wenaha River cuts a valley about 1200 ft. deep (avg.) with average side slopes of 50-60% (Toretta 1991). In general, canyon depth

Figure 3. Map of study area in northeast Oregon and southeast Washington.
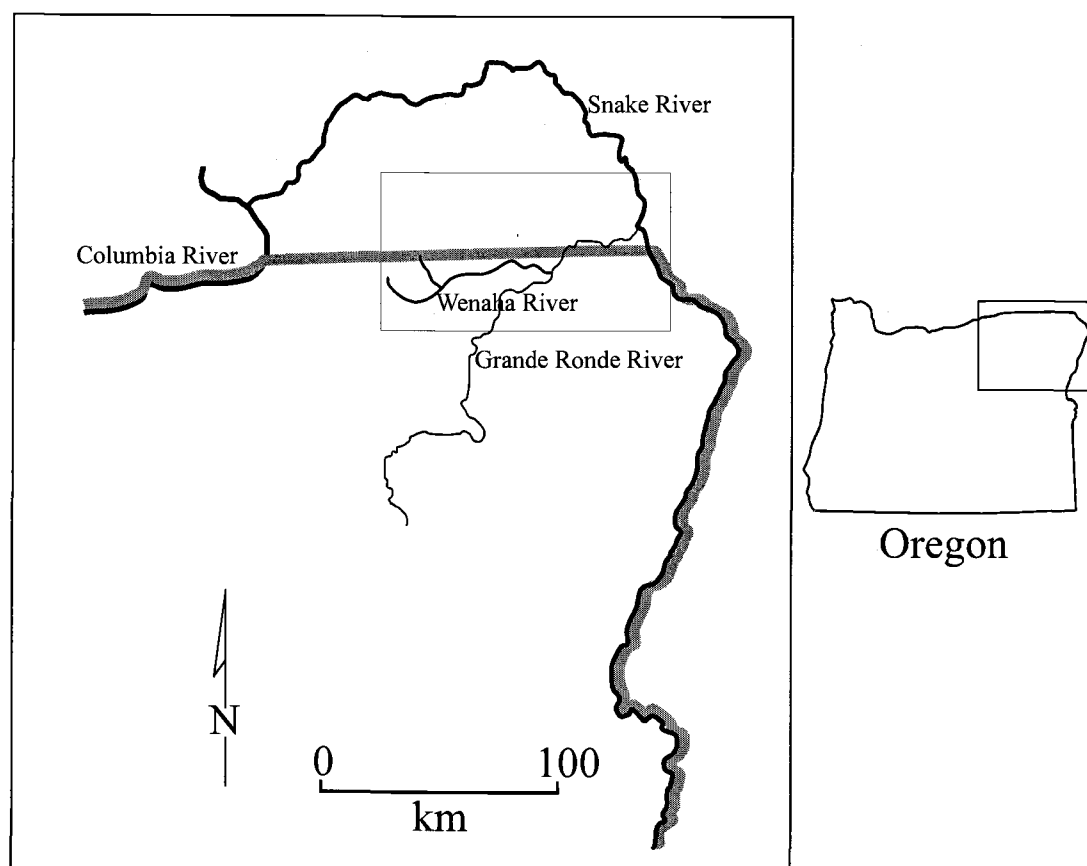
Figure 4. Images of the study area from locations throughout the river network.



S. Fork of the Wenaha     Floodplain reach of the upper Wenaha River     Lower Wenaha River
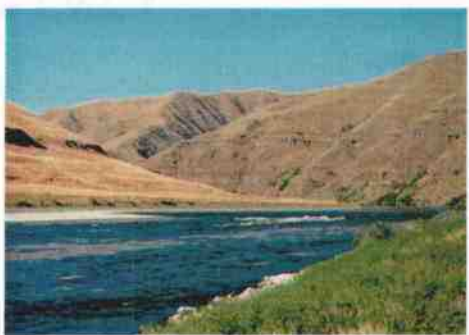


Lower Grande Ronde River     Snake River downstream of Hell's Canyon



Aerial views of lower Wenaha River, forks of the Wenaha River, and the lower Grande Ronde River

increases and valley side slopes become steeper lower in the study area. The Wenaha River possesses a relatively lower gradient and broader valley bottom than is found in the more entrenched lower Grande Ronde and Snake River portions of the study area. Consequently, the Wenaha drainage possesses the most extensive floodplain reaches in the study area.

The area also spans a climactic transition, from a moist, Mediterranean character in the headwaters of the Wenaha, to a much drier, intermountain west character in the reaches of the lower Grande Ronde and Snake River. Most precipitation in this area falls as snow, and peak discharge generally occurs from March to May. Summer cloudbursts and rain-on-snow events commonly result in flash flooding and debris flows in steeper terrain. Air temperatures may exceed 30 °C in summer and fall below -5 °C in winter.

The vegetation of the area reflects the climactic and elevation (range 1200-240 m) gradients. Uplands of the headwaters are characterized by ponderosa pine/mixed conifer forest (*Pinus ponderosa, Abies grandis, Abies lasiocarpa, Pseudotsuga menziesii, Picea engalmanii, Pinus contorta, Larix occidentalis*) and these give way to drier forests and shrub/grassland steppe (*Physocarpus sp., Symphoricarpus sp., Agropyron sp., Festuca sp.*) in the lower reaches. Valley bottom vegetation includes hardwood shrubs and trees (*Salix sp., Alnus sp., Populus sp., Creataegus columbiana and Cornus nutalli*). The more extensive floodplain reaches of the Wenaha River possess dense vegetation of trees and woody shrubs, while the riparian zones along the Grande Ronde and Snake River are generally restricted to narrow riverside ribbons (see Figure 4).

The Wenaha River may be the only low elevation watershed in the Columbia Basin that is protected entirely by designated wilderness and is virtually unaltered by human activity. The Wenaha drainage is rare in that it has not experienced notable logging, mining, or cattle grazing (Thompson & Haas 1960, Wissmar et al. 1994). Locally, segments of the Wenaha River possess an extensive, densely vegetated floodplain. The waters of this basin are home to three endangered fish species; the bull trout *Salvelinus confluentus*, and Snake River spring chinook salmon *Oncorhynchus tshawytscha* and steelhead trout *Oncorhynchus mykiss*. The Wenaha River provides critical habitat for these endangered salmonids and is considered a basin-scale refuge (Li et al. 1995,

Buchanan et al. 1997). Though collection of data in this basin is logistically
challenging (the area is only accessible by trail), I felt that study in this area might
provide unique insights not evident in other river systems of the region. Furthermore, I
expected that this information might serve as a critical reference for other drainages in the
region that have experienced extensive human impacts and whose fish communities are
imperiled.

## 2.2    *Natural History Observations*

As I have described, the Wenaha drainage is perhaps the most ecologically intact low
elevation watershed of its size remaining in the mid-Columbia basin. Consequently, any
natural history information from this area, even in the form of qualitative descriptions, is
of potential importance. With this in mind, we made an effort during this study to collect
data and record observations on many species in addition to stream fish. As the river is
only accessible via backpacking, each of our snorkel survey trips involved hiking along
approximately 40 km of the river. We viewed this hike as a transect and recorded
observations of wildlife we encountered along the trail as well as at each of the intensive
survey sites. These natural history observations were recorded for species with which we
were familiar, and those that were easily seen during our surveys. Consequently, while
my hope was to provide useful information, these records should not be considered a
rigorous natural history survey of the area, a task as worthwhile as it would be
challenging. What follows is a summary of some of our observations on the mammals,
birds, reptiles, amphibians, invertebrates and plant life we encountered. I present these
observations in order to help set the ecosystem context for the study area, and to serve as
a record of natural history observations in this unique place.

<u>2.2.1 Mammals</u>

River otters were observed at sites along the Wenaha River from its confluence with the Grande Ronde to as far upstream as rkm 25. Otter were seen in the Wenaha River from May through December, though most sightings occurred in summer and fall. In contrast, we observed river otter in the Grande Ronde River predominantly during the winter and early spring. Mink were also seen at several sites along the Wenaha River, with most sightings occurring in floodplain reaches of the lower river. On two occasions we observed river otter predation on fishes, once on adult rainbow trout and once on an unknown species of juvenile salmonid. On another occasion, we also observed a mink to prey on a juvenile salmonid.

Black bear were common in the Wenaha drainage. During one trip in September, we observed 5 bears, including a mother and two cubs. Bears appeared to be most abundant along the Wenaha River during late summer and early fall when berries were ripe on the river floodplain. It was often difficult hiking the river trail during this time due to the many hawthorn bushes that had been broken or bent down by bears for their greater ease in removal of berries. This period also seemed to correspond to the time of greatest density of spruce grouse (see below) in the valley bottoms. We observed ample evidence that bears foraged on berries and grouse during this time. In addition, we observed two instances of bears preying on fish, both during late summer. We saw one bear chasing after a sucker in the river shallows, and observed that another had foraged on the carcass of a chinook salmon. Finally, we observed one bear tearing apart a rotted log and foraging on insects.

Beaver were observed on only two occasions, though signs of their current occupation of the Wenaha River were evident in several areas, particularly in floodplain reaches of the upper river. In these areas their activity appeared to have the greatest impact on aquatic habitat, and their dams contributed to habitat complexity through the formation of ponds, floodplain wetlands, side channels, and spring brooks.

We often observed bighorn sheep, deer, and elk during our hikes through the drainage. Bighorn sheep were seen year-round and most frequently on the hillsides and

cliffs in lower reaches downstream of Crooked Creek. White tail and mule deer were also seen year-round. Elk were commonly observed along the ridge tops during spring, summer and fall. Elk were rarely seen in the valley bottom except during late fall and winter months, when deer and elk were observed there in larger numbers. Additional mammals observed (or whose sign were observed) during our surveys included bats, bobcat, coyote, and mountain lion.

### 2.2.2 Humans (Mammals contd.)

The amount of time we spent in the Wenaha River drainage also gave us a perspective on the present-day use of the area by another mammal—human beings. Even to the eyes of those trained to detect human impacts on the landscape, the Wenaha River valley appears to possess a wilderness character. Historically, there was some commercial harvest of timber along the river, though we only observed evidence of this in a small plot of private land in the reach downstream of Crooked Creek. Though the Eden grazing allotment parallels the south side of the Wenaha Canyon, these cattle were never observed in the valley bottom. The only cattle we observed in the river bottom were the small herd associated with the Wenaha grazing allotment (Pomeroy Ranger District). We never saw more than 20 of these animals at a time. However, they were seen to actively graze on the river floodplain, particularly in the vicinity of the confluence of Crooked Creek. Other than one small cabin on a private inholding tract near rkm 5, the only private residences are at the mouth of the Wenaha River in the village of Troy. A broad terrace about 0.5 km upstream of Troy was historically the site of a lumber mill, though nothing remains of this but the remnants of a concrete bridge abutment. On this flat is a cabin owned by the Oregon Department of Fish and Wildlife that we were fortunate to use as our base camp during our winter research. This area is used for public camping as well as a target practice area for the local black powder club, and it gets heavy use during the annual "rendezvous."

In general, we observed very few people during our many trips along the Wenaha River. I estimate that we observed a total of 30-40 individuals during the course of all of our surveys, and these were almost entirely limited to summer and fall seasons. During these periods, we often made entire trips without seeing another party, though it was typical to meet 1-3 small groups. Particularly during the hunting season, we occasionally saw groups on horseback. The most we observed in a single trip was two small (< 4 horses) groups.

Despite the small number of people using the area, many campsites showed signs of heavy use. Ground vegetation had been worn away at many campsites, there was evidence that tethering of stock had resulted in tree and riverbank damage, and trash (including improperly disposed of human waste) was abundant at several sites. These observations, along with others, yielded the impression that some small groups were having an impact disproportionate to their numbers.

Furthermore, there was evidence that angling pressure may also be disproportionate to the number of people visiting the area. Trash at campgrounds often included packaging for lures, hooks, and occasionally live bait. Though we observed few anglers, many of those we spoke to stated that they returned on an annual basis to fish the Wenaha River, and frequently reported having captured (and presumably released, under current regulations) large numbers of bull trout. The two largest groups of people we saw during the study were anglers that had camped at sites between Butte and Rock Creeks in mid-July. This was a period when high densities of large bull trout were to be found in this stretch of river, a fact of which these anglers were aware. Using artificial lures, these anglers reported that they had captured and released many "dollies." Though these anglers were using single hooks, we observed one instance of a bull trout mortality that was induced by their activities. During our dives we also observed two instances in which bull trout had lures (both treble hooks) stuck in their mouths. During our trips through the Wenaha, we encountered only one warden (a mounted state policeman), though we did meet several other fisheries workers doing surveys for state and federal agencies. As there is currently no check-in at the trailhead in Troy, there does not appear to be a mechanism in place for monitoring recreational use along the river.

2.2.3  Birds

Though we did not take the time (or possess the skills) to identify many bird species, we did observe that a diverse array of birds used the Wenaha River floodplain corridor during different times of the year.  Our observations focused on those species associated with the river or floodplain environment.  We made a large number of observations of American dippers, belted kingfisher, osprey and bald eagles.  We observed dippers feeding on aquatic and terrestrial insects and recorded several instances of kingfishers, osprey and eagles preying on river fish.  Kingfishers and dippers were observed to nest near several of the intensive dive sites and were observed at nearly every site along the length of the river.  We observed numerous bald eagles along both the Grande Ronde and the lower Wenaha River, though we saw them only between October and March.  Osprey, on the other hand, were very common along the middle and lower reaches of the Wenaha as well as the Grande Ronde, while they were largely absent during the time period that eagles were present.  The timing of the return of osprey in the spring seemed to correspond to the timing of the largescale sucker spawning migration up into the Wenaha River.  In fact, we observed instances of osprey preying on suckers and, in our capture of suckers for radio-tagging, we noted several fish with talon injuries, both fresh wounds and old scars.  We also observed many Canada geese using the floodplain of the Wenaha River, particularly in spring, and especially in the lower river floodplain.  During one hike in May along the lower 3 km of the river, we observed about 30 geese.  During this same time period, we also observed many mergansers in and along the river.  We observed that both these species used the floodplain for nesting.  Particularly in spring, we observed that numerous songbirds utilized the dense floodplain vegetation of the Wenaha canyon, including warblers, finches, chickadees, tanagers and other unknown (to us) species.  Throughout the year, we observed winter wrens, brown creepers, ravens, crows, woodpeckers (pileated and downy), and spruce grouse using this valley bottom habitat.

### 2.2.4 Reptiles and Amphibians

The Wenaha River and its floodplain are home to abundant reptiles and amphibians. Adult western spotted frogs and western spotted toads were commonly observed, and their tadpoles were present in locally high densities in floodplain ponds, alcoves, and wetland areas throughout the river in summer. Larval tailed frogs, *Ascaphus truei* were also abundant in 1-2$^{nd}$ order reaches of the upper Wenaha River, though they were not observed at all lower in the river.

From the perspective of one who has surveyed many rivers of the Pacific Northwest, it seemed that the numbers of snakes encountered was exceptionally high. For instance, the largest number of rattlesnakes seen in a single day during surveys of the Wenaha River was 11. That's a lot of rattlesnakes. Rattlesnake sightings were most common from Butte Creek downstream, and were most frequent along the Wenaha River and floodplain during early evenings of late summer. Garter snakes and rubber boas were also abundant in and along the river. Garter snakes were repeatedly seen preying on small fish and amphibians (both adults and larvae). Interestingly, we also observed several occasions when garter snakes disappeared into the saturated and porous cobble bed of the river, a behavior that did not appear to be based on avoiding our presence, but might be associated with feeding activities in the hyporheic zone.

### 2.2.5 Aquatic Invertebrates

During our underwater surveys we had ample opportunity to form an impression of the aquatic invertebrates present in the Wenaha River. Local anglers describe the Wenaha River as being "incredibly full of fish food." We concur. Our visual observations suggested that aquatic macroinvertebrate densities were quite high in comparison to other rivers of this size and character that we have surveyed in northeast

Oregon (e.g., North Fork of the John Day River, upper Grande Ronde River). Caddis species of the families Brachicentridae, Hydropsychidae and Limnephilidae were common. Stonefly species, including large *Pteronarcys sp.*, and other species of the families Perlodidae and Chloroperlidae were abundant. Mayfly species, including *Drunella sp.* and others of the families Heptageniidae and Baetidae were also abundant, as were larval Chironomidae. Densities of emerging insects were quite striking at times. For example, we observed a concentrated emergence of large stoneflies that occurred in late September and a similar emergence of large caddis adults in November.

Other aquatic invertebrates we observed included crayfish and freshwater mussels. Crayfish were most abundant in the mid to lower reaches of the Wenaha. It was common (particularly at night) to observe from 1-5 crayfish during a dive of one of our intensive sites. The most we observed was 12 individuals in a night dive of our site just upstream of the Crooked Creek confluence. In contrast to the insect densities, we observed relatively few mussels. We estimate that we observed 20-30 individuals, along with some empty shells, during the course of the entire study. These were only seen in long glide-like habitats in the reaches downstream of Crooked Creek. I tentatively identified these individuals as belonging to the species *Margaritifera falcata.*

## 2.2.6 Riparian Vegetation

The vegetation along the Wenaha River and on its floodplain is in places so dense as to make walking through it nearly impossible. There is a marked vegetation transition from upstream to downstream that reflects the moisture gradient (see also section 2.1), though there is also variation in valley bottom vegetation that reflects shifts in valley segment type (see Figures 4 and 7). Most of the riparian vegetation biomass and diversity appeared to be in woody species of shrubs and trees, including *Salix sp., Alnus sp., Populus sp., Creataegus columbiana* and *Cornus nutalli.* These species tended to characterize alluvial valley segments and alluvial fan-influenced segments, particularly in the mid-upper sections of the river. These segments often included an over-story of large

cottonwood trees. In contrast, terrace-bound valley segments usually possessed plant associations of the drier ponderosa pine/mixed-conifer forest, shrubs and grasses. Alluviated canyon segments included a mixture of these vegetation types. Some floodplain wetland complexes occurred in alluvial valley segments, and these frequently possessed more herbaceous plants. In the reaches below Crooked Creek, the dominant herbaceous riparian plant was the non-native reed canary grass. Other than the presence of this species, the riparian vegetation of the Wenaha River drainage appeared to reflect a state relatively unaltered by human activity.

## 2.3  *Background Information on Study Development*

There were several elements specific to the study region that combined to form some of the motivation for my research project. Previous studies of fish and habitat in the Wenaha River are relatively few and the reports have not been published (Thompson & Haas 1960, Toretta 1991, Frissell et al. 1996, Keefe et al. 1996, Price 1998). These studies were generally conducted in summer and tended to focus on the salmonid species present in the drainage. When questioned in conversation, however, several local fishermen claimed considerable movement of resident fishes, including rainbow trout, mountain whitefish, bull trout and suckers in the Grande Ronde River, with the general pattern being upstream in spring and downstream in the fall. We performed reconnaissance snorkel observations in the lower Wenaha River during September of 1997, and when these data were compared to summer stream survey observations by Toretta (1991) there appeared to be significant differences in fish numbers (particularly for largescale suckers).

In addition, this study was interactive with another (Torgersen 2002). A cooperative goal of our two studies was to gain a more spatially and temporally continuous perspective on stream fish and their habitat than is achieved in most single studies. The emphasis of Torgersen's (2002) study was on detecting patterns through spatially continuous summer surveys of fish and habitat along the length of several rivers of

northeast Oregon (including the Wenaha). Natural questions that arose during that work included, "Do fish and habitat patterns observed in summer remain the same year-round?" and "To what extent do fish move?" This background and cooperation informed the generation working hypotheses and helped provide the focus of my study on seasonal fish assemblage dynamics and movement.

## 2.4     *Study Approach and Methods*

In this study, I applied an empirical approach to addressing multiple working hypotheses, *sensu* Chamberlin (1890). Several primary working hypotheses and their alternatives were developed and formed the basis for the research. In the first phase, my primary working hypotheses were that fish assemblage patterns along the length of the Wenaha River were either 1) seasonally dynamic or 2) relatively static throughout the year. Our observations of seasonal dynamics during the first year of the study led naturally to my hypotheses that these dynamics were either 1) primarily driven by the migrations of several fish species, 2) largely a function of the population dynamics of non-mobile fish species, or 3) an artifact of our sampling approach. Linked to the previous hypotheses and my questions regarding fish movement was my interest in assessing the nature and extent of landscape habitat relationships, particularly complementation (Figure 1) (*sensu* Dunning et al. 1992, Schlosser 1995). Were fish moving? If so, did that result in occupation of distinct habitats that could represent (or be associated with) non-substitutable resources? At what spatio-temporal scale or scales did this occur? I hypothesized that the nature and degree of fish movement among species in the assemblage would reflect the extent to which potentially important fish habitat resources were spatially separated in the river network. Likewise, I expected that the expression of various migratory and/or resident life history strategies among and within fish species would reflect this landscape (or "riverscape") context.

To address these hypotheses, my study objectives were to 1) assess spatial and temporal patterns of potentially important aspects of fish habitat within the riverscape, 2)

quantify fish assemblage dynamics, 3) characterize the nature and extent of movement by representative fish species in the assemblage, and 4) evaluate fish assemblage patterns and the expression of fish behaviors and life histories in the context of the riverscape.

To assess fish assemblage dynamics and the nature and extent of fish movement throughout the riverine landscape, we employed multiple complementary methods (Figure 5). The dynamics of stream fish populations and assemblages in the riverscape unfold in a way that can be envisioned as an on-going movie, of which researchers can only see portions. In order to piece together the main characters and the plot of this movie, we applied complementary methods including underwater surveys, radio telemetry, aerial surveys of river habitat, and both spatially extensive and temporally intensive mapping of habitat and fish distribution. Using these techniques, we varied sampling strategy to increase our ability to detect ecological patterns (see also Torgersen 2002). We used both site-based (intensive) and continuous (extensive) underwater sampling in a mutually informative manner, and we quantified fish assemblage dynamics and tracked fish movements at multiple, nested spatial and temporal scales.

## 2.5    Field Methods:  Underwater Surveys of Fish Assemblage Dynamics

Site-based and continuous fish assemblage surveys were performed using snorkeling techniques (Northcote & Wilke 1963, Helfman 1983). A team (consisting of a diver and a note taker) moved upstream with the diver reporting species and numbers from each channel unit and the note-taker collecting additional data on physical habitat factors. As fish of different life stages are known to occupy different ecological niches (Polis 1984, Werner & Gilliam 1984), we recorded size classes of each species separately. Spatially continuous data on summertime fish distributions were obtained August 4-9, 1998 and again July 19-23, 1999 through extensive snorkel surveys along the length of the Wenaha River from its 3$^{rd}$ order headwaters to its confluence with the Grande Ronde River (Figure 6). In order to gain added perspective on the fish assemblage of the headwaters, during August of 1999 we surveyed four additional sites along the South Fork of the

Figure 5. Schematic illustrating the multiple methods and sampling approaches that were applied to gain the most thorough perspective on fish movement and assemblage dynamics.



Aerial surveys

Underwater surveys

Radio telemetry

Extensive and intensive fish and habitat surveys
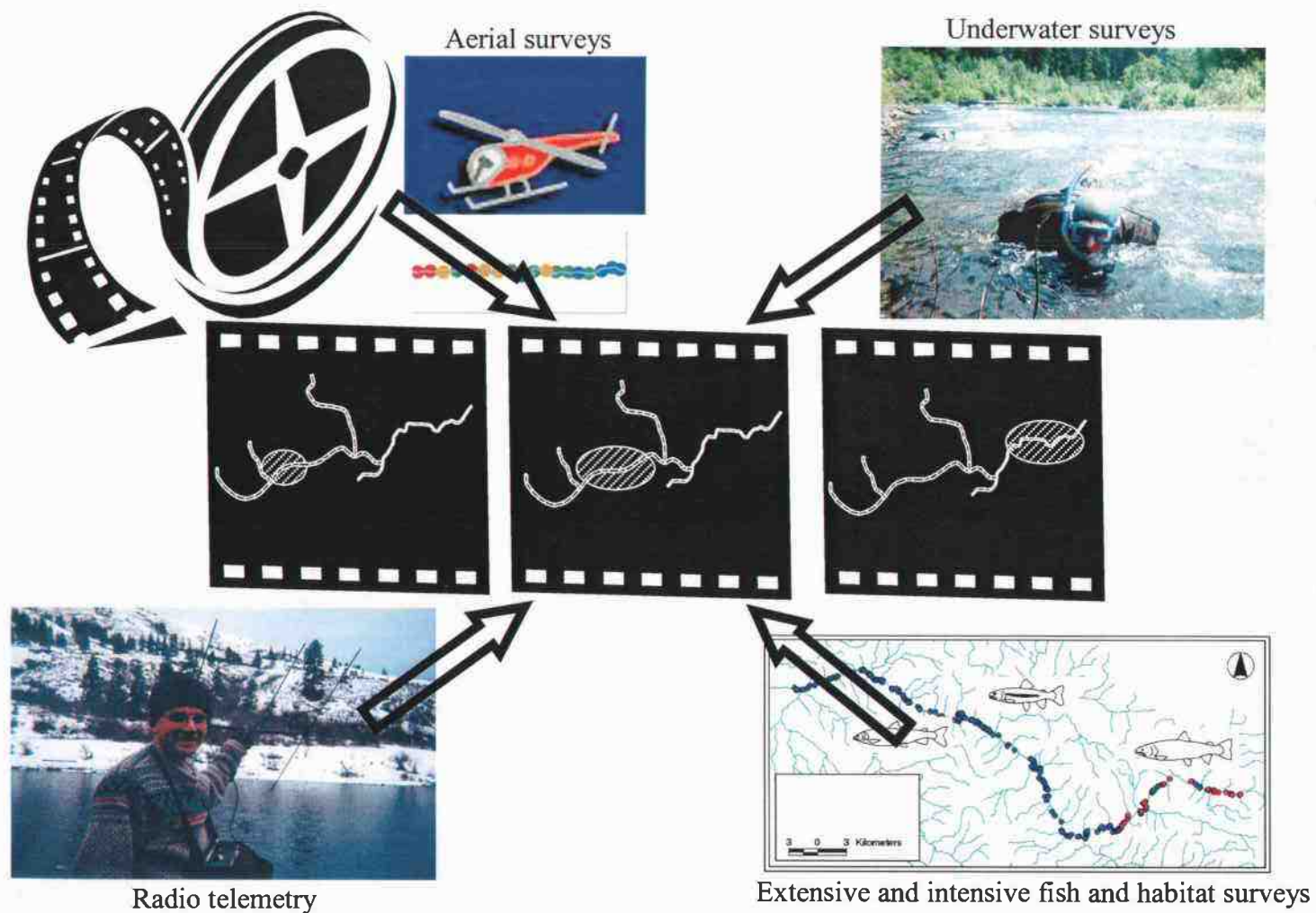
Figure 6. Map showing summer extensive survey (closed dots) and sites selected for repeated intensive surveys (ends of each reach delineated by red flags), 1998-2000.
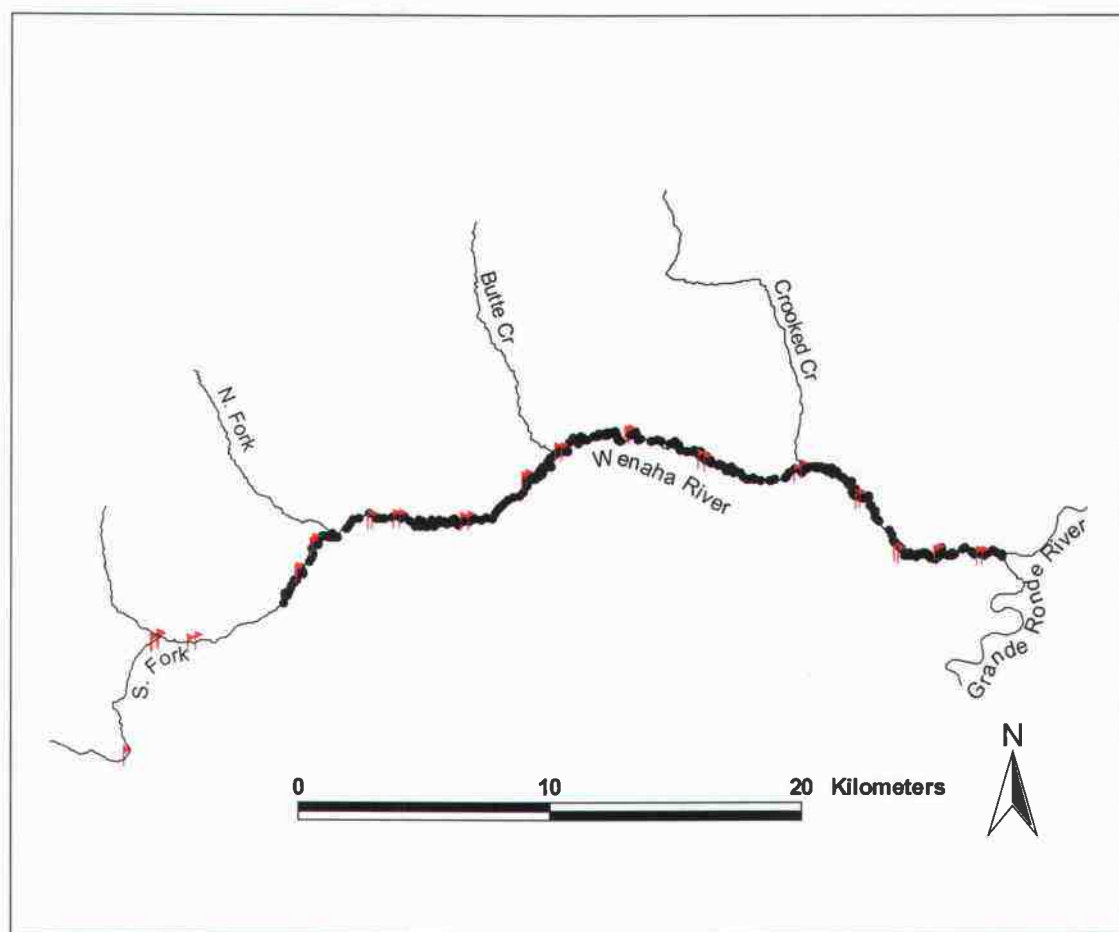
Wenaha; two were 3$^{rd}$ order, one was 2$^{nd}$ order, and one (just below Timothy Springs) was 1$^{st}$ order. The summer extensive survey data and a valley segment classification of the drainage (Frissell et al. 1986) were utilized to stratify the basin and select 13 reaches (200-300m length) (Figure 6) that were deemed representative of the large-scale habitat and fish assemblage variation in the main-stem Wenaha River. These sites (referred to as "intensive sites") were then sampled repeatedly over a two-year period on a monthly to bi-monthly basis. Some longer intervals resulted at some sites due to difficulties with access during winter and high flows in early spring months. In order to detect diel shifts in assemblage structure, a subset of at least three sites (upper, middle, and lower basin) were snorkeled both in the day and at night during each sampling period. Though the Wenaha was too large a stream for us to operate a two-way weir, I found that frequent surveys (weekly and even daily in some cases) of the most downstream site in the drainage during times of the most dramatic change in assemblage structure yielded a more continuous perspective on seasonal movements of fish in and out of the Wenaha River. Finally, though it was not the focus of this work, throughout the study period we collected observations on feeding behavior and the location and timing of spawning by fish species using the Wenaha River (data on salmon and bull trout spawning were collected by ODFW biologists). These observations were meant to aid in the interpretation of species movements and assemblage dynamics, and to provide the basis for further hypothesis generation.

## 2.6    Analysis: Underwater Survey Data

Spatial and temporal patterns in species distribution and fish assemblage structure were assessed directly through use of a geographical information system (GIS) and indirectly through multivariate ordination techniques and non-parametric statistical tests. Fish assemblage data were entered for organization and data analysis into a geographical information system (ArcView GIS v. 3.2), using the stream network (1:100,000) as a

template. Assemblage data were then compiled into matrices for entry into PC-ORD, a multivariate statistical software package (McCune & Mefford 1999).

I used several techniques to search for, quantify and graphically depict assemblage level patterns. I used non-metric multi-dimensional scaling (NMDS) in PC-ORD to generate ordinations of fish assemblage structure and explore patterns of similarity and difference between sites and between survey times based on the relative abundance of fish species. I chose to use NMDS because it is robust to violations of normality and other characters of complex ecological community data sets (Clarke 1993). Due to the inefficiency of daytime snorkel surveys during winter months (see section below), only night survey data were included in our assemblage analyses for winter months. In addition, due to high variation in sampling efficiency for young-of-the-year suckers and dace (whose summer numbers were often so high that they eclipsed the abundance of any other species and were not easily assessed by snorkeling techniques) and benthic species (that were difficult to assess by snorkeling due to their cryptic behavior), dace (*Rhynichthys* sp.), sculpins (*Cottus* sp.) and larval largescale suckers (*Catostomus macrocheilus*) were excluded from the fish assemblage ordination analysis. Finally, to reduce the influence of rare species on ordination solutions, I excluded those species that were present in fewer than 5% of the site-time combinations (Gauch 1982).

The data from our summer extensive surveys were analyzed directly through use of the GIS, and indirectly through use of ordination. I compiled matrices for both the 1998 and 1999 summer extensive survey data and examined them for fish assemblage gradients via NMDS ordination. The 1998 extensive survey data were analyzed for reach-scale patterns in faunal similarity, and I made an effort to encompass these patterns, along with valley segment scale habitat variation (see below), in my selection of sites for repeated, intensive surveys. For the purpose of comparing the patterns detected via summer intensive site surveys vs. those detected via the summer extensive surveys, I pooled the extensive survey data points (channel units) into 3 km bins (roughly the spacing of the intensive survey sites) for analysis.

Using the repeated intensive survey data, I compiled two different fish assemblage matrices, a monthly and a seasonal matrix. For the monthly matrix, I combined survey

data of raw fish counts to generate mean estimates of the assemblage structure for each site during each month. Due to the lack of night surveys at some sites during some winter months, only 8 of the 13 sites were included in this monthly matrix. For the seasonal matrix, I combined data to generate mean estimates of the assemblage structure for all of the 13 sites during each of the four seasons. Based on the general patterns of seasonal discharge and flow, seasons were defined as: spring (March 1-June 15), summer (June 15-September 15), fall (September 15-October 31) and winter (November 1-February 28). Summary statistics were calculated for each matrix to help assess the need for relativization, and the data were screened for multivariate outliers. Subsequently, I performed NMDS ordinations on data relativized by site totals (this transformation places all sites on equal footing). Overlays (Pearson correlations) of individual species relative abundance helped determine which species contributed most strongly to the assemblage gradients described in each ordination. Similarly, overlays of site position (rkm) provided a means of assessing which assemblage gradients were associated with the longitudinal profile, while overlays of survey year on ordinations of site-month combinations allowed us to evaluate the inter-annual variation in assemblage dynamics.

To quantify the similarity of the fish assemblage between survey times, and between survey sites during a given survey period, I used Schoener's Proportional Similarity Index (PSI) (Schoener 1970):

$$PSI = 1 - \frac{1}{2} \sum |P_{ij} - P_{ik}|$$

Where $P_{ij}$ = the proportion of individuals of species i in sample j, and $P_{ik}$ = the proportion of individuals of species i in sample k. PSI values range from 0 (when no taxa are shared between samples) to 1 (when all taxa are of equal importance between samples). To characterize faunal similarity over time at each site, we calculated PSI for each site over all months and seasons sampled. To characterize between-site faunal similarity, I calculated PSI for all possible combinations of sites during each month and season.

## 2.7    *Assessing the Precision and Accuracy of Underwater Surveys*

Underwater surveys via snorkeling are considered a reliable standard technique for assessing patterns in stream fish distribution (Helfman 1983).  Though researchers generally apply standardized protocols for sampling, snorkeling techniques are still evolving, and there has been relatively little assessment of how factors such as stream character, survey conditions (e.g., visibility), and survey timing may influence the reliability of data gathered using this approach.  Furthermore, there is some evidence that snorkeling efficiency varies among different species.  For example, snorkel surveys in coastal streams of Oregon have been shown to be reliable for population estimation of juvenile coho and chinook salmon, but only useful for detecting trends in the abundance of trout (Jeff Rodgers, ODFW, Corvallis, personal communication).  Though several studies have identified the need to assess efficiency and precision (Northcote & Wilke 1963, Cunjak et al. 1988), few studies utilizing the method have done so.  I wanted to assess the accuracy and precision of the snorkel survey technique used in this study.  Of course, a somewhat circular indication of the reliability of the method was evident from the results of this study.  If patterns detected using this technique were simply an artifact of sampling variability or inefficiency, I would not expect to have detected ecologically intuitive or meaningful relationships in our analyses using this information.  As I did detect what appeared to be meaningful patterns and associations, this suggests that the data were relatively accurate.  However, I felt it was necessary to collect this additional information in order to provide for a more objective assessment of the technique and to aid in decisions and interpretations regarding the significance of observed patterns in fish distribution.

To gauge the precision of our surveys, we performed repeated surveys of the same site during the course of a day.  We did these repeated dives at several sites along the length of the river during the summer, and again in the winter.  Due to logistical, legal and ethical constraints (i.e., regulations associated with endangered species protection), we were unable to carry out surveys in the Wenaha River using alternative sampling techniques (e.g., backpack electro-shocking, electric seining, or rotenone) that might have

provided estimates of the efficiency and accuracy of our snorkeling counts. Even had they been possible, it is unlikely that any of the electro-shocking techniques would have yielded more accurate estimates due to the size and velocity of the river which prevented block-netting of the channel. However, I felt that one way to assess the accuracy of the technique was to compare the relative abundance estimates from day dives with those from night dives. In the course of performing over 180 intensive reach dives of this river, we found that diving at night almost always resulted in observation of more individuals of most species, thus we felt they could be used a kind of check as to the efficiency of day-time surveys. In addition, as diving conditions and fish assemblage patterns varied most dramatically between summer and winter, we repeated these comparisons in both seasons.

During the summers of '98 and '99, four sites (distributed from upstream to downstream) were each surveyed 3-4 times within one day on an approximately 4hr interval. During the winters of '98 and '99, three sites (distributed from upstream to downstream) were each surveyed 3 times in the same manner. The surveys were done by the same observer and under similar visibility conditions (> 7 m for summer surveys and > 5 m for winter surveys). There was no evidence of fish behavior observed that indicated any significant migration out of these reaches as a result of the surveyor's presence. The coefficient of variation was calculated for each species for each site. Fish assemblage composition changes significantly from upstream to down in the Wenaha River. By doing repeat surveys at sites along the longitudinal profile, we were able to include, for most species, locations where they were abundant and where they were rare.

During the summers of '98 and '99, seven sites (distributed from upstream to downstream) were each surveyed in both the day and the night within one 24hr period. During the winters of '98 and '99, three sites (distributed from upstream to downstream) were each surveyed in the same manner. As in the case of the daily repeat sampling, the surveys were done by the same observer and under similar water-clarity conditions. Again, the coefficient of variation (COV) was calculated for each species for each site. At four of the seven sites we had collected multiple daytime dives, but the mean daytime values were used for the purposes of this comparison. As in the daily comparisons, we

calculated a mean coefficient of variation for each species in cases where that species was common as well as for reaches where it was rare.

I wanted to assess the precision and accuracy of the technique with respect to estimated relative abundance as well as absolute abundance. For each site survey, I calculated the relative abundance of each fish species. I then calculated all of the same COV's that were obtained using the absolute values and made the same comparisons between repeated daily surveys and day-night surveys during summer and winter.

Repeated surveys during the daytime showed that survey precision was somewhat greater for assessing relative abundance than for assessing absolute abundance (compare Tables 1 and 2). Precision of absolute and relative abundance estimates between daytime dives was similar in summer and winter. As expected, however, COV's for abundance and relative abundance among repeated dives were significantly higher for benthic species (i.e., sculpin, dace) than for mid-water column fishes. In addition, the precision of relative or absolute abundance estimates for a species was higher when it was abundant than when it was rare. Though fewer species were present in the river in winter and the physical conditions for snorkeling were much more challenging, there appeared to be little difference in daytime survey precision between seasons. The lower precision for rare species among winter vs. summer day dives was due to the fact that total numbers of fish observed were much lower in winter.

We almost always observed more fish of every species during night vs. day dives. This was especially true during winter surveys. Importantly, while estimates of relative abundance did not differ significantly between day and night dives during the summer, they did vary substantially between day and night dives in winter (Table 2). For example, the COV for relative abundance estimates of juvenile chinook salmon between summer day and night dives was 18.3, while it was 115.9 between day and night surveys during winter. Consequently, though snorkel surveys appeared to yield reasonable estimates of relative abundance for most species during late spring, summer and fall, winter daytime snorkel surveys did not yield reliable estimates of species relative abundance.

Table 1. Mean coefficients of variation in absolute abundance of fish species observed during repeated snorkel surveys of sites in the Wenaha River. If the species was not present in an abundance category, "na" was reported.

| Season | Comparison | Survey Design | Abundance | CHj | Cha | RBTj | RBTa | MWj | MWa | BTj | Bta | LSSj | LSSa | NPMa | Psa | Tsa | SCj | LNDa | SPDa | RBTy |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| summer | day-day | 4 sites/4 repeats | common | 9.9 | na | 16.4 | 11.6 | 16.9 | 34.4 | na | 34.8 | na | 11.5 | na | 44.9 | 91.1 | na | na | na | na |
| summer | day-day | 4 sites/4 repeats | rare | na | 115.5 | na | na | 92.7 | 86.6 | 173.2 | 76.6 | 200.0 | 200.0 | na | 81.6 | na | 115.5 | 76.6 | 105.2 | na |
| summer | day-night | 7 sites/diel pair | common | 18.3 | na | 24.1 | 13.7 | 51.2 | 29.9 | na | 33.7 | na | 16.8 | na | na | na | na | na | na | na |
| summer | day-night | 7 sites/diel pair | rare | na | 141.4 | na | na | 141.4 | 141.4 | 141.4 | 106.1 | 130.5 | 141.4 | 141.4 | 74.3 | 130.0 | 44.3 | 120.6 | 88.1 | 33.5 |
| winter | day-day | 3 sites/3 repeats | common | 7.8 | na | na | 19.3 | na | 17.5 | na | na | na | na | na | 43.9 | 34.6 | 24.7 | na | na | na |
| winter | day-day | 3 sites/3 repeats | rare | 40.1 | na | 56 | 91.65 | na | na | na | 83.7 | na | na | na | na | na | na | na | na | na |
| winter | day-night | 3 sites/diel pair | common | 97.2 | na | 132.4 | 105.8 | 141.4 | na | na | na | na | na | na | 47.5 | 130.9 | na | na | na | na |
| winter | day-night | 3 sites/diel pair | rare | na | na | na | na | na | 75.9 | 141.4 | 80.8 | na | na | na | na | na | 141.4 | 141.4 | na | na |

* j = juvenile, a = adult, y = young of year, ch = chinook salmon, rbt = rainbow trout, mw = mountain whitefish, bt = bull trout, lss = largescale sucker npm = northern pikeminnow, ps = piute sculpin, ts = torrent sculpin, lnd = longnose dace, spd = speckled dace

Table 2. Mean coefficients of variation in relative abundance of fish species observed during repeated snorkel surveys of sites in the Wenaha River. If the species was not present in an abundance category, "na" was reported.

| Season | Comparison | Survey Design | Abundance | CHj | Cha | RBTj | RBTa | MWj | MWa | BTj | Bta | LSSj | LSSa | NPMa | Psa | Tsa | SCj | LNDa | SPDa | RBTy |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| summer | day-day | 4 sites/4 repeats | common | 6.1 | na | 12.3 | 6.5 | 8.5 | 33.8 | na | 35.7 | na | 2.6 | na | 44.5 | 80.1 | na | na | na | na |
| summer | day-day | 4 sites/4 repeats | rare | na | 115.8 | na | na | 90.1 | 89.2 | 173.2 | 78.3 | 200.0 | 200.0 | na | 82.3 | na | 115.5 | 115.8 | 127.3 | na |
| summer | day-night | 7 sites/diel pair | common | 11.7 | na | 19.5 | 7.9 | 41.3 | 34.9 | na | 33.9 | na | 27.2 | na | na | na | na | na | na | na |
| summer | day-night | 7 sites/diel pair | rare | na | 151.8 | na | na | 167.0 | 167.0 | 167.0 | 110.0 | 114.9 | 169.8 | 130.9 | 72.3 | 118.5 | 45.9 | 106.0 | 108.0 | 42.8 |
| winter | day-day | 3 sites/3 repeats | common | 1.4 | na | na | 18.4 | na | 29.0 | na | na | na | na | na | 37.4 | 65.5 | 9.5 | na | na | na |
| winter | day-day | 3 sites/3 repeats | rare | 43.6 | na | 52.0 | 141.4 | na | na | na | 23.0 | na | na | na | na | na | na | na | na | na |
| winter | day-night | 3 sites/diel pair | common | 115.9 | na | 251.9 | 285.7 | 141.4 | na | na | na | na | na | na | 323.1 | 8.8 | na | na | na | na |
| winter | day-night | 3 sites/diel pair | rare | na | na | na | na | na | 340.1 | 141.4 | 198.6 | na | na | na | na | na | 141.4 | 282.8 | na | na |

* j = juvenile, a = adult, y = young of year, ch = chinook salmon, rbt = rainbow trout, mw = mountain whitefish, bt = bull trout, lss = largescale sucker
npm = northern pikeminnow, ps = piute sculpin, ts = torrent sculpin, lnd = longnose dace, spd = speckled dace

During winter only night surveys appeared to be useful, and due to logistical and safety concerns, we were able to accomplish only a subset of our study sites at night (2 from upper, 2 middle and 3 from lower Wenaha) during the winter months (November-February). Further limiting our underwater survey technique was the fact that habitats in the Wenaha River during high flow months (typically April and May) and all waters downstream of the Wenaha River were impossible to sample through snorkeling due to high flows and turbidity.

There are several possible factors that could have contributed to the variation among repeat day dives and the differences between day and night dives. The differences we observed in relative and absolute abundance between winter days and nights appeared to be due primarily to the more cryptic behavior of most fish species during this season. On winter days we only observed the largest-bodied fish holding in the mid-water column or out in the open of the channel where they would be most visible. In fact, by digging in the streambed we routinely found fishes hiding in the crevices between rocks or in amongst woody debris. As soon as it was night, we observed a dramatic movement of these fish into open water areas of the main channel, and often into slack-water, side channels, or alcoves. Variation between day and night dives in summer was probably also influenced by fish hiding during the daylight hours, though this was not as dramatic as in winter. Some fishes, particular the smaller individuals, appeared to be seen easier at night as the dive light shining on them created a higher level of contrast, making them stand out for easier counting. Finally, the diel movements of fish between the times of dive surveys could also be an important factor influencing the variation we observed.

Underwater surveys generally appeared to provide reliable estimates of species relative abundance and insight into fish assemblage dynamics in the Wenaha River. However, uncertainty regarding the extent of movement, the lack of underwater surveys during high flow periods, the unreliable nature of daytime surveys in winter, and the lack of underwater surveys in the Grande Ronde River made it clear to me that this technique was not sufficient in itself to glimpse the full range of these dynamics or assess the movements of fishes.

## 2.8    Field Methods:  Radio Tracking of Individual Fish

Because of the "blind-spots" inherent in the application of underwater surveys, and because I wanted to directly assess movement by following individual fish, I chose to complement the perspective gained from snorkeling by applying radio telemetry techniques.  As I was interested in movements by all species in the fish assemblage but could not track them all due to logistical limitations, I chose to track those species whose movements were least understood.  Information exists for this basin on migrations by adult chinook salmon (Price 1998, B. McIntosh and H. Li, unpublished data) and steelhead, patterns of juvenile chinook salmon and steelhead out-migration (Keefe et al. 1996), movements of resident rainbow trout (in the Salmon River, another tributary of the Snake basin) (Bjornn & Mallett 1964) and northern pikeminnow *Ptychocheilus oregonensis* (James Petersen, U.S.G.S., Columbia River Research Lab, Cook, Washington, personal communication).  In contrast, very little is known about three of the most abundant native species in the system; largescale suckers *Catostomus macrocheilus*, mountain whitefish *Prosopium williamsoni*, and bull trout *Salvelinus confluentus*.  The bull trout is a native char that has recently attracted increased research attention since it was listed as a threatened species.  However, little information exists on their life history and ecology in this basin, despite the fact that the bull trout population associated with the Wenaha drainage is considered one of the healthiest in the lower 48 United States (Buchanan et al. 1997).  The mountain whitefish is one of the most common species in rivers of the Pacific Northwest, and yet its basic ecology and life history is poorly understood (Northcote & Ennis 1994).  Finally, the largescale sucker is often the most abundant native fish in rivers of this region and it undoubtedly plays important ecological roles, yet its basic life history is also largely unknown (Wydoski & Whitney 1979).

In the spring of 1999, we tagged 25 adult mountain whitefish and 25 adult largescale suckers from sites along the length of the Wenaha River.  To track adult bull trout, we

cooperated with Oregon Department of Fish and Wildlife researchers who, as a part of
an on-going study, radio-tagged bull trout in the Wenaha River in the summers of 1997,
1998 and 1999 (see also Hemmingsen et al. 2001). For the purposes of this study, we
tracked only those fish tagged in 1999, and fish tagged in earlier years whose tags were
still transmitting and were confirmed as living. Consequently, we tracked 4 fish tagged
in 1997, 11 fish tagged in 1998, and 13 that were tagged in 1999. We tagged suckers and
whitefish from throughout their range in the drainage, while we also attempted to tag a
number proportional to their abundance in different reaches. The bull trout were also
tagged from throughout their range in the Wenaha River, however tagging in 1997 and
1998 focused on large adults (mean FL = 49 cm) while smaller adult and/or subadult fish
(mean FL = 34 cm) were tagged in 1999. It was hypothesized that the different size
classes might represent either 1) different life history types, or 2) distinct life stages that
might exhibit movement patterns different from the largest adults. Angling (with barb-
less lures and artificial flies) was used to capture the mountain whitefish and bull trout
that were to be tagged, while largescale suckers were all captured via snorkeling with a 1
m diameter dip net. There were no mortalities during capture or tagging of fish.
However, fish that appeared overly stressed by the capture or appeared to be in poor
condition were released without tagging. This was rare for mountain whitefish or bull
trout, but more common with the suckers, which were being tagged immediately
following their spawning season. All surgeries were performed within 10 minutes of
capture.

Immediately following capture, each fish was anesthetized (a solution of clove oil
was used for whitefish and suckers, and MS-222 for bull trout) in a tub equipped with
aerators, and length and condition factors were noted. The presence of nuptial tubercles
and a larger anal fin in males (Dauble 1986) allowed us to differentiate the sexes among
largescale suckers that were tagged, though this was not possible for the other species.
Fish were removed from the anesthesia solution when they could no longer stay upright
or did not respond to being touched. For surgery, a fish was placed on a v-shaped
operating cradle covered with neoprene. During surgery, an assistant using a turkey
baster bathed the fish's gills with anesthesia solution. This assistant carefully monitored

the respiration of the fish and the progress of the surgery. At any signs of respiratory distress, or when the end of the surgery was approaching, the assistant began bathing the fish's gills with plain aerated water.

To implant a transmitter, a 2 cm incision was made anterior of the pelvic girdle and slightly to the side of the mid-line of the ventral surface. A hollow needle was then used to puncture a small hole immediately posterior of the pelvic girdle; internal organs were protected from the needle by a plastic shield tube held from the incision. The end of the antenna was placed in the hollow needle and the needle withdrawn, threading the antenna through the hole. The transmitter was then placed in the coelom on the pelvic girdle. Two to four non-absorbable synthetic sutures and a thin layer of veterinary glue were used to close the incision, and a topical antibiotic was applied after the glue had dried. Surgeries lasted for an average of 6 minutes (range 4-10 minutes). After surgery, fish were held in river water until equilibrium was recovered, then released. The entire surgery set-up was cleaned after each fish and sterilized prior to its next use. The transmitters emitted signals at 148-151 MHz, were active for a year, weighed 7 g each, and did not exceed 2 % of weight for any tagged fish (Winter 1983).

After tagging, the movements of each fish were then tracked at nested spatial and temporal scales, from ground and air, over the following year. Tagged fish locations were determined at multiple spatial and temporal resolutions. Coarse-resolution ($\pm$ 400-600 m) aerial surveys were performed roughly every month via a plane equipped with antennae and a g.p.s. unit. These surveys allowed the reach-scale location of a fish to be determined. Higher resolution ($\pm$ 5-10 m) surveys were conducted from the ground using a backpack-portable, 3-element Yagi antenna. In some areas of the lower Grande Ronde and Snake rivers that were accessible by road we also used a truck-top whip antenna to find fish from the road, and subsequently used the hand-held Yagi antenna to get a more accurate location. The higher resolution surveys were conducted monthly and allowed the channel unit-scale (e.g., pool, riffle) location of a fish to be determined. During these surveys, habitat maps were constructed for the area where each fish was located. The highest resolution ($\pm$ 2-4 m) surveys we performed involved triangulation using the hand-held Yagi antenna. Locations of this resolution were obtained on a subset of fish during

each month, and sampling at this micro-habitat scale was usually combined with intensive tracking of diel movements and detailed mapping of habitat within the channel unit(s) occupied by the fish. These methods were applied for tracking of all tagged largescale suckers and mountain whitefish. As described, the seasonal movements of 28 adult bull trout were monitored through cooperation with ODFW researchers. During the period from spring 1998 to spring 1999, only aerial surveys were used to track 15 of these bull trout whose tags were transmitting signals during this period. From spring 1999 (when 13 additional fish were tagged) to summer 2000, however, the bull trout were tracked according to the same nested-scale protocol as described above.

## 2.9    Analysis: Radio Tracking Data

Spatial and temporal patterns in fish location and movement were assessed directly through use of a geographical information system (GIS). The GIS provided a framework for spatial analysis. A map of locations was created for each radio tracked fish, and descriptive characters of their movement and ranges were calculated at nested temporal scales. The annual range of a fish was calculated from the most upstream location (usually in summer or fall, depending on species), to the winter location furthest downstream (or, in the case of fish that over-wintered in the Grande Ronde upstream of the Wenaha, down and then up), and back to the most upstream location the following year. For the bull trout that were tracked over more than one year, ranges were calculated for each year. Particularly in the case of bull trout that rapidly ascended and descended tributary streams for spawning, these annual range estimates were likely conservative because temporal resolution of tracking was not always sufficient to capture the full range of a fish's movement. For the purposes of analysis, I did not include annual range values for years in which a fish was not tracked throughout the entire year (as was the case in 1999-2000 for some of the fish tagged in 1997 and 1998).

I also calculated the distance moved by each fish during each season, excluding in this calculation any fish-season combinations that did not include at least 2 locations

within the season. Finally, using the fine resolution tracking data, I estimated diel movement for the fish of each species that had been tracked in this fashion during each season. Fish movement was examined for patterns with respect to size, sex (for suckers), and factors associated with tagging (e.g., surgery duration and quality for each fish). Among the tracked fish of each species we observed distinct groups associated with seasonal movement patterns which provided a basis for grouping them for certain additional analyses (see below).

## 2.10    Field Methods: Riverscape Habitat Heterogeneity

We mapped the heterogeneity of habitat within the riverscape at nested spatial and temporal scales. To characterize spatial habitat heterogeneity at large scales, I applied a valley segment classification (Frissell et al. 1986, Frissell 1992, Ebersole 1994) to the length of the Wenaha, Grande Ronde and Snake rivers within our study area. Using ArcView GIS software, digitized topographic quads (1:24,000), digital elevation models (DEM's), and low-elevation video shot from a helicopter, five segment types were delineated based on measures of valley bottom width, stream gradient, the ratio of channel width to floodplain width, and adjacent hill slope gradient. Qualitative ground and aerial field observations aided in classification in instances where segment type was uncertain. Segments (any stream length > 0.5 km) were classified as canyon (C), alluviated canyon (AC), alluvial valley (AV), alluvial fan influenced valley (AFV), and terrace bound valley (TBV) (Figure 7, Table 4).

We quantified habitat variation at small spatial scales as well. During our summer extensive surveys of the Wenaha River stream habitat data collected included classification of each channel unit and its length, mean width, mean and maximum depth.

Figure 7. Representative topographic map sections and air photos depicting valley segment types identified in the study area (map scale 1:8000). Box indicates location of photo.



Alluvial Valley, Wenaha River



Terrace-bound valley, Wenaha River



Alluvial fan-influenced valley, Wenaha River

Figure 7, continued.



Alluviated Canyon, Wenaha River
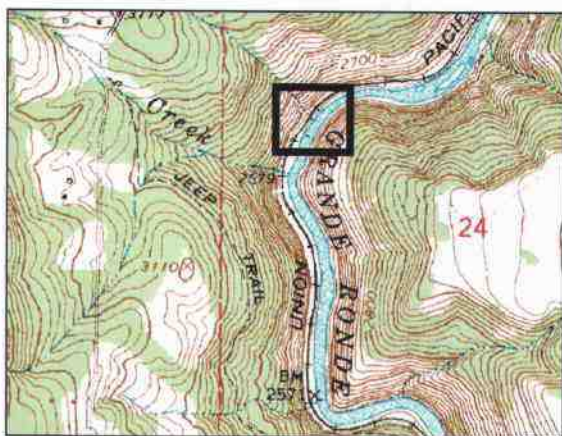


Canyon segment, Grande Ronde River

Table 3. Key characteristics of five valley segment classes in Wenaha, Grande Ronde, Snake Rivers. AV = alluvial valley, AFV = alluvial-fan influenced valley, TBV = terrace bound valley, AC = alluviated canyon, C = canyon, ACW = active channel width. Based on Frissell (1992) and Ebersole (1994).

| Valley segment type | Valley slope | Valley width | Floodplain width | Channel pattern | Geomorphic description |
|---|---|---|---|---|---|
| Alluvial Valley (AV) | mean 1.0% | > 2 x ACW | >2 x ACW | Anastomosed to meandering or sinuous | Broad floodplains; active, unstable channels; local terraces and contact with hillslope |
| Alluvial-fan-influenced valley (AFV) | mean 1.0% | > 3 x ACW | > 3 x ACW | Anastomosed to meandering or sinuous | Complex floodplains influenced by alluvial fan deposits; relict channels and wetlands |
| Terrace-bound valley (TBV) | mean 1.2% | > 2 x ACW | < 2 x ACW | Single channel, meandering or sinuous | Broad valley floor, channel constrained by alluvial terrace, banks consolidated alluvium; local contact with hillslope |
| Alluviated Canyon (AC) | mean 1.3% | 1.2-2 x ACW | 1.2-2 x ACW | Sinuous to straight | Narrow, discontinuous floodplains, bounded by hillslope on alternating sides |
| Canyon (C) | mean 2% | = ACW | = ACW | Sinuous to straight | No floodplain; local alluvial bar deposits; bounded on both sides by hillslope |

We also created detailed habitat maps for each of the sites selected for intensive, repeated underwater surveys. These maps included regularly spaced channel transects measuring depth, velocity, temperature, substrate category, large wood, and percent cover. Changes in habitat characteristics of the site were mapped once each season. Water temperatures were recorded every 15 minutes at a well-mixed location within each site using Optic Stowaway data loggers. A logger also monitored temperature at a site in the lower Grande Ronde River. Though a channel unit survey was not performed on the Grande Ronde or Snake Rivers, a habitat map was constructed wherever a radio-tagged fish was located (from the ground). To aid in assessing thermal habitat heterogeneity, infrared and real color video imagery (Torgersen et al. 2001) were collected along the length of the Wenaha River via helicopter during a typical hot summer afternoon in August of 1998. In conjunction with the data from the loggers, this information was used to assess reach-scale thermal patterns and map locations of potentially important groundwater-influenced habitats such as spring-brooks or alcoves. In addition, in August of 1999 the Oregon Department of Environmental Quality performed a similar infrared video survey of the main-stem Grande Ronde River that provided a thermal profile of this portion of the study area. Daily discharge of the Grande Ronde River was obtained from a USGS gauging station just below the confluence of the Wenaha River at the town of Troy, Oregon.

## 2.11    Analysis: Spatial Habitat Relationships

One of the goals of this study was to assess the relationship between fish movement and processes that depend on the spatial arrangement and composition of habitat features within the riverscape. I expected that fish movement patterns might reflect processes such as habitat complementation, habitat supplemention, source-sink dynamics, and neighborhood or connectivity effects. In particular, I wanted to evaluate whether the nature and extent of movement by fishes was associated with the spatial distribution of similar (i.e., habitat supplementation) and/or non-substitutable habitat resources (i.e.,

complementation). Consequently, patterns of stream habitat were assessed at multiple scales, and, using fish data from both underwater surveys and radio tracking, I characterized associations between fish and habitat variables. In doing so, I paid particular attention to the temporal dynamics of habitat associations. These analyses do not constitute an exhaustive treatment of habitat-use by species in this fish assemblage, but rather serve to 1) point out certain strong associations we observed that might reflect important habitat requirements for some species, 2) to provide a temporal context within which to evaluate fish-habitat relationships detected in any given season, and 3) to explore possible linkages between fish movement and habitat arrangement and composition in the riverscape.

Habitat preferences of radio-tracked fish were assessed at nested scales directly via use of maps in a GIS framework and indirectly via analysis of use vs. availability. For each habitat factor of interest, electivity indices were calculated and compared (White & Garrot 1990). Ivlev's electivity index is a dimensionless number that compares the proportion of a resource used by an animal to the proportion available in a specified area of study (Manly et al. 1993). The index ranges from $-1$ to 1, where negative values suggest avoidance and positive values suggest selection. Simultaneous Bonferroni confidence intervals ($\alpha = 0.05$) were calculated to determine whether preference or avoidance responses were statistically significant (White & Garrot 1990).

A similar technique was applied to assess multi-scale habitat associations and preferences using the fish assemblage data from underwater surveys of the Wenaha River. Direct analysis of maps and longitudinal profiles in the GIS helped me identify habitat patterns associated with fish assemblage structure as well as the distribution of individual species. In addition, using the PC-ORD software and matrices of habitat variables for each sample unit, I explored correlations between habitat factors and gradients in fish assemblage structure that had been derived from NMDS ordinations. Significant associations that were identified were subsequently assessed qualitatively and statistically through use vs. availability analysis as described above.

# CHAPTER 3: RESULTS

### 3.1 Riverscape Heterogeneity at Multiple Scales

Dramatic gradients in habitat character occur in this riverscape. At the drainage scale, there are differences among the Wenaha tributaries, the main-stem Wenaha River, the Grande Ronde River, and the Snake River that reflect the broad range in their sizes ($1^{st}$- $9^{th}$ order), as well as the geologic, physiographic, and climactic transitions from the upper Wenaha to the Snake canyon (see also section 2.1). Potentially important heterogeneity is evident in both relatively fixed (e.g., valley geomorphology) and more dynamic (e.g., temperature, flow) factors. For example, summer temperatures in the Wenaha River are much cooler than those in the Grande Ronde or Snake rivers (Figure 8). A longitudinal temperature profile based on infrared thermal imagery collected by Oregon DEQ in August of 1999 showed that the Wenaha River contributes a plume that cools the Grande Ronde for many kilometers downstream of the confluence (Figure 8). Interestingly, the main-stem Wenaha River is also cooler than most of its major tributaries (Figure 9), such as Rock, Butte, Weller, and Crooked Creeks which are all south-facing sub-basins (see study sites map, Figure 6). Stream temperature patterns were also evident at intermediate spatial scales. Summer temperature in the Wenaha River increases gradually from upstream to downstream reaches (Figure 10). However, in fall this thermal gradient becomes less prominent, in winter it is largely absent, and the gradient is re-established in spring (Figure 10).

Though streams in the study area naturally exhibit a similar discharge regime, there are some interesting departures. Discharge of the lower Grande Ronde River, while it certainly integrates the influences of its entire watershed, is strongly affected by the flow of its primary tributary, the Wallowa River, which enters upstream of the Wenaha. The Wallowa River drains the Eagle Cap Wilderness, a higher elevation area than the Wenaha drainage, and consequently differs from the Wenaha River in its flow regime. This seems to be particularly true during the rising and falling limbs of the annual hydrograph. Consequently, the Wenaha and Grande Ronde flows may be out of synch at times, creating heterogeneity in the local habitat template as a function of precipitation and run off in subbasins of the watershed that are far away. This phenomenon also occurs

Figure 8. Paired mosaics of real color and thermal infrared video frames showing the confluence of the Wenaha (19.9 C) and the Grande Ronde (23.9 C) rivers at Troy, Oregon on August 19, 1999. The Wenaha has a dramatic cooling effect on the Grande Ronde River that extends many kilometers downstream. The Wenaha flows in from the top right of the image and the Grande Ronde River flows from top to bottom of the image. The color legend below corresponds to different temperatures in the thermal image.
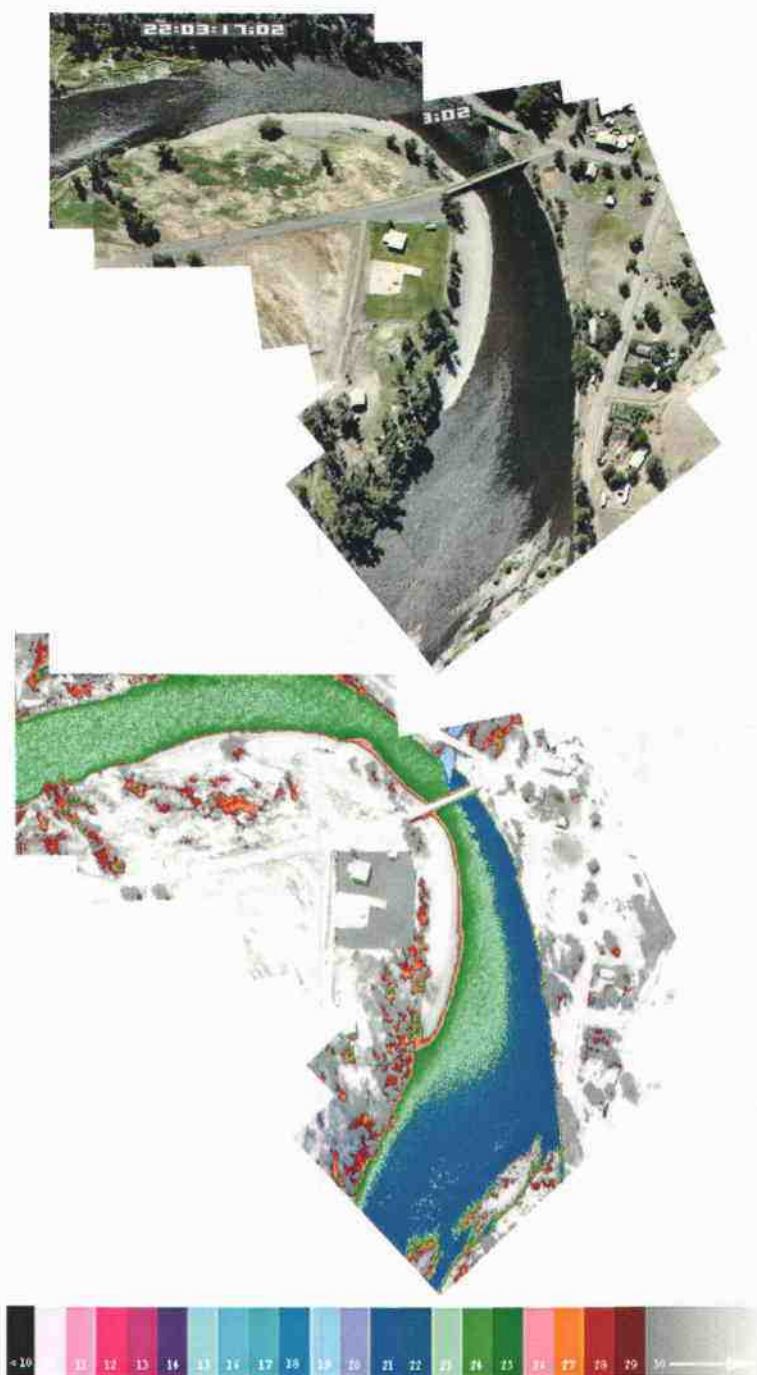
Figure 9. Longitudinal temperature profile of the Wenaha River derived from infrared video imagery shot by helicopter at mid-afternoon on August 9, 1998. The thermal profile is representative of water temperatures on a warm day in mid-summer. Squares represent temperatures of major tributaries at their confluence with the Wenaha River.
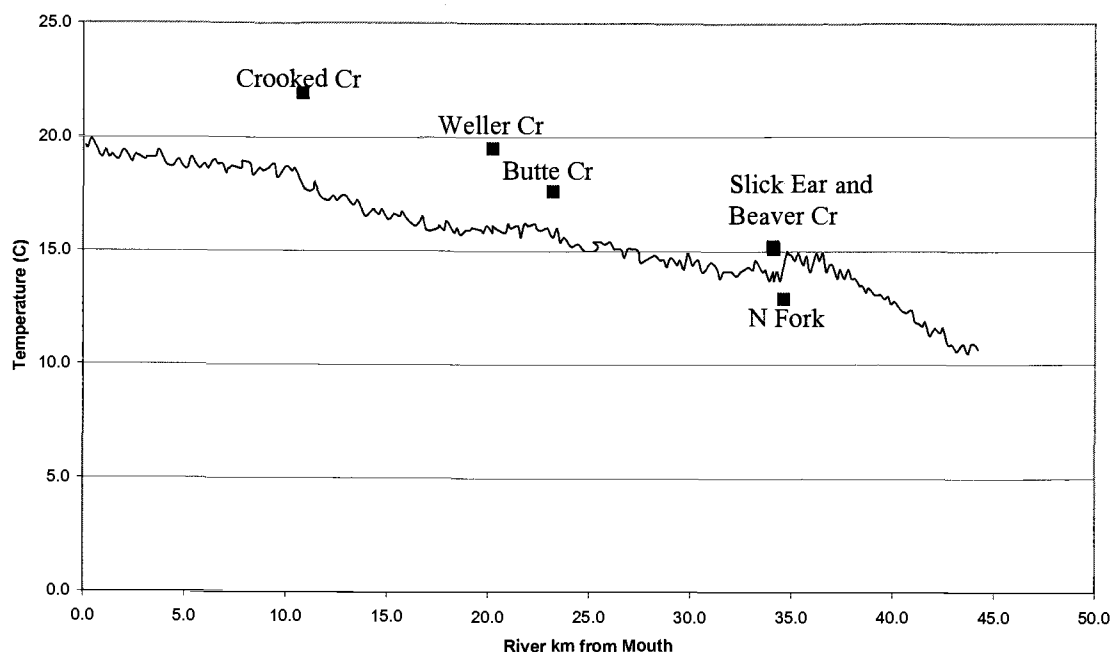
Figure 10. Temperature along the length of the Wenaha River during different times of the year. Profiles describe temperature at 1300 hrs on August 9 1998 (line from FLIR survey), September 15 1998 (diamonds), November 17 1998 (x's), January 10 1999 (triangles), and June 24 1999 (circles).
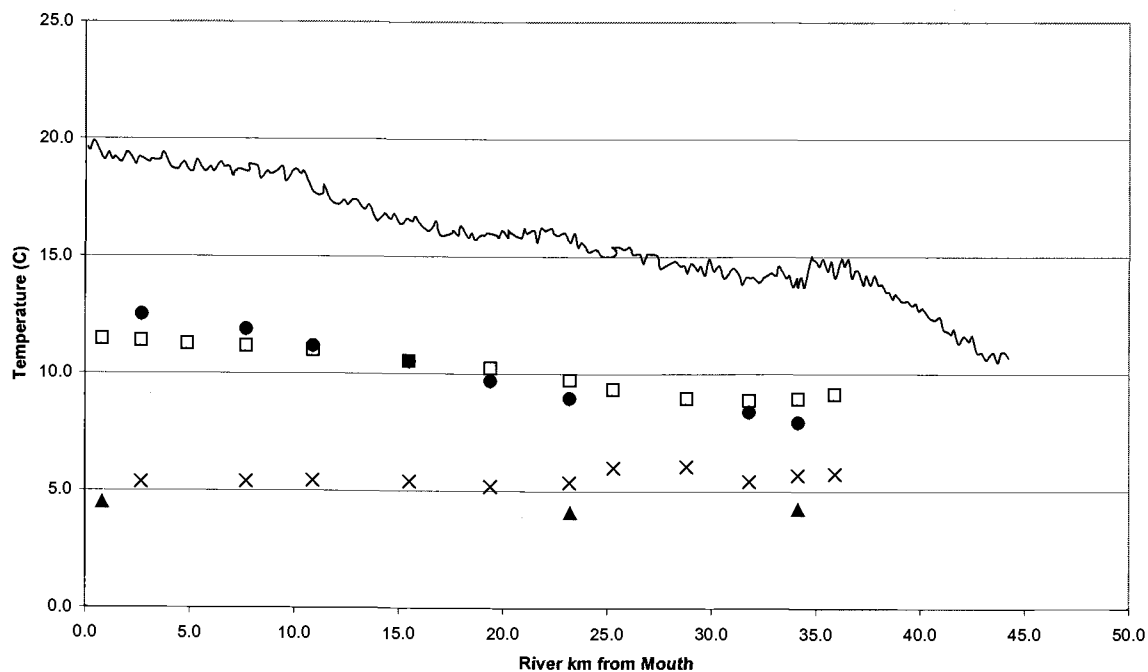
between the Grande Ronde and the Snake River, as the Snake's flow regime is partially regulated by hydropower dams.

These transitions in dynamic as well as relatively fixed habitat factors set the context for the expression of habitat at smaller scales nested within the drainage network. I found that landscape structure transitions between the Wenaha drainage and the lower Grande Ronde and Snake River portions of the study area were reflected in the distribution and extent of valley segment types within the study area (Figure 11). My classification showed the main-stem Snake and lower Grande Ronde portions of the study area were dominated by canyon (58%) and alluviated canyon (46%) segment types. Alluviated canyon and canyon segments were not evenly distributed, but exhibited an aggregated pattern. For example, from rkm 50-75, the Grande Ronde River flows primarily through alluviated canyon segments, while canyon segments dominated sections downstream, and particularly upstream, of this stretch (Figure 11). In contrast, the main-stem Wenaha River was characterized by greater diversity of valley segment types, the most common of which were alluvial valleys (45%), followed by alluviated canyons (21%), alluvial fan-influenced valleys (17%), and terrace-bound valleys (17%) (Figure 12). The distribution of these segment types was less aggregated than was observed for the Grande Ronde-Snake sections, with confined segments typically alternating in occurrence with more unconfined segments. However, a few additional patterns were apparent. Much of the alluviated canyon habitat in the Wenaha River occurs between the Weller Creek and Butte Creek confluences, whereas the majority of the terrace bound valley habitat exists in the most downstream section. Alluvial or alluvial fan valleys were often juxtaposed with terrace bound valley segments in a manner that appeared to reflect sediment supply 'waves' from tributaries.

The valley segment classification demonstrated that habitat features at this large scale were separated into distinct regions in the riverscape. This, in turn, resulted in spatial separation of habitat features at smaller spatial scales. Variation in the spatial extent and arrangement of valley segments in the riverscape had consequences for the distribution of smaller scale habitat features nested with them. Within the Wenaha River the distribution of channel-unit scale habitat features of potential importance to fish were associated with

Figure 11. Map of valley segment types throughout the study area. AV = alluvial valley, AFV = alluvial-fan influenced valley, TBV = terrace bound valley, AC = alluviated canyon, C = canyon.
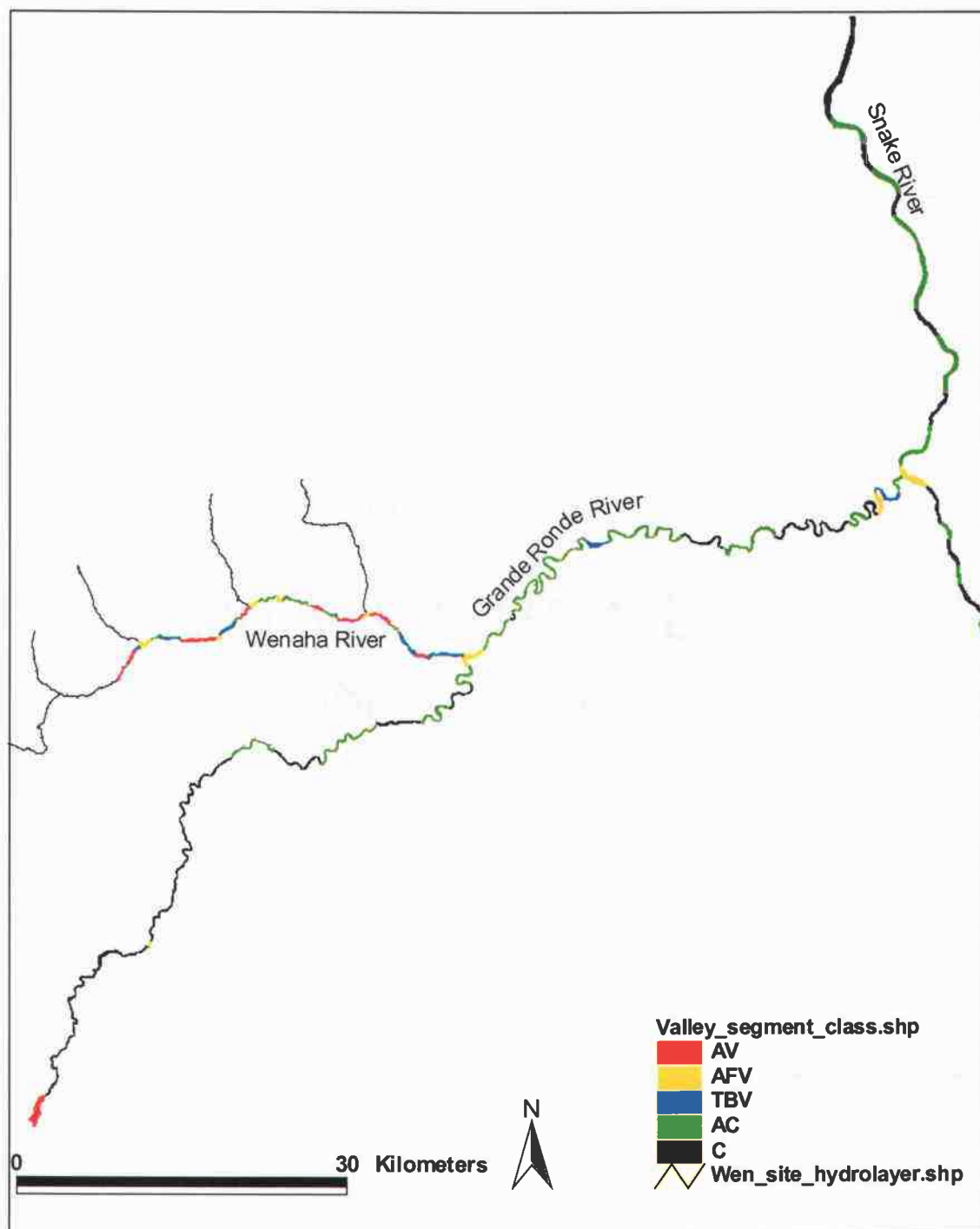
Figure 12. Map of valley segment types along the length of the Wenaha River. Map legend is as in Figure 11.
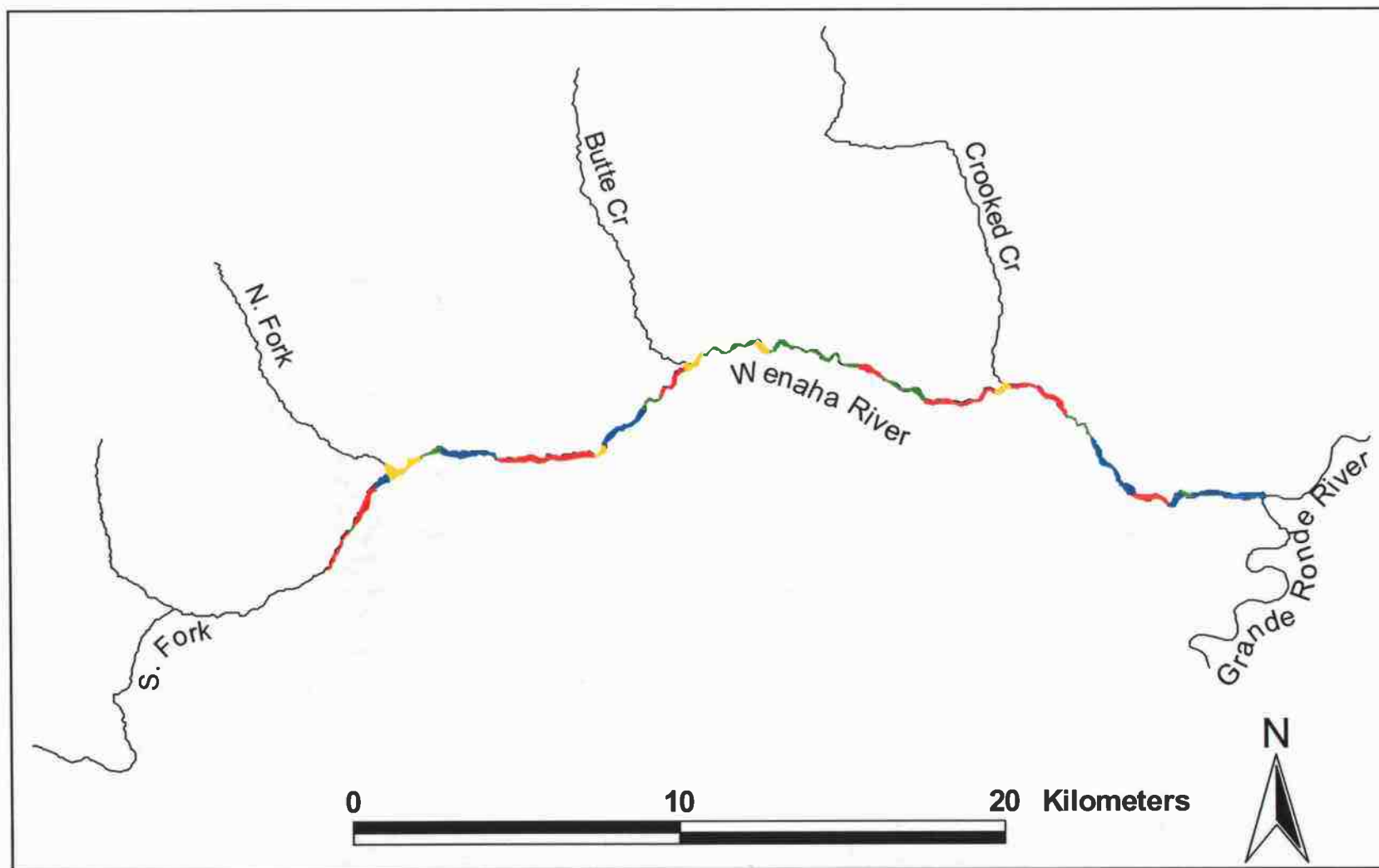
valley segment type. For example, the density of deep pools (> 2.0 m max depth) was significantly greater (Bonferroni confidence interval: $P < 0.05$) in alluviated canyon segments than in other segment types, while the density of long glide-like habitats was greatest in terrace bound valleys (Figure 13). In contrast, the density of side channel and alcove habitat was significantly greater in alluvial valleys than in other segment types (Figures 13 and 14).

We observed thermal heterogeneity at the channel unit scale as well. Habitat units lateral to the main channel, such as alcoves and spring-brooks, often exhibited markedly different thermal characteristics. Thermal differences appeared to be due to the influence of upwelling groundwater and zones of decreased mixing within these habitat types. Both alcove and spring-brook habitats possessed patches of habitat with moderated thermal regimes temperatures that were cooler than the main channel in summer and warmer in winter (Figure 15). Though their highest density was in alluvial valley segments, these groundwater-influenced habitats were present throughout the Wenaha River. In many instances within the lower river segments they were associated with patterns of intragravel flow through large cobble bars and local bedrock knickpoints. However, in alluvial valley segments of the upper drainage they were often observed to occur in association with beaver dam and floodplain wetland areas.

We did not observe any dramatic inter-annual changes in habitat structure or dynamics. Over the time period of the study, the one obvious difference between years was the character of the spring run-off. Flow levels of the Grande Ronde and to a lesser extent the Wenaha River, were significantly higher in June and early July 1999 than in the same period of 1998 or in 2000 (Figure 16). By the end of July 1999, however, flow conditions were relatively similar to the previous year, and assemblage structure was not significantly different between years during any other month surveyed. The difference in early summer flows also corresponded to cooler temperatures in the Wenaha River during summer 1999 than 1998 (Figure 17). Other differences in habitat character between years were of lesser magnitude. Though we monitored our repeated dive sites for dynamics in channel structure and large wood throughout the study period, we observed very little change. We observed no marked channel changes at these sites between years,

Figure 13. Density of deep pools and side channels in different valley segment types along the length of the Wenaha River, adjusted for the length of stream available in each type.
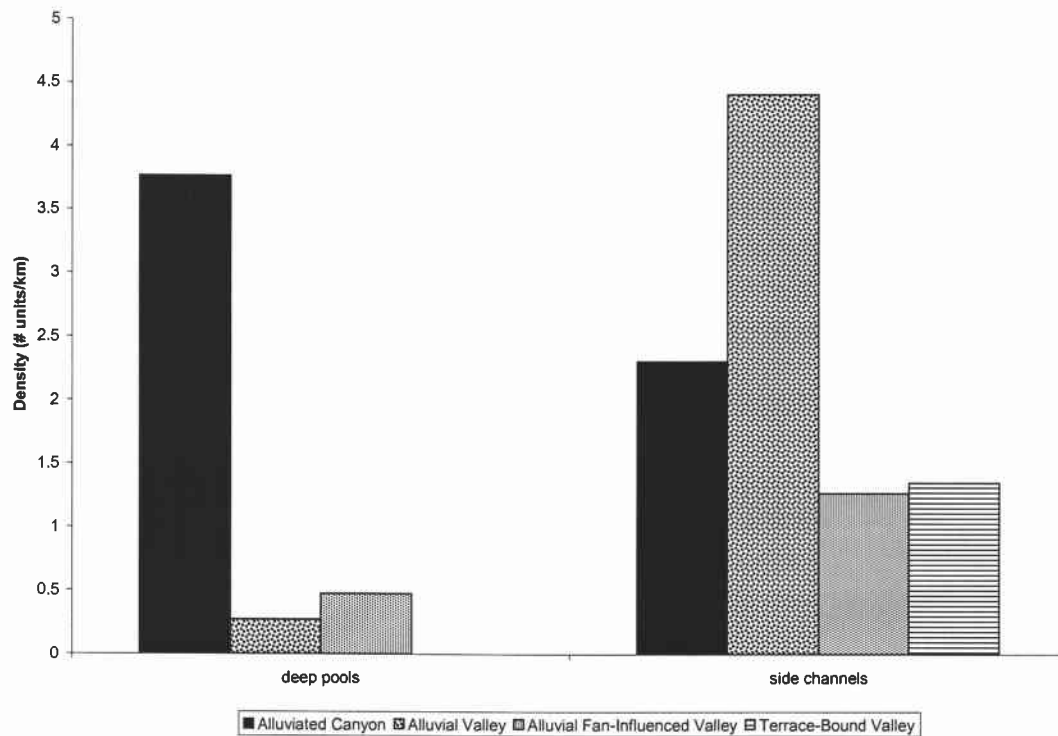
Figure 14. Map of the distribution of deep pools (> 2m max depth, pink dots) in the Wenaha River overlaid on the map of valley segment types, showing the association between deep pools and alluviated canyons. Valley segment legend is as in Figure 11.
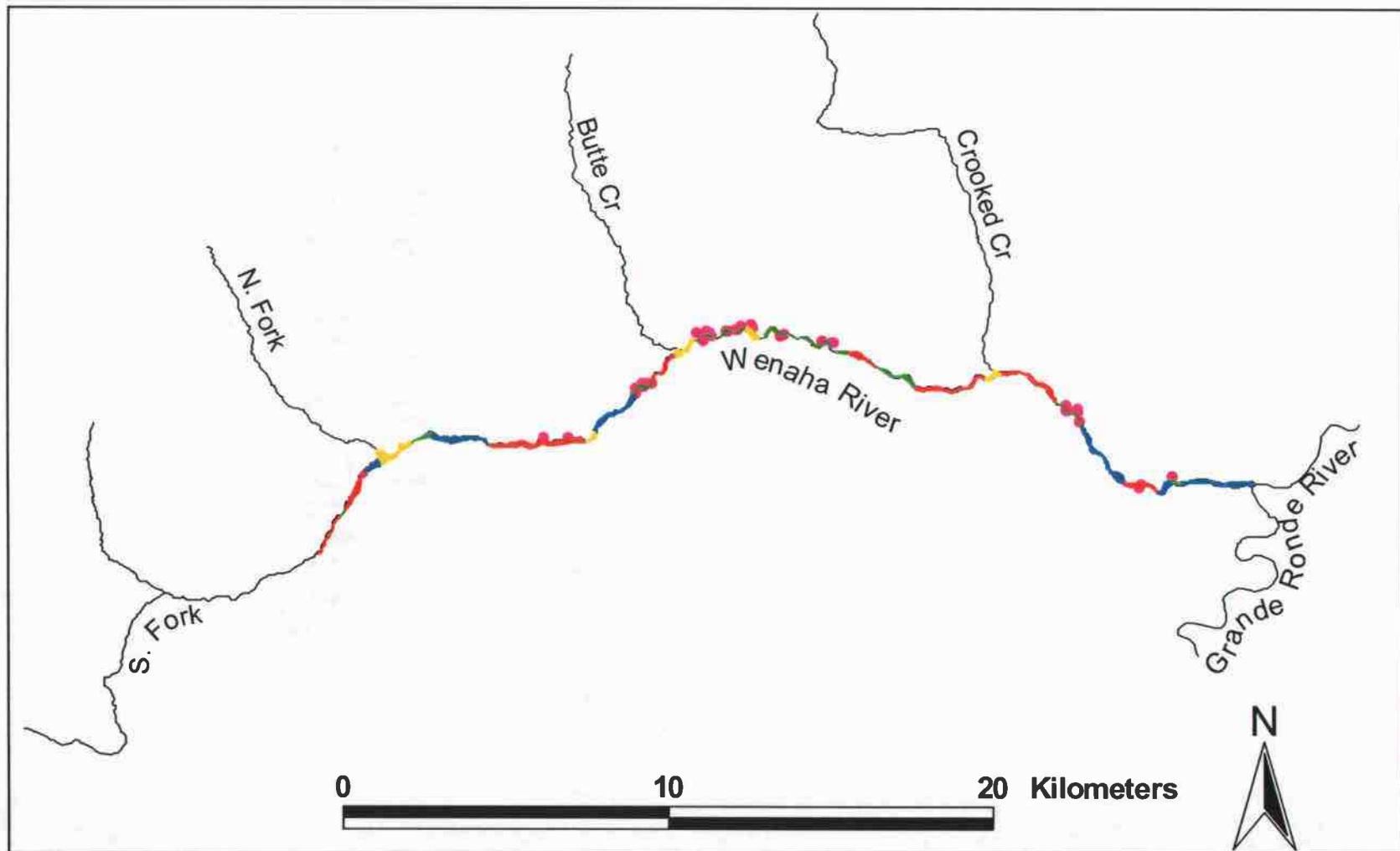
Figure 15. Graphs showing temperature regimes for main channel and alcove habitat over 4 typical summer days and 4 winter days, superimposed on a photo of the same alcove. Note the difference in temperature scales.
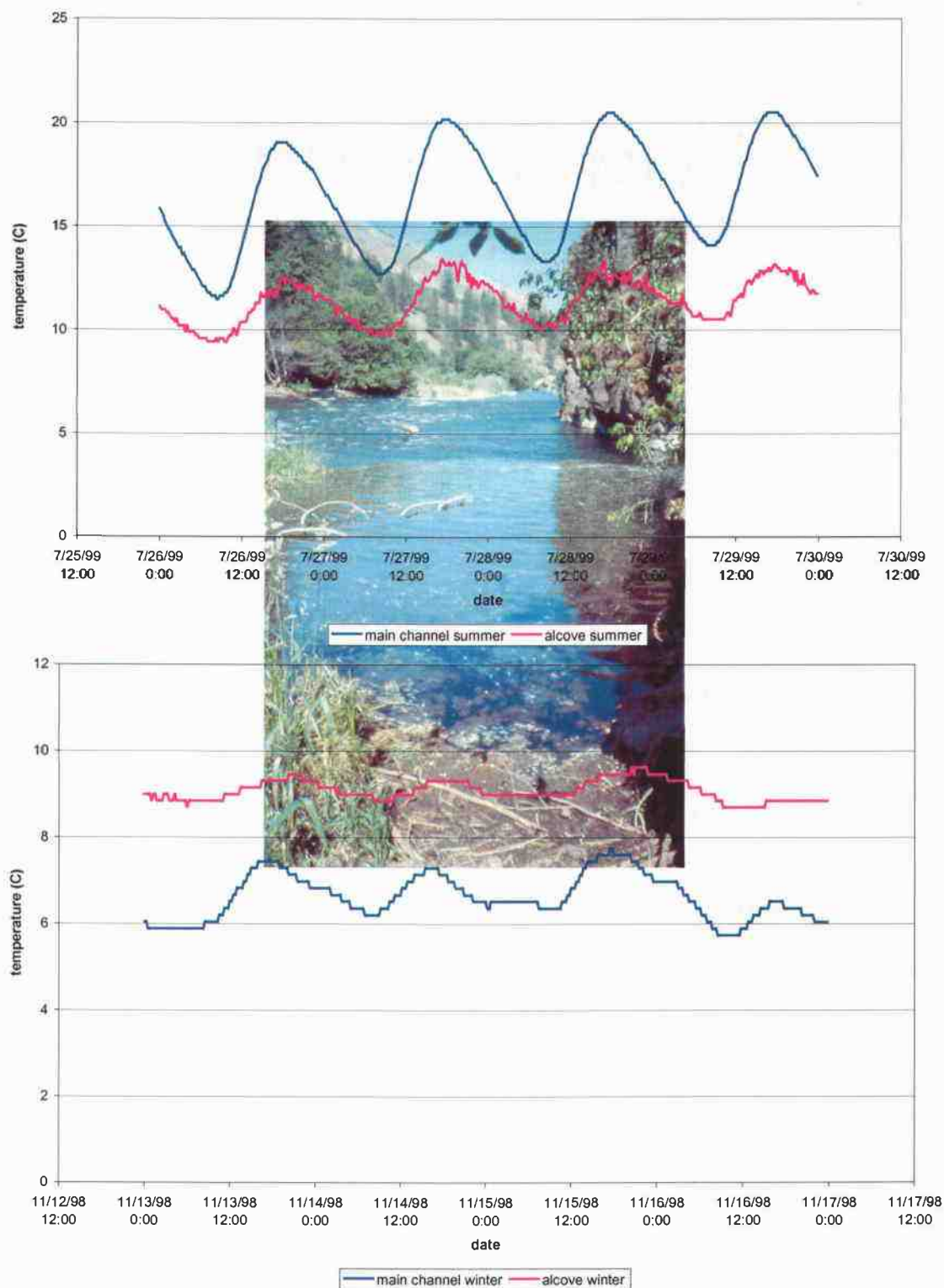
Figure 16. Mean monthly discharge of the Grande Ronde River in Troy, Oregon at the confluence of the Wenaha River for the period fall 1998 to summer 2000. Differences in the spring-early summer flow regime between 1999 and 2000 are circled.
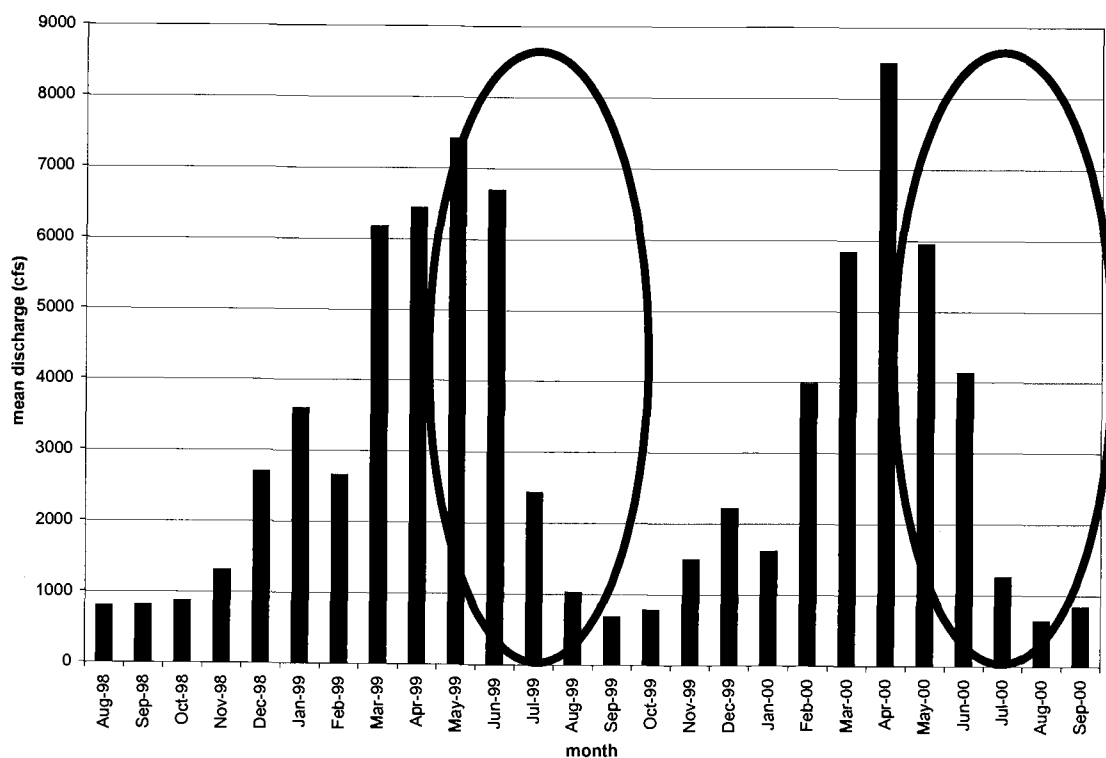
Figure 17. Temperature profiles at a site in the lower Wenaha River during the summer of 1998 (pink) and 1999 (black).
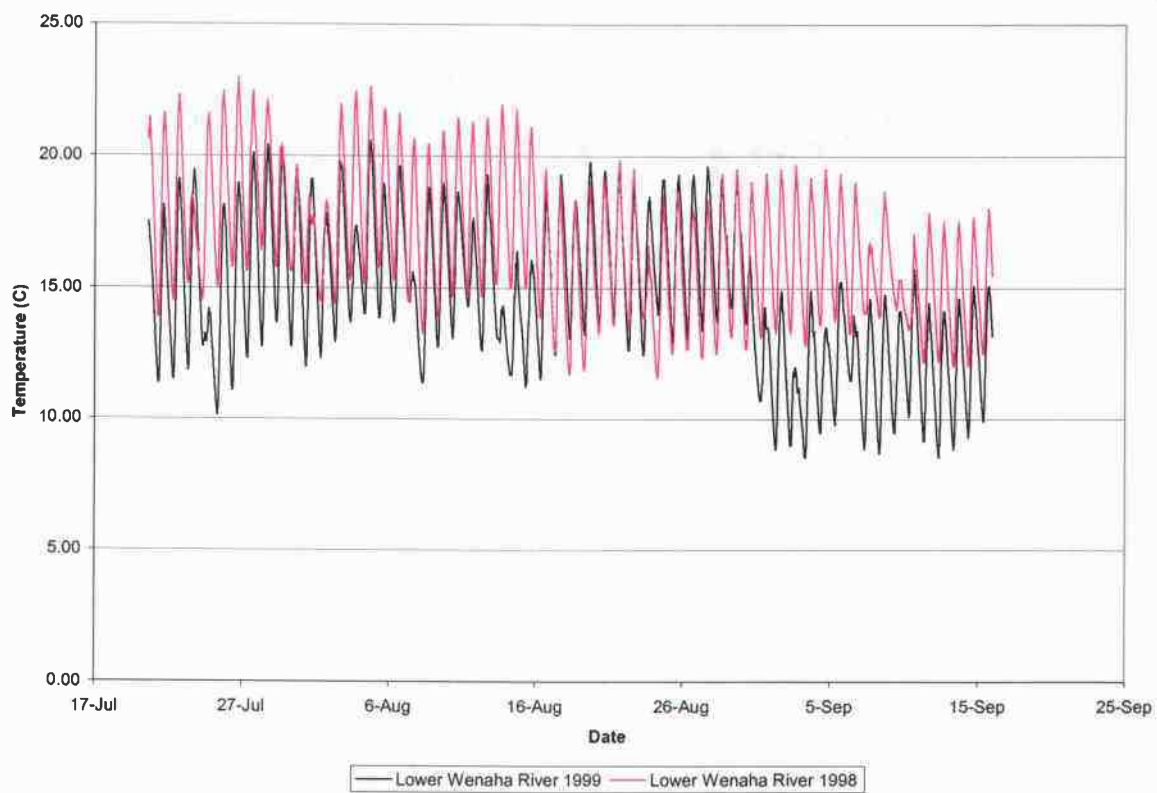
and no dramatic shifts in large wood numbers or position. Between years two sites gained a single large tree each, but in both cases they were oriented parallel with the flow and had little influence on channel form (though they did result in an increase in fish cover).

## 3.2    Fish Assemblage Dynamics at Multiple Scales

Two continuous snorkel surveys of the Wenaha River, combined with over 180 dives of the intensive survey sites, yielded a thorough perspective on fish assemblage patterns and their dynamics along the length of this river system. Direct assessment of individual species distribution patterns and life history observations, along with analysis of assemblage level patterns, provided insight into the nature and drivers of the patterns observed. The theme that emerged was one of context; the changes in fish assemblage patterns were a function of temporal context, while the dynamics of the assemblage at any given location reflected the context of that locality in the overall riverscape.

### 3.2.1  Inter-annual Variability in Fish Assemblage Patterns

Analysis of extensive summer surveys and intensive repeated surveys performed during 1998 and 1999 revealed relatively little difference in assemblage structure or seasonal dynamics between years. The only difference we detected was that assemblage structure at most sites in June of 1998 departed from that of June 1999. This difference was primarily a function of the larger number of bull trout and mountain whitefish (particularly in the lower reaches) at sites in June 1998 than in June 1999. Based on this analysis, we concluded the observations from both years could be lumped together for further assemblage level analyses.

### 3.2.2  Direct Observations, by Species, of Reach-scale Seasonal Patterns

During the time of our surveys of the Wenaha River (spring 1998-spring 2000) we observed 12 fish species (Table 4).  Two species, the chiselmouth, *Acrocheilus alutaceus*, and the bridgelip sucker *Catostomus columbianus*, were extremely rare.  We observed only a single individual adult chiselmouth, *Acrocheilus alutaceus*, 0.9 km above the confluence with the Grande Ronde River on June 29, 1999.  We observed bridgelip suckers (total = 11 fish) at three of the lower Wenaha sites (rkm 0.9, 2.7, and 10.9).  These fish were only observed during a few dives in summer months, were seen predominantly at night exhibiting very cryptic behavior, and were significantly smaller (20-25 cm) than the adult largescale suckers in the river.  We did observe some morphological variation among adult largescale suckers in the Wenaha River, suggesting the possibility that larger bridgelip suckers and/or bridgelip-largescale hybrids (as described by Dauble & Buschbom 1981) may have been present, but not differentiated via underwater surveys.  However, we did not detect any differences when suckers were captured for radio tagging.

Adult largescale suckers were present in the Wenaha River from May through September.  During fall and winter we saw no adults of this species in the river, while they were one of the dominant species of the assemblage in spring and summer months (Figure 18).  In June and July surveys, largescale suckers were most abundant in downstream reaches, particularly from rkm 0-10.9, with moderate densities from 10.9-23.2 km, and few found from 23.2-27.1 km (Figure 19).  Intensive site dives and the July '99 and August '98 extensive surveys showed that adult largescale suckers ranged furthest upriver during June and early July, after which the entire distribution began to shift downstream.  Based on the distribution of larval suckers, spawning was presumed to occur throughout their range in the river.  Direct observation of spawning was made at two sites in the lower river during mid-June, 1999, and we collected eggs from the streambed at the most downstream site between late May and mid-June, 1999.  Adult suckers were observed feeding throughout the time of their stay in the Wenaha River, both by grazing the rocks of the stream bottom and consuming detritus in slack water

Table 4. A list of fish species observed in the Wenaha River (fall 1998-spring 2000) via underwater survey techniques.

| Species | Common name |
|---|---|
| *Salvelinus confluentus* | bull trout |
| *Oncorhyncus mykiss* | rainbow trout and steelhead |
| *Oncorhyncus tshawytscha* | chinook salmon |
| *Ptychocheilus oregonensis* | northern pikeminnow |
| *Catostomus macrocheilus* | largescale sucker |
| *Prosopium williamsoni* | mountain whitefish |
| *Cottus beldingi* | piute sculpin |
| *Cottus rhotheus* | torrent sculpin |
| *Rhinichthys osculus* | speckled dace |
| *Rhinichthys cataractae* | longnose dace |
| *Catostomus columbianus* | bridgelip sucker* |
| *Acrocheilus alutaceus* | chiselmouth* |

* Very rare, < 10 individual fish observed.

Figure 18. Seasonal shifts in observed fish assemblage composition (relative abundance) summarized for upstream (rkm 24-36), middle (rkm 12-24), and downstream (rkm 0-12) sites along the length of the Wenaha River.

Upstream

Downstream

| | | | |
|---|---|---|---|
| **summer** | **fall** | **winter** | **spring** |
| □ ls sucker adult | ■ n pikeminnow adult | ■ p sculpin adult | ■ t sculpin adult | ■ dace adult |
| ■ chinook juvenile | □ rainbow trout juvenile | □ rainbow trout adult | ■ mtn whitefish juv | ■ mtn whitefish adult | ■ bull trt adult |

Figure 19. Abundance of largescale suckers (from extensive survey) along the
Wenaha River in July 1999. Larger dots indicate higher abundance. The asterisk
represents the upstream extent of the survey (see also Figure of survey sites).
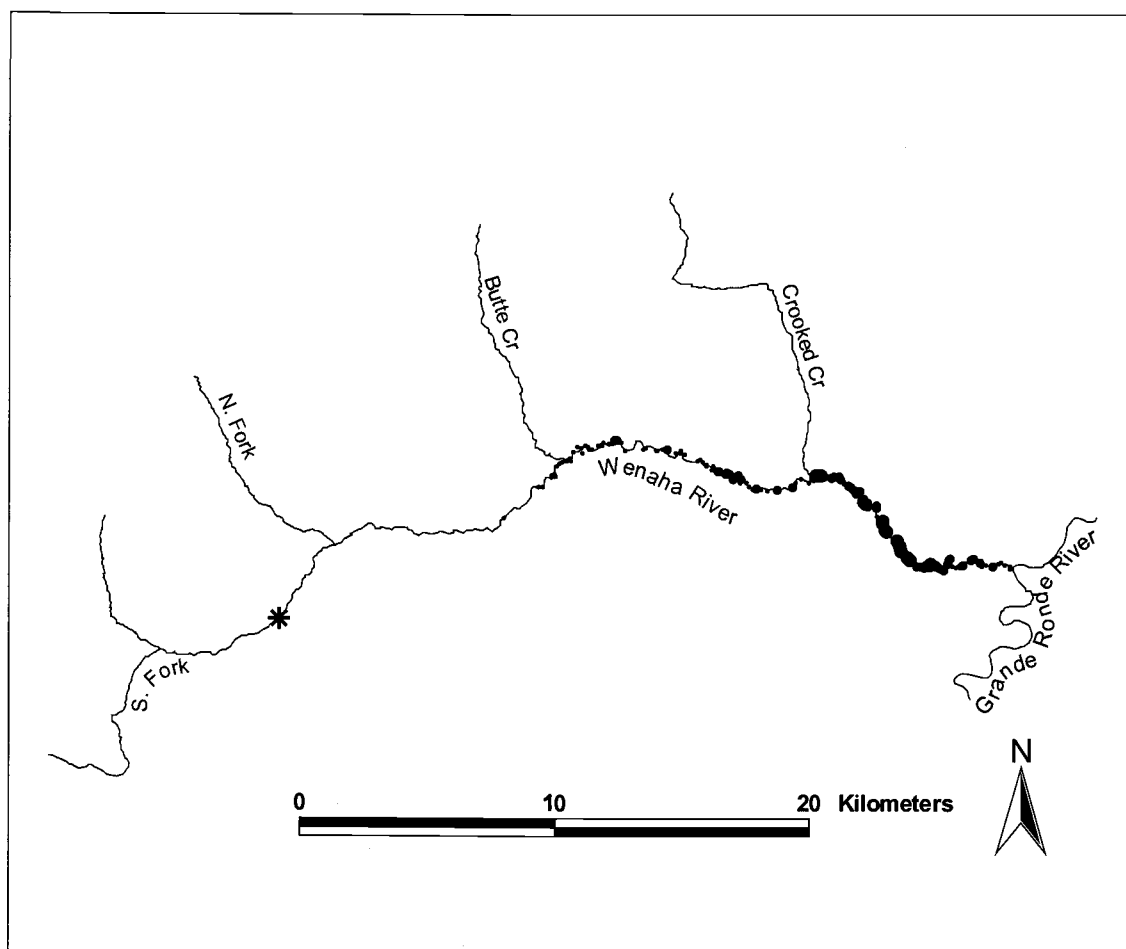
areas. Larval suckers were observed in slack-water areas of the Wenaha from mid-July to mid-October, 1999, with emergence occurring later in upstream than in downstream reaches, and largest densities observed from late July to early August (a coarse estimate suggested > 10,000 in one 200m reach of the lower river). Despite the high densities of larval suckers, juvenile suckers (< 15 cm) were rarely observed in the Wenaha (typically 0-15 individuals) and were found exclusively at the most downstream sites, while no sub-adult largescale suckers were observed.

Mountain whitefish adults were observed in the Wenaha River year-round. During the winter, adult mountain whitefish were distributed throughout the length of the main-stem Wenaha River in relatively low numbers. In addition, the largest adult fish (~50-55 cm) were not observed in the Wenaha during winter. However, during spring, summer, and fall we observed that adult mountain whitefish numbers were greater by nearly an order of magnitude than in winter months, and there was a pronounced longitudinal gradient in their abundance (Figure 18). In July and August, adult mountain whitefish were distributed throughout the length of the main-stem Wenaha, though their numbers were highest (relative and absolute abundance) in downstream reaches, and no individuals were found at sites above rkm 38.8 on the S. Fork (Figure 20). By late August, numbers of adult whitefish in the Wenaha had declined at most sites, with the exception of one downstream site (rkm 4.9) where we observed a congregation of over 300 individuals. By October, numbers at this site had dropped as well. At this site we captured ripe individuals, collected eggs from the gravel, and made direct observations of spawning in mid-October, 1998. The greatest decline in adult mountain whitefish abundance occurred at those sites in the lower river that had the highest abundance during summer months, while abundance at sites in the upper basin (particularly above rkm 25) were more constant. Juvenile (< 10 cm) and sub-adult (10-20 cm) mountain whitefish were observed year-round in the Wenaha, though they were relatively rare compared to other juvenile fishes (e.g., rainbow trout and chinook salmon) and were primarily observed in a few of the downstream sites (Figure 18). Beginning in March, but especially following the peak run-off, we saw the highest densities of young-of-the-year whitefish utilizing secondary channels and floodplain habitats, but as the fish grew

Figure 20. Abundance of mountain whitefish adults (from extensive survey) along the Wenaha River in July 1999. Larger dots indicate higher abundance. The asterisk represents the upstream extent of the survey (see also Figure of survey sites).
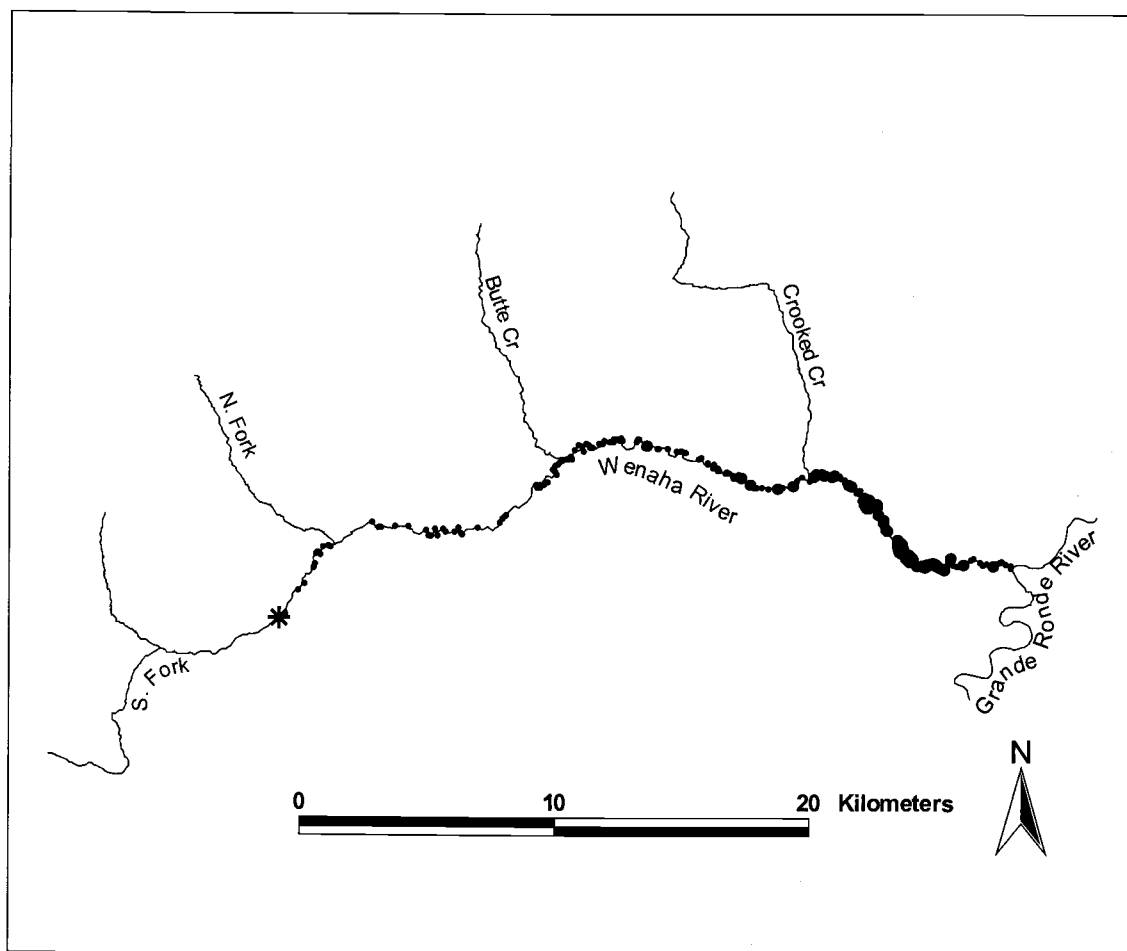
and water levels dropped, they were more often found in the main channel. We observed feeding by adult and sub-adult whitefish throughout the year in the Wenaha, though they appeared to differ in their foraging strategies. While adults seemed to focus on drifting invertebrates from a stationary vantage point in the main channel, sub-adults were more often observed moving about and feeding opportunistically from the bottom as well as the drift.

Bull trout were also observed year-round in the Wenaha River. In the winter, they were found in relatively low numbers at sites throughout the river, though their relative abundance was highest in upstream reaches. In spring, summer and fall bull trout were present in the Wenaha in much higher numbers, and many of these were of a significantly larger size than most of those observed in winter. During these seasons, longitudinal patterns in their abundance were clear (Figure 18). Numbers of bull trout in the main-stem Wenaha were highest in the spring and early summer, when they were found at all sites along the length of the river. By mid-July a significant upstream-downstream gradient in their abundance was evident, and the strongest gradient was seen during mid to late summer, during which period no bull trout were observed at any sites downstream of rkm 10.9 (Figure 21). Our surveys of headwater reaches showed small bull trout (range 3-20 cm) were present all the way to the 2$^{nd}$ and 1$^{st}$ order sites; in fact, they were the only fish species observed in the 1$^{st}$ order site (larval tailed frogs, *Ascaphus truei*, were the only other aquatic vertebrate encountered). In September and October, numbers of adult bull trout in the main-stem Wenaha were lower than in spring and summer, though they were observed at sites along the entire length of the river. In October of 1999, we observed large bull trout holding near spawning redds in the S. Fork Wenaha and in Butte Creek, a major tributary to the Wenaha. Juvenile bull trout (< 10 cm) were rarely observed during extensive surveys or at any of our intensive dive sites, though small bull trout (maturation status unknown) were common in the headwater sites of the S. Fork surveyed in August 1999. In the main-stem Wenaha, small (< 10 cm), presumably juvenile, bull trout exhibited cryptic behavior and were most often seen during night-time surveys. No small bull trout were seen below rkm 23, near the

67

Figure 21. Abundance of adult bull trout (from extensive surveys) along the Wenaha River in July and August. Larger dots indicate higher abundance. Arrow highlights observed differences. Asterisk represents upstream extent of survey.
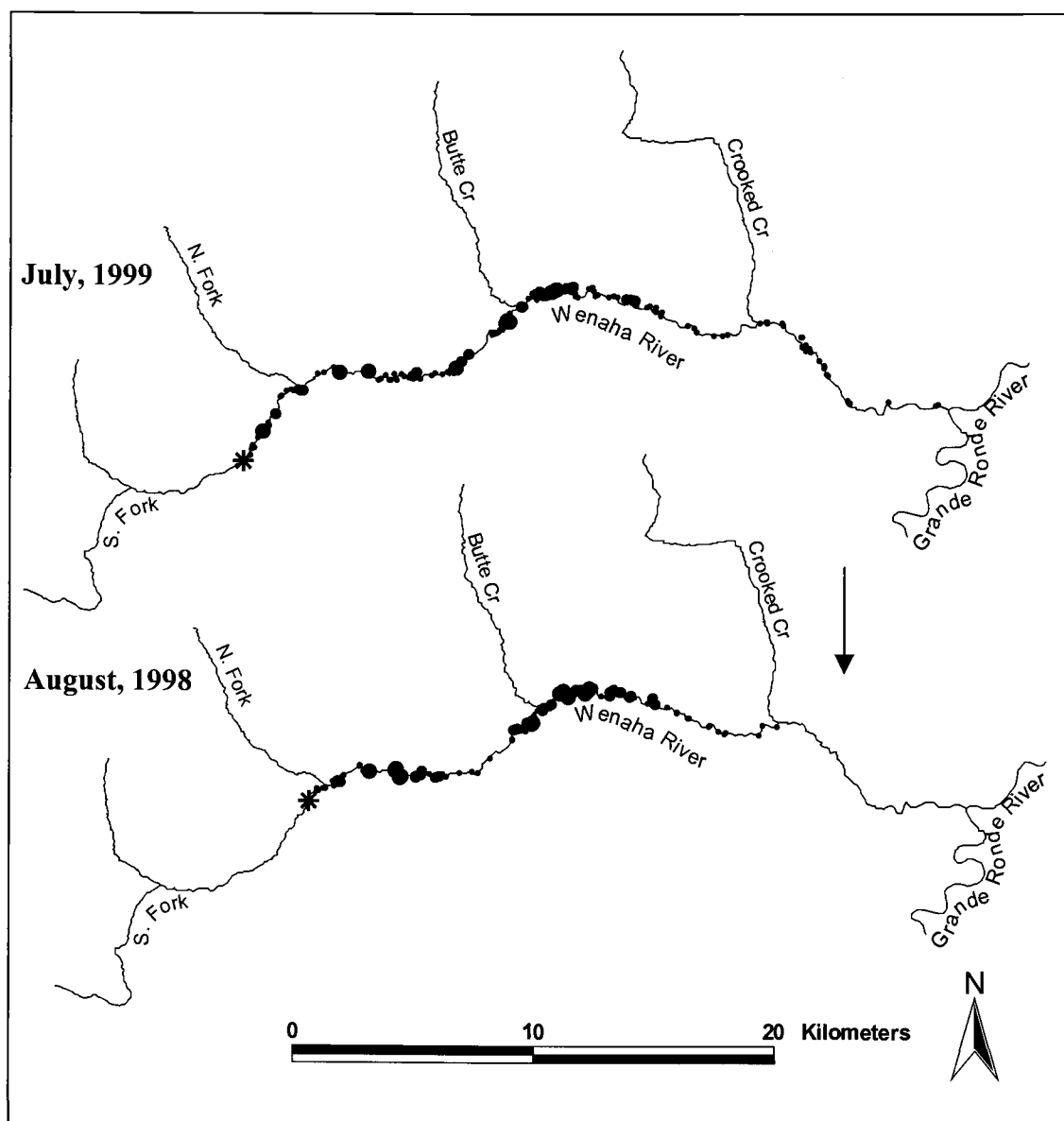
confluence with Butte Creek. During the course of our study we observed adult bull trout feeding on drifting invertebrates and, in a few cases, on sculpin and juvenile salmonids.

Adult chinook salmon were rarely encountered during our surveys. During all intensive site surveys over two years we made only 18 observations. During the August 1998 and July 1999 extensive surveys we saw only 44 and 10 individuals, respectively. The annual ODFW chinook salmon redd surveys of the main-stem and S. Fork of the Wenaha in September 1998 and 1999 yielded respective counts of 76 and 25 redds, and no spawning was observed to occur downstream of Fairview Creek (rkm 16.4). Despite the low numbers of adults, juvenile chinook salmon were consistently the most abundant fish (other than larval suckers) in our surveys of the Wenaha River. Juvenile chinook salmon were found at sites throughout the length of the river during all seasons. In the spring, summer, and fall their relative abundance was higher in upstream than downstream sites (Figure 18). However, they were the most abundant in the S. Fork and particularly in the main-stem section between rkm 14 and 26 (Figure 22). We observed no juvenile chinook in the 2nd or 1st order headwater sites. During spring surveys, we saw the highest densities of young-of-the-year fish utilizing secondary channels and floodplain habitats, and as the fish grew and water levels dropped, they were more often found in the main channel. A pronounced longitudinal gradient in juvenile chinook relative abundance was evident in spring, became stronger by mid-July, was most dramatic by mid-August, and persisted into the fall. By November, however, there was a significant decline in the number of juvenile chinook observed in the Wenaha across all sites except the two furthest downstream, after which numbers appeared to gradually decline or remain constant throughout the winter. We observed the lowest densities of juvenile chinook during our March surveys, though high water prevented snorkeling in April and May.

Rainbow trout were the second most common fish species observed in the Wenaha River, and were present throughout the main-stem during all times of the year. Though there was no clear upstream-downstream gradient in their absolute abundance, in summer rainbow trout relative abundance was higher in upstream than downstream sites (Figure
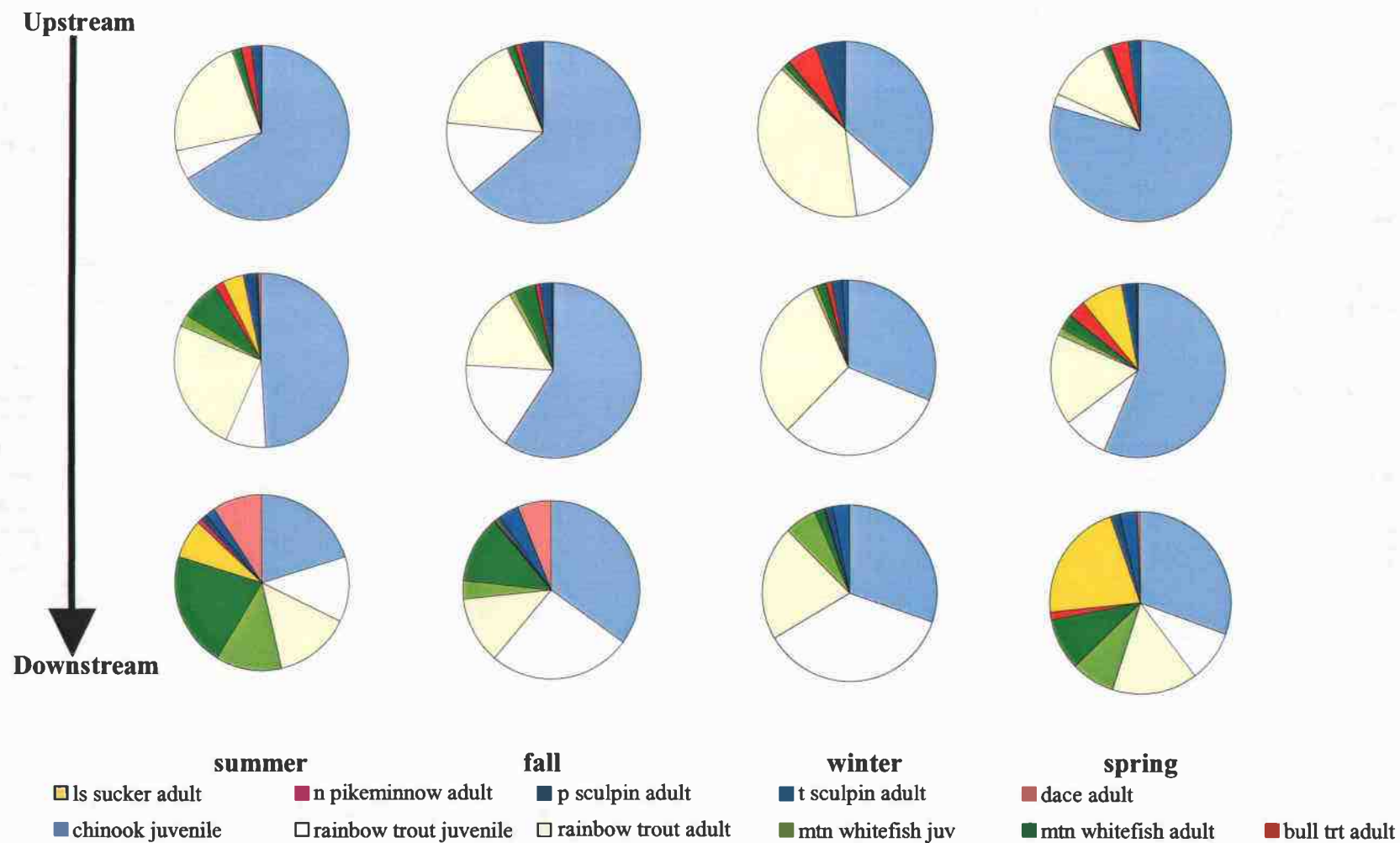
Figure 22. Abundance of juvenile chinook salmon (from extensive survey) along the Wenaha River in July 1999. Larger dots indicate higher abundance. The asterisk represents the upstream extent of the survey.
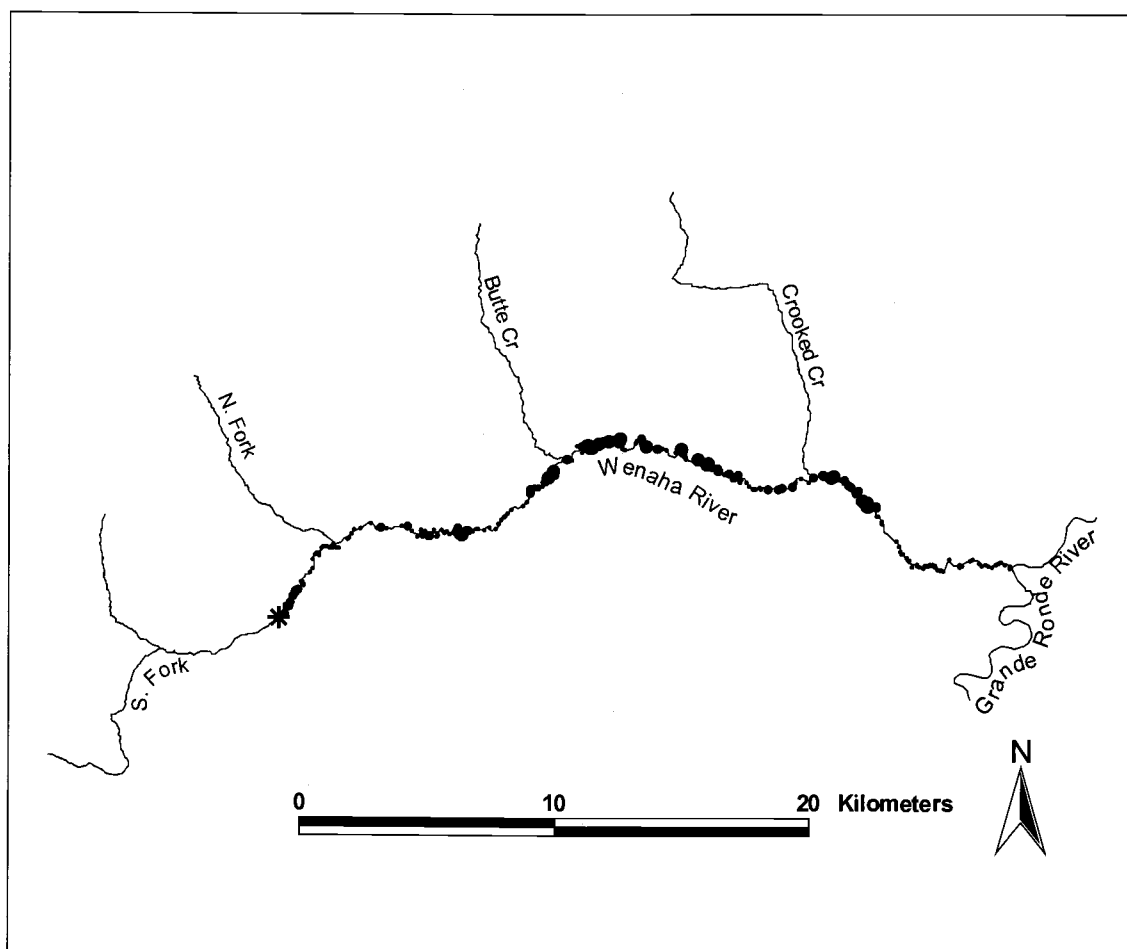
18). In addition to the longitudinal gradient, there were other distinct patterns in their distribution that changed with the seasons. In particular, spring intensive surveys and the July 1999 extensive survey indicated that rainbow trout adults were abundant in the reach between rkm 5.0 and 11.0 during these times (Figure 23). However, by August there was a dramatic decrease in their numbers in this reach, which is located just downstream of the confluence with a large, warm tributary (Crooked Creek), and a corresponding increase in their numbers in the reach just upstream of the tributary (Figure 23). Over the same time interval there was a significant increase in the numbers of adult rainbow trout observed in the lower 2 km of the Wenaha, which is dramatically cooler than the Grande Ronde River, where rainbow trout are also known to reside (Figure 8, Figure 23). In addition to differences within a year, these extensive survey patterns may partly reflect differences between years, though data from our intensive dive sites do not support this idea. Juvenile rainbow trout were present throughout the main-stem Wenaha throughout the year. As was the case with the adults, we did not observe a particularly strong longitudinal gradient in their absolute abundance during any season, though their relative abundance tended to be greater in downstream than upstream sites (Figure 17). This was particularly true in spring, as young-of-the-year rainbow trout reached larger sizes and were more abundant at an earlier date in the lower river sites than in upper reaches.

Northern pikeminnow were relatively rare in the Wenaha River during the study period, and were observed in the months of July and August only (Figure 18). Only adult fish were seen, and these individuals were large (estimated average size ~40-50 cm). During the August 1998 and July 1999 extensive surveys we saw only 46 and 79 individuals, respectively. During the extensive (Figure 24) and the intensive site surveys (Figure 18) most of the fish were found in the mid to lower reaches of the river. However, in July we observed fewer northern pikeminnow distributed lower in the basin (none above rkm 12.6) than in August, when we observed them as high as rkm 21.3 and relatively few below rkm 12.6 (Figure 24). Distribution within these ranges was very patchy, with long stretches of river where no individuals were seen punctuated by locations where we observed small schools of 6-12 individuals. We observed several

Figure 23. Abundance of adult rainbow trout (from extensive surveys) along the lower 15 km of the Wenaha River in July 1999 and August 1998. Larger dots indicate higher abundance. Arrows denote reach-level changes in abundance from July to August.
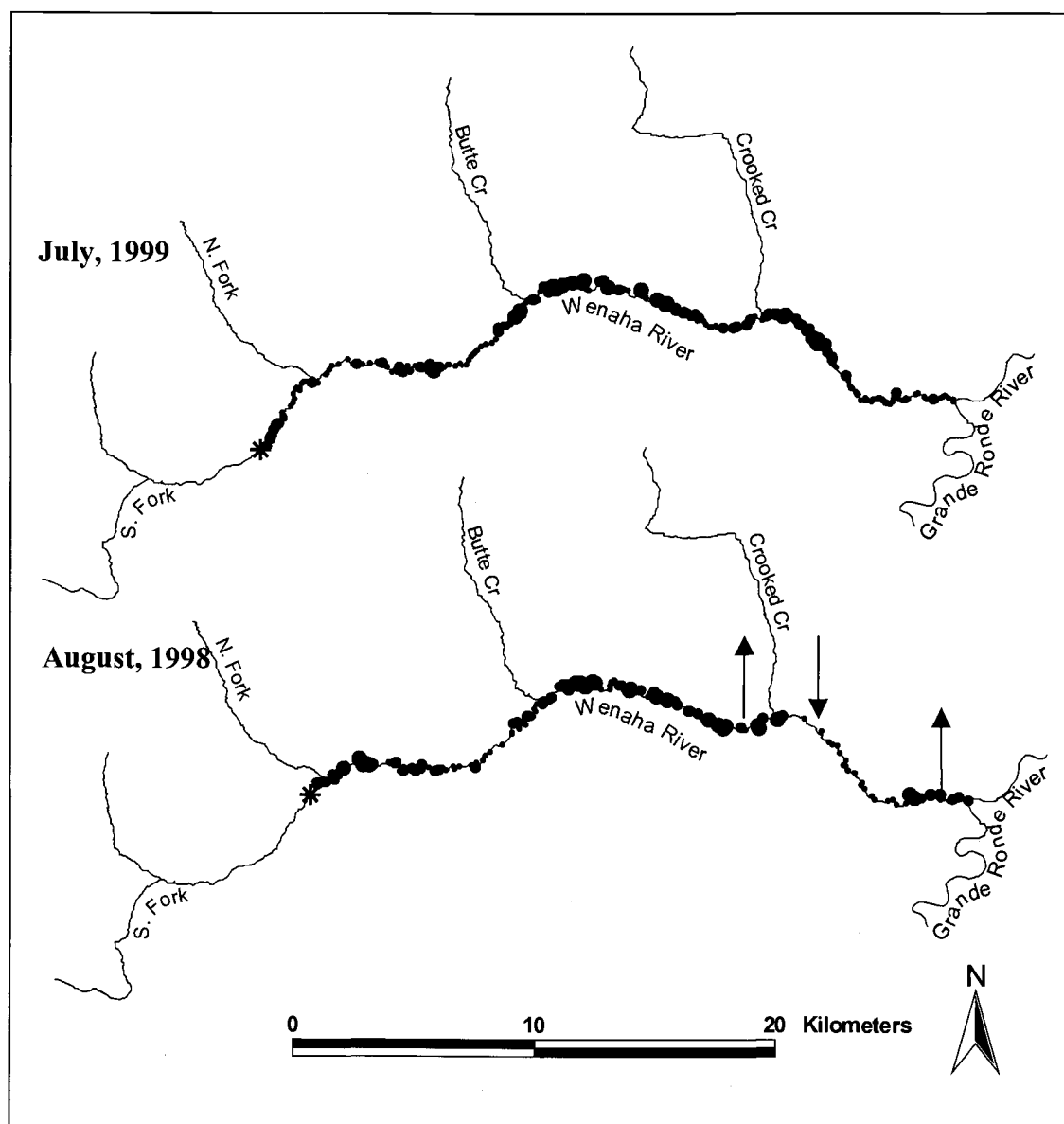
Figure 24. Abundance of northern pikeminnow (from extensive surveys) along the Wenaha River in July 1999 and August 1998. Larger dots indicate higher abundance. Arrow highlights observed differences. Asterisk represents upstream extent of survey.
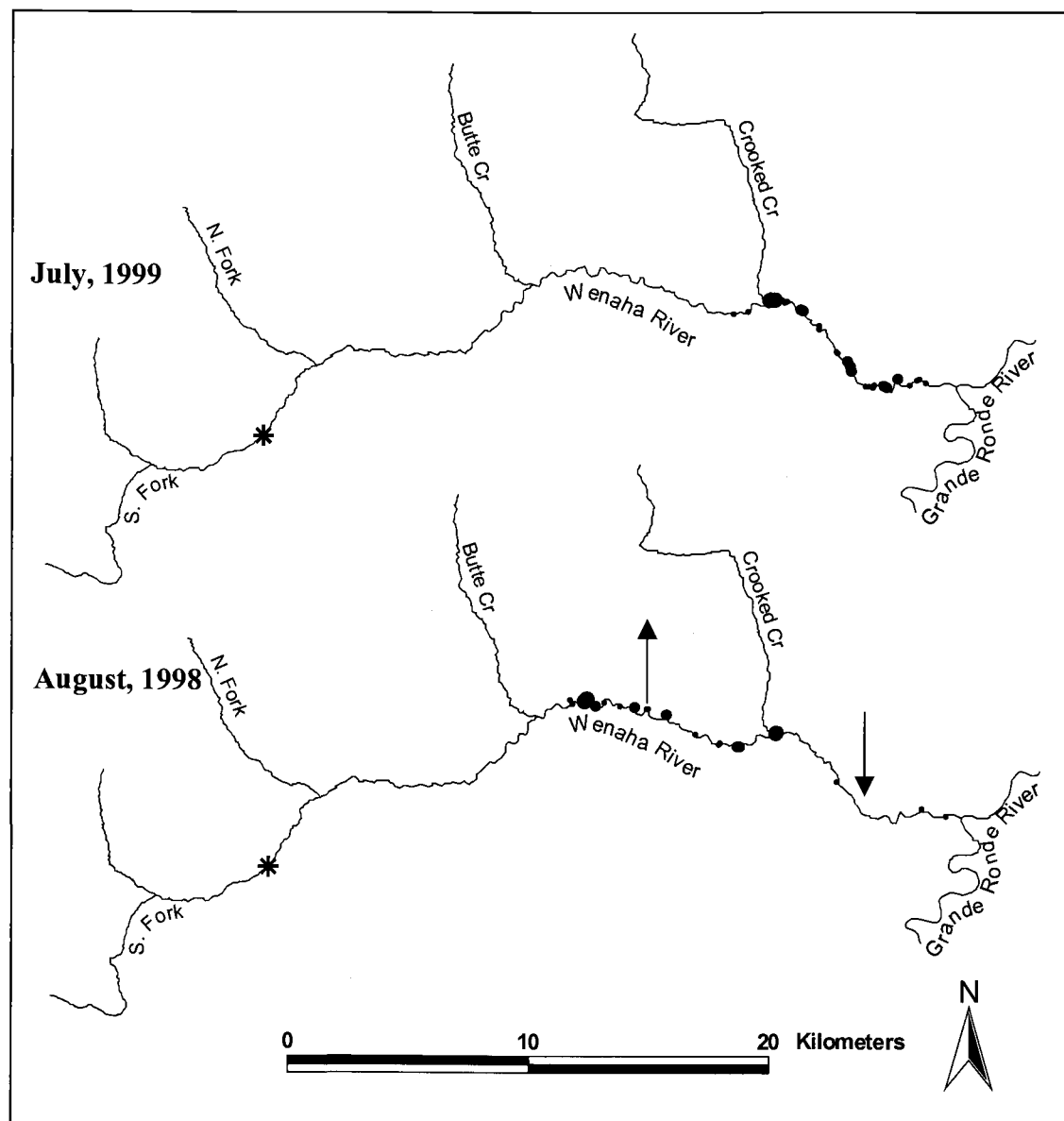
instances of northern pikeminnow feeding on both juvenile fishes and aquatic invertebrates.

We observed speckled *Rhinichthys osculus* and long nose *R. cataractae* dace in the Wenaha River. There appeared to be significant variation in morphology within these two types, suggesting that other species may be present that could not be delineated via snorkeling. Adults of the two species were differentiated from one another (by body and head shape) during underwater surveys, however dace juveniles and fry had to be lumped together. Though I determined that the surveys of benthic fishes had low efficiency, coarse patterns in dace presence/absence were evident from our observations. Dace were only observed in lower reaches of the river, and were never seen above the substratum during late fall, winter, or early spring months (Figure 18). In the winter of 1999, three long nose dace were discovered at rkm 0.9 by excavating the stream substratum over a square meter to a depth of about 20 cm. During summer months, adult speckled dace were commonly observed in the lower 5 km of the river (max observed at a site = 35). Adult long nose dace were seen at sites as far upstream as rkm 15.5, though it was uncommon to see more than 1-5 individuals during the survey of a site. Dace fry were observed in the lower Wenaha River beginning in late July. During July and August surveys at our most downstream site (rkm 0.9) they were too numerous to accurately count. We commonly observed large schools of mixed dace and sucker fry (thousands of individuals) in slack-water areas along channel margins of the lower river.

We also observed two species of cottids in the Wenaha River, torrent *Cottus rhotheus* and piute sculpin, *C. beldingi*. As was the case for dace, there may be other less common sculpin species present that could not be delineated via snorkeling. Several snorkeling observations at sites in the upper portions of the drainage (above Butte Cr.—rkm 23.2) suggested shorthead sculpin, *C. confusus*, might have been present, though they were either 1) relatively rare or 2) not consistently distinguished from piute sculpin during underwater surveys. Though piute and torrent sculpin adults were easily differentiated during underwater surveys, juveniles and fry were lumped. Piute sculpin were observed throughout the main-stem Wenaha River and the S. Fork Wenaha with the exception of the 2nd and 1st order sites. Torrent sculpin were most abundant at sites downstream of

rkm 10.9 (Crooked Creek confluence), though individuals (always large adults, sometimes found dead) were occasionally sighted much further upstream in the basin. The furthest upstream sighting of a torrent sculpin was a very large (15 cm) individual observed at rkm 25.3 in November of 1998. At sites downstream of rkm 10, torrent sculpin were relatively more abundant than piute sculpin during all seasons, while the opposite was true at sites upstream of this point (Figure 18). Dead adult sculpin, presumably post-spawning mortalities, of both species were commonly observed throughout spring and summer surveys, and sculpin eggs were frequently seen at sites throughout the river. We made numerous incidental observations of sculpin feeding on invertebrates and larval fish during the course of our study. On several occasions during summer months in sites of the lower Wenaha River, we observed high densities of adult torrent sculpin in alcove habitat at night, and we observed active predation by these sculpin on the larval suckers and dace that were also abundant in these habitats during this season.

### 3.2.3  Indirect Analysis of Reach-scale Seasonal Assemblage Patterns

In each season, we observed distinct longitudinal fish assemblage patterns. However, these patterns changed dramatically with season (Figure 18). Both extensive (Figure 25) and intensive survey data (Figures 18 and 26) from summer describe a marked gradient from headwaters to mouth of the Wenaha River. When the extensive survey data from August 1998 were summed into twelve 3-km bins and analyzed, ordination results were similar to those obtained from the intensive dive sites only, though analysis of the extensive survey data revealed two assemblage gradients and the intensive survey data only one. The extensive survey data ordination solution accounted for 96 % of the variation in assemblage structure between bins (Figure 25). Axis 1 accounted for 76% of the variation and was strongly correlated with river kilometer (Pearson's correlation, r = -0.89), suggesting significant separation of assemblage types between upstream and downstream sites. This assemblage structure pattern was driven by variation in mountain

Figure 25. NMDS ordination plot of August 1998 extensive survey sites (data summed in 3 km bins) in species relative abundance ordination space. Percent of variation explained = 76% for axis1 and 20 % for axis 2. Correlations (Pearson's r > 0.4) between ordination axis scores and site position (rkm) and individual species are shown.



Axis 2

| Factor | r |
|---|---|
| rainbow trout | -0.94 |
| largescale sucker | -0.41 |
| mountain whitefish | 0.54 |
| adult chinook | 0.52 |

Axis 1

| Factor | r |
|---|---|
| river km | -0.89 |
| bull trout | -0.79 |
| juvenile chinook | -0.79 |
| mountain whitefish | 0.95 |
| largescale sucker | 0.46 |

Figure 26. NMDS ordination plot of sites in species relative abundance ordination space based on summer season intensive site survey data. Percent of variation explained = 97% for the single axis solution. Correlations (Pearson's r > 0.4) between ordination axes scores and site position and individual species are shown. Polygons describe longitudinal position of sites.



| Factor | r |
|---|---|
| river km | 0.79 |
| juvenile chinook | 0.97 |
| adult bull trout | 0.74 |
| adult rainbow trout | 0.72 |
| adult mountain whitefish | -0.96 |
| adult largescale sucker | -0.87 |

whitefish (r = 0.95), which were found in greater relative abundance in downstream reaches, while bull trout (r = -0.79), and juvenile chinook (r = -0.79) were relatively more abundant in upstream reaches. Axis 2 explained 20% of the variation among bins and was largely driven by differences in rainbow trout relative abundance (r = -0.94). Ordination of summer intensive survey data yielded a single axis solution that accounted for 97% of the variation in site assemblage differences (Figure 26). This axis was also correlated with river kilometer (r = -0.79). As in the case of the extensive survey analysis, this gradient was driven by variation in juvenile chinook salmon, adult rainbow trout and adult bull trout which were all found in higher relative abundance in upstream reaches (r = 0.97, 0.74, 0.72, respectively), as well as adult mountain whitefish and largescale suckers which were more abundant in downstream sites (r = -0.96, -0.87, respectively).

Fall surveys also showed a gradient from upstream to downstream in the Wenaha River, though the species driving these patterns were different from the summer season. The NMDS ordination identified a two-axis solution that accounted for 97% of the variation in fish assemblage structure among the sites (Figure 27). Axis 1 accounted for 74% of the fall variation among sites, and it was largely driven by variation in juvenile chinook (r = 0.95) and adult mountain whitefish (r = -0.89). Particularly along axis 2 (which explained 23 % of the variation), upstream sites were clearly separated from those downstream (r = -0.74 for river km). Axis 2 was also negatively correlated with juvenile rainbow trout (r = -0.91) and juvenile mountain whitefish (r = -0.90), while it was positively correlated with the relative abundance of adult rainbow trout (r = 0.62), adult bull trout (r = 0.51), and juvenile chinook (r = 0.50).

During winter, patterns in fish assemblage structure were also evident among sites, and these were also different from those observed during other seasons. The NMDS ordination identified two major gradients that captured most of the variance (99%) in winter fish assemblage structure between sites (Figure 28). The first dimension contained 4% of the information and was primarily associated with relative abundance of adult rainbow trout (r = 0.98). Axis 2 accounted for 95% of the variation among sites in winter and was positively correlated with juvenile rainbow trout (r = 0.96) but negatively

Figure 27. NMDS ordination plot of sites in species relative abundance ordination space based on fall season survey data. Percent of variation explained = 74% for axis 1 and 23% for axis 2. Correlations (Pearson's r > 0.4) between ordination axes scores and site position and individual species are shown. Polygons describe longitudinal position of sites.



Axis 2

| Factor | r |
|---|---|
| adult rainbow trout | 0.62 |
| adult bull trout | 0.51 |
| juvenile chinook | 0.50 |
| juv. mountain whitefish | -0.90 |
| juvenile rainbow trout | -0.91 |
| river km | -0.74 |

Axis 1

| Factor | r |
|---|---|
| juvenile chinook | 0.95 |
| adult mountain whitefish | -0.89 |
| adult rainbow trout | -0.49 |
| juv. mountain whitefish | -0.45 |
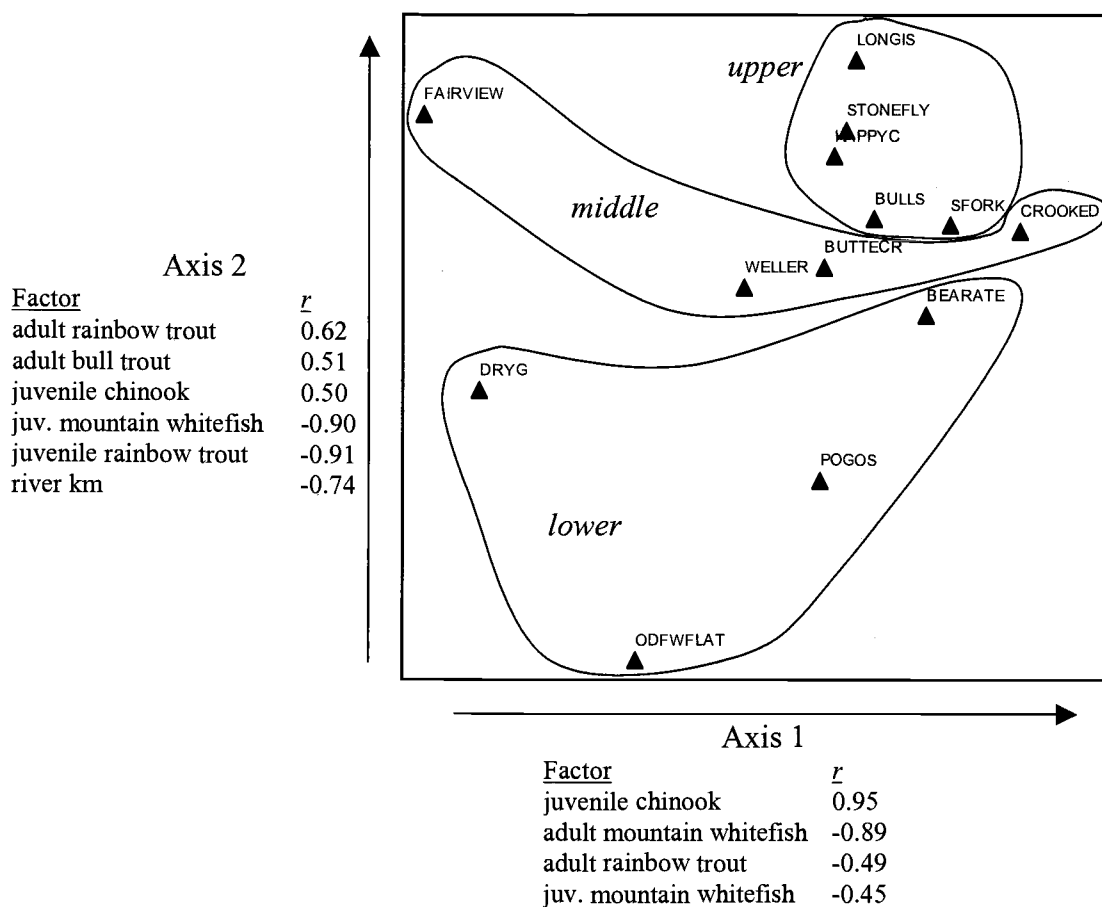
Figure 28. NMDS ordination plot of sites in species relative abundance ordination space based on winter season survey data. Percent of variation explained = 4% for axis 1 and 95% for axis 2. Correlations (Pearson's r > 0.4) between ordination axes scores and site position and individual species are shown. Polygons describe longitudinal position of sites.



Axis 2

| Factor | r |
|---|---|
| river km | 0.67 |
| juvenile rainbow trout | 0.96 |
| adult bull trout | -0.69 |
| juvenile chinook | -0.97 |

Axis 1

| Factor | r |
|---|---|
| adult rainbow trout | 0.98 |
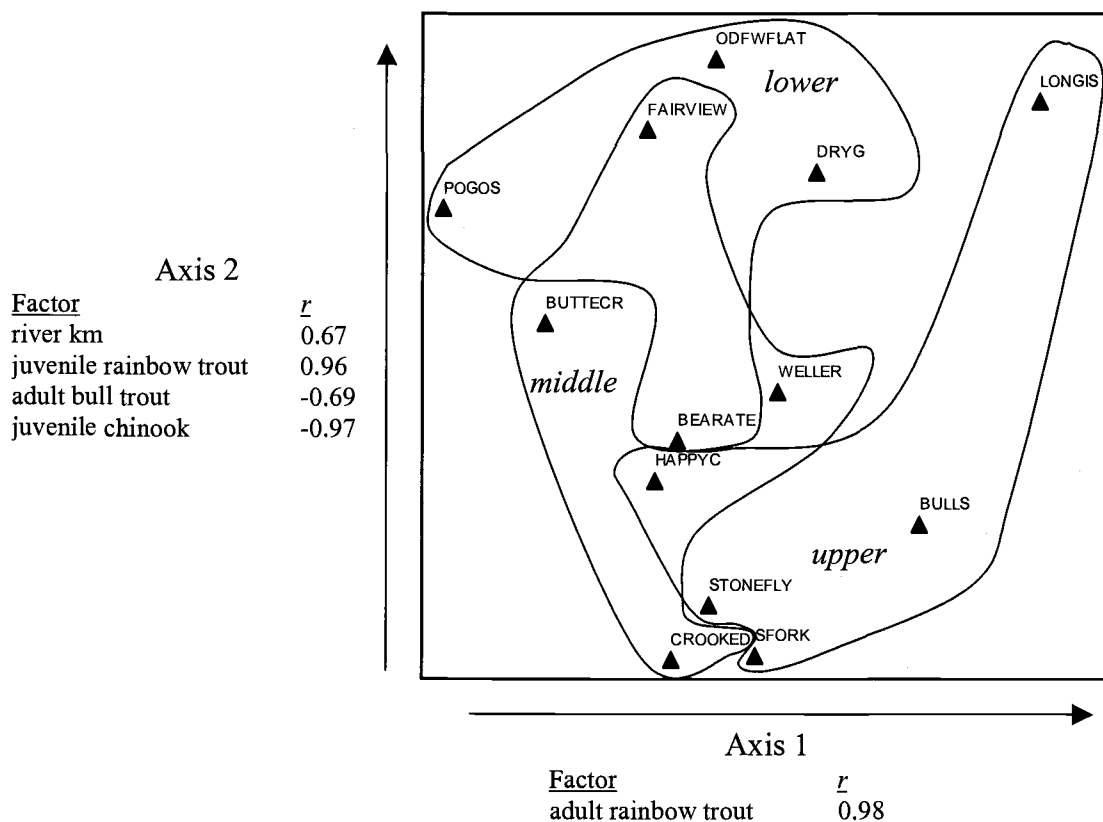
with juvenile chinook (r = -0.97) and adult bull trout (r = -0.69). During winter, the upstream downstream grouping of sites was not evident, though scores on axis 2 were still weakly correlated with river km (r = 0.67).

Stronger upstream-downstream gradients in fish assemblage structure were re-established during spring months in the Wenaha River. The NMDS ordination identified two gradients that accounted for 93% of the variation in fish assemblage structure among the sites (Figure 29). Axis 1 accounted for 36% of the spring variation among sites, and it was driven by variation in adult (r = 0.80) and juvenile (r = 0.78) rainbow trout, juvenile mountain whitefish (r = 0.64) and juvenile chinook (r = -0.80). Particularly along axis 2 (which explained 57 % of the variation), upstream sites were clearly separated from those downstream (r = -0.81 for river km). Axis 2 was also negatively correlated with juvenile chinook (r = -0.76) and adult bull trout (r = -0.63), while it was positively correlated with the relative abundance of adult largescale suckers (r = 0.94).

Temporal similarity was greater among upstream sites than among downstream sites (Figures 30 and 31). Analysis of percent similarity indices yielded a similar perspective to that gained through ordination. Shifts in species relative abundances were reflected by changes in the positions of sites within community NMDS ordination space (Figure 30). In this ordination on data from all site-season combinations, NMDS gave a 3-dimensional solution, describing 97% of the variation. Axis 1 described 46% of the variation between site-season combinations and was driven by differences in juvenile rainbow trout (r = 0.76), largescale suckers (r = -0.73) and adult mountain whitefish (r = -0.48). Axis 2 explained 35% of the variation and was positively correlated with juvenile chinook (r = 0.88) and adult bull trout (r = 0.58), while it was negatively associated with adult mountain whitefish (r = -0.68), juvenile mountain whitefish (r = -0.64), and juvenile rainbow trout (r = -0.56). Axis 3 explained 16% and was primarily driven by differences in adult rainbow trout (r = 0.79) and juvenile chinook (r = -0.76) relative abundance. There was no correlation between site river km and scores on any of the ordination axes. However, upstream sites all tended to follow a similar path of community shifts through the seasons, as did those from mid and lower reaches (Figure 31). Upper sites underwent

Figure 29. NMDS ordination plot of sites in species relative abundance ordination space based on spring season survey data. Percent of variation explained = 36% for axis 1 and 57% for axis 2. Correlations (Pearson's r > 0.4) between ordination axes scores and site position and individual species are shown. Polygons describe longitudinal position of sites.



Axis 2

| Factor | r |
|---|---|
| river km | -0.81 |
| adult largescale sucker | 0.94 |
| juvenile chinook | -0.76 |
| adult bull trout | -0.63 |

Axis 1

| Factor | r |
|---|---|
| adult rainbow trout | 0.80 |
| juvenile rainbow trout | 0.78 |
| juv. mountain whitefish | 0.64 |
| juvenile chinook | -0.81 |
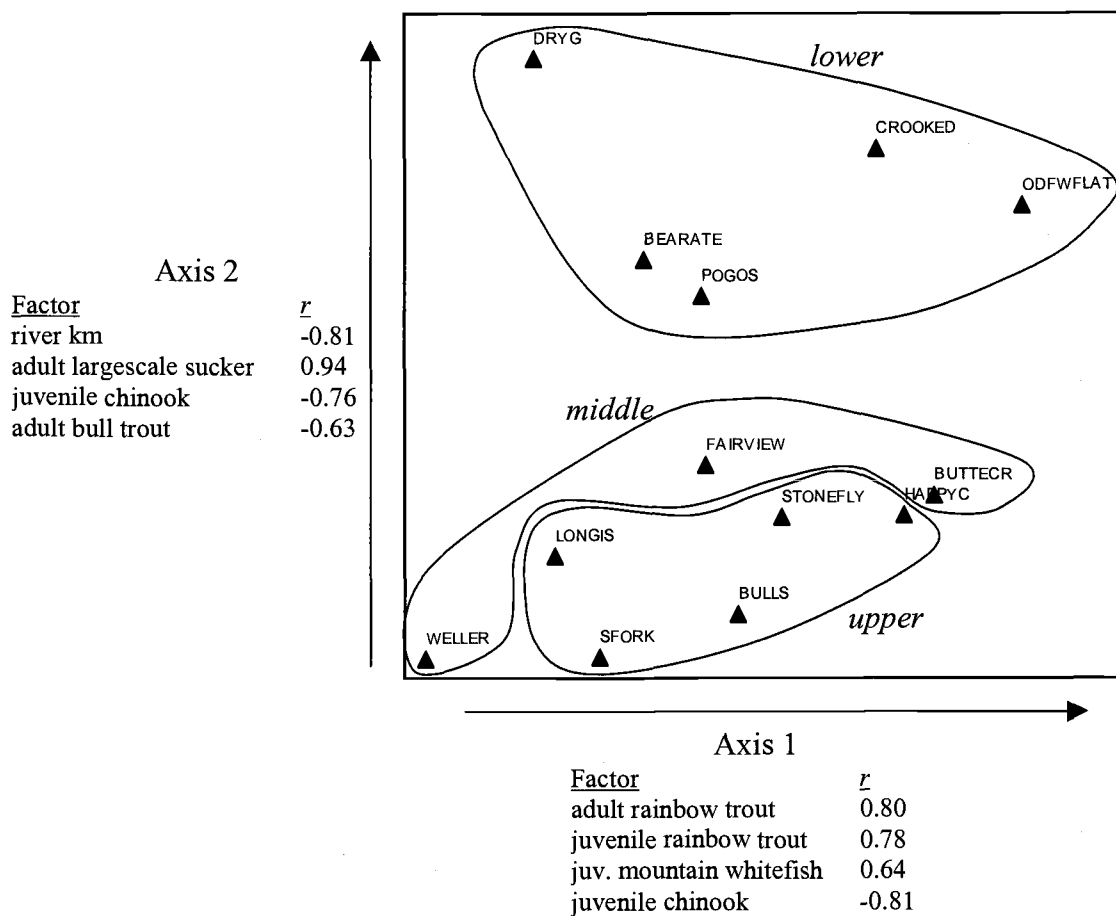
Figure 30. NMDS ordination plot of sites in species relative abundance ordination space. The positions in community space of each of the 13 sites for each of the four seasons (labeled sp, su, fa, wi) are connected by successional vectors. Percent of variation explained = 46% for axis 1 and 35% for axis 2. Axis 3 (not pictured) explained 16% of the variation (see results text). Correlations (Pearson's r > 0.4) between ordination axis scores and site position and individual species are shown.



Axis 2

| Factor | r |
| --- | --- |
| juvenile chinook | 0.88 |
| adult bull trout | 0.58 |
| adult mountain whitefish | -0.68 |
| juv. mountain whitefish | -0.64 |
| juvenile rainbow trout | -0.56 |

Axis 1

| Factor | r |
| --- | --- |
| juvenile rainbow trout | 0.76 |
| adult largescale suckers | -0.73 |
| adult mountain whitefish | -0.48 |
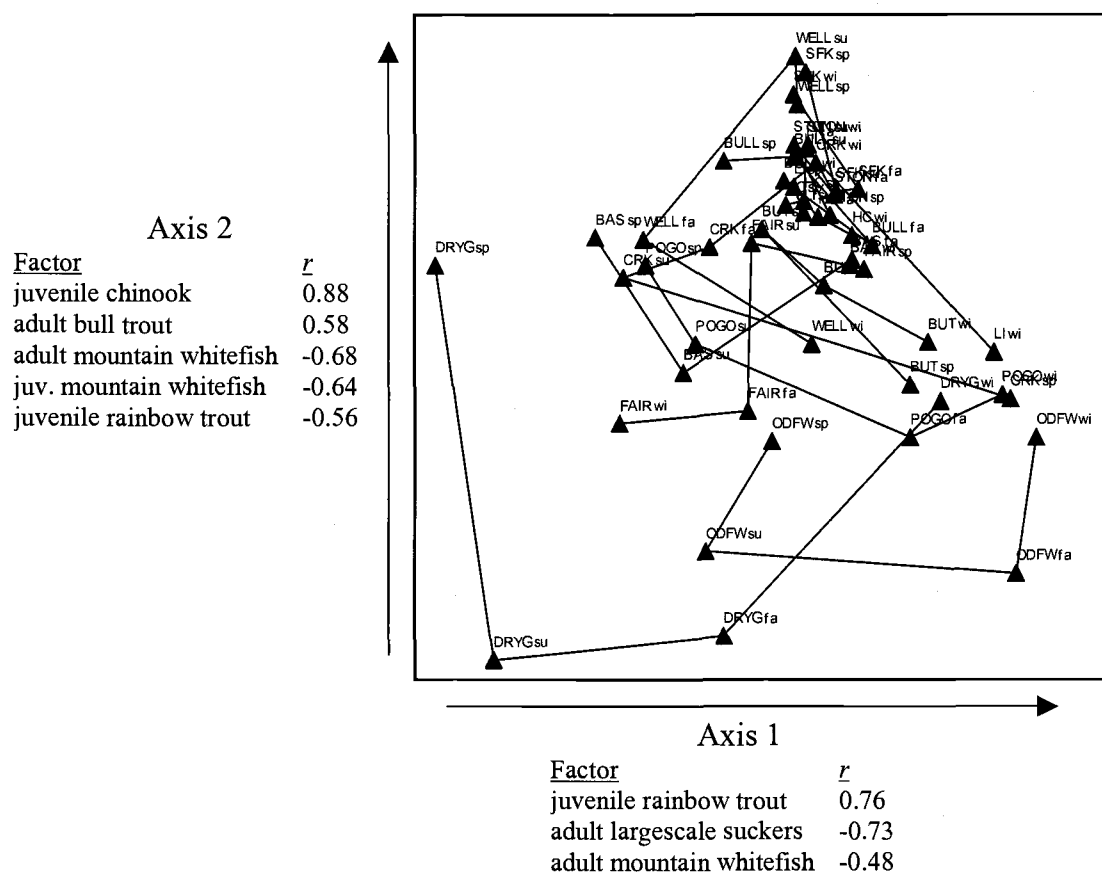
Figure 31. The positions in community space of each of the 13 sites for each of the four seasons (as in Figure 30), with generalized patterns of seasonal change for sites in the upper (green), middle (blue), and lower (red) portions of the drainage traced. As in Figure 30, percent of variation explained = 46% for axis 1 and 35% for axis 2. Axis 3 (not pictured) explained 16% of the variation (see results text). Correlations (Pearson's r > 0.4) between ordination axis scores and site position and individual species are shown.
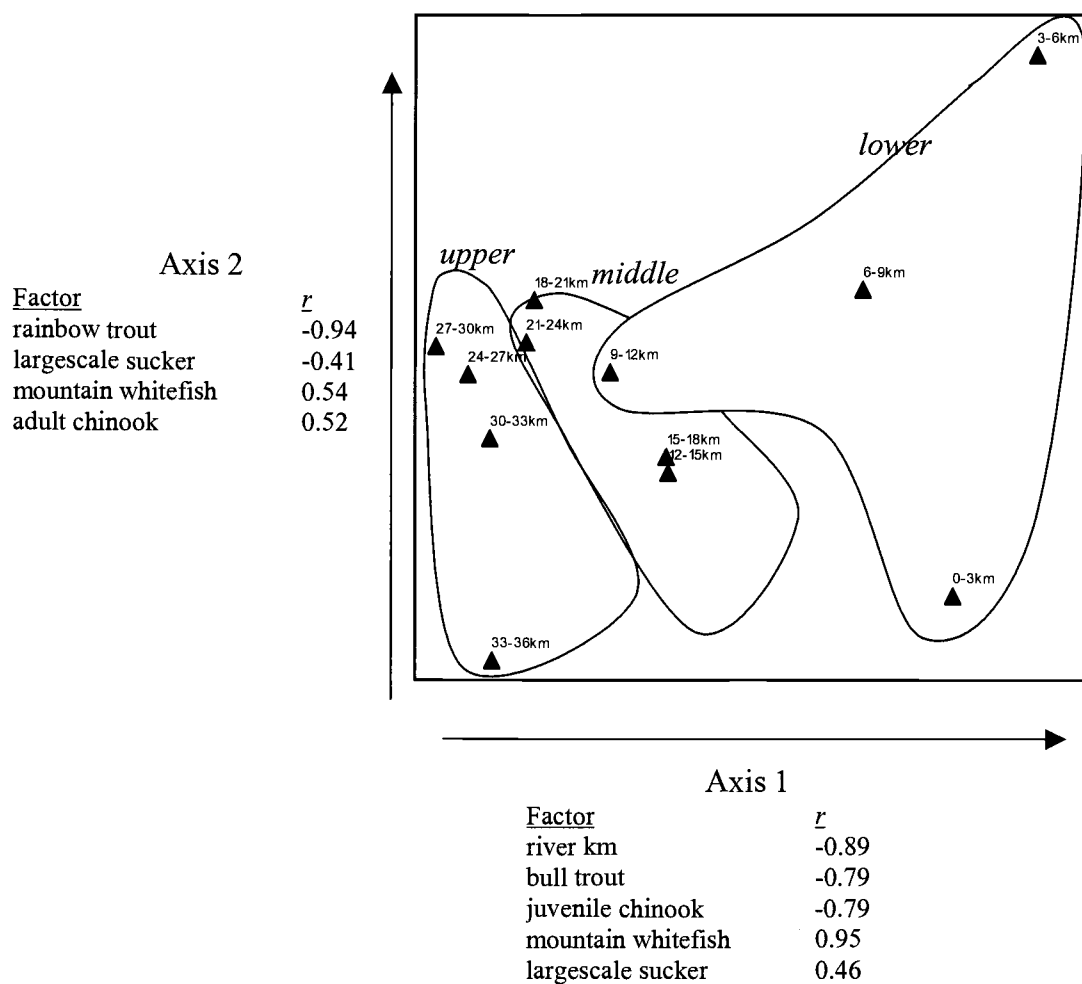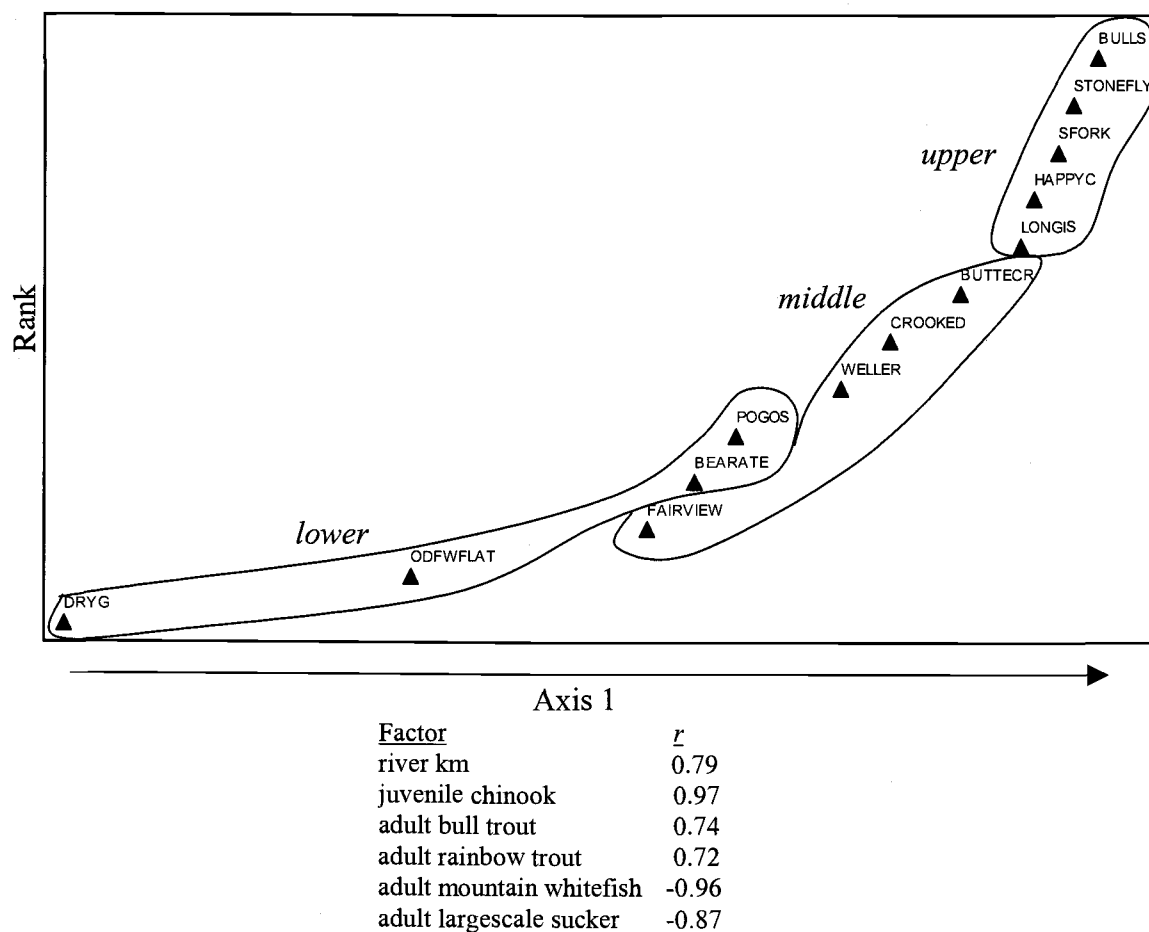


Axis 2

| Factor | r |
|---|---|
| juvenile chinook | 0.88 |
| adult bull trout | 0.58 |
| adult mountain whitefish | -0.68 |
| juv.mountain whitefish | -0.64 |
| juvenile rainbow trout | -0.56 |

Axis 1

| Factor | r |
|---|---|
| juvenile rainbow trout | 0.76 |
| adult largescale suckers | -0.73 |
| adult mountain whitefish | -0.48 |
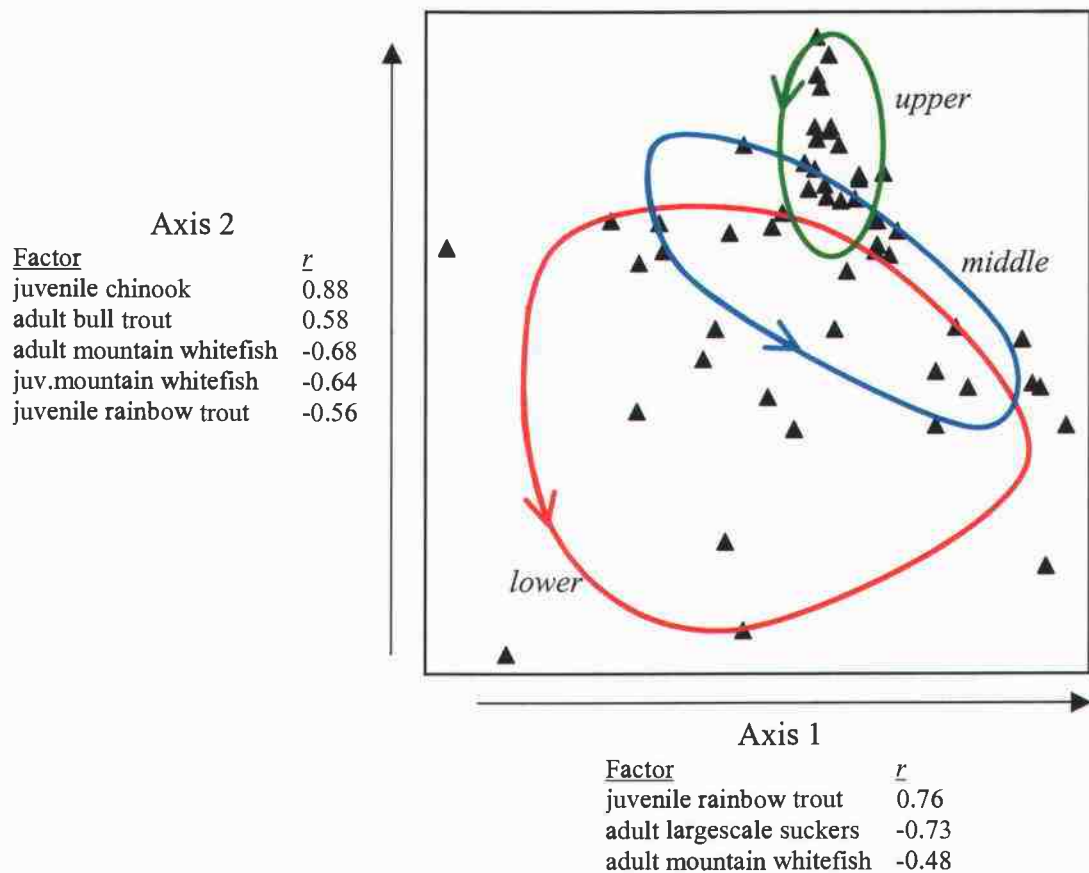
smaller shifts in community composition than those in mid-reaches, while lower reaches displayed the most dramatic seasonal dynamics (Figure 31).

### 3.2.4 Seasonal and Diel Dynamics of Fish Assemblage Structure at the Channel Unit-scale

The longitudinal context of a reach imposed constraints on the dynamics of assemblage structure in channel units within the reach. As described above, reaches in the lower section of the Wenaha River were the most seasonally dynamic. Consequently, channel units within these reaches showed more assemblage changes between the seasons. Superimposed on this pattern, however, were dynamics that reflected distribution at the channel unit scale between day and night.

Diel surveys often showed changes in the abundance of fish. As described (see section 2.7), we almost always observed greater abundance of all species at night, and this difference was most dramatic during the winter months. During spring-fall months, the observed relative abundance of fishes within a given study reach tended to remain the same between day and night observations. In winter, however, the observed relative abundance was different between day and night surveys. These results, combined with daytime observations of fish hiding within the streambed, undercut banks, wood jams, and other sources of cover, suggested that fish were present, but not visible during these surveys. By staying in the water continuously at the onset of dark, we were able to observe a striking increase in the number of fish of all species on several occasions.

Paired day-night underwater surveys of sites revealed diel changes in the fish assemblage structure in different channel unit types. These diel dynamics also differed with season. The greatest diel changes in observed fish distribution were seen during the winter, though much of this shift must be attributed to the inefficiency of daytime snorkel surveys during this season (see section 2.7). Of the different channel habitat types, alcoves and side channels exhibited the greatest diel shift in assemblage structure, and this was the case during all seasons (see details below). We also observed relative abundance changes in pools and glide-like units, though this was most dramatic in winter.

Riffles tended to be fairly stable in winter, when few fish of any species were seen in riffles during day or night. Riffles exhibited greater day-night dynamics during other seasons, particularly during summer when the numbers of fish seen in this channel type were greatest.

## 3.3 Fish Movement Patterns from Radio Telemetry at Nested Scales

Many of our observations of assemblage dynamics were consistent with the hypothesis that dynamics were driven by migration patterns within the Wenaha River, as well as in and out of the drainage. Radio tracking of adult mountain whitefish, largescale suckers, and bull trout revealed that many individuals of these three species migrated long distances (up to 300 km) to occupy habitats distributed throughout the Wenaha, Grande Ronde, Snake river system during different times of the year, though considerable variation occurred within each species (Figures 32-45). In addition, tracked fish showed distinct movement patterns at smaller spatial and shorter temporal scales.

### 3.3.1 Seasonal, Large-scale Movements: Mountain Whitefish

Seasonal migrations by radio-tagged adult mountain whitefish were perhaps the most complex of the three species tracked. Annual home range size varied dramatically among tagged adult mountain whitefish (Figure 32), ranging from 0.2 to 190 km, with an average of 61.4 km (SD = 62.2). Sizes of the 25 fish tagged were fairly consistent, averaging 39.7 cm (SD = 3.6). I observed no significant association between fish size and the total distance moved by a fish, nor was size correlated with any other aspect of whitefish movement (Pearson's correlation, $P > 0.05$). In addition, there was no association between the distance moved by a fish or suspected mortalities and any factor associated with capture or tagging surgery (e.g., duration or quality of surgery).

Figure 32. Frequency histogram of annual range for radio tracked mountain whitefish.
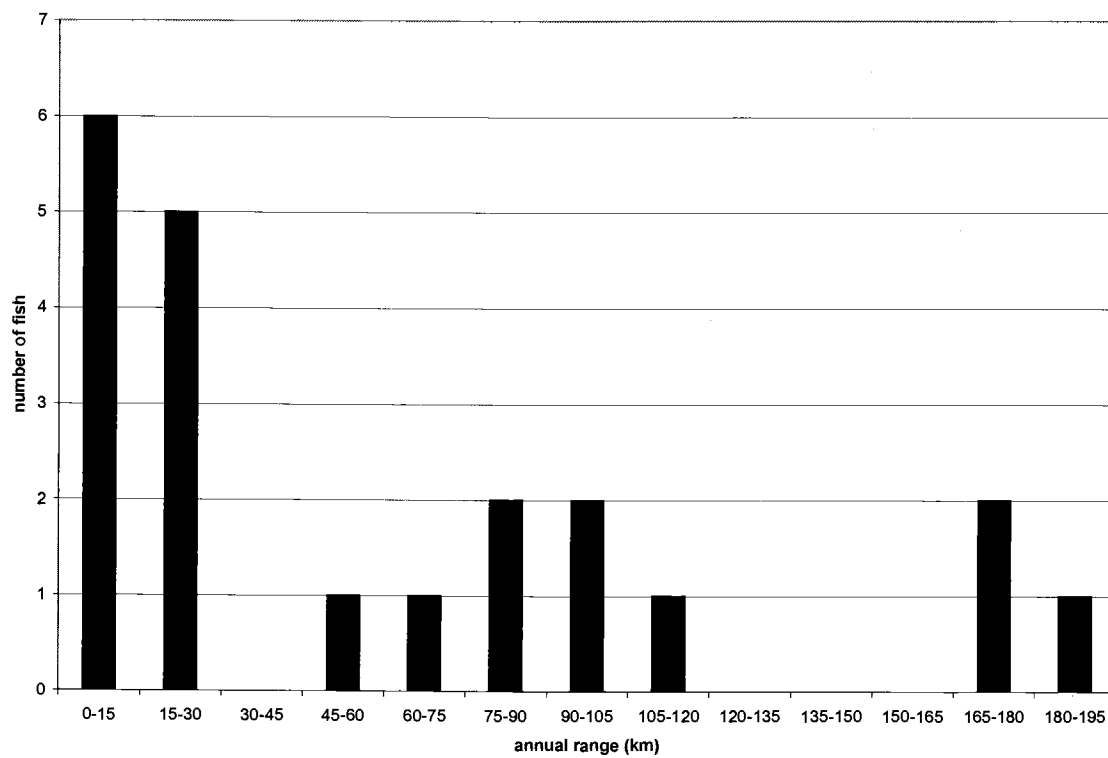
The behavior of tagged mountain whitefish appeared to reflect five different types of seasonal behavior. The first two types remained in the Wenaha River throughout the year (Figure 33). Two fish that were tagged in the lower Wenaha River (rkm 10.9) moved very little, remaining in a single reach throughout the entire year. Four fish that were tagged in the upper reaches (rkm 23-33) also stayed in the Wenaha, but exhibited a pronounced seasonal migration (avg. annual range = 10.6 km). All four of these fish remained in the reaches where they were captured until September, when they moved downstream 3-10 km to over-winter in the reach near the confluence of Butte Creek. The following spring (April-June), each of these fish moved back upstream to the same reaches (and in two cases the same channel unit) they had occupied the previous summer.

Most of the radio-tagged mountain whitefish (16) spent part of the year outside the Wenaha drainage, and of these there were three distinct types. The first group (Figure 34) consisted of 4 fish that were tagged in the upper Wenaha between rkm 23 and 35, spent the summer in these reaches, and then made a rapid downstream migration of 25-54 km to the Grande Ronde River in October or early November. These fish spent the winter months in the Grande Ronde and exhibited little movement (< 0.5 km) during this time. However, in March and April, all four of these individuals made the return migration to the same reaches (three of them to the exact channel unit) of the upper Wenaha River they had occupied during the previous summer.

The second group of fish that left the Wenaha drainage (Figure 34) consisted of 9 fish that were tagged in the mid to lower reaches of the Wenaha. Following their tagging in June and early July, these fish either 1) spent the summer in the reach where they were tagged (4 fish), 2) dropped downstream slightly (0.5-1.0 km) and held for the summer (2 fish), 3) moved up-river during July and August (2 fish), or 4) moved 100-200 m into the lower reaches of a nearby tributary in July or August (2 fish). Regardless of their summer behavior, in either September or October all of these fish migrated down into the Grande Ronde River. Distance traveled to an over-wintering site varied considerably among fish in this group (7.3-94.5 km). However, 7 of these 9 fish traveled further than 35 km. This group included the fish that traveled the furthest total distance. In particular two fish traveled 89-90 km down the Grande Ronde and up the Snake River to over-

Figure 33. Mountain whitefish tracking locations showing three of the five types of seasonal movement patterns: 1) those that were resident in the Wenaha River but undertook significant seasonal migration, 2) those that were resident and moved very little, and 3) those that moved into the Grande Ronde and did not return the following year.
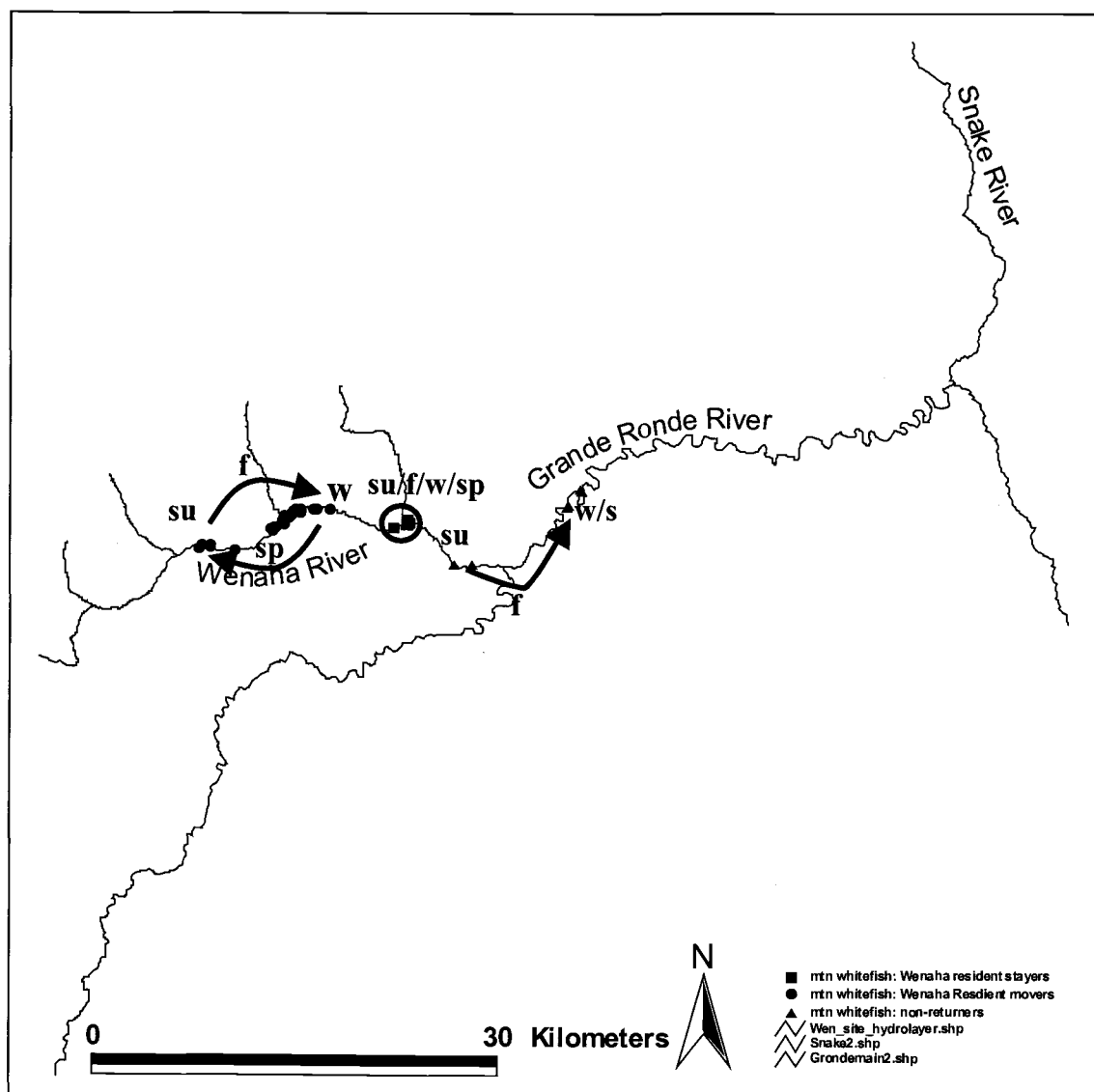
Figure 34. Mountain whitefish tracking locations showing two of the five types of seasonal movement patterns: 1) those tagged in the upper Wenaha that moved short distances into the Grande Ronde and returned early the following spring, and 2) those tagged in the mid to lower Wenaha that moved long distances in the Grande Ronde and Snake and returned later in the spring the following year.
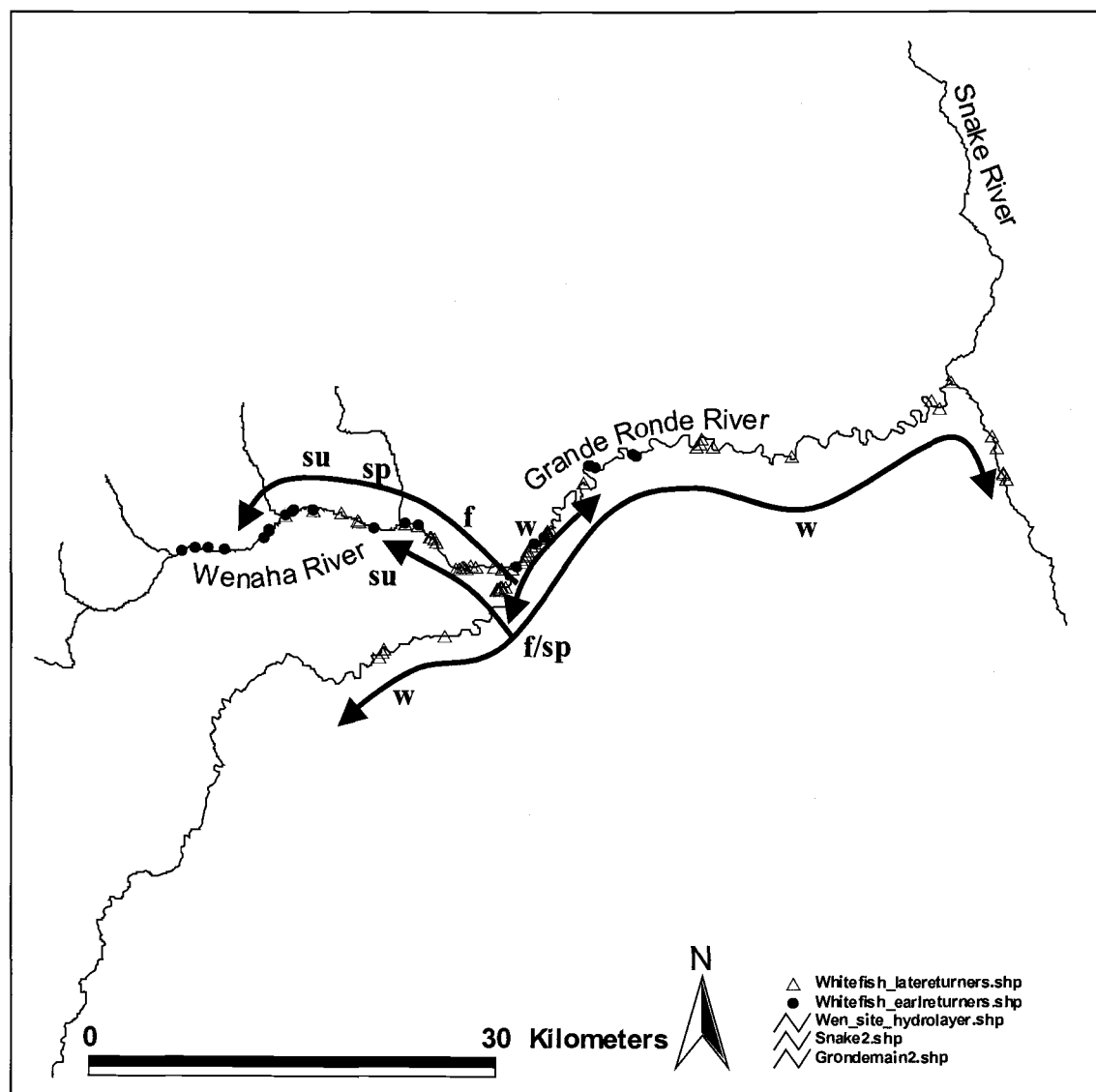
winter in the Hell's Canyon reach, and one fish migrated 95 km down the Wenaha and up the Grande Ronde River to over-winter near the confluence of the Wallowa River. These fish also exhibited little movement (< 0.5 km) during the winter months, but starting in March or April, began a migration back to the Wenaha River. This migration was more gradual than the other group's, and these fish (including the 2 that migrated only short distances from the Wenaha) did not actually re-enter the Wenaha River until late May, June, or even early July. Though tracking during June and July 2000 was limited to aerial surveys that allow only reach-scale spatial resolution, it appeared that at least 6 of these 10 fish had returned to the reaches where they were found the previous summer.

The third group of fish that left the Wenaha drainage consisted of two fish (Figure 33) that were tagged in the lower Wenaha, spent the summer in the reach in which they had been captured, and then migrated into the Grande Ronde during September or October. Though these fish were confirmed (via observations of small-scale diel movements) to be living in March 2000, they had not undertaken any significant movement when we ceased tracking in July 2000.

Finally, of the remaining 4 mountain whitefish we tagged, an angler captured 1 in the lower Wenaha just weeks after tagging. The other 3 dropped downstream after tagging and remained in a single location throughout the year. After several unsuccessful attempts to view them underwater and/or detect movement, I presumed that these three fish had either died or their tags had been shed. Other than these, we were able to confirm the live status (through underwater observation or tracking of diel movements) of all of our tagged mountain whitefish. In numerous instances, we observed active feeding by our tagged fish. In several cases we were able to make close observations of the surgery wound site on fish, and always found that the fish appeared to have healed well.

### 3.3.2 Seasonal, Large-scale Movements: Largescale Suckers

Seasonal movements by largescale suckers involved the longest distances moved by any of the three species we tracked. Seasonal home range for tagged adult largescale suckers ranged from 17.2 to nearly 300 km, with an average of 111 km (SD = 71.7) (Figure 35).

We tagged 11 male and 14 female suckers. The females were slightly larger on average but varied more in size (mean FL = 45.4 cm, SD = 5.63) than the males (mean FL = 43.8 cm, SD = 2.09). We observed no significant association between fish size and the total distance moved by a fish (Pearson's correlation, $P > 0.05$). We did not detect any association between distance moved and a fish's sex (T-test, $P > 0.05$). Neither were there any associations between distance moved by a fish or observed mortalities and any factor associated with capture or tagging surgery (e.g., duration or quality of surgery).

Following their tagging in late-June and July, the individuals we tracked remained in the main-stem Wenaha River for variable amounts of time. During the summer (Figure 36), thirteen of the suckers moved downstream into the Grande Ronde River within 5 days of their tagging date, 6 fish stayed 10-25 days, and 3 fish remained in the Wenaha for 30-50 days before moving into the Grande Ronde. The length of stay in the Wenaha tended to be greater for male fish (avg. 14 days) than for females (avg. 9 days). However, there were 2 females that stayed longer than 20 days, and 6 males that left within 5 days of their tagging. Once in the Grande Ronde, suckers migrated quickly up and downriver; most fish reached what was to be their over-wintering reach in less than 1 week. Eight fish moved to reaches in the Grande Ronde upstream of the Wenaha River confluence, five moved to reaches in the Grande Ronde downstream of the confluence, and 7 fish traveled downstream to reaches of the Snake River. Three tagged fish (all females) were tracked out of the Wenaha River, but were then lost entirely and their signals were not detected again during the study.

By the fall (Figure 37), the amount of sucker movement had declined. Fish spent the winter months in the Grande Ronde or Snake River (Figure 38) and exhibited little movement (< 0.5 km) during this time. In the spring, however, we observed 16 of the

Figure 35. Frequency histogram of annual range for radio tracked largescale suckers.
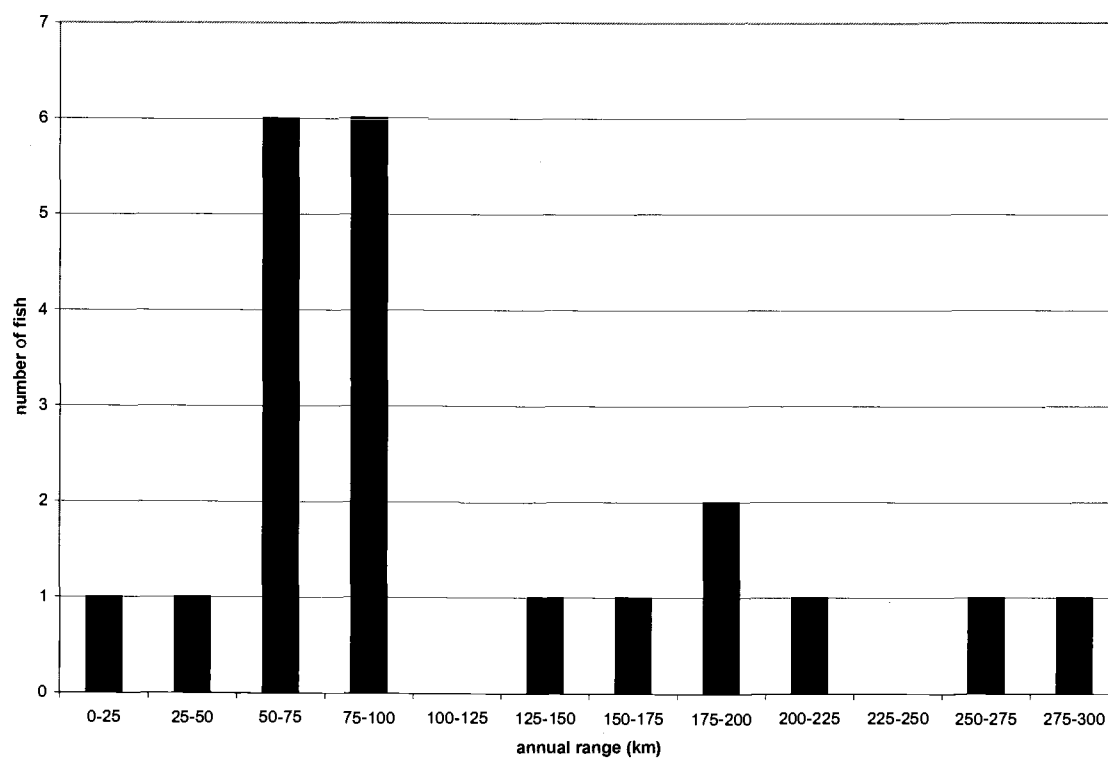
Figure 36. Tracking locations of largescale suckers in July and August of 1999, showing their migration into the Grande Ronde and Snake rivers during this time period.
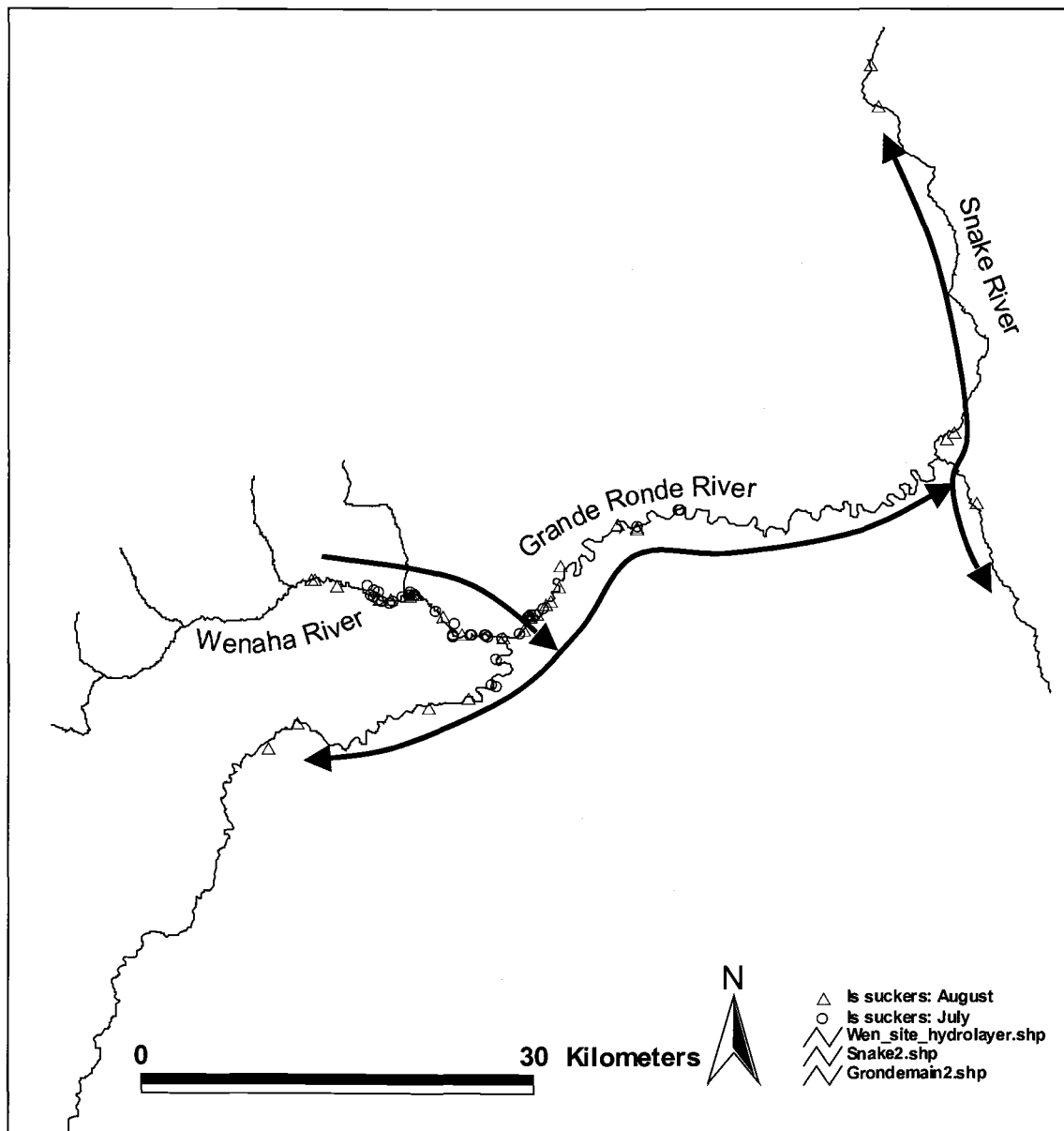
Figure 37. Tracking locations of largescale suckers in September and October of 1999, showing their migration throughout the lower Grande Ronde and Snake rivers during this time period.
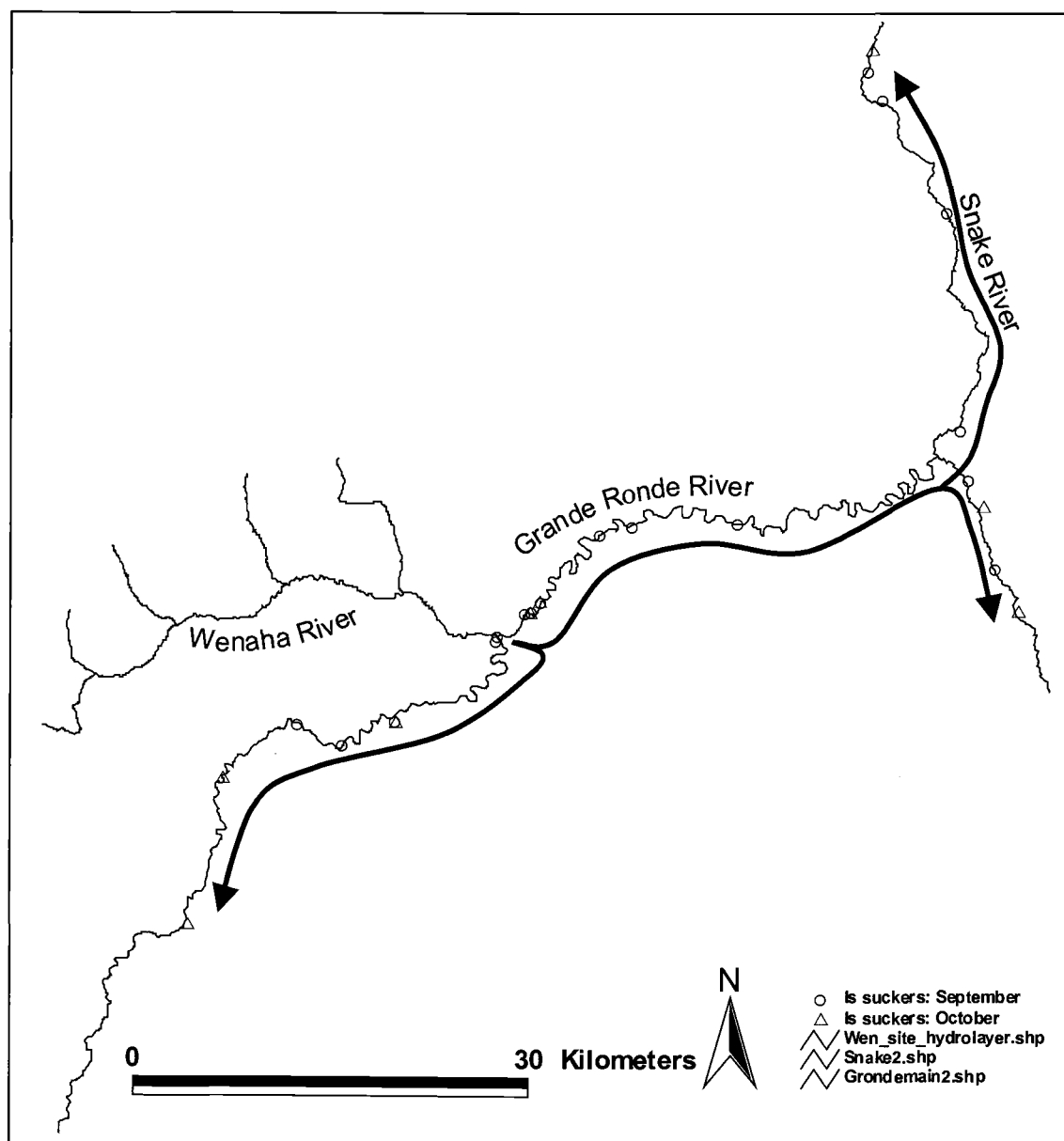
Figure 38. Tracking locations of largescale suckers from November, 1999 to March of 2000, showing their over-wintering range in the lower Grande Ronde and Snake rivers. Largescale suckers exhibited little large-scale movement during the winter (hah! no pun intended!).
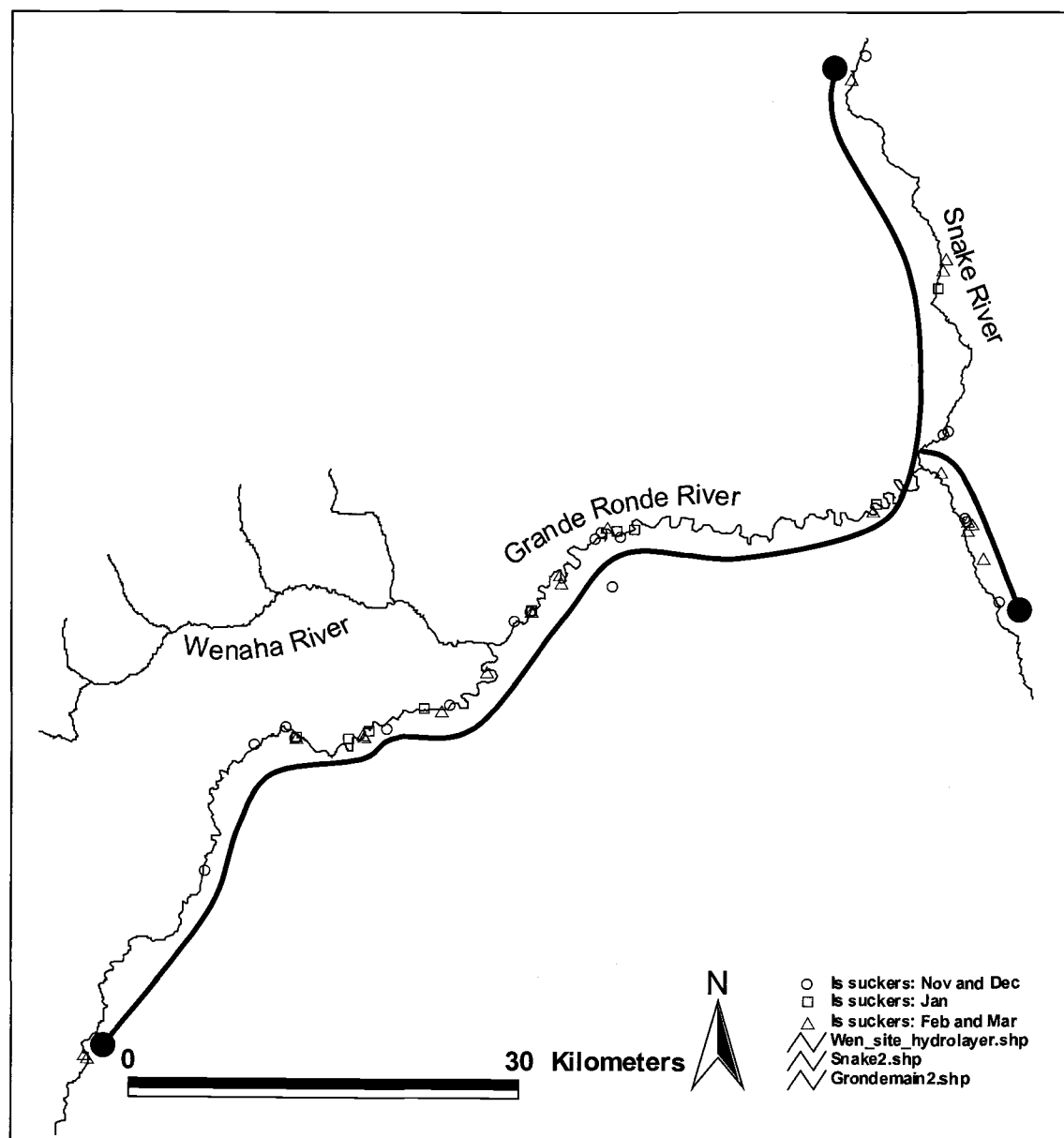
tagged fish migrated back to the Wenaha River (Figure 39). Among these returners there seemed to be two groups, a group (7 fish) that moved up into the Wenaha in May and early June, and another (9 fish) that moved in during July. Four fish (all males) that we had tracked through the winter did not return, and though they had been confirmed alive during early winter, this could not be confirmed in the spring. A greater proportion of the tagged females returned (71.4%) than the tagged males (54.5%). Of the 6 males that did return, 3 returned in May/June and 3 in July. Of the 10 female suckers that returned, 4 returned in May/June and 6 in July. There was no association between size and whether a fish returned or not; nor was size associated with the timing of return migrations.

During our tracking, we confirmed (via carcass observation) two mortalities among our tagged suckers. One of these, a large female died in the Wenaha within a week of tagging. The other, a male, was found along the lower Snake River in the February of 2000. We also made underwater observations of several tagged fish, documented their feeding on several occasions, and found that surgery wound sites appeared to have healed well.

### 3.3.3 Seasonal, Large-scale Movements: Bull Trout

Through the efforts of Oregon Department of Fish and Wildlife biologists (see also Hemmingsen et al. 2001 for details of this cooperative research), we observed extensive seasonal migrations by radio-tagged adult bull trout, and were able to identify several distinct movement patterns. We gained additional perspective on bull trout migration and life history patterns because some fish were tracked over multiple years. Annual home

Figure 39. Tracking locations of largescale suckers in April, May and June of 2000, showing the general pattern of their return migration into the Wenaha River during this time period.
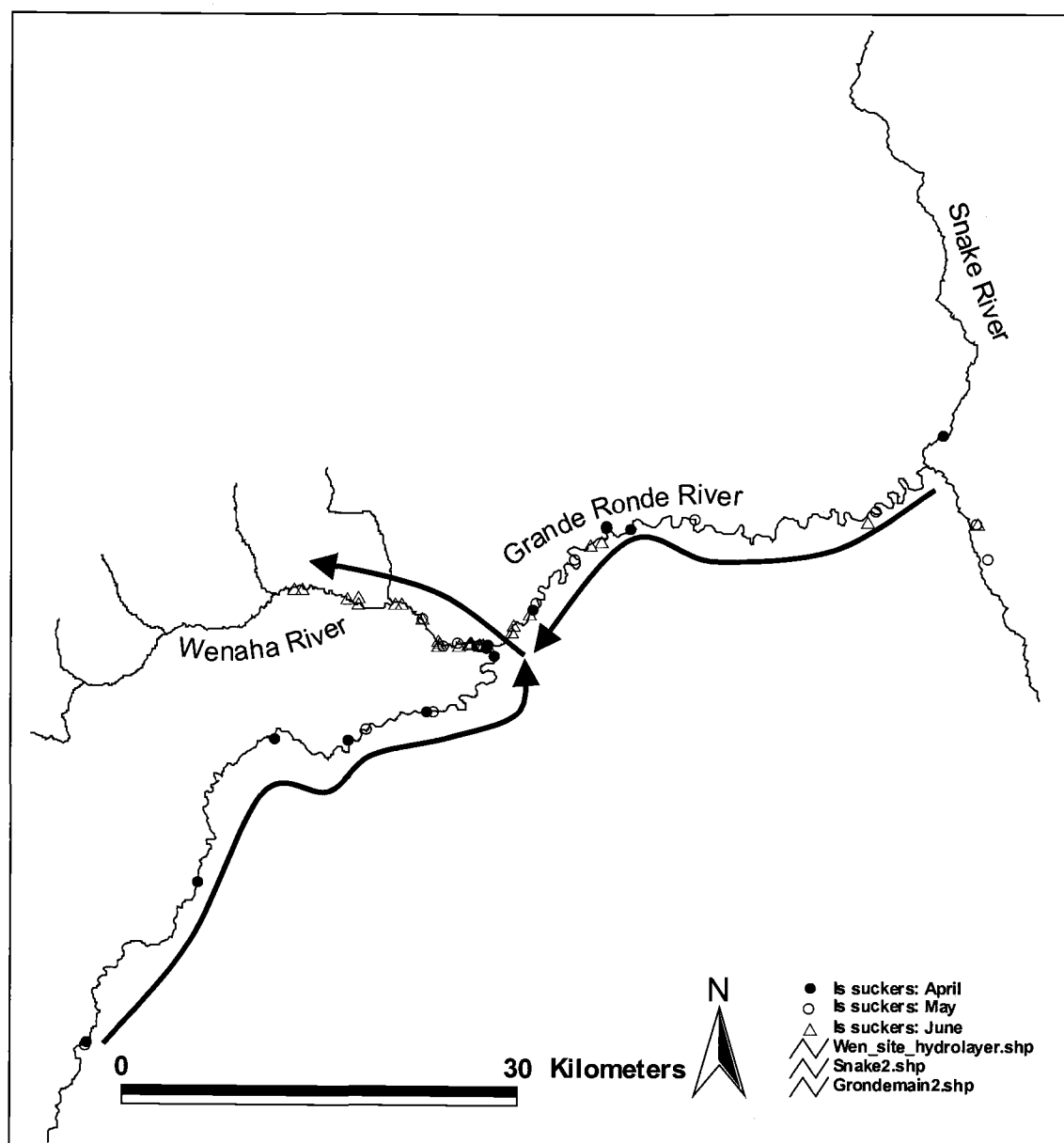
range varied significantly among tagged adult bull trout (Figure 40), ranging from 20 to 280 km, with an average of 108 km (n = 31 complete track years, SD = 62). As indicated above, there were two distinct size classes of fish tracked. The 15 fish tagged in 1997 and 1998 were large adults (mean FL = 490 mm), while smaller adult or sub-adult fish (mean FL = 340 mm) were tagged in 1999. Among the fish we tracked, there was no association between fish size and the annual range of a fish. Five fish between 310 and 350 mm in length were tagged, and, while these fish did not exhibit the longest movements, their average annual range was 100 km (range 76-116 km). The only difference in movements we observed associated with fish size was that individuals that we observed in tributaries of the Wenaha River generally did not include the smallest fish tagged. Though it is possible that additional fish ascended and descended these spawning tributaries without our detection, we observed 11 fish in different tributaries (South Fork, North Fork, Slick Ear Cr., Butte Cr., and Crooked Cr.) and these averaged 462 mm in length (range 350-589 mm). There was no association between the distance moved by a fish and any factor associated with capture or tagging surgery (e.g., duration or quality of surgery).

The behavior of tagged adult bull trout appeared to reflect several different types of seasonal behavior. One type (3 fish, 51-53 cm) remained in the Wenaha drainage throughout the year, but undertook significant seasonal migrations (Figure 41). Included in this type were two fish that were tagged in the upper reaches (rkm 32-35), spent the summer and fall there, but moved downstream to spend winter and early spring in the reach below Butte Creek (rkm 22-25), and then returned to the upstream reaches the following spring and summer. Both of these fish were tracked through two full years of this same cycle (annual range 21-29 km), and were found in some of the same habitat units each year. Another fish that was tagged in the upper drainage (rkm 30) spent summer and fall 15-20 km up the North Fork of the Wenaha, moved back to the main river for the winter, and then returned to the North Fork the following spring (annual range 49 km).

Figure 40. Frequency histogram of annual range for radio tracked bull trout.
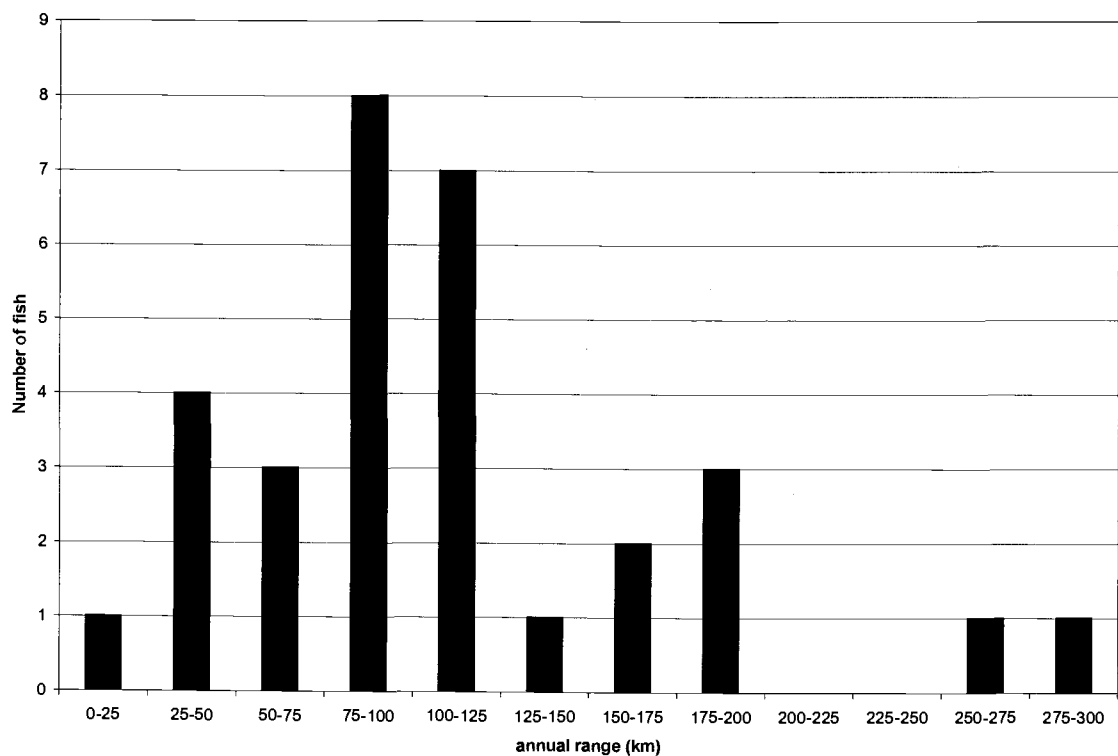
Figure 41. Bull trout tracking locations of 3 fish that stayed in the Wenaha drainage, but undertook significant seasonal migrations.
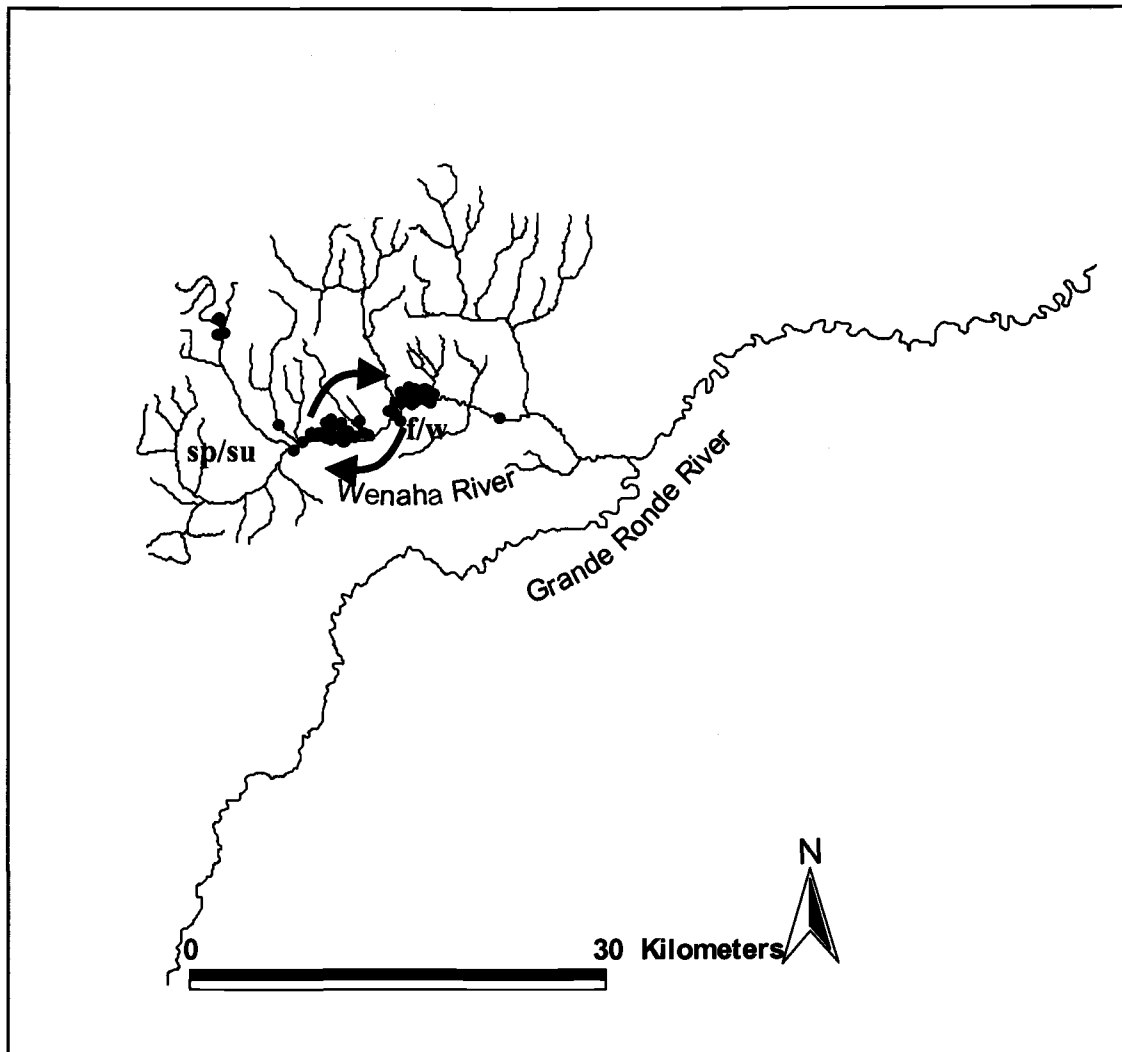
Most of the tagged bull trout (25 fish) spent part of the year outside the Wenaha drainage. Among these, over-wintering locale varied. Some fish were observed to return to the Wenaha River the next year, others the year after, and a few did not return at all. Following their tagging in early summer, the general pattern for these fish was to spend the summer in the mainstem Wenaha River, during which they tended to exhibit either little movement or movement upstream (Figure 42). Fish typically reached their most upstream location in the mainstem or in a tributary sometime between mid-August and early September (Figure 43). From our observations and those of others (B. Knox and B. Smith, ODFW, personal communication), most spawning appeared to occur between mid-September and mid-October. Most fish had moved down the Wenaha into the Grande Ronde River by mid-October to early November and typically reached their furthest distance from the Wenaha anywhere from late October to mid-December (Figure 44). Among these fish, return migration to the Wenaha occurred in the spring between May and early July (Figure 45).

Of the 25 fish that migrated out of the Wenaha drainage, 14 were tracked for one full year, while 11 were followed over the course of at least 2 years. Of the fish that were tracked over just one full year, all but 4 were observed to return to the Wenaha the following spring. Of these 4, 2 may have returned but data were lacking due to transmitter expiration. The other 2 remained, one in the Grande Ronde and the other in the Snake River, throughout the next year and both showed significant upstream movement (i.e. they were alive) the following spring before their transmitters expired. Among the 11 fish that were tracked over at least 2 full years, 4 returned to the Wenaha in the 2 years following tagging and 1 fish (with exceptional transmitter life) actually returned a 3rd consecutive spring. Three fish returned the next year but not the following year, while 3 fish (confirmed alive) did not return at all over the two-year period. There was no association between fish size and when or whether a fish returned.

Bull trout that moved out of the Wenaha drainage over-wintered in the Grande Ronde River, both upstream (15 fish) and downstream (7 fish) of the Wenaha River confluence,

Figure 42. Tracking locations of bull trout in July and August: most were distributed within the Wenaha River, though a few individuals spent the summer months in the Grande Ronde River. While some tagged fish exhibited upstream movement during these months, others made no large-scale movements.
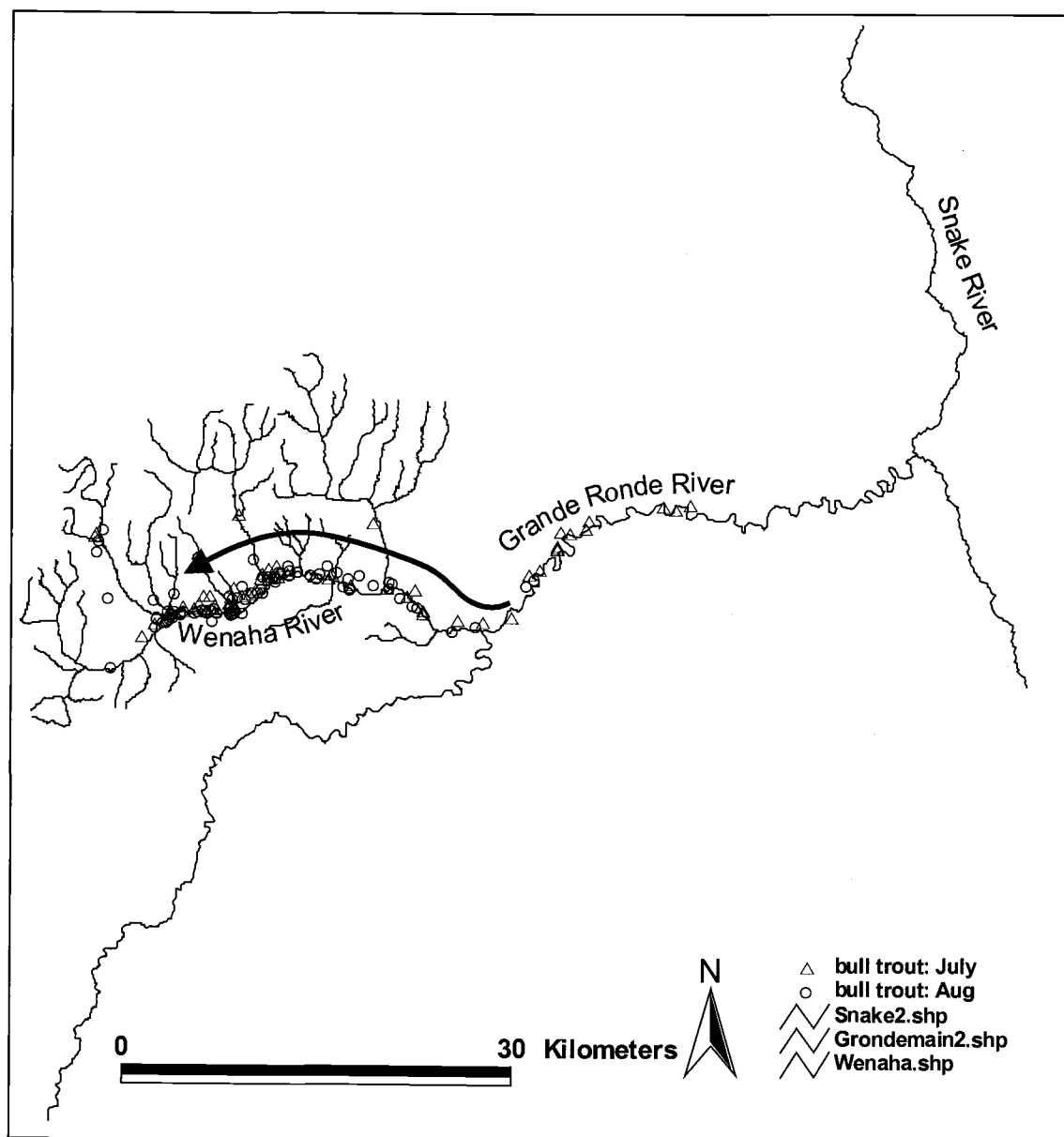
Figure 43. Tracking locations of bull trout in August, September and October.
During the fall, most tagged bull trout migrated down into the Grande Ronde River, while
some fish were tracked into tributaries of the Wenaha (presumably for spawning) prior to
their leaving the basin.
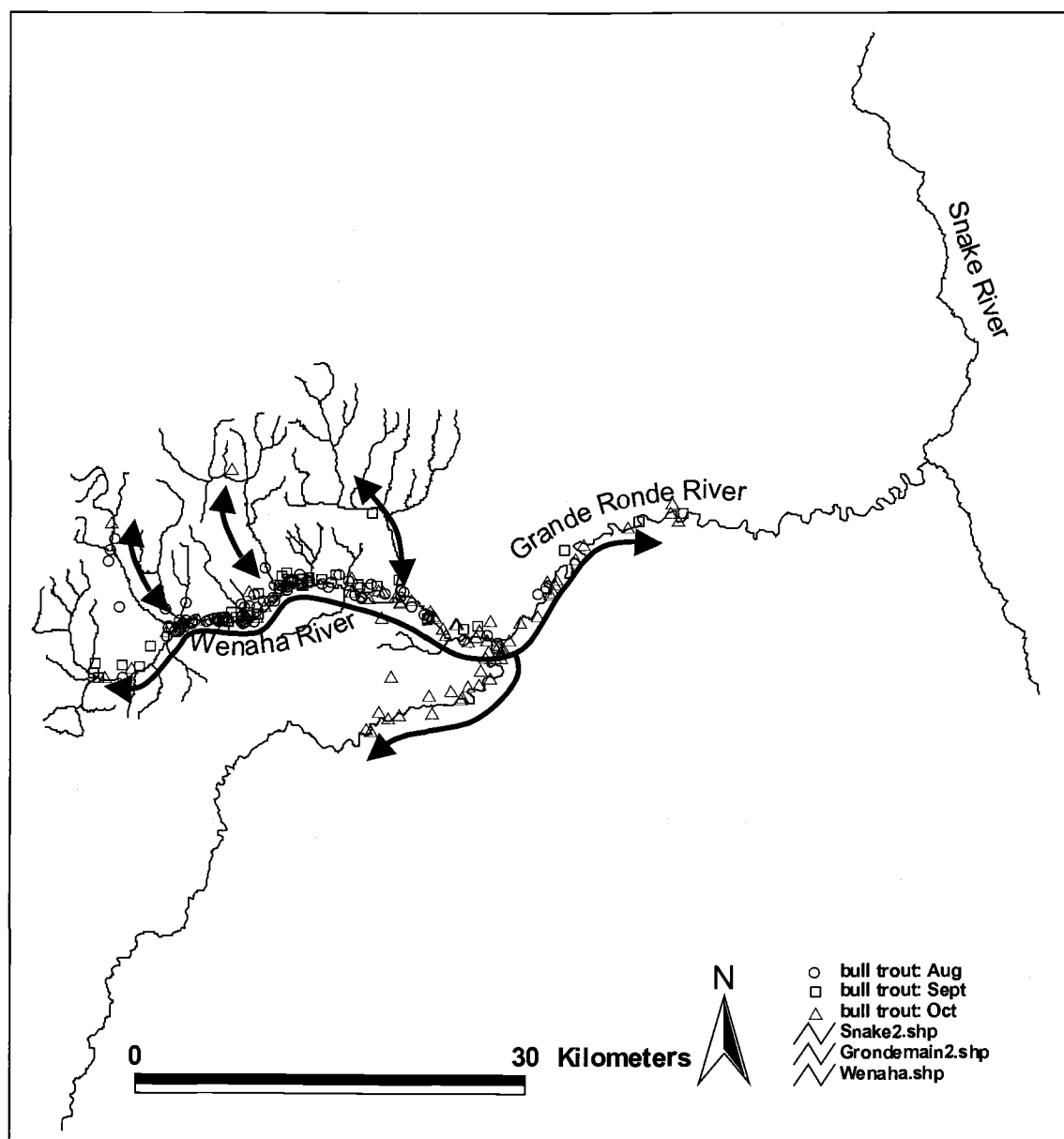
Figure 44. Tracking locations of bull trout from November through March showing their over-wintering range in the lower Grande Ronde and Snake rivers. Though some fish were still moving in November, adult bull trout exhibited little large-scale movement during the winter months December-March.
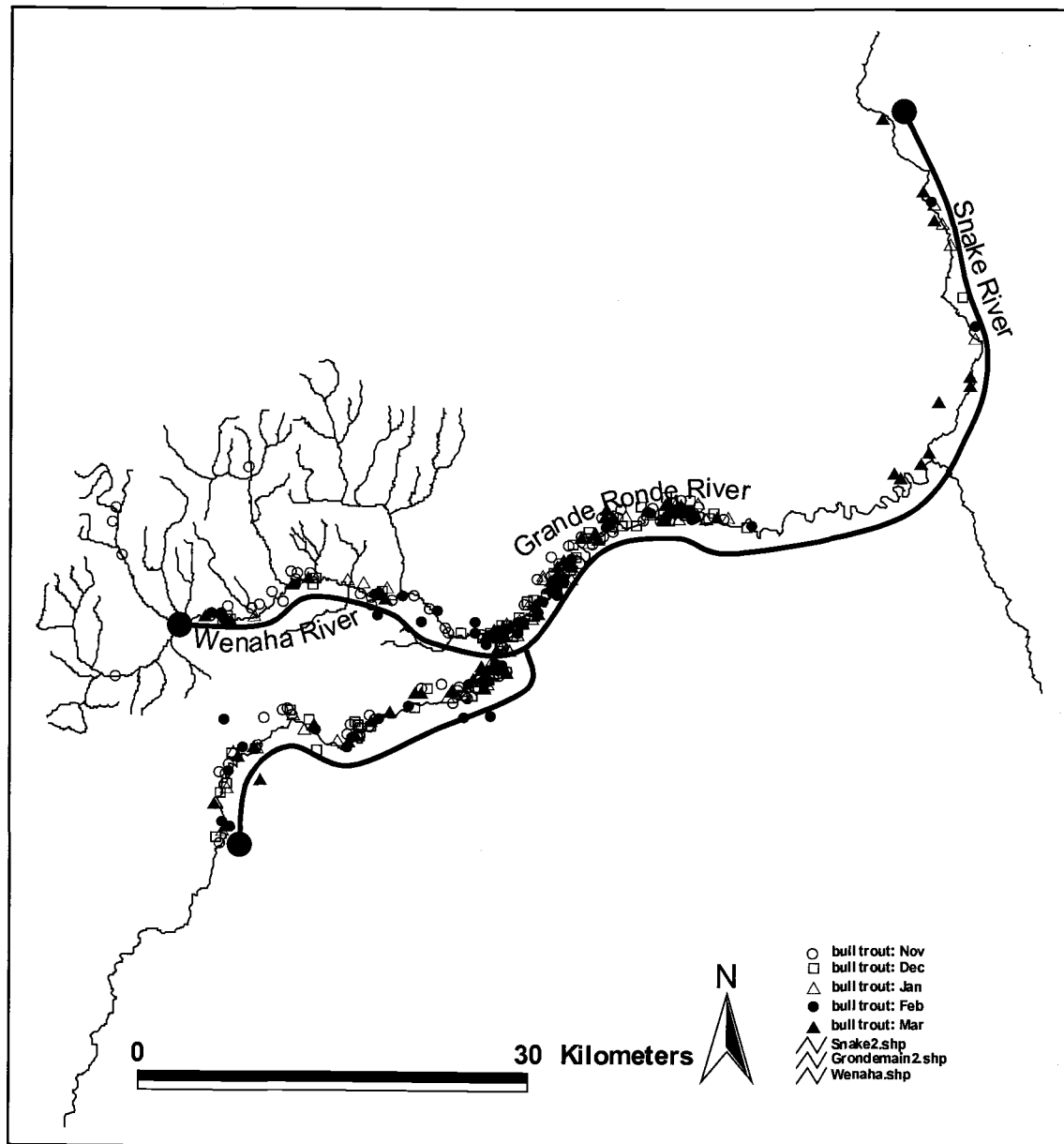
Figure 45. Tracking locations of bull trout in May and June showing their general pattern of return migration back into the Wenaha River during this time period.
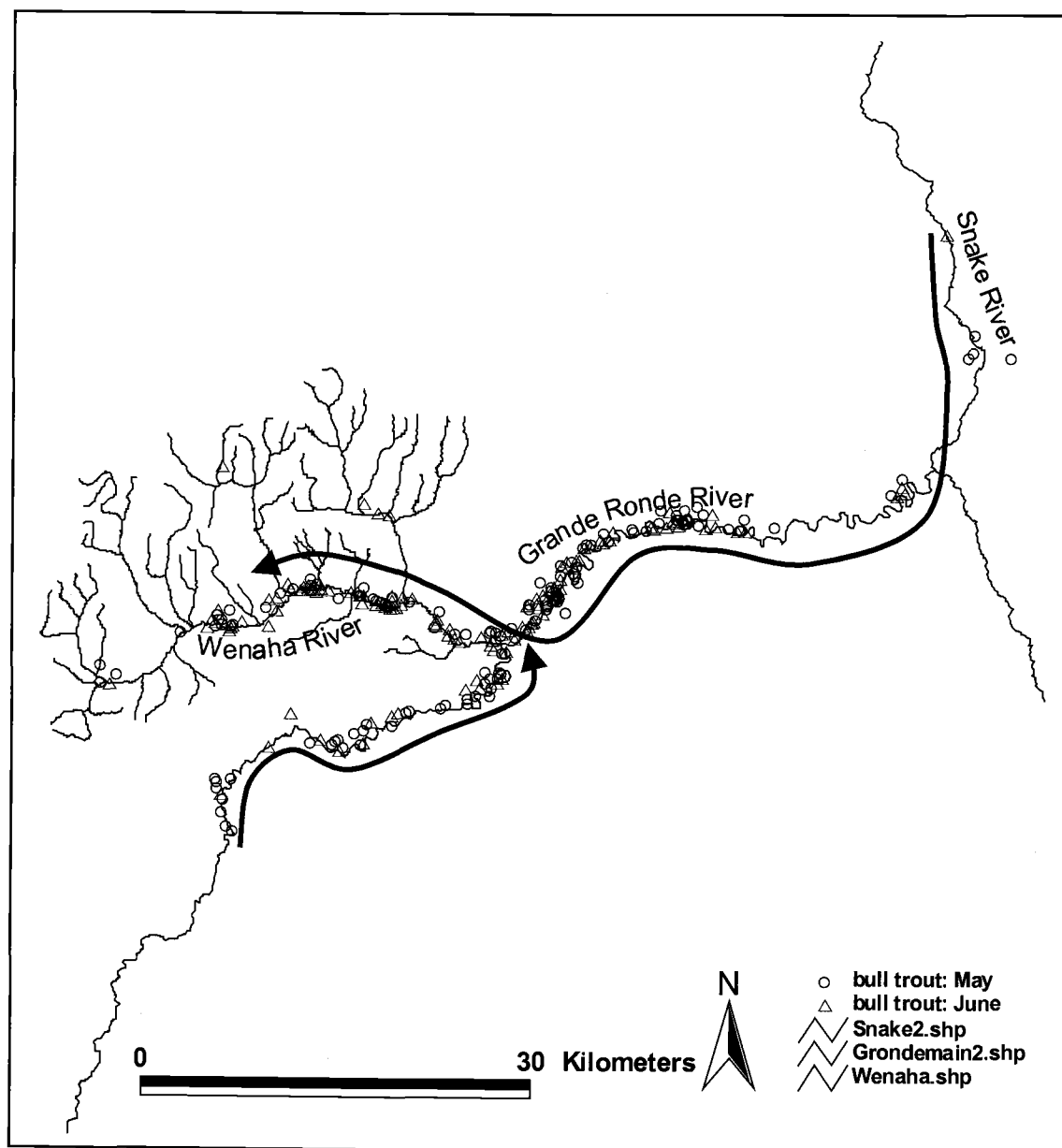
as well as in the Snake River (3 fish). Fish that were tracked through more than one cycle of migration to and from the Wenaha River did not always over-winter in the same reach. For example, one fish that returned to the Wenaha in 2 consecutive springs after tagging spent the first winter in the Grande Ronde River above the Wenaha confluence, and then spent the next winter in the Snake River.

Tracking fish over multiple years gave us the opportunity to detect interannual differences in the timing of movement. Within a given year, the timing of bull trout migration was similar among fish. However, we observed one difference between years. In the spring of 1999, which had higher flow levels than usual (Figure 16), bull trout returned to the Wenaha River significantly later (mean date 6/28/99) than in the spring of 2000 (mean date 6/15/00).

We did not observe any mortality among bull trout radio-tagged in 1999, though a few fish that were tagged in 1998 and were still transmitting could not be confirmed (via upstream movement or underwater observation) to be alive. These were excluded from all analyses. In general, bull trout appeared resilient to the capture and tagging process. We made numerous underwater observations of tagged fish and observed no complications associated with the surgical wound site or antennae. We also observed active feeding by tagged fish, including, on one occasion, predation on a sculpin that was spooked out of cover by the diver.

### 3.3.4 Diel Movements by Radio-tracked Fish

Radio-tracked fish exhibited distinct diel movement patterns. A common theme in the movement of mountain whitefish, largescale suckers, and bull trout was the tendency for the large-scale migrations (e.g., from spawning to over-wintering habitat) to occur over very short time periods. We observed that most of these movements (which, as described, frequently exceeded 100 km one-way) occurred within a 1-3 week period. For example, one largescale sucker moved 125 km from over-wintering habitat in the Grande Ronde to the lower Wenaha River in 4 days. Due to this rapid movement and the

frequency of our tracking surveys, we rarely had the opportunity to map the diel movements of fish that were in the midst of a large-scale migration, except on 4 occasions. These occurred twice with mountain whitefish and once with a sucker during the spring migrations back to the Wenaha, and once with a bull trout during its fall migration down the Wenaha to the Grande Ronde. During these episodes, the 2 mountain whitefish moved sporadically upstream. One moved during the day (1.1 km) and night (3.2 km) for a total of 5.3 km, while the other moved only during the night for a total of 10.2 km upstream. The largescale sucker moved 15.4 km upstream in an 18 hr period, all of which occurred during the night. Similarly, the bull trout we tracked moved downstream a distance of 17.3 km overnight.

There were several diel patterns observed that could be generalized for all three species that were tracked. Most fish that were tracked on a diel basis stayed within a given reach, usually moving less than 400 m total distance. It was also common for fish to stay within the same channel unit throughout a 24 hr period. It was rare, however, for a fish of any of the three species to remain in the same portion of the channel throughout the day-night time frame.

## 3.4 *Fish-habitat Associations: Habitat Complementation at Multiple Scales*

I found that several species of fish exhibited distinct movement patterns at different spatio-temporal scales, ranging from dramatic seasonal migrations to marked diel movements. We also observed that these movements resulted in their use of different habitats at different times and that these habitats were not uniformly distributed, but were spatially separated within the riverscape. Thus, it appeared that movement resulted in the complementary use of non-substitutable habitat resources at nested scales. The integrated results of underwater surveys and radio telemetry yielded a more full perspective on this phenomenon. Through these approaches, I identified the general relationship between life history and large-scale habitat needs of each species.

## 3.4.1  Seasonal, Drainage Scale Complementation

The majority of the species found in the Wenaha River exhibited at least one life history form that seasonally utilized some combination of habitat, ranging from tributaries of the Wenaha River to the Grande Ronde, the Snake River, and, in the case of chinook salmon and steelhead trout, the Columbia River and Pacific Ocean. Species differed in the times and potential reasons for their occupation of these different streams and rivers. Though we observed a general theme of migration into the Wenaha in the spring and back to the Grande Ronde in fall, there was significant variation among and within the radio-tracked species. Underwater observations augmented the interpretation of these patterns and yielded a riverscape perspective on the complement of habitats required for the life history of each species.

Our observations showed that different life history forms of mountain whitefish used somewhat different drainage scale complements of habitat. However, all adult mountain whitefish appeared to use portions of the Wenaha River for spawning and/or spring-summer feeding, most adults used parts of the Grande Ronde and Snake Rivers for over-wintering habitat, and most juvenile rearing appears to occur in the larger river environment. As described, some tagged mountain whitefish remained year-round in the Wenaha River, though most migrated out of the drainage. These observations corresponded to what we observed via underwater surveys. Mountain whitefish tended to have somewhat smaller annual ranges than the other two tracked species (though a few fish did over-winter in the Snake River). Tagged whitefish did not exhibit substantial use of Wenaha River tributaries. We observed only two instances, both during summer, in which tagged whitefish entered the lower reaches of a tributary (Crooked Creek and Butte Creek) for a brief period (< 1 month). Among those whitefish that moved out of the Wenaha there was variation in the time spent in the Wenaha. Some individuals entered as early as March and left as late as mid-November, and others (including those that traveled the furthest) remained in the Wenaha for a shorter period of time, arriving

later in the summer and leaving by September of October. Consequently, though the timing of whitefish presence in the Wenaha may include their spawning period (mid October-November), and some individuals do use the river for spring-summer feeding and fall spawning, it is clear that many adult whitefish that use the Wenaha do so for reasons other than spawning. Our observations showed active feeding by whitefish throughout the time of their stay in the Wenaha. Juvenile and sub-adult mountain whitefish were found throughout the river, though in relatively low densities compared to the number of adults using the river in summer.

We found that most migratory adult bull trout used tributaries to the Wenaha for fall spawning, while both adult and sub-adult fish used the main-stem Wenaha River for summer holding and feeding, and many adult and sub-adult fish over-wintered at sites in the Grande Ronde and Snake Rivers. During our dive surveys we saw many small (< 20 cm) bull trout in the Wenaha River (mostly in the upper reaches) on a year-round basis, indicating that 1) juvenile rearing habitat is an important function of the upper Wenaha to migratory bull trout and 2) a non-migratory life history form, characterized by small size at maturity, likely occurs in the basin. All of the radio-tagged bull trout undertook significant seasonal migrations. Tagged bull trout did exhibit a migratory type that stayed within the Wenaha River, though most moved out to the Grande Ronde, and in several cases to the Snake River, where they typically stayed from late fall to early spring. Some bull trout remained in the Grande Ronde River throughout the full year following their tagging, while others made consecutive return trips to the Wenaha. Among those that left the Wenaha drainage, we observed less variation in the duration of time spent in the Wenaha by bull trout than by whitefish.

Largescale suckers used reaches of the Wenaha River primarily for spawning and early larval rearing, and used reaches of the Grande Ronde and Snake Rivers for over-wintering and juvenile rearing. When compared to mountain whitefish and bull trout, largescale suckers spent less time in the Wenaha River. While some suckers spent most of the summer in the Wenaha, others appeared to spend only 1-2 weeks in the lower reaches before returning to the Grande Ronde, and in several cases, the Snake River. Radio tracked largescale suckers were never observed in tributaries of the Wenaha River.

The time period when suckers were present in the Wenaha overlapped closely with the time during which we observed their spawning, though the variable length of stay and the active feeding we observed indicate the Wenaha may have served as spring-summer feeding grounds for some members of this species as well. Our survey data showed that reaches of the Wenaha were utilized by large numbers of larval suckers in the first 1-2 months of their lives, but most of these underwent downstream movement out of the river by fall and there appeared to be relatively little use of the Wenaha River for rearing by juvenile suckers. In contrast, large numbers of juvenile suckers were observed in the shallows of the Grande Ronde River.

Based on our underwater surveys, we observed some evidence for drainage scale habitat complementation by species other than those we radio-tracked. For example, it was clear from our surveys that northern pikeminnow utilized reaches of the Wenaha River during the summer (Figure 24), but spent the rest of the year in the Grande Ronde and/or Snake rivers. We observed no juvenile or sub-adult pikeminnow in the Wenaha River, nor any spawning behavior. However, as we did observe active predation by adult pikeminnow on both juvenile fishes and aquatic invertebrates, it appeared that the main function of the Wenaha River for this species was as summer feeding habitat, though for a relatively small number of adults. Interestingly, the shift in their distribution from early to late summer corresponded to an increase of their density in those reaches where the highest densities of juvenile fishes also occurred (see Figure 22, for example).

Another example of complementation at the drainage scale was suggested by the shifts in abundance of rainbow trout in lower reaches of the Wenaha River. As previously described, there was a significant increase from early to late summer in the numbers of adult rainbow trout observed in the lower 2 km of the Wenaha River. It was during this time that the Wenaha River became dramatically cooler than the Grande Ronde River (Figure 8), where rainbow trout are also known to reside (Figure 23). These observations indicated that the lower Wenaha River might have served as a summer thermal refuge for rainbow trout that otherwise spent most of the year in reaches of the Grande Ronde River.

Finally, while chinook salmon were not the focus of radio telemetry in this study (but see Price 1998) our observations clearly demonstrated the importance of the mainstem Wenaha River as summer holding habitat for adult chinook, and both the mainstem Wenaha and its tributaries as spawning and rearing habitats. Though, as described above, we observed relatively few adult chinook salmon, most summer holding sites in the mainstem Wenaha appeared to be in the upper two-thirds of the river. Most spawning appeared to occur upstream of rkm 17 and in tributaries (B. Jonassen, ODFW, personal communication). Juvenile chinook, while they were present throughout the mainstem Wenaha River, were more abundant in upstream reaches, particularly in the section between Butte and Weller Creeks. Similarly, our few observations of adult steelhead trout indicated that they use the mainstem Wenaha River for holding and some spawning. Juvenile steelhead could not be distinguished from other *O. mykiss* juveniles, which were found throughout the mainstem Wenaha from 2nd order tributaries downstream.

## 3.4.2 Seasonal, Valley Segment Complementation

Set within the context of drainage scale migrations, we observed that fish species displayed other large-scale complementary habitat use. Fish species distribution and radio tracking locations were associated with large-scale habitat heterogeneity, but these associations changed with season. In the summer, reach-scale fish assemblage patterns along the length of the Wenaha River were strongly associated with water temperature, which (as described above) increased gradually in a downstream direction. Axis scores from the NMDS ordination of summer extensive survey data were strongly associated ($P < 0.05$) with this gradient in temperature and river km. In contrast, stream temperature was not as strongly associated with gradients in reach assemblage structure in fall and spring, and not at all during winter. Though there was not an association between winter assemblage structure and pool depth, we did observe winter assemblage structure was

correlated with the volume of alcove habitat present within a reach ($r = -0.70$, axis 1, Figure 28), a factor we explore further below.

Among the species we radio tracked, I found that most fish used a mosaic of habitats distributed throughout several valley segment types during the course of a year. While fish were spatially associated with certain valley segment types and appeared to select habitat within them, this selection changed with the seasonal context.

Observations of tracked mountain whitefish showed associations with certain valley segment types and these associations changed with season (Table 5). During the winter, mountain whitefish used habitat in alluviated canyon segments proportionately more than their availability in the study area. During this time period (nov-feb), 67% of mountain whitefish locations were in alluviated canyons, and electivity for this segment type was significant (Bonferroni confidence interval: $P < 0.05$). In contrast, fish appeared to avoid (relative to its availability) habitat in both alluvial valleys and canyons ($P < 0.05$), and few were found in terrace bound or alluvial fan influenced valley types. In spring (mar-may) these associations shifted slightly, with whitefish showing less of an affinity for alluviated canyons (61% of locations), more occurrences in alluvial fan valleys (21%) and terrace bound valleys (7%), but continuing avoidance of canyon habitat ($P < 0.05$). There was a dramatic shift in segment use vs. availability in summer months (jun-aug). During this time period, though the majority of whitefish occurrences were in alluviated canyon segments, the proportion (38%) was much lower than in other seasons. Whitefish occurrences were more evenly distributed among segment types, and they displayed selection ($P < 0.05$) for valley segments (23 % in alluvial fan, 21% in terrace bound, and 18% in alluvial valley types) and avoidance of habitat in canyon segments. From summer to fall there was little change in valley segment associations. In the fall (sept-oct) whitefish continued to select habitat in valley segment types relative to its availability ($P < 0.05$), while avoiding canyon segments.

Electivity analysis of largescale sucker use of habitat at the valley segment scale also revealed seasonally dynamic associations with valley segment types (Table 6). During winter months, suckers showed significant ($P < 0.05$) preference for habitat in alluviated canyons (76% of locations), and significant avoidance of all other types with the

Table 5. Analysis of valley segment type availability and seasonal use by radio tracked mountain whitefish. Valley segment selection by mountain whitefish is described using an electivity index and 95% confidence intervals indicating statistically significant preference or avoidance.

| Valley segment type* | Species-season | Proportion of habitat in range of species | | Bonferroni confidence intervals | | | |
| | | Available | Occupied | Lower 95% | Upper 95% | Significant (P < 0.05) | Electivity |
|---|---|---|---|---|---|---|---|
| AV | mwf-spring | 0.08 | 0.07 | -0.51 | 0.65 | no | -0.12 |
| AFV | mwf-spring | 0.05 | 0.21 | -0.74 | 1.16 | no | 0.62 |
| TBV | mwf-spring | 0.05 | 0.09 | -0.57 | 0.75 | no | 0.28 |
| AC | mwf-spring | 0.42 | 0.61 | -0.52 | 1.75 | no | 0.19 |
| C | mwf-spring | 0.40 | 0.02 | -0.32 | 0.37 | yes | -0.89 |
| AV | mwf-summer | 0.08 | 0.18 | 0.11 | 0.25 | yes | 0.37 |
| AFV | mwf-summer | 0.05 | 0.23 | 0.15 | 0.31 | yes | 0.65 |
| TBV | mwf-summer | 0.05 | 0.21 | 0.13 | 0.28 | yes | 0.61 |
| AC | mwf-summer | 0.42 | 0.38 | 0.29 | 0.47 | no | -0.05 |
| C | mwf-summer | 0.40 | 0.00 | 0.00 | 0.00 | yes | -1.00 |
| AV | mwf-fall | 0.08 | 0.18 | 0.07 | 0.28 | no | 0.36 |
| AFV | mwf-fall | 0.05 | 0.26 | 0.14 | 0.38 | yes | 0.68 |
| TBV | mwf-fall | 0.05 | 0.23 | 0.12 | 0.35 | yes | 0.65 |
| AC | mwf-fall | 0.42 | 0.33 | 0.20 | 0.46 | no | -0.12 |
| C | mwf-fall | 0.40 | 0.00 | 0.00 | 0.00 | yes | -1.00 |
| AV | mwf-winter | 0.08 | 0.06 | 0.00 | 0.12 | no | -0.15 |
| AFV | mwf-winter | 0.05 | 0.15 | 0.06 | 0.24 | yes | 0.50 |
| TBV | mwf-winter | 0.05 | 0.11 | 0.03 | 0.19 | no | 0.38 |
| AC | mwf-winter | 0.42 | 0.67 | 0.54 | 0.79 | yes | 0.23 |
| C | mwf-winter | 0.40 | 0.01 | -0.02 | 0.04 | yes | -0.94 |

* AV = alluvial valley, AFV = alluvial-fan influenced valley, TBV = terrace bound valley, AC = alluviated canyon, C = canyon

Table 6. Analysis of valley segment type availability and seasonal use by radio tracked largescale suckers. Valley segment selection by largescale suckers is described using an electivity index and 95% confidence intervals indicating statistically significant preference or avoidance.

| Valley segment type* | Species-season | Proportion of habitat in range of species | | Bonferroni confidence intervals | | | |
| | | Available | Occupied | Lower 95% | Upper 95% | Significant (P < 0.05) | Electivity |
|---|---|---|---|---|---|---|---|
| AV | lss-spring | 0.08 | 0.01 | -0.02 | 0.05 | yes | -0.70 |
| AFV | lss-spring | 0.05 | 0.07 | 0.00 | 0.15 | no | 0.19 |
| TBV | lss-spring | 0.05 | 0.22 | 0.10 | 0.34 | yes | 0.63 |
| AC | lss-spring | 0.42 | 0.57 | 0.43 | 0.71 | yes | 0.16 |
| C | lss-spring | 0.40 | 0.12 | 0.03 | 0.21 | yes | -0.55 |
| AV | lss-summer | 0.08 | 0.13 | 0.07 | 0.19 | no | 0.21 |
| AFV | lss-summer | 0.05 | 0.12 | 0.06 | 0.18 | yes | 0.42 |
| TBV | lss-summer | 0.05 | 0.30 | 0.22 | 0.39 | yes | 0.72 |
| AC | lss-summer | 0.42 | 0.40 | 0.31 | 0.50 | no | -0.01 |
| C | lss-summer | 0.40 | 0.04 | 0.01 | 0.08 | yes | -0.80 |
| AV | lss-fall | 0.08 | 0.00 | 0.00 | 0.00 | yes | -1.00 |
| AFV | lss-fall | 0.05 | 0.09 | -0.05 | 0.22 | no | 0.27 |
| TBV | lss-fall | 0.05 | 0.13 | -0.03 | 0.29 | no | 0.45 |
| AC | lss-fall | 0.42 | 0.74 | 0.53 | 0.95 | yes | 0.28 |
| C | lss-fall | 0.40 | 0.04 | -0.06 | 0.14 | yes | -0.80 |
| AV | lss-winter | 0.08 | 0.00 | 0.00 | 0.00 | yes | -1.00 |
| AFV | lss-winter | 0.05 | 0.00 | 0.00 | 0.00 | yes | -1.00 |
| TBV | lss-winter | 0.05 | 0.12 | 0.00 | 0.24 | no | 0.41 |
| AC | lss-winter | 0.42 | 0.76 | 0.61 | 0.91 | yes | 0.29 |
| C | lss-winter | 0.40 | 0.12 | 0.00 | 0.24 | yes | -0.54 |

* AV = alluvial valley, AFV = alluvial-fan influenced valley, TBV = terrace bound valley, AC = alluviated canyon, C = canyon

exception of terrace-bound valleys (12% of locations). In the spring, the preference for alluviated canyons became weaker (57%), while fish also showed selection (P < 0.05) for terrace bound valleys (22%), some occurrence in alluvial fan valleys (7%), and weaker avoidance of canyon segments (12%). During the summer months there was a dramatically different use of segment types. The majority of sucker locations were in valley types (30% in terrace bound, 12% in alluvial fan, and 13% in alluvial valleys), for which they showed significant selection (P < 0.05). Canyon segments returned to being strongly avoided (P < 0.05). Fall showed another shift in habitat preference by suckers, with significant preference (P < 0.05) being shown for habitat in alluviated canyons (74%), a lesser number of occurrences in terrace bound valleys (13%), and continued avoidance of canyons.

Finally, bull trout also displayed patterns of habitat association at the valley segment scale that changed with the seasons (Table 7). During the winter, bull trout also selected habitat in alluviated canyon segments (61 % of locations, P < 0.05). However, while they showed avoidance of valley segment types in winter, they were found using habitats in canyon segments to a greater degree (20%) than either suckers or whitefish. In particular, when compared to suckers or whitefish that we tracked, a greater proportion of bull trout over-wintered at sites in the Grande Ronde River upstream of its confluence with the Wenaha, a section dominated by canyon habitat. In the spring, bull tout showed a somewhat weaker use of alluviated canyon (58%) and canyon (12%) segments, with a slight increase in the proportion of sightings in the three valley types (15% in alluvial fan, 8% in terrace bound, and 7% in alluvial valley types). In contrast, summer habitat use by tagged bull trout showed a decrease in the use of alluviated canyons (40%), significant avoidance of canyon segments (3%) and selection of habitat in alluvial valleys (30%) (P < 0.05). Similarly, in the fall tagged bull trout continued to occupy alluviated canyon segments (43%), while selecting habitat in alluvial valley segment types (28%), and avoiding canyon segments (P < 0.05). During this period they also showed a significant selection (19%) of alluvial fan-influenced valley segments relative to the availability of this habitat type (P < 0.05).

Table 7. Analysis of valley segment type availability and seasonal use by radio tracked bull trout. Valley segment selection by bull trout is described using an electivity index and 95% confidence intervals indicating statistically significant preference or avoidance.

| Valley segment type* | Species-season | Proportion of habitat in range of species | | Bonferroni confidence intervals | | | |
|---|---|---|---|---|---|---|---|
| | | Available | Occupied | Lower 95% | Upper 95% | Significant (P < 0.05) | Electivity |
| AC | bt-spring | 0.08 | 40.00 | 0.05 | 0.11 | no | -0.02 |
| AC | bt-spring | 0.05 | 75.00 | 0.11 | 0.19 | yes | 0.50 |
| AC | bt-spring | 0.05 | 35.00 | 0.04 | 0.10 | no | 0.17 |
| AC | bt-spring | 0.42 | 290.00 | 0.53 | 0.63 | yes | 0.17 |
| AFV | bt-spring | 0.40 | 60.00 | 0.09 | 0.15 | yes | -0.54 |
| AFV | bt-summer | 0.08 | 249.00 | 0.36 | 0.45 | yes | 0.65 |
| AFV | bt-summer | 0.05 | 80.00 | 0.10 | 0.16 | yes | 0.44 |
| AFV | bt-summer | 0.05 | 43.00 | 0.05 | 0.09 | no | 0.16 |
| AV | bt-summer | 0.42 | 230.00 | 0.33 | 0.42 | no | -0.06 |
| AV | bt-summer | 0.40 | 18.00 | 0.01 | 0.04 | yes | -0.86 |
| AV | bt-fall | 0.08 | 162.00 | 0.24 | 0.32 | yes | 0.54 |
| AV | bt-fall | 0.05 | 87.00 | 0.12 | 0.18 | yes | 0.50 |
| C | bt-fall | 0.05 | 52.00 | 0.06 | 0.12 | yes | 0.28 |
| C | bt-fall | 0.42 | 249.00 | 0.38 | 0.48 | no | 0.02 |
| C | bt-fall | 0.40 | 29.00 | 0.03 | 0.07 | yes | -0.78 |
| C | bt-winter | 0.08 | 23.00 | 0.03 | 0.07 | yes | -0.25 |
| TBV | bt-winter | 0.05 | 32.00 | 0.04 | 0.10 | no | 0.16 |
| TBV | bt-winter | 0.05 | 32.00 | 0.04 | 0.10 | no | 0.16 |
| TBV | bt-winter | 0.42 | 280.00 | 0.56 | 0.66 | yes | 0.19 |
| TBV | bt-winter | 0.40 | 92.00 | 0.16 | 0.24 | yes | -0.33 |

* AV = alluvial valley, AFV = alluvial-fan influenced valley, TBV = terrace bound valley, AC = alluviated canyon, C = canyon

### 3.4.3 Diel, Channel Unit Complementation

Fish also exhibited complementary use of different habitat types on a day-night time scale. In almost all cases among the radio tagged fish, regardless of species or season, I found they tended to move from a position in the main channel to shallower, slower water at night and then back into the channel the following morning. The timing of the movement seemed to be closely tuned to light, as the fish usually moved to shallower water as soon as it was fully dark, and back again when the sun came up. In several instances, we repeated diel tracking on a fish within a season. In these cases, we usually observed a recurring diel pattern, such that the fish seemed to follow a habitual 'path' through each day-night cycle.

Largescale suckers exhibited distinct diel movement patterns associated with the use of different habitats. Among the tracked largescale suckers, we frequently observed use of off-channel alcove habitats during the night. In nearly every case, we observed night time occupation of shallower, lower velocity habitats by radio tagged fish. We observed this pattern during all seasons. On several occasions in the lower Wenaha River, adult suckers were observed feeding on algae and detritus in backwaters or alcoves at night. During the summer, underwater surveys and radio telemetry showed that adult suckers used shallow riffle and glide-like habitats to a greater degree than in other seasons, and most of this use occurred at night. Some of this use may have been associated with spawning, as eggs were collected in these habitats on a few occasions (see section 3.2.2). During our summer dives of slack-water areas in the lower Wenaha River, we also observed a pattern of diel movement by larval suckers. Sucker larvae were seen to stay close to the substratum at night, moved to occupy the top layer of the water column at first light, and then distribute in the upper portions of the water column during the day. Interestingly, during night surveys larval suckers often left the bottom and swam toward the dive light.

Mountain whitefish also showed diel shifts in channel unit habitat use. As with suckers, radio tracked mountain whitefish used alcoves and slower, shallower habitat at night during all seasons. During the daytime, adult mountain whitefish tended to select

deeper, faster habitats. Our tracking and underwater observations suggested that they moved little during the day, usually staying within a 10-15 m radius of a particular holding position. From this holding location, we observed adult mountain whitefish actively feeding on drifting invertebrates. Disturbing the substrate to increase drifting prey appeared to increase their foraging rate, but did not result in a shift in their position. In contrast, juvenile and sub-adult mountain whitefish tended to exhibit a roaming behavior and fed from both the drift and from the bottom. On several occasions, juvenile and subadult fish were observed to follow closely behind a diver, foraging on prey that were dislodged by the diver's hands and feet.

Paired day-night underwater surveys revealed shifts in the distribution, as well as abundance (see section 3.2.4) of fish species among channel units within reaches. The most striking of these dynamics involved fish use of alcove habitats (Figure 46). Three of our sites in the lower drainage included alcoves, and all of these possessed patches thermally moderated by the influence of upwelling groundwater (Figure 14, section 3.1). Temperatures in these habitats were cooler than the main channel in summer and warmer in winter. This thermal difference was most pronounced during the daytime in summer and at night during winter. Because the bed materials of these alcoves were primarily bedrock and/or cobble with fine-grained material deposited over-top, it was difficult for fish to avoid the sight of a diver. Hence, we could be reasonably certain of the accuracy of our surveys in these habitat units, both during day and night and regardless of season. During daytime surveys in the summer, we observed large numbers of larval suckers and dace, many juvenile rainbow trout, juvenile whitefish and chinook salmon, and some adult rainbow trout. It was common to observe adult rainbow trout holding near the coldest patch within the alcove. During summer nights our observations were similar, except that we observed larger numbers of sculpin and also saw adult largescale suckers, mountain whitefish, and occasionally adult bull trout utilizing the alcoves. When approached by a diver, fish (particularly the larger individuals) would frequently spook and move rapidly in avoidance.

In contrast to the summertime dynamic, winter differences between day and night use of alcoves was more dramatic (Figure 46). During winter days we rarely observed fish of

any kind using these alcoves. However, repeated dive observations showed that as soon as it was fully dark fish began moving into the alcoves in large numbers. During winter nights we observed more total fish in alcoves than during summer nights (excluding larval suckers and dace, which were not observed in the Wenaha River in winter). For example, on one occasion we saw no fish in an alcove (~10 m x 3 m x 0.30-0.50 m) 30 min before sunset and then, 45 min after sundown, we counted a total of 180 fish in that same area. Fish we observed using alcoves on winter nights included large numbers of juvenile chinook salmon, juvenile and adult rainbow trout, as well as smaller numbers of juvenile and adult mountain whitefish and adult bull trout. We also observed that many of these fish exhibited torpid behavior and little movement when approached by the diver.

Figure 46. Seasonal shifts in the day-night use patterns of the main channel and groundwater-influenced alcove habitat at a site in the lower Wenaha River. Silhouette representations are as defined in figure 47, and their numbers are roughly indicative of observed relative abundance. Sculpin and dace species are not represented, but are described in text.

*SUMMER (DAY)*

Alcove (cooler than main channel)                    Main Channel

*SUMMER (NIGHT)*

Alcove (slightly cooler than main channel)           Main Channel

*WINTER (DAY)*

Alcove (slightly warmer than main channel)           Main Channel

*WINTER (NIGHT)*

Alcove (warmer than main channel)                    Main Channel
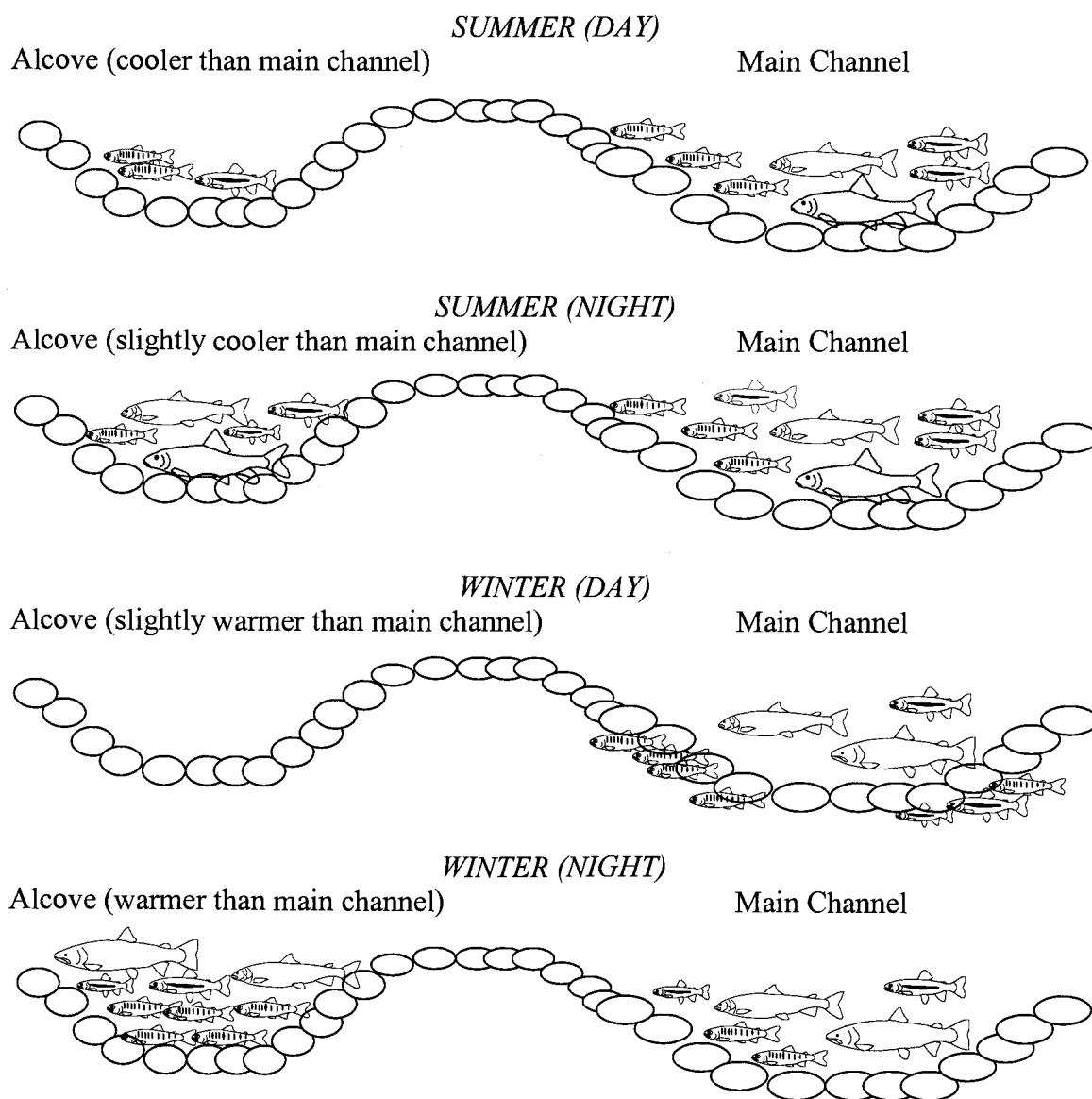
# CHAPTER 4: DISCUSSION

## 4.1 Summary of Findings and Discussion Overview

I found that spatial patterns in fish assemblage structure at multiple scales were not static. Rather, they exhibited marked change over diel to seasonal temporal scales. Seasonal changes in longitudinal fish assemblage patterns were primarily driven by the migration of prominent members of the assemblage, several of which have not received much previous research attention. Similarly, movement of fishes at smaller spatial scales influenced the diel dynamics of fish assemblage patterns. Potentially important habitat features, from sub-basins and valley segments to channel units, were separated spatially, and many fish species exhibited diverse migratory life history forms that reflected the complementary use of habitats distributed throughout this riverscape. Below I describe the consequences of these findings for understanding and conservation of the individual fish species and fish assemblage of this riverscape, I explore the implications of this research for stream fish and stream community ecology conceptual frameworks, and I raise questions regarding the nature of ecological communities in general. In this discussion, I first address several species from an individualistic perspective, dealing primarily with issues associated with their autecology. I then discuss fish movement, life histories and habitat relationships in the context of riverscapes. Next I move to a more holistic perspective, discussing species within the context of the entire fish assemblage and stream communities. I then explore some of the consequences of our work for theory and practice in the ecology of stream fish assemblages, stream communities, and communities in general. Finally, I describe a few of the implications of this study for research and conservation of stream fishes.

## 4.2 Consequences for the Ecology of Individual Fish Species

The life histories of stream fishes, including their movement patterns, reflect the evolution of species and populations in the context of particular riverscapes. Habitat heterogeneity in the riverscape (its abundance, arrangement, temporal changes, etc.)

provides the templet (Southwood 1977) for the expression of life history strategies in fishes. It has been recognized that salmonid species display exceptional plasticity in life history character (e.g., Noakes et al. 1989, Healey & Prince 1995). While our observations reinforce this idea, they also suggest that other non-salmonid species present in rivers of the Pacific Northwest have the potential for this diversity, dependent on riverscape context. Below I discuss the life history strategies, biology and ecology of individual species in light of our findings, with special emphasis on the species we studied via both underwater surveys and radio telemetry; largescale suckers, mountain whitefish and bull trout.

## 4.2.1 Largescale Suckers

Largescale suckers are generally known to exhibit a migratory life history strategy (Wydoski & Whitney 1979). In fact, aboriginal cultures of the Pacific Northwest were attuned to these migrations and largescale suckers played an important role in the subsistence of many tribes (Dave Close, Umatilla Tribal Biologist, Pendleton, Oregon, personal communication). However, this is the first scientific study I am aware of that describes the nature and spatial extent of their migrations throughout the year. In the context of the Wenaha, Grande Ronde, Snake River network, largescale suckers undertake seasonal migrations ranging from tens to hundreds of kilometers. These movements are associated with spring and early summer spawning in the Wenaha River, followed by a return to the Grande Ronde and Snake Rivers. Some fish may die after spawning and others may not return to the Wenaha River the following spring. Our observations suggest that after spending the fall and winter in reaches of the Grande Ronde and Snake a large proportion of these fish do return to the Wenaha River the following spring, demonstrating both extensive migration and repeat homing to spawning streams. Based on a mark-recapture study of the species, Dauble (1986) hypothesized that the majority of the largescale sucker population in the Hanford reach of the Columbia River was transient. Though his recapture rate was quite low and recapture

efforts were limited to this reach of the main-stem Columbia River, tags were recovered as far as 60 km downstream and 14 km upstream from release sites. Our telemetry observations suggest that his speculations were correct, but that the extent of migration exhibited is much greater than detected through his mark and recapture study. A closely related species common in Canada and the midwest and eastern United States, the white sucker, *Catostomus commersoni*, has also been observed to migrate between large rivers and small streams for spawning (Clifford 1972), and homing to spawning streams has been shown in this species (Werner 1979). Spawning migrations have also been documented for numerous other catostomids such as razorback sucker *Xyrauchen texanus* (Modde & Irving 1998) and species of redhorse, *Moxostomoa sp.* (Hall 1972).

The timing and function of sucker migrations are poorly understood. Dauble (1986) reported that, based on fish ladder counts at Priest Rapids Dam, seasonal movements of suckers (all species) were greatest in June when nearly half of the upstream migration occurred. He speculated that this movement could have been associated with feeding and/or migration to spawning tributaries. We also observed the greatest upstream movement in May and June, and noted fish spawning and feeding in the Wenaha River. I am uncertain whether fish that return to the Wenaha River in consecutive years actually spawned repeatedly. Dauble (1986) found some mature female largescale suckers possessed undeveloped ovaries or lacked atrophic eggs prior to the spawning season in the Columbia River. Thus, he speculated that some females did not spawn annually, but that the large size range he observed suggested that most survived to spawn more than once. In contrast, he observed greater post-spawning mortality among males, and suggested that they may be less likely to spawn again. We also observed a greater size range among adult female suckers we captured, and frequently observed both dead and spent males, or "railbacks." However, we selected only fish in good condition for radio tagging, and subsequently did not observe any difference between sexes in the extent of movement or return migration the next year.

The timing of spawning and the factors influencing this timing are also uncertain, and knowledge of this is important to understanding life history diversity in the species. Dauble (1986) observed that largescale sucker spawning occurred from early April to

early July in the Hanford reach of the Columbia River, with peak spawning in late May and June. Similarly, largescale suckers spawning in the Stave Lake system, B.C. were observed to spawn over a long spring period (McCart & Aspinwall 1970). In the Wenaha River we also observed a protracted spawning season in close accord to Dauble's (1986) reports. However, both radio telemetry and underwater surveys showed two 'waves' of adult largescale suckers moving into the Wenaha River, one in May and early June and another in early July, suggesting that distinct spawning runs may exist. The timing of stream temperatures has been suggested as a key factor influencing the timing of sucker spawning in adfluvial (Nelson 1968, McCart & Aspinwall 1970) and fluvial (Dauble 1986) populations. Though the beginning of the spawning period may be limited by temperature, the long spawning season and the presence of multiple runs of fish in the same system indicates that additional factors are likely at work. In addition, based on Dauble's (1986) observations of spawning in the large river environment of the Columbia, it is likely that some largescale suckers carry out their full life cycle in reaches of the Grande Ronde and Snake Rivers. Density-dependent processes, such as dispersal and colonization, may also influence some of the sucker movements we observed. The timing of migrations and spawning is probably a function of many factors that vary with the riverscape context and the life histories expressed within that setting.

Our observations of largescale sucker fry and juveniles were similar to those for other sucker species (e.g., Geen et al. 1966, Clifford 1972, Corbett & Powles 1986, Modde & Muirhead 1994). We observed high densities of larval suckers in slack-water areas of the Wenaha River from mid-July to mid-October, with emergence occurring later in upstream than in downstream reaches, and highest densities observed from late July to early August. These fish all migrated downstream into the Grande Ronde River by late fall, and no young-of-the-year suckers were present in the Wenaha River until the following spring. Despite the high densities of larval suckers, juvenile suckers were very rare in the Wenaha River, and no sub-adult largescale suckers were observed. Consequently, fluvial migratory largescale suckers appear to utilize the Wenaha River primarily for spawning, a period of adult summer feeding, and larval rearing. Further growth of fish to maturity appears to occur mostly in the large river environment,

regardless of whether they were spawned in tributary streams like the Wenaha or in the large river reaches.

Our observations of largescale sucker life history and migration, as well as habitat associations at different scales represent one of the first attempts to document habitat requirements for the species. The broad-scale habitat needs of this species are virtually unknown. Largescale suckers are often considered to be poorer swimmers than salmonids, as well as fishes associated with warm, slow waters. However, this perception seems largely based on field studies conducted during summer months that do not take into account the range of habitats used and distances covered by individuals of this species. I did see a strong association between stream temperature and adult largescale sucker distribution within the Wenaha River in summer months, with fewer found higher up in the drainage where temperatures were lower. However, this association could as easily be explained by other co-varying factors such as stream size. We observed these fish ascending long distances in the river system during times of very high flow to reach habitats whose spring temperatures were very cold ($< 10°C$), reflecting run-off of melting snow. No largescale suckers occupied habitat in the Wenaha River year-round. Why this habitat appears unsuitable for year-round residency is unclear. In the Middle Fork of the John Day River, another northeast Oregon stream of similar size, small numbers of largescale suckers and large numbers of bridglelip and mountain suckers, *C. platyrhynchus* are to be found year-round as far upstream as $3^{rd}$ order headwater reaches (Baxter, C., unpublished data). This stream possesses warmer temperatures than the Wenaha River in summer and the winter thermal regime is influenced by warm springs in the headwaters. In addition, it exhibits less seasonal discharge fluctuation. The mechanisms influencing large-scale distribution patterns and life history expression of largescale suckers remain unclear. However, as in the case of any migratory species, connectivity among habitat elements is likely to be critical. For example, Dauble (1986) suggested that dams present barriers to sucker movement in the Columbia River, pointing out that since the construction of Priest Rapids Dam, net upstream passage of suckers at this site has declined from ~200, 000 to 20, 000 fish a year.

I also found associations between largescale suckers and habitat factors at nested, smaller spatial scales, and these associations changed with temporal context. Radio-tracked suckers showed selection of habitats in different valley segment types during different portions of the year. For example, alluvial valleys (most common in the Wenaha) were selected in summer but avoided in winter while alluviated canyons (most common in Grande Ronde and Snake) were selected in winter and avoided in summer. This valley segment context was reflected in the selection of habitats at smaller scales as well. During the summer, we observed that adult suckers used shallow riffle and glide-like habitats (most common in valley as opposed to canyon segments) to a greater degree than in other seasons, while they were found in deeper pools and glides (most common in alluviated canyons) during the winter. Radio-tracked suckers were observed in all seasons to use off-channel alcove and slack-water margin habitats at night. Larval suckers, on the other hand, were found exclusively in slack-water habitats such as alcoves and channel margins during both day and night. However, our summer dives of these habitats did reveal diel pattern of habitat use by larval suckers; larvae were found in the water column during the day but stayed close to the bottom at night.

This study has contributed to a riverscape perspective on the distribution, movement, habitat use, and species associations of largescale suckers. I found that changes in sucker distribution in the Wenaha River and dynamics of their associated fish assemblage reflected complex movement patterns. These movements were associated with seasonal shifts in habitat preference at nested spatial scales. In the context of this particular riverscape, largescale suckers exhibit at least one migratory life history strategy that reflects the complementary use of habitats distributed throughout the river network. I hope these efforts will serve to raise new questions and encourage the research needed to understand more of the biology and ecology of this important native species.

## 4.2.2 Mountain Whitefish

While they are among the most abundant species present in many rivers of the west (Northcote & Ennis 1994), mountain whitefish have received relatively little research attention. There has only been one other intensive study of migratory behavior in mountain whitefish, that of Davies & Thompson (1976) in the Sheep River system, Alberta. They demonstrated that mountain whitefish exhibit complex seasonal migratory behavior, documenting that adults generally moved upstream in the spring and early summer, remained in the local area until late fall or early winter, and then moved back downstream to spend the winter in deep pools. Interestingly, Davies & Thompson (1976) found that, while the majority of adult fish migrated, a few adult fish did not migrate, but remained as residents of upper river reaches or tributaries year-round. Similarly, I found that most adult mountain whitefish in the Wenaha, Grande Ronde, Snake River system undertook marked seasonal migrations, while a few remained as residents of the Wenaha River year-round.

This study also documents additional life history variation and complexity in the movement patterns of adult mountain whitefish. I found that, among fish that remained in the Wenaha River, some fish resided year-round within a single reach (< 0.5 km), while others undertook significant round-trip migrations (6-20 km) between upper (spring-fall) and mid-reaches (winter). In addition, though the majority of tracked fish migrated out of the Wenaha River and over-wintered in the Grande Ronde or Snake rivers, there were distinct groups that either 1) spent most of the year in the mid-upper reaches of the Wenaha River or 2) spent only summer-fall in its mid-lower reaches. Nearly all of these fish returned to the Wenaha River the following year, many to the reaches or channel units in which they were tagged. This fidelity to holding locations has been documented in other fishes, and may, as suggested by Smith (1985), benefit fish through intimate knowledge of feeding and hiding places at a particular location. There was no correlation between movements and size, and thus no indication that migratory types were associated with different life stages. These observations demonstrate that mountain whitefish are capable of expressing multiple life history strategies within the

context of a single river system. This has not been previously described for the species, though multiple life histories, stock structure and even anadromy have been shown in related species of coregonids in Europe and Canada (Ihssen et al. 1981, Morin et al. 1982, Lehtonen & Himberg 1992). In addition, this study presents clear evidence that mountain whitefish often repeatedly migrate to the same areas for feeding and spawning, an idea advanced by Pettit & Wallace (1975) based on their observations of a few tagged fish that returned to a tributary in the year following their marking.

The timing and reasons for adult mountain whitefish migrations are still poorly understood. Davies & Thompson (1976) suggested that complex movements might be associated with both feeding and spawning, an idea supported by the results of this study. Fish occupied summer holding locations from which they moved relatively little. Movement downstream generally preceded the onset of the spawning period, during which some fish appear to spawn in the Wenaha River and others in the larger river environment. After the spawning period, fish made additional movements to over-wintering habitat, both downstream (in the case of those who went down the Grande Ronde or to the Snake River) and up (in the case of those who went up the Grande Ronde after leaving the Wenaha River). The following spring, most of these fish made the return migration to the Wenaha River, though a few fish had not returned before their transmitters failed. We do not know whether large numbers of mountain whitefish occupy the Grande Ronde or Snake Rivers during summer months. During a few dives in the lower Grande Ronde River in summer we did not observe adult mountain whitefish (Baxter, C., unpublished data), however these were not extensive surveys and visibility was very poor. It is uncertain whether mountain whitefish exhibit annual spawning, or if they do not, whether non-spawners still undertake the return migration for other purposes (e.g., feeding, avoidance of environmental conditions or predators in the lower river, etc.).

It is also unclear what role environmental or biological factors may play in the timing of migrations. Davies & Thompson (1976) described associations between environmental factors and movements in the Sheep River watershed, Alberta. My findings generally supported their hypotheses, though the diversity of migratory

strategies observed confounds any full generalizations. The spring migration of some fish into the Wenaha River corresponded to a period of increasing discharge, turbidity, and temperature in the lower Grande Ronde and Snake Rivers, factors that either singly or synergistically could be related to this movement. During this same time of lengthening photoperiod, the Wenaha remains clearer than the Grande Ronde River, its increases in flow and temperature are less dramatic, and aquatic macroinvertebrate densities undergo a pronounced increase. Our observations of feeding by adult mountain whitefish suggested that the majority of their prey while they were in the Wenaha River were drifting invertebrates. Capture of drifting prey may require a certain level of visibility. If so, both availability of food and favorable foraging conditions may be mechanisms influencing this spring migration. Mountain whitefish are considered a cool water species, and summer water temperatures where they are found generally range from 11 to 20 °C (Ihnat & Bulkley 1984). Consequently, it is also possible that warm summer water temperature in the lower Grande Ronde (daily maximum often exceeds 25 °C) precludes large numbers of adult mountain whitefish from surviving there during this season.

This study suggests that mountain whitefish may spawn across a range of habitat types, though the precise distribution of spawning was not clear from this study. We documented a fall aggregation and spawning at one site in the lower Wenaha River, and we observed young-of-the year whitefish throughout the mid to lower reaches of the Wenaha in spring. However, the small numbers of these fry relative to the numbers of adults present in summer and fall, combined with spring observations of many more fry in shallows of the Grande Ronde, lead me to speculate that the majority of the spawning by migratory fish occurred in the Grande Ronde River. Davies & Thompson (1976) also observed movement to downstream habitat for spawning, while other populations reportedly spawn in upstream tributaries (Brown 1952, Pettit & Wallace 1975). We observed mountain whitefish spawning at night in the Wenaha River during mid-October, which is similar to other reports that spawning is nocturnal and that it typically occurs in late fall (Brown 1952, Stalnaker et al. 1974, Thompson & Davies 1976).

Our observations of mountain whitefish fry and juveniles were similar to those described by others (Brown 1952, Brown 1972, Pettit & Wallace 1975, Davies & Thompson 1976). Beginning in March, and especially following the peak run-off, we saw high densities of young-of-the-year whitefish utilizing secondary channels and floodplain habitats, but as the fish grew and water levels dropped, they were more often found in the main channel. As the summer progressed, many of these fish appeared to migrate downstream into the Grande Ronde River. Juvenile and sub-adult mountain whitefish were observed year-round in the Wenaha, though they were relatively rare compared to other juvenile fishes and the numbers of adult whitefish in the river during summer. They were primarily observed in a few of the downstream sites. It is unclear what kind of movements these fish may undertake. Davies & Thompson (1976) and Pettit & Wallace (1975) suggested that they remained in lower river reaches until reaching sexual maturity at 3 years of age. It is possible they do the same in this river system.

In addition to observations of mountain whitefish life history and migration, I identified significant habitat associations. The broad scale habitat requirements of mountain whitefish are poorly understood. Mountain whitefish are one of the most abundant species in this river system, and adults (particularly of the migratory types) frequently reach sizes in excess of 500 mm, which generally exceeds the size range reported for adults in other stream systems (Scott & Crossman 1973, Northcote & Ennis 1994). Mechanisms governing the production and growth of this species are largely unknown. As in the case of suckers, mountain whitefish distribution patterns are generally thought to be associated with temperature. I found a negative correlation between temperature and whitefish abundance in the Wenaha River during summer months, with more being found in downstream than upstream reaches. Again, however, factors such as stream size and/or distance from the Grande Ronde River could also explain this gradient in abundance. Competition with other salmonids has also been suggested as a mechanism limiting whitefish production (Baxter & Simon 1970, Donald 1987). Though this study did not address competition directly, we observed high densities of other salmonids in this river system and little to indicate that such limitation

actually occurs. Rather, we speculate that the abundance of mountain whitefish in this system and the sizes attained reflect the availability of the Wenaha River, with its highly productive floodplain and aquatic invertebrate fauna, for spring and summer feeding. In addition, the fact that connectivity remains intact between the free-flowing Grande Ronde and the Wenaha Rivers likely favors the production of whitefish in the system as it maintains accessibility among critical habitat elements and fosters the continued expression of diverse life history strategies. The importance of this connectivity was emphasized by Northcote & Ennis (1994), who listed several examples in which mountain whitefish sizes and or numbers have declined since damming and impoundment of river systems.

I also found associations between mountain whitefish distribution and abundance and habitat factors at nested, smaller spatial scales, and these associations changed with temporal context. As was the case for suckers, radio-tracked whitefish showed selection of habitats in different valley segment types during different portions of the year. For example, alluvial valleys (most common in the Wenaha) were selected in summer but avoided in winter while alluviated canyons (most common in Grande Ronde and Snake) were selected in winter and avoided in summer. This shift was true for both fish that migrated outside of the Wenaha River as well as those that migrated between upper (where alluvial valley segments were more common) and middle reaches (where the most alluviated canyon segments occurred) within the Wenaha River. This valley segment context was reflected in the selection of habitats at smaller scales as well. During the summer, I found that adult mountain whitefish used shallow riffle and glide-like habitats (most common in valley as opposed to canyon segments) to a greater degree than in other seasons, while they were found in deeper pools and glides (most common in alluviated canyons) during the winter. This observation is consistent with other studies that have shown whitefish utilizing deeper habitats for over-wintering (Northcote & Ennis 1994). As with suckers, radio tracked mountain whitefish often used alcoves and slower, shallower habitat at night during all seasons. During the daytime, adult mountain whitefish tended to select deeper, faster habitats and remained relatively stationary except to pick off drifting invertebrates. During spring and early summer, young of the year

mountain whitefish were associated with slack-water habitats such as alcoves and channel margins during both day and night, though they began to shift to deeper, faster habitats as they attained larger sizes in late summer and fall. Sub-adult fish were typically associated with shallower habitats than the adults, and appeared to exhibit a roaming behavior that involved foraging from both the drift and the stream bottom.

This study has also contributed to a riverscape perspective on the distribution, movement, habitat use, and species associations of mountain whitefish. I found that changes in whitefish distribution in the Wenaha River and dynamics of their associated fish assemblage reflected complex movement patterns. These movements were associated with seasonal shifts in habitat preference at nested spatial scales. Within the context of this riverscape, mountain whitefish appear to express multiple life history strategies, some of which require the complementary use of habitat resources separated by long distances. As in the case of the largescale sucker, this important native species deserves greater research attention, and I hope these efforts will help encourage such activity.

## 4.2.3  Bull Trout

Though bull trout have attracted greater research interest in recent years, there is still much to be learned regarding their life history, population structure, movements, habitat requirements, and other elements of their basic ecology. Bull trout are known to exhibit both migratory and non-migratory life history types within the same river system (Fraley & Shepard 1989, Rieman & Dunham 2000). We observed both migratory fish and many bull trout that were present year-round in the Wenaha River and its tributaries, suggesting that migratory and non-migratory forms exist in this river system. Individual bull trout have been shown to travel hundreds of kilometers (Bjornn & Mallett 1964, McLeod & Clayton 1997, Swanberg 1997). However, the distances of migrations followed in this study (up to 280 km) represent some of the longest documented for the species (see also Hemmingsen et al. 2001 for further details of this cooperative research). Migratory bull

trout are known to include those that move back and forth between lakes (adfluvial) or large rivers (fluvial) and smaller tributary streams. Much of what is known of the fluvial life history is borrowed from studies of adfluvial populations. For example, in the Flathead Lake and River system of northwest Montana, Fraley & Shepard (1989) reported that adfluvial fish lived from 1 to 4 years in the smaller tributaries, then moved into large lakes where they spent 2-4 years growing before reaching sexual maturity, after which they returned to tributaries to spawn. The only intensive study published on the movements of fluvial migratory bull trout is Swanberg's (1997) radio telemetry study of adult fish in the Blackfoot River, a tributary of the Clark Fork River in Montana. As was generally observed in this study, Swanberg (1997) described the seasonal movements and habitat use of fish as they moved from the main river environment to spawning tributaries in early summer and back into the main river after spawning in fall. Similar observations were made by McLeod & Clayton (1997), who radio tracked a small number of adult fish in the Athabasca River, Alberta.

This research (see also Hemmingsen et al. 2001) represents perhaps the most extensive telemetry study of fluvial bull trout to date, and the number of fish tracked provided data on variations in migratory patterns suggestive of additional diversity in bull trout life history strategies. While the majority of the bull trout we tracked moved between the Grande Ronde River, the Wenaha River, and Wenaha tributaries, several of the fish remained in the Wenaha River drainage on a year-round basis but exhibited pronounced seasonal movements within the basin. These fish spent the summer in upper reaches of the Wenaha River, moved into and back out of spawning tributaries in the fall, downstream to middle reaches of the Wenaha for over-wintering, and then returned to upper reaches the following spring. In addition, among fish that over-wintered in the Grande Ronde River, some used reaches upstream of the Wenaha River confluence while others moved downstream. Similarly, but over a greater distance, we observed several fish that migrated back and forth between the Wenaha drainage and over-wintering sites in the Snake River. The range of movement strategies we observed likely reflects the diversity and connectivity of habitats in this river system. In contrast, Swanberg (1997) suggested that life histories were limited in his study system by the presence of a dam

lacking upstream passage facilities on the Clark Fork River near its confluence with the Blackfoot River. Interestingly, a dam was once proposed on the Grande Ronde River near the confluence of the Wenaha (Thompson & Haas 1960). Had this dam been built, I suspect that we would not have observed the same life history variation among bull trout in this river system.

The timing of migratory bull trout movement and durations spent in different habitats appears to vary with watershed context. Swanberg (1997) found that fish began upstream migrations in June as temperature in the main river increased and discharge decreased from peak flows. He showed that fish entered spawning tributaries in late June or early July, 2-3 months prior to spawning. He hypothesized that high temperatures in the main river (> 20 °C) prompted this movement into cooler tributary streams. In contrast, in large mainstem rivers with cooler summer temperatures (e.g., Flathead River, Montana), adults often remain in the main river longer and typically do not enter spawning tributaries until late summer or early fall (Shepard et al. 1984, Fraley & Shepard 1989). Our observations reflected both of these scenarios, though an additional stream level (or levels in the case of fish that used the Snake River) was involved in the migration process. We found that bull trout moved towards the Wenaha River (up or downstream, depending on their over-wintering locale) as flows began to fall and temperatures were rising in the Grande Ronde and Snake rivers. These fish moved into the Wenaha River in June and early July. However, fish did not enter spawning tributaries, which in several cases had warmer summer temperatures than the main Wenaha River, until late summer and early fall, and many fish were not observed to enter smaller tributaries at all.

Though migrations of bull trout are often referred to as 'spawning migrations,' I expect that the reasons for this movement may also vary among river systems. For example, Swanberg (1997) found that nearly all bull trout, both spawning and non-spawning, undertook an early summer migration into cooler tributaries of the Blackfoot River. Again, the bull trout of the Flathead system provide a contrast. In the Flathead basin, sub-adult and adult bull trout alike can be found year-round in the larger river environment (Shepard et al. 1984, Fraley & Shepard 1989). In the context of our study area, high summer water temperatures make it seem unlikely that large numbers of adult

or sub-adult bull trout would be found year-round in the lower Grande Ronde or Snake rivers. Nonetheless, we did observe 2 radio-tagged fish that spent an entire summer in these habitats; one in the Grande Ronde just downstream of the Wenaha River confluence and the other in the Snake River. Similarly, Swanberg (1997) observed 2 radio-tagged fish that summered in the Blackfoot River near the confluence of a cold tributary. Rather than being aberrant behaviors, we speculate that these few observations point to an additional facet of the full life history suite of the species, as well as the potential importance of local thermal refugia. While we did not track the movements of bull trout < 300 mm, we did track fish that ranged from 310-630 mm. Based on the size-age-maturity relationships observed by others (Fraley & Shepard 1989, Swanberg 1997) some of the smaller fish we tracked were probably immature sub-adults. However, even the smallest individuals exhibited extensive seasonal movements. The only difference in movement associated with size we observed was that fish tracked into tributary streams of the Wenaha River did not include the smallest individuals. Consequently, I expect that both sub-adult and adult fish move throughout the Wenaha, Grande Ronde, Snake River network, and that water temperature is an important factor driving the seasonal migration patterns of bull trout in this system.

Factors other than water temperature may influence the timing of bull trout movement and/or provide additional reasons for migration to occur. For example, the movement of bull trout into the Wenaha River in early summer not only corresponds to increases in temperatures of the Grande Ronde River, it also corresponds to a time of increased abundance of potential prey, both invertebrate and young-of-year fish, in the Wenaha River. During underwater surveys we frequently observed bull trout foraging on both insects and small fish. In addition, influences on migration timing may not simply be a function of local conditions. For instance, by virtue of its influence on flow and temperature of the Grande Ronde River, the hydrograph of the Wallowa River (a larger tributary upstream ~70 km) could have consequences for the timing of movements into and out of the Wenaha River by all species, including bull trout.

Our observations of bull trout fry and juveniles were limited. This was likely due to the fact that this study did not include extensive or repeated underwater surveys of

tributaries to the Wenaha River. Bull trout fry and small (presumably juvenile and/or mature non-migratory) bull trout were occasionally seen at sites in the upper main stem Wenaha River, more frequently observed at sites in the lower S. Fork of the Wenaha, and were abundant in the most upstream sites of the S. Fork that we visited only once in the summer of 1999. In the main river they were almost never seen during the daytime, while at the most upstream sites of the S. Fork they were visible at all times. These observations match those of previous studies that generally suggest the use of spawning tributaries as juvenile rearing habitat (Rieman & McIntyre 1993). However, our limited observations suggest that the diel use of habitat by juvenile bull trout may be context-dependent, which contrasts with observations by (Bonneau & Scarnecchia 1996) and the results of an experiment by (Baxter & McPhail 1997) that both suggested cryptic daytime behavior was generally the rule for juvenile bull trout.

The Wenaha River is considered a stronghold of regional significance for endangered bull trout (Li et al. 1995, Buchanan et al. 1997, Rieman et al. 1997). Indeed, the numbers and sizes of fish we observed are suggestive of high productivity for bull trout in the study area, though it has become more apparent through this study that this productivity is not linked to the character of the Wenaha River alone, but rather to an entire riverscape of which it is a part. It is not certain why this area is so productive, but there are numerous possible factors involved. Though I did not perform a rigorous analysis of habitat use by bull trout, I did observe habitat associations, and temporal shifts in those associations, that may be of importance. As bull trout are classified a stenothermic species (Buchanan & Gregory 1997), water temperature is generally at the top of the list of environmental factors influencing the broad scale distribution and abundance of the species. Summer water temperatures in excess of about 15 °C are thought to limit adult bull trout distribution, and optimal fry and juvenile development is known to require temperatures less than about 10 °C (Buchanan & Gregory 1997). In accordance with this, we saw fry and juvenile bull trout only in the upper reaches and tributaries of the Wenaha River where summer temperatures typically meet this standard. Nevertheless, there are relatively long lengths of stream in the drainage that likely meet these standards and may provide optimal rearing habitat. I also observed an association between the

summer distribution of sub-adult and adult sized bull trout and water temperature along the length of the Wenaha River, with almost no fish seen in the lowermost reaches during the warmest periods of the summer. Despite this apparent limitation, relative to other rivers of its size in the region the main-stem Wenaha River includes a large amount of thermally acceptable habitat for bull trout. Of course, there are many other factors that may be related to their productivity in the area. Habitat within the Wenaha drainage is largely unaltered by humans. This fact combines with the natural occurrence of floodplain segments that are known to be important to bull trout (Baxter et al. 1999, Baxter & Hauer 2000) and are thought to be hotspots for aquatic productivity in general (Stanford & Ward 1993) to make the Wenaha drainage a unique resource for this species. In addition and inseparably, the free-flowing nature of the Grande Ronde River and the connectivity that exists from headwater tributaries all the way to the Snake River is undoubtedly essential to the productivity of bull trout in this area.

I also found associations between bull trout distribution and abundance and habitat factors at nested, smaller spatial scales, and these associations changed with temporal context. As was the case for suckers and whitefish, radio-tracked bull trout showed selection of habitats in different valley segment types during different portions of the year. For example, alluvial valleys (most common in the Wenaha drainage) were selected in summer but avoided in winter while alluviated canyons (most common in Grande Ronde and Snake) were selected in winter and avoided in summer. Interestingly, while both mountain whitefish and largescale suckers avoided habitat in canyon segments during all seasons, a greater proportion of bull trout were found in canyon segments during winter. This was related to the fact that many bull trout migrated up the Grande Ronde from the confluence of the Wenaha River (this section was dominated by the canyon type), while most whitefish and bull trout went downriver (where much more alluviated canyon type was present). The reason for this difference is unclear, though one possible explanation may have to do with the proximity of the upstream section to the Wallowa River and Lookingglass Creek, which could serve as prey sources of out-migrating juvenile salmon and steelhead. For bull trout that migrated seasonally within the Wenaha River, I also found a shift from upper reaches (where alluvial valley

segments were more common) in summer to use of mid-reaches (where the most alluviated canyon segments occurred) in winter. This valley segment context was reflected in the selection of habitats at smaller scales as well, with deeper habitats (typically pools) being used in winter and more use of shallow habitats occurring in spring, summer and fall. As with suckers and whitefish, radio tracked bull trout frequently used alcoves and slower, shallower habitat at night during all seasons. During the daytime, adult bull trout also tended to select deeper, faster habitats. Though they exhibited a similar pattern, bull trout tended to exhibit greater overall diel movement than the other species. Though an individual typically remained in a single channel unit during a day or during a night, movement within this area was quite variable. This difference may reflect a more mobile mode of foraging by bull trout than by suckers or whitefish.

A riverscape perspective on the distribution, movement, habitat use, and species associations of bull trout may be essential to effective conservation and management. This study showed that changes in bull trout distribution in the Wenaha River and dynamics of their associated fish assemblage reflected complex movement patterns. As with other migratory fish species, these movements were associated with seasonal shifts in habitat preference at nested spatial scales. Within the context of this riverscape, bull trout display multiple life history strategies and migratory behaviors, some of which require the complementary use of habitat resources separated by long distances. The fact that migratory bull trout in this system may use habitat ranging from headwaters to the Snake River has important consequences for defining the population and area of concern for conservation and management of bull trout and habitat in this river network.

### *4.3  Movement, Life Histories and Habitat Relationships of Fishes in the Riverscape*

#### 4.3.1  Fish Movements and Life Histories

Rather than the restricted movement long presumed to be characteristic of non-anadromous fishes (e.g., Gerking 1959, Gatz & Adams 1994), I found that many species in the Wenaha, Grande Ronde, Snake river system exhibited dramatic movements of up to hundreds of kilometers, providing further evidence that such mobility may be more the rule than the exception among stream fishes, particularly of this region (Gowan et al. 1994, Fausch & Young 1995) (Figure 47).  In a recent modeling and synthesis effort, Rodriguez (2002) argued that stream fish do conform to the restricted movement paradigm, but that a mobile component may occur within many populations.  Rodriguez (2002) also argued that critics of the restricted movement paradigm have overemphasized the spatial extent of movement and the proportional representation of mobile fishes within populations.  The findings of my study contradict Rodriguez's argument and suggest that the concept of restricted movement may have little applicability in river systems of the Pacific Northwest.

Nonetheless, while the restricted movement paradigm may not have general applicability to entire stream fish assemblages, some species exhibit less movement than others (e.g., Hill & Grossman 1987).  In the context of this study, for example, we did not observe evidence of large-scale migrations by species of sculpin or dace.  Even among those species for which we did detect significant movement, there were different strategies exhibited by groups within species, including some fish that moved very little.  Consequently, I expect that generalizations regarding movement among stream fishes may be less important than specific knowledge of life history complexity among and within species.  Furthermore, I suspect that the context of a species within a particular riverscape has important consequences for the extent of movement and the range of life histories that it will exhibit in that setting.  This idea is supported by comparison of our

Figure 47. Members of the Wenaha River fish assemblage by family. Those that are shaded exhibited at least one large-scale migratory life history form. Young of the year and juveniles of all species occurred in the Wenaha River with the exception of *Ptychocheilus oregonensis* (only large adults were observed in the Wenaha) and *Catostomus sp.* (fry were seasonally common, but juveniles were rare in the Wenaha).
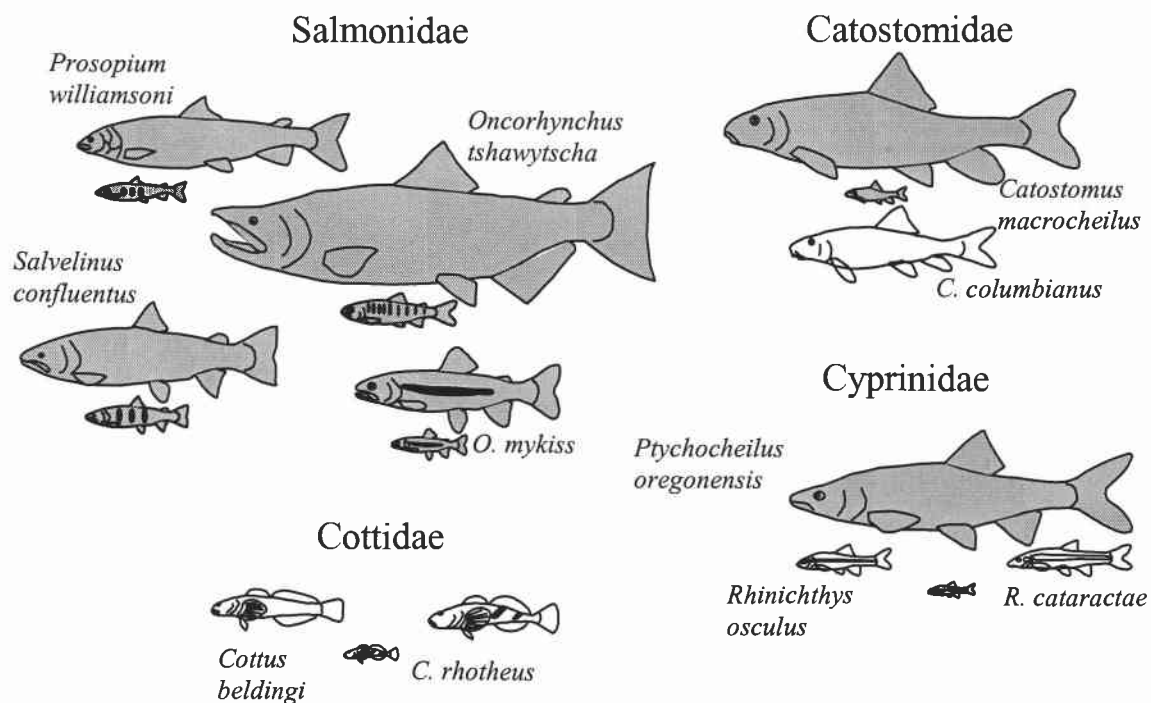
observations of individual species such as largescale suckers, mountain whitefish and bull trout with those of studies done elsewhere.

Indeed, the nature of species migration patterns, the distribution of different life stages, and the associations with large-scale arrangement of habitat resources in the study area indicate that, as was suggested by Southwood (1977), heterogeneity in the habitat templet provides the context for life history expression. For example, the spatial arrangement of alluvial valley segment habitat within the study area is such that there is little of it located along the sections of the lower Grande Ronde and Snake rivers. For species that require habitat of this kind at some stage of their life history, this may necessitate movement between the larger rivers and drainages such as the Wenaha where large amounts of this habitat type occur (higher in the Grande Ronde Basin, fish may move to use alluvial valley habitat in the Wallowa or upper Grande Ronde rivers). The findings of this study also show that, in free flowing river systems that maintain their connectivity to large areas of relatively pristine habitat, many species will exhibit multiple life history forms, with variations on the general "migratory" and "resident" themes. Such life history diversity is increasingly recognized as common in fishes, particularly salmonids, and as having evolutionary significance and importance to the long-term resiliency of populations and species (Noakes et al. 1989, Healey & Prince 1995, Smith & Skúlason 1996).

## 4.3.2 "Landscape Habitat Relationships" for Fish in the Riverscape

The factors responsible for the fish movement patterns we observed likely include a complex array of biological interactions and habitat relationships. Though this study was not designed to explicitly describe such causal mechanisms, our results do point to some important possibilities. In particular, the results of this study suggest that the life histories of many fish species we observed require the complementary use of habitat resources that are often separated by long distances within the river network. Dunning et al. (1992) described the movement to obtain non-substitutable resources found in

different areas of the landscape as 'landscape habitat complementation.' They pointed out several examples of its importance to other mobile species, from birds (e.g., Petit 1989) to butterflies (e.g., Weiss et al. 1988). My study shows that landscape habitat relationships (*sensu* Dunning et al. 1992) appear to be important factors to consider in our attempt to understand the processes that affect populations, assemblages, and communities in riverine landscapes or "riverscapes." Schlosser (1995) explored the concepts of landscape habitat relationships described by Dunning et al. (1992) in the context of stream fish ecology and described a dynamic landscape model of stream fish life history in which fish movement plays a critical role in transporting different life stages across landscape scales to occupy patches of critical habitat required to complete their life cycles. Our observations support the applicability of Schlosser's model, and emphasize the need for a "riverscape perspective" in the research and management of stream fish (Fausch et al. in press).

This study is one of the first to explicitly examine the nature and importance of large-scale habitat complementation to stream fishes. One of the principal hypotheses advanced regarding landscape habitat complementation is that settings in which non-substitutable resources are closer together in space should be more productive for fish populations than areas where these resources are widely distributed (Dunning et al. 1992, Schlosser 1995). Though this hypothesis seems intuitive, our observations do not necessarily support it. In this study we did not examine other watersheds to draw comparison of habitat complementation and productivity for different fish species. However, the numbers and sizes of fish we observed for species such as bull trout, whitefish and suckers were suggestive of high productivity in this system, while the distances moved by many individuals were among the furthest documented for these species. Upon consideration, there seem to be many other examples of fishes that exhibit high productivity despite having to migrate long distances to carry out their life cycle. For instance, I know of no evidence suggesting that populations of Pacific salmon that travel longer distances are less productive, and the same seems to hold true for tropical migrant species such as *Prochilodus sp.* (Welcomme 1985). What does seem likely, however, is that landscape changes that reduce the amount of important habitat resources,

reduce connectivity to these resources, or increase the travel distance to reach them to a degree that departs from conditions under which populations have evolved, may lead to their reduced productivity.

There have been few studies that have explicitly examined fish movements and/or productivity in relation to the spatial arrangement of habitat resources. However, observations of migration by fish to use habitats separated by long distances are well known. For example, researchers in temperate zones have known for decades of migrations by species of the family Salmonidae, including the well studied migrations of anadromous salmon and trout (Thorpe 1988) and many examples of potamodromous migrations as well (Northcote 1997). In addition, researchers in the tropics are well aware of both diadromous and potamodromous migrations as common among the riverine fishes of these latitudes (e.g., Welcomme 1985, Bruton et al. 1987). Despite this empirical background, information on fish migration is not always coupled with an understanding of river habitat heterogeneity at large scales. I feel that a perspective on the spatial arrangement and temporal dynamics of habitat in the riverscape added considerably to the interpretation of movement patterns, and sets the stage for well-informed tests of hypotheses in future studies.

With a perspective on habitat heterogeneity in the riverscape and detailed information on the movements of fishes, it is possible to ask questions regarding the importance of other "landscape habitat relationships." In addition to complementation, other processes linked to the spatial arrangement and physiognomy of resources in the riverscape may include habitat supplementation, source-sink dynamics, neighborhood effects, and connectivity (Dunning et al. 1992, Taylor et al. 1993, Schlosser 1995). As described, there was considerable variation in movement among individual fish, with some traveling much further distances than others. We commonly observed individuals of a species to move through habitats that appeared suitable to others in their population to occupy habitat that required additional migration. This phenomenon is likely the result of interactive processes, including density-dependent processes, learned behavior patterns, evolutionary context, as well as biological and physical characteristics of which we are unaware. However, it also indicates that some fish movement occurs to supplement

habitat resources of similar character (i.e., habitat supplementation). These observations suggest that habitat supplementation is also an important process in this river system. For instance, adult mountain whitefish migrated variable distances up the Wenaha River to reach specific summer feeding habitats. There are either 1) many miles of apparently similar summer feeding habitat, or 2) these variable habitats are effectively substitutable as summer feeding habitat for adult mountain whitefish. Regardless, the extent of the patches of this resource available and their spatial proximity likely has a positive influence on the productivity of the area for this species.

Landscape processes such as these may act in concert to influence the patterns we observe. For example, high summer water temperatures in the Grande Ronde River may make the boundary between the Wenaha and the Grande Ronde rivers largely impermeable (an example of a neighborhood effect) during this time period to species like mountain whitefish or bull trout that may utilize non-substitutable resources in both rivers (habitat complementation). Similarly, some rainbow trout from the Grand Ronde River may use the lower reaches of the Wenaha River as a thermal refuge during peak temperatures of summer (an example of habitat complementation), yet fish may be more likely to undertake this movement if they are closer to the mouth of the Wenaha River than if they are further away (another example of a neighborhood effect).

While landscape habitat relationships such as habitat complementation are generally conceived as occurring at large spatial scales, "landscapes" can come in many sizes (often depending on the organism, community, or questions being addressed), and attention to the spatial arrangement of resources can yield insight at smaller spatial scales as well (Turner 1989). Our observations of habitat complementation at small spatial scales (e.g., channel units) and over short temporal scales (e.g., diel) support the idea that these processes are important across a hierarchy. For example, we observed that adult largescale suckers often utilized slack-water areas such as alcoves at night, while they tended to be found only in main channel habitats during the day. We observed many fish species utilizing these alcove habitats, which were low energy environments, sites of detritus accumulation, and often were thermally influenced by upwelling groundwater. The spatial proximity of appropriate main channel habitat to alcoves may be an important

aspect of habitat physiognomy at this scale for many species. Additionally, one reason fish did not use these off-channel habitats during the day may have been that they were effectively impermeable due to greater predation susceptibility in these habitats during this time period. These are but a few examples. Based on the kind of information we collected on fish movement and habitat heterogeneity, it will be possible to raise questions regarding many more relationships and processes such as these.

## 4.4    *Consequences for Understanding Stream Fish Assemblages*

### 4.4.1  Factors Operating Over Long Time Scales

This study represents an intense effort to describe and better understand the dynamics of a river fish assemblage. However, no matter how thorough this effort, the dynamics we observed must be set within the context of the long-term history of the ecosystem and the changes in this system that occur on longer temporal scales than the years encompassed by our research. The dynamics of fish assemblages can be explained by factors operating across a hierarchy of scales, from ultimate factors such as evolution and zoogeography to proximal abiotic or biotic factors (Matthews 1998). Long-term fish assemblage dynamics include changes in species abundance and membership through immigration and emigration, local extinction and recolonization. Ecologists are used to thinking of these kinds of dynamics as occurring on geologic time scales. However, in this river system they are evident in recent history, largely due to human impacts that have occurred outside of the Wenaha River drainage.

Perhaps the most dramatic of these influences has been the decline of salmon populations in the area. Prior to their extinction in the late 1980's, coho salmon, *O. kisutch*, were once plentiful enough in the Wenaha River that adults were captured there in large numbers (Thompson & Haas 1960). Numbers of Wenaha River steelhead and chinook salmon in recent years have been a degree of magnitude lower than historic estimates (Thompson & Haas 1960, Keefe et al. 1996), though the numbers of juvenile

chinook salmon we observed in the Wenaha River were quite high relative to the number of spawning adults. Nevertheless, the consequences of the salmon population decline for assemblage and community dynamics is likely significant, both in terms of the living presence of these fish and the subsidy of marine-derived nutrients they historically represented to this drainage.

While the construction of the Snake River dams has had many direct and indirect impacts on salmon populations of the basin, there have been affects on other species as well. These impoundments drowned most of the alluvial valley-type habitat in the lower mainstem Snake River. Our observations emphasize the importance of habitat in these floodplain segments to the life histories of many native stream fishes. In this study we observed migratory forms of species such as bull trout, mountain whitefish and largescale suckers moved long distances to utilize habitats of this kind. It is likely that the movements, ecology and productivity of fish populations in this riverscape have been affected by the loss of the large river floodplain habitat. Though bull trout and mountain whitefish are found in seeming abundance at present, several local residents stated that they believed their numbers have also decreased from historic levels. While these species may be negatively impacted by the loss of mainstem Snake River habitat, non-native species such as smallmouth bass, *Micropterus dolomieui*, appear to flourish in the reservoirs created by the dams. Interestingly, smallmouth bass were absent from any of our surveys, though they were observed (and their spawning documented) in the lower Wenaha River in the summers of 1994 and 1995 (Frissell et al. 1996). This dynamic may well reflect a source-sink process (*sensu* Dunning et al. 1992) in the riverscape, with the reservoirs of the Snake River serving as a source area, and areas such as the Grande Ronde and Wenaha Rivers currently functioning as sinks. The ebb and retreat of species (both native and non-native) has important consequences for fish assemblage membership and, subsequently, for the structure and function of the river ecosystem.

### 4.4.2 Migration: Consequences for Fish Assemblage Structure and Definition

Set within the context of the long-term dynamics described above, the findings of this study have important implications for our understanding of factors governing stream fish assemblage structure. This study demonstrated that the seasonal migrations of fish species have dramatic effects on the dynamics of the fish assemblage in this river system. In particular, I found that longitudinal patterns in fish assemblage structure changed significantly with season as a function of these movements. Investigations of the seasonal dynamics of longitudinal assemblage patterns have been relatively rare (Matthews 1998). Rather, many studies of stream fish assemblages result in a summertime snapshot of the distribution and abundance of species along the length of a river section, and these observations have formed the basis for conceptual frameworks describing fish assemblage patterns. For example, concepts of longitudinal zonation of stream fishes (Matthews 1998) are almost exclusively based on studies that involved collection or observation of fishes during summer base flow periods (e.g., Sheldon 1968, Horwitz 1978, Rahel & Hubert 1991) with little or no discussion of fish movement as a possible complicating factor. Consequently, while debate over whether longitudinal patterns represented species "addition" or species "replacement" has been extensive in the literature (e.g., see Matthews (1986) and references within), in light of increased awareness of fish movements, these discussions may have less relevance than previously thought.

While some studies of seasonal assemblage dynamics in temperate stream systems have been done, these have typically not placed the dynamics in the context of individual species life histories or movements, but rather have focused on assemblage level phenomenon such as changes in species diversity or assemblage stability (e.g., Grossman et al. 1985, Gelwick 1990, Meador & Matthews 1992, Taylor et al. 1996, Gido et al. 1997). In part, this may be due to the fact that many species life histories and movements are unknown. This is likely to be especially true in settings such as the Mississippi or in tropical basins such as the Amazon where diversity is very high and new species continue to be discovered. However, investigations in the Amazon Basin have yielded

perspectives of dynamic assemblages driven by spectacular longitudinal and lateral (i.e., floodplain) migrations (Lowe-McConnell 1975, Goulding 1980, Welcomme 1985). The results of my study indicate that migratory species can have important consequences for temporal dynamics of fish assemblages in temperate systems as well. Knowledge of these movements is essential to any interpretation of observed species-habitat associations, assemblage patterns, or the results of experiments done in an attempt to understand factors governing assemblage structure.

Our observations of stream fish migrations raise questions about defining fish assemblages themselves. What constitutes a "local fish assemblage?" Furthermore, what does "local" mean? In a recent text, Matthews (1998) (p. 30) states, "a locality is a place in a stream or lake that would be included in a single typical collection or observation sample by an ichthyologist (e.g., one to a few hundred meters of a stream or shoreline)." In light of the distances moved by many fishes we observed, the spatial limits of Matthews (1998) 'locality' seem quite small. A local assemblage, Matthews (1998) states, will "include the individual fish that occur together at a locality at a given time or over a brief period of ecological time, having reasonable probability of encountering each other within the course of feeding, resting, movements, and so forth in a given day." As part of the basis for this definition, he cites several examples of studies demonstrating small home range among stream fish (Scalet 1973, Helfman 1981, Hill & Grossman 1987). When applied to a river system dominated by migratory fishes, such a definition would seem to yield a bewildering array of different assemblages. For instance, movements in the lower Wenaha River are such that very different 'assemblages' could exist in the same 'locality' from one month to the next. As Matthews (1998) later qualifies, the spatial and temporal boundaries to an assemblage can be difficult to define. I suspect that they may be even more difficult to define than has been generally perceived.

In the context of the riverscape we studied, two possible scenarios suggest themselves for defining fish assemblages. One possibility would be to extend the spatial boundary of the local assemblage to include the full movement ranges of the species in the system. In a system possessing anadromous fishes, however, this would yield an assemblage whose

spatial extent would seem far from 'local.' Alternatively, one could define a locality as a single reach of stream, but include all fish species that might occur there together over an entire year. In this fashion, different reaches could be conceived as possessing distinct assemblages, yet these assemblages are seasonally dynamic in nature and movements among reaches would be included as an important driving mechanism. I explore this possibility in greater detail below (see Figure 49).

With these uncertainties in mind, the dramatic migrations of many species we observed have implications regarding the mechanisms responsible for fish assemblage structure. In his recent text, Matthews (1998) synthesized much of the existing literature pertaining to factors influencing local fish assemblage structure. While he identified a complex web of possible mechanisms influencing the composition of local assemblages, he did not include the movement of fishes as one of these. A common theme in the study of fish assemblages, and indeed in the study of communities in general, has been to question the relative role of individual species response to abiotic factors vs. the role of biotic interactions in governing assemblage structure. While it is generally assumed that elements of both factors are responsible for the patterns we observe, I submit that the full nature of fish-habitat relationships and the strengths of inter-specific interactions are difficult to evaluate without knowledge of fish movement.

## 4.5    *Consequences for Stream Communities and Conceptual Frameworks*

### 4.5.1  Consequences for Existing Stream Community Frameworks

The results of this study and the questions I have raised have consequences for understanding not only stream fish assemblages, but also entire stream communities. The dominant conceptual framework for explaining stream community structure is the River Continuum Concept (RCC) (Vannote et al. 1980). This framework has served as an invaluable heuristic foil in stream ecology, and has inspired many advances in the field. The basic tenet of this framework is that stream communities vary in a predictable

fashion that reflects gradients in physical factors, productivity, and sources of organic material from headwater streams to large rivers. However, the perspective on stream fish described in this framework reflects a largely static perspective, suggesting that fish species and assemblages are associated with only portions of the river continuum. In contrast to this perspective, I found that many fish species in the study area used habitats positioned from headwater $2^{nd}$ and $3^{rd}$ order streams to $7^{th}$ and $9^{th}$ order large river reaches throughout the river continuum, and that fish assemblages were not static in time (Figure 48).

Though our observations do support the general idea that stream communities reflect the physical templet of the river network, our results also point to the importance of habitat heterogeneity not encompassed by the generalized longitudinal gradients described in the RCC. For example, valley segments with extensive floodplains existed at sites of lower stream order, and the spatial arrangement of valley segment types appeared to have important consequences for stream fish distribution, and hence stream community patterns. The results of my study, particularly the valley segment scale associations we observed, support the claim by Fausch et al. (in press) that heterogeneity at intermediate spatial scales plays an important role in the life histories of many stream fishes. The idea that this kind of heterogeneity is important, rather than noise about some general longitudinal theme, is one of the premises of the "patch dynamic concept" for stream systems (Pringle et al. 1988, Townsend 1989), as well as Montgomery's (1999) concept of "process domains." In particular, I feel our observations lend additional support for the concept of process domains, which embraces a perspective on heterogeneity in riverscapes at nested scales and acknowledges the importance of spatio-temporal context in interpretations of ecological patterns. I suspect that the tenets of this concept will be important elements in the evolving frameworks for fish species, assemblages, and stream communities.

Concepts regarding the mechanisms underlying stream community structure are tied to the results of manipulative experiments whose outcomes and subsequent interpretations often do not fully account for the physical or biological context within which they were performed. The results of my study suggest that the seasonal movement

Figure 48. In contrast to the more static perspective on fish assemblage structure depicted, for example, in the river continuum concept (Vannote et al. 1980), we observed several of the most abundant resident species moving seasonally to occupy habitats distributed across many stream orders. See figure 47 for fish silhouette identification.

of organisms may provide an important aspect of biological context within which community ecology experiments should be evaluated. Similarly, the heterogeneity in the riverscape we observed was linked to species movements and assemblage patterns, and hence provides important physical context for experimental approaches. Many experimental studies of the role of fishes in stream communities have been based on small spatial scale manipulations over short summer field seasons (e.g., Power et al. 1985, Power 1990, Flecker 1996) with little attention given to the physical context of the study reach, the prospect of temporal dynamics, or the role of movement in governing species associations or ecosystem processes. Research in tropical rivers has suggested the importance of seasonal context and fish movement. For example, Winemiller (1996) showed that food web character exhibits seasonal fluctuation in tropical rivers (Winemiller 1990), and that these dynamics are largely a function of the migration patterns of fishes, which, in these river systems, are often poorly understood (Winemiller & Jepsen 1998). Similarly, Zaret & Rand (1971) found evidence for distinct shifts in competitive interactions among fishes between wet and dry seasons. In addition, there have been numerous studies documenting the influence of fish migration on the energy and nutrient dynamics of stream ecosystems (Hall 1972, Durbin et al. 1979, Bilby et al. 1996). Consequently, the results of our study are not without precedent in other river systems of the world. Rather, these observations suggest that the full dynamics and complexity of stream communities and the subsequent importance of context are only beginning to be grasped by stream ecologists.

### 4.5.2 Thoughts on an Alternative Framework for Stream Fish Species, Assemblages and Communities

With the importance of fish movements, assemblage dynamics, habitat heterogeneity, and a contextual perspective in mind, I introduce the beginnings of an alternative approach to conceptualizing stream fish species, fish assemblages and stream communities. I believe that, rather than using a single generalized framework such as the RCC, it would be fruitful to integrate themes from multiple conceptual models that span

the biological hierarchy from populations and species to communities. This approach may provide the appropriate context within which to understand the requirements of stream fish, the nature of fish assemblages, and the role of fish in stream communities. The results of my study highlight the importance of a riverscape approach to understanding fish populations, species and assemblages (Torgersen 2002, Fausch et al. in press). Consequently, any useful framework for stream fishes should incorporate the full life histories of fishes, their movement, and their large-scale habitat relationships (Schlosser 1995, Schlosser & Angermeier 1995). To do so requires that we embrace more of the full heterogeneity of habitat and habitat-forming processes within the riverscape (Frissell et al. 1986, Montgomery 1999).

I also perceive the need for a conceptual model of stream fish assemblages and their dynamics that can be set within the riverscape context (Figure 49). The "community as a kaleidoscope" idea developed through modeling of lake plankton communities (Lane 1986) provides a useful analogy for fish assemblages and communities in streams. Within any given stream reach, there are fish species, species life stages, or life history forms that may represent a "core assemblage" whose composition is relatively stable throughout a year. For example, in a given reach of the lower Wenaha River, the core fish assemblage may consist of sculpin and dace species, along with adult and juvenile rainbow trout, and mountain whitefish. Interacting with this core structure is a suite of species, life stages, or life history forms whose presence in the local assemblage is seasonally dynamic. This dynamic element can be thought of as "turning" about the core structure, with different members entering into the local assemblage as a function of seasonal migrations, seasonal dynamics of populations, and habitat changes. For example, in reaches of the lower Wenaha River, northern pikeminnow, adult and larval largescale suckers, adult and juvenile chinook salmon, migratory bull trout and migratory mountain whitefish are all seasonal members of the local assemblage. The seasonal alignment of the outer dynamic element and the central core structure determines the local assemblage within a season, and hence sets the context within which biological interactions among fish species may occur.

Figure 49. Fish assemblage kaleidoscope for a given reach of the lower Wenaha River depicting a core assemblage structure that persists year-round and fish species and/or life history types that are seasonal members of the local assemblage. Fish silhouette identities are as depicted in previous figure, with those shaded denoting migratory types. Interactive factors that drive seasonal assemblage shifts are shown.
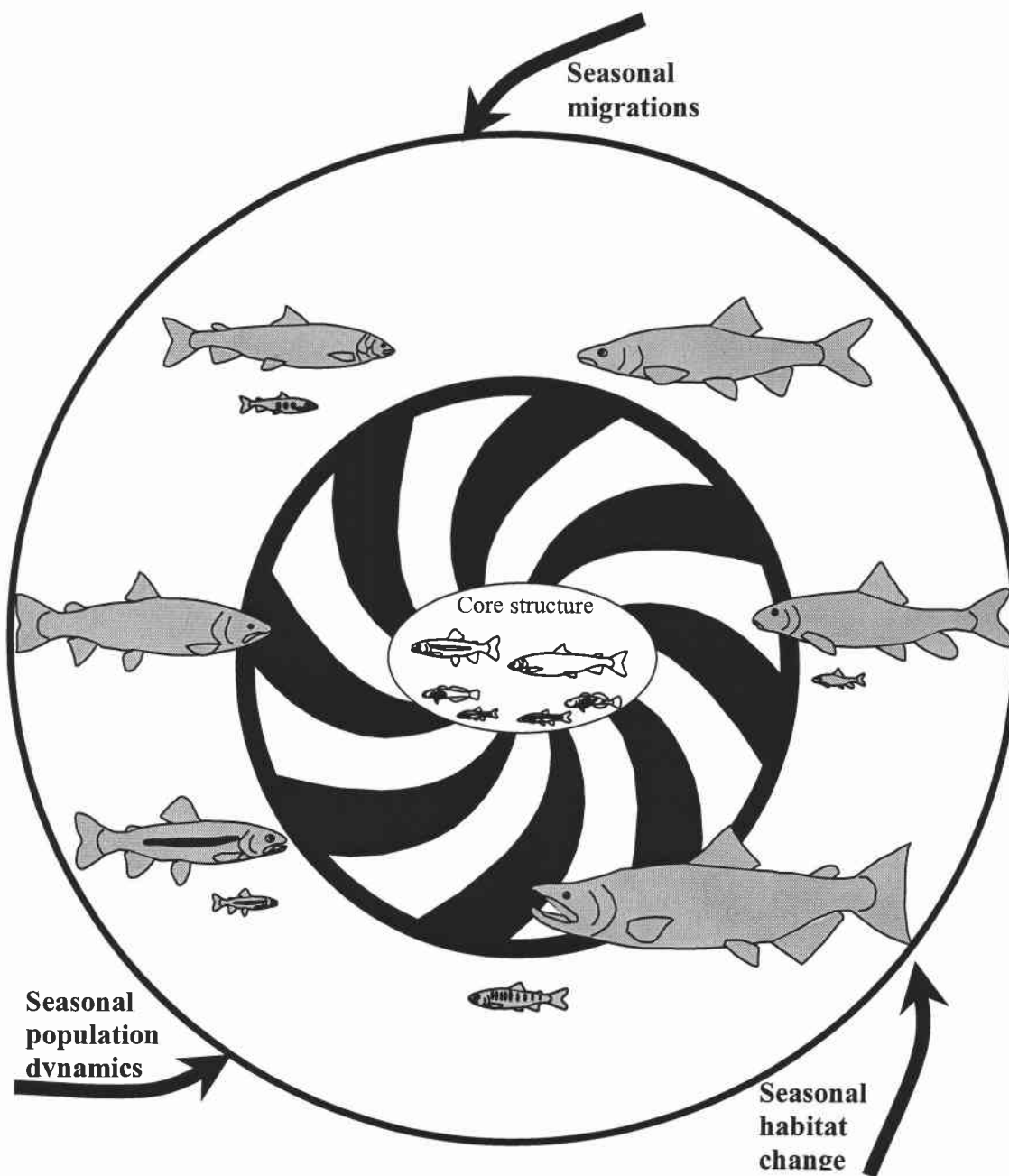
To extend this model in a spatial dimension, we must ask the question, "What are the spatial boundaries of an assemblage?" One can draw the boundaries of the dynamic assemblage (i.e., the "kaleidoscope") at different scales. Following one line of thought, the assemblage kaleidoscope could be defined at the scale of the Wenaha or Grande Ronde basins, or even the entire region ranged by Pacific salmon. However, if we subscribe to Matthews' (1998) view that a local fish assemblage includes those fish in an area that have reasonable probability of encountering each other in a day, we can envision reaches along the length of a river network functioning like a string of kaleidoscopes, whose characters and dynamics reflect their unique context in the riverscape (Figure 50).

This concept could be extended to include the entire stream community. In fact, this is clearly necessary in order to reflect the reality of important biological relationships that involve non-fish organisms. Stream ecologists have known for decades that stream communities undergo distinct seasonal changes such as shifts in organic matter input and processing (e.g., Webster & Meyer 1997) and a suite of seasonal dynamics associated with floods (e.g., Junk et al. 1989). In addition, the seasonal dynamics of benthic invertebrate assemblages within a given reach can be dramatic (e.g, Tavares-Cromar & Williams 1996). Despite this empirical experience, we suggest that these dynamics have not truly been incorporated into our conceptual frameworks for stream communities. Extension of the kaleidoscope model to include other members of the aquatic community may be a useful conceptual step. Furthermore, the community boundary need not be the water's edge. Our natural history observations suggest that a large suite of terrestrial species could, and possibly should, be integrated into our vision of "the stream community."

In addition, the kaleidoscope model, with its core and dynamic elements, can be applied to dynamics of assemblages or communities on time scales longer than a single year. As such, one can visualize "kaleidoscopes within kaleidoscopes" representing the dynamics of assemblages and communities that occur over different time scales as a consequence of different driving forces. For instance, while the kaleidoscope structure of a particular reach may remain relatively constant over a single year or even several years,

Figure 50. Extending our model in a spatial dimension, local fish assemblages in reaches along the length of a river network can be envisioned as a string of kaleidoscopes whose characters and dynamics reflect their unique context in the riverscape.
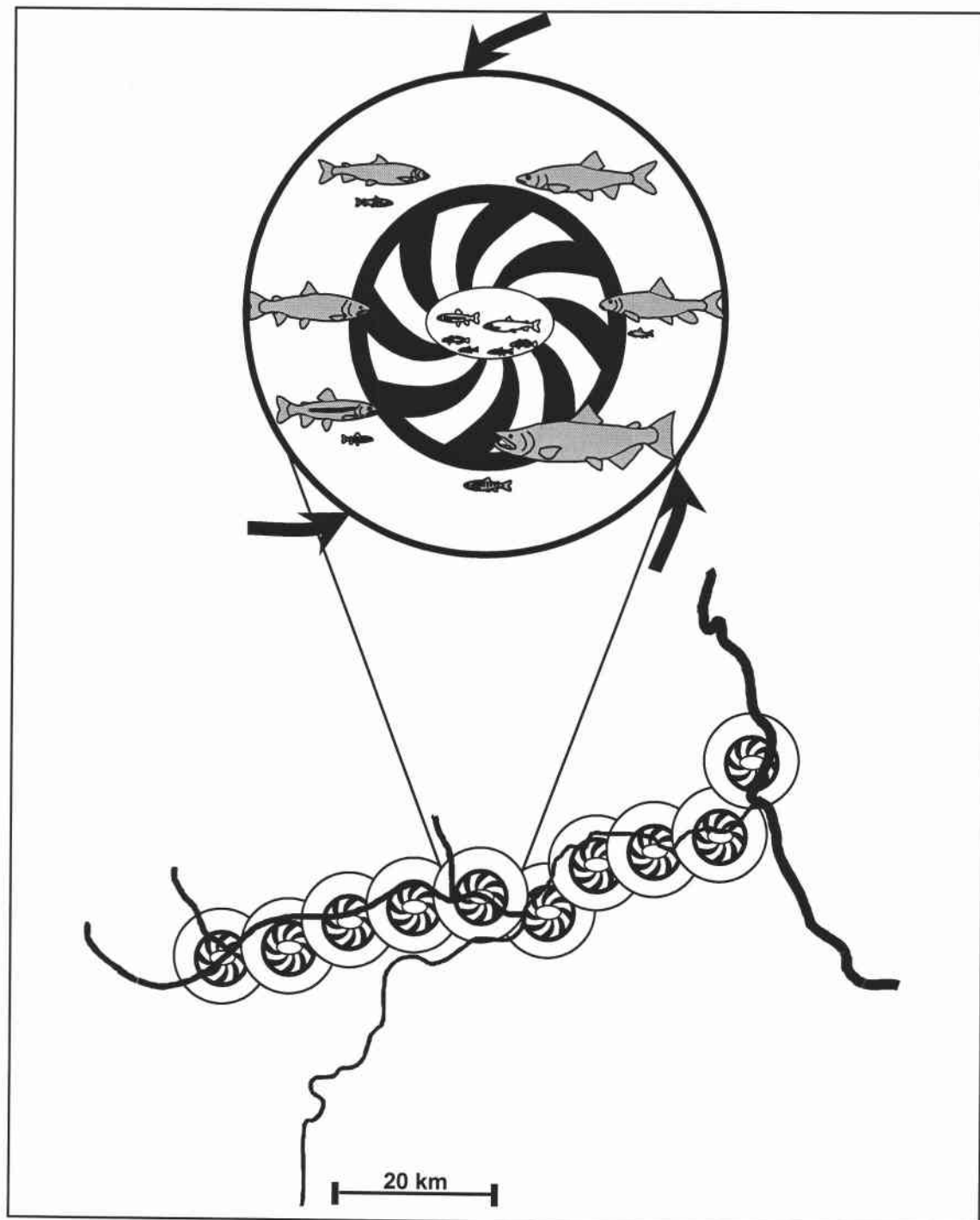
as a consequence of factors such as decadal climate shifts, changes in species management, or introduction of non-native species, this membership may change. For example, our observations suggest that shifts of this nature may be responsible for the ebb and retreat of non-native smallmouth bass in the lower Wenaha River. Similarly, changes in the management of terrestrial species such as river otters or bald eagles could have consequences for community membership as well. Regardless, it seems that a dynamic model of this kind could be quite useful for conceptualizing stream assemblages and communities.

## 4.6    Consequences for General Ecological Theory of Communities

The results of this study raise questions regarding the nature of ecological communities in general. Are communities groups of co-evolved populations closely-knit by strong biotic interactions? Are they loosely associated populations of species whose shared distribution is primarily driven by the physiological constraints of the environment? If these ideals represent ends of a continuum, where do particular communities lie along this gradient? The extent of movement we observed among fishes and the resultant ephemeral nature of many species associations at a given locality suggest that, while strong biotic interactions may play important roles in the stream community, these interactions likely exhibit significant changes with the seasons. Consequently, if strong, co-evolved relationships among organisms are important in this stream system, the roots of these linkages are not in year-round contact within small spatial areas.

The results of this study emphasize the need for explicit knowledge of life histories and movements in order to identify potentially important biotic interactions and estimate the strength of these connections. Community ecologists such as Paine (1980) called for a research focus on determining interactions strengths in real communities, and this has since become an important theme in the work of community ecologists. However, only with more complete information on species contact times can researchers truly hope to

make accurate estimates of the strengths of biological interactions. Information on the contact time and numbers of organisms in contact with one another establishes what might be termed "interaction potential," without which estimates of "interaction strength" lack the required context to be truly useful. Studies such as this one provide the necessary background for asking questions regarding the nature of relationships that characterize the structure and function of ecological communities.

The movement of organisms is a factor that reflects organisms' biotic and abiotic interactions, while it also influences or sets the context for these interactions, a fact acknowledged decades ago by Charles Elton (1927), yet under appreciated. For example, the movement patterns of migratory bull trout in our study area may be influenced by the relationship between bull trout physiology and stream temperature. In turn, these movement patterns have consequences for the nature and extent of interactions between bull trout and other species throughout the basin. There are many other ecological systems in which migration has been shown to be a critical factor contributing to seasonal community dynamics. For example, a significant component of bird assemblages in tropical or temperate zones may be migratory species whose seasonal presence and absence contributes significantly to assemblage dynamics and possible community interactions in any given locality (e.g., Trippe 1874). Likewise, the landscape scale migrations of animals in grassland ecosystems is well known, including the spectacular migrations of animals and consequent community and ecosystem dynamics in the Serengeti of Africa (e.g., Sinclair & Norton-Griffiths 1979, Wolanski et al. 1999).

This kind of evidence notwithstanding, the potential importance of movement and its role in the expression of ecological phenomena has not been fully incorporated into theory regarding ecological communities. Though community ecologists have, in the past, emphasized that assemblages and communities are dynamic in their nature (e.g., Menge & Sutherland 1987, Paine 1988), only recently have they begun to explore the full import of species life histories, the landscape context of communities, and temporal dynamics for understanding the structure and function of communities (Holt 1996, Winemiller 1996, Polis et al. 1997). In part, this may reflect scientists' desire for simple, elegant conceptual frameworks. Some might submit that greater theoretical integration of

the complexity that characterizes real communities could yield frameworks of such intricacy that they lose their utility as general models. I suggest, however, that embracing the complexity of ecological systems, along with the importance of contextual thinking, will yield more realistic and more useful frameworks for understanding, conserving and managing natural systems. My efforts at conceptualizing the dynamics of stream fish assemblages and communities in the context of riverscape heterogeneity represent another step in this direction. I believe that conceptual constructs such as the "kaleidoscope" model for stream fish assemblages can provide both useful abstractions and more realistic representations of complex ecological systems.

### 4.7 Consequences for Research and Conservation of Stream Fish in the Pacific Northwest

The results of my study and the questions I have raised have implications for research and conservation of streams and stream fish, particularly in the Pacific Northwest. They support the idea that a perspective of the full riverscape is critical to understanding and conserving stream fish (Torgersen 2002, Fausch et al. in press). Our observations of life histories and movements suggest that research at small spatial scales must be placed in a larger scale context to be useful. In addition to the need for research at larger spatial scales, it is clear that study of stream fishes must be conducted during times of the year other than summer base-flow periods if the full needs of these organisms are to be understood. Though this can involve considerable logistical difficulty, it remains an important task and must not be overlooked. In addition, it seems that the use of multiple complementary methods yields a much fuller perspective on the life histories, habitat relationships, and assemblage dynamics of stream fish. Integration of methods such as underwater surveys and radio telemetry leads to an emergent perspective greater than that gained through either one or the other alone. Applying variable sampling approaches may also enhance researchers ability to detect important ecological patterns (see also Torgersen 2002). For example, I found that coupling spatially extensive underwater surveys with intensively repeated surveys of select sites provided a very thorough

perspective on fish life histories and assemblage dynamics. Similarly, the nested sampling scheme we used to track the movements of radio tagged fish yielded much more information than a single, systematic approach.

The links I found between movement, life history, and the use of habitat in the riverscape have important consequences for conserving stream fishes in this region. These results indicate that effective conservation plans for individual species must often incorporate large areas to address the full habitat needs of fishes. While most researchers and managers would not consider a conservation plan for an anadromous species complete without addressing issues related to habitats used throughout the salmon life cycle (Mobrand et al. 1997), this same kind of attention has not been focused on non-anadromous species. Future conservation and habitat restoration plans must be conceived at a scale that reflects the full life history patterns of the species involved. Furthermore, effective management must take into account the spatial arrangement of species' resources and the importance of maintaining connectivity among them. Along these lines, managers of fish may learn from on-going efforts to address life history needs and landscape ecology of other mobile wildlife species (e.g., grizzly bears, wolves, whales, migratory birds).

Our observation of fishes' seasonal use of large river habitat has special consequences for their management in this region. From the results of this study, it is clear that the long-term health of populations of native species such as bull trout, mountain whitefish and largescale suckers depend on the availability and character of habitat in large river sections like the lower Grande Ronde and Snake Rivers. Many efforts to restore habitat and bolster populations of native fishes have focused on headwater tributary stream reaches. While native species such as bull trout may exhibit life history forms that remain resident in such headwater streams, expression of the full complement of their life histories and the long-term resilience of these populations likely depends on the maintenance of, and connectivity to, large river habitats. More research into the nature of these habitats and their use will be necessary for a full understanding of the role they play in the life cycles of fishes in Pacific Northwest Rivers.

Finally, the questions raised by this study regarding the nature of stream communities have consequences for their management and conservation. Most management and conservation of stream fishes in the Pacific Northwest is centered on single species. Actions are often taken with little regard for these organisms' place in the ecological community. If stream fish truly are a part of an integrated community, then no matter how much effort is put into developing conservation plans for species of concern, this single species approach is not viable in the long-term. Setting the context with information like that collected in this study, scientists can begin to gain a better understanding of the importance of community relationships to stream fish and the role fish play in the structure and function of these communities.

# REFERENCES

Bates, M. 1960. Ecology and evolution. pp. 547-568. *In:* S. Tax (ed.) The evolution of life (Evolution after Darwin, Vol. I), University of Chicago Press, Chicago, IL, USA.

Baxter, C.V., C.A. Frissell & F.R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. Transactions of the American Fisheries Society 128: 854-867.

Baxter, C.V. & F.R. Hauer. 2000. Geomorphology, hyporheic exchange and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57: 1470-1481.

Baxter, G.T. & J.R. Simon. 1970. Wyoming fishes.

Baxter, J.S. & J.D. McPhail. 1997. Diel microhabitat preferences of juvenile bull trout in an artificial stream channel. North American Journal of Fisheries Management 17: 975-980.

Begon, M., J.L. Harper & C.R. Townsend. 1986. Ecology; individuals, populations and communities. Sinauer Associates, Sunderland, MA, USA.

Bilby, R.E., B.R. Fransen & P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53: 164-173.

Bjornn, T.C. & J. Mallett. 1964. Movements of planted and wild trout in an Idaho River system. Transactions of the American Fisheries Society 100: 423-438.

Bonneau, J.L. & D.L. Scarnecchia. 1996. Distribution of juvenile bull trout in a thermal gradient of a plunge pool in Granite Creek, Idaho. Transactions of the American Fisheries Society 125: 628-630.

Brown, C.J.D. 1952. Spawning habits and early development of the mountain whitefish, *Prosopium williamsoni*, in Montana. Copeia: 109-113.

Brown, L.G. 1972. Early life history of the mountain whitefish *Prosopium williamsoni* (Girard) in the Logan River, Utah, Utah State University, Logan Utah. 47 pp.

Bruton, M.N., A.H. Bok & M.T.T. Davies. 1987. Life history styles of diadromous fishes in inland waters of southern Africa. American Fisheries Society Symposium 1: 104-121.

Buchanan, D.V. & S.V. Gregory. 1997. Development of water temperature standards to protect and restore habitat for bull trout and other cold water species in Oregon. pp. 119-126. *In:* W.C. Mackay, M.K. Brewin & M. Monita (ed.) Friends of the bull trout conference, Bull Trout Task Force (Alberta), c/o Trout Unlimited, Calgary, Calgary, Alberta, Canada.

Buchanan, D.V., M.L. Hanson & R.M. Hooton. 1997. Status of Oregon's bull trout. pp. 168, Oregon Department of Fish and Wildlife, Portland, OR, USA.

Camp, V.E. & P.R. Hooper. 1981. Geologic studies of the Columbia Plateau: Part I. Late Cenozoic evolution of the southeast part of the Columbia River basalt province. Geological Soc. Amer. Bull. 92: 659-668.

Chamberlin, T.C. 1890. The method of multiple working hypotheses. Science 15 (reprinted in 148): 754-759.

Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clifford, H.F. 1972. Downstream movements of White Sucker, *Catostomus commersoni*, fry in a brown-water stream of Alberta. Journal of the Fisheries Research Board of Canada 29: 1091-1093.

Corbett, B.W. & P.M. Powles. 1986. Spawning and larva drift of sympatric walleyes and white suckers in an Ontario stream. Transactions of the American Fisheries Society 115: 41-46.

Cunjak, R.A., R.G. Randall & E.M.P. Chadwick. 1988. Snorkeling versus electrofishing: a comparison of census techniques in Atlantic salmon rivers. Naturaliste can. (Rev. Ecol. Syst.) 115: 89-93.

Dauble, D.D. 1986. Life history and ecology of the largescale sucker (Catastomus macrocheilus) in the Columbia River. The American Midland Naturalist 116: 356-367.

Dauble, D.D. & R.L. Buschbom. 1981. Estimates of hybridization between two species of catastomids in the Columbia River. Copeia: 802-810.

Davies, R.W. & G.W. Thompson. 1976. Movements of mountain whitefish (*Prosopium williamsoni*) in the Sheep River watershed, Alberta. Journal of the Fisheries Research Board of Canada 33: 2395-2401.

Donald, D.B. 1987. Assessment of the outcome of eight decades of trout stocking in the mountain national parks, Canada. North American Journal of Fisheries Management 7: 545-553.

Dunning, J.B., B.J. Danielson & H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

Durbin, A.G., S.W. Nixon & C.A. Oviatt. 1979. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. Ecology 60: 8-17.

Ebersole, J.L. 1994. Stream habitat classification and restoration in the Blue Mountains of northeast Oregon, Oregon State University, Corvallis, OR, U.S.A. 59 pp. pp.

Elton, C.A. 1927. Animal ecology. Sidgwick and Jackson Ltd.

Fausch, K.D., C.E. Torgersen, C.V. Baxter & H.W. Li. in press. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience.

Fausch, K.D. & M.K. Young. 1995. Evolutionary significant units and movement of resident stream fishes: a cautionary tale. American Fisheries Society Symposium 17: 360-370.

Fenneman, N.M. & D.W. Johnson. 1946. Physical divisions of the United States, U.S. Geological Survey, Washington D.C.

Flecker, A., S. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77: 1845-1854.

Forbes, S.A. 1887. The lake as a microcosm. Bulletin of the Peoria Scientific Association, Reprinted 1925, Bulletin of the Illinois Natural History Survey 15: 537-550.

Fraley, J.J. & B.B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63: 133-143.

Frissell, C.A. 1992. Cumulative effects of land use on salmon habitat in southwest Oregon coastal streams. Doctoral, Oregon State University, Corvallis, OR, USA. 227 pp.

Frissell, C.A., J.L. Ebersole, W.J. Liss, B.J. Cavallo, G.C. Poole & J.A. Stanford. 1996. Potential effects of climate change on thermal complexity and biotic integrity of streams: seasonal intrusion of non-native fishes, Environmental Protection Agency, Duluth, MN.

Frissell, C.A., W.J. Liss, C.E. Warren & M.D. Hurley. 1986. A hierarchical framework for stream habitat classification. Environmental Management 10: 199-214.

Gatz, A.J., Jr. & S.M. Adams. 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. Ecology of Freshwater Fish 3: 35-48.

Gauch, H.G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, New York, USA.

Geen, G.H., T.G. Northcote, G.F. Hartman & C.C. Lindsey. 1966. Life histories of two species of catastomid fishes in Sixteenmile Lake, British Columbia, with particular reference to inlet stream spawning. Journal of the Fisheries Research Board of Canada 23: 1761-1788.

Gelwick, F.P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. Copeia 4: 1072-1082.

Gerking, S.D. 1959. The restricted movement of fish populations. Biological Review 34: 221-242.

Gido, K.B., D.L. Propst & J. Manuel C. Molles. 1997. Spatial and temporal variation of fish communities in secondary channels of the San Juan River, New Mexico and Utah. Environmental Biology of Fishes 49: 417-434.

Goulding, M. 1980. The fishes and the forest: explorations in Amazonian natural history. University of California Press, Berkely, CA, USA. 280 pp.

Gowan, C., M.K. Young, K.D. Fausch & S.C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51: 2626-2637.

Grossman, G.D., M.C. Freeman, P.B. Moyle & J.O. Whitaker. 1985. Stochasticity and assemblage organization in an Indiana stream fish assemblage. The American Naturalist 126: 275-285.

Hall, C.A.S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53: 585-604.

Healey, M.C. & A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and conservation of phenotype and genotype. American Fisheries Society Symposium 17: 176-184.

Helfman, G. 1983. Underwater methods. pp. 349-370. *In:* L.A. Neilson & D.L. Johnson (ed.) Fisheries techniques, American Fisheries Society, Bethesda, MD, USA.

Helfman, G.S. 1981. Twilight activities and temporal structure in a freshwater fish community. Canadian Journal of Fisheries and Aquatic Sciences 38: 1405-1420.

Hemmingsen, A.R., S.L. Gunckel & P.J. Howell. 2001. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon. pp. 42, Oregon Department of Fish and Wildlife, Portland, OR, USA.

Hill, J. & G.D. Grossman. 1987. Home range for three North American fishes. Copeia 1987: 376-378.

Holt, R.D. 1996. Temporal and spatial aspects of food web structure and dynamics. pp. 255-257. *In:* G.A. Polis & K.O. Winemiller (ed.) Food webs: integration of patterns and dynamics, Chapman and Hall, New York.

Horwitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs 48: 307-321.

Ihnat, J.M. & R.V. Bulkley. 1984. Influence of acclimation temperature and season on acute temperature preference of adult mountain whitefish, *Prosopium williamsoni*. Environmental Biology of Fishes 11: 29-40.

Ihssen, P.E., D.O. Evans, W.J. Christie, J.A. Reckhan & R.L. DesJardine. 1981. Life history, morphology, and electrophoretic chracteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences 38: 1790-1807.

Junk, W.J., P.B. Bayley & R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. pp. 110-127. *In:* D.P. Dodge (ed.) International large river symposium.

Keefe, M., D.J. Anderson, R.W. Carmichael & B.C. Jonasson. 1996. Early life history study of Grande Ronde River Basin chinook salmon. pp. 39, U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, Portland, Or, USA.

Lane, P.A. 1986. Symmetry, change, perturbation, and observing mode in natural communities. Ecology 67: 223-239.

Lehtonen, H. & M.K. Himberg. 1992. Baltic Sea migration patterns of anadromous *Coregonus lavaretus* and sea-spawning European whitefish, *C. widegreni*. Polish Archives of Hydrobiology 39: 463-472.

Li, H.W., K. Currens, D. Bottom, S. Clarke, J. Dambacher, C. Frissell, P. Harris, R. Hughes, D. McCullough, A. McGie, K. Moore, R. Nawa & S. Thiele. 1995. Safe havens: refuges and evolutionary significant units. American Fisheries Society Symposium 17.

Lowe-McConnell, R.H. 1975. Fish communities in tropical freshwaters. Longman, London. 337 pp.

Manly, B.F.J., L.L. McDonald & D.L. Thomas. 1993. Resource selection by animals: statistical design and analysis. Chapman and Hall, London, UK.

Matthews, W.J. 1986. Fish faunal 'breaks' and stream order in the eastern and central United States. Environmental Biology of Fishes 17: 81-92.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York.

McCart, P. & N. Aspinwall. 1970. Spawning habits of the largescale sucker, *Catastomus macrocheilus*, at Stave Lake, British Columbia. Journal of the Fisheries Research Board of Canada 27: 1154-1158.

McCune, B. & M.J. Mefford. 1999. Multivariate analysis of ecological data on the PC-ORD system, MjM Software, Gleneden Beach, Oregon, USA.

McLeod, C.L. & T.B. Clayton. 1997. Use of radio telemetry to monitor movements and locate critical habitats for fluvial bull trout in the Athabasca River, Alberta. pp. 413-419. *In:* W.C. Mackay, M.K. Brewin & M. Monita (ed.) Friends of the bull trout conference, Bull Trout Task Force (Alberta), c/o Trout Unlimited, Calgary, Calgary, Alberta, Canada.

Meador, M.R. & W.J. Matthews. 1992. Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. American Midland Naturalist 127: 106-114.

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

Mobrand, L.E., J.A. Lichatowich, L.C. Lestelle & T.S. Vogel. 1997. An approach to describing ecosystem performance "through the eyes of salmon". Canadian Journal of Fisheries and Aquatic Sciences 54: 2964-2973.

Modde, T. & D.B. Irving. 1998. Use of multiple spawning sites and seasonal movement by razorback suckers in the middle Green River, Utah. North American Journal of Fisheries Management 18: 318-326.

Modde, T. & N. Muirhead. 1994. Spawning chronology and larval emergence of June Suckers (*Chasmistes liorus*). Great Basin Naturalist 54: 366-370.

Montgomery, D.R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 35: 397-410.

Morin, R., J.J. Dodson & G. Power. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*) and round whitefish (*Prosopium cylindriceum*) populations of eastern James-Hudson Bay. Canadian Journal of Fisheries and Aquatic Sciences 39: 958-967.

Nelson, J.S. 1968. Hybridization and isolating mechanisms between *Catastomus commersoni* and *C. macrocheilus* (Pisces: Catastomidae). J. Fish. Res. Bd. Canada 25: 101-150.

Noakes, D.L.G., S. Skúlason & S. Snorrason. 1989. Alternative life history styles in salmonine fishes with emphasis on arctic charr, *Salvelinus alpinus*. pp. 329-346. *In:* M. Bruton (ed.) Alternative life history styles of animals, Kluwer Academic Publishers, Dordrecht, Netherlands.

Northcote, T.G. 1997. Potamodromy in Salmonidae--living and moving in the fast lane. North American Journal of Fisheries Management 17: 1029-1045.

Northcote, T.G. & G.L. Ennis. 1994. Mountain whitefish biology and habitat use in relation to compensation and improvement possibilities. Reviews in Fisheries Science 2: 347-371.

Northcote, T.G. & D.W. Wilke. 1963. Underwater census of stream fish populations. Transactions of the American Fisheries Society 92: 145-151.

Orr, E.L., W.N. Orr & E.M. Baldwin. 1992. Geology of Oregon.

Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49: 667-685.

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

Petit, D.R. 1989. Weather-dependent use of habitat patches by wintering woodland birds. Journal of Field Ornithology 60: 241-247.

Pettit, S.W. & R.L. Wallace. 1975. Age, growth, and movement of mountain whitefish, *Prosopium williamsoni*, in the North Fork Clearwater River, Idaho. Transactions of the American Fisheries Society: 68-76.

Pickett, S.T.A. & M.L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269: 331-334.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? The American Naturalist 123: 541-564.

Polis, G.A., W.B. Anderson & R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289-316.

Postlethwait, J.H. & J.L. Hopson. 1989. The nature of life. McGraw-Hill, Inc., New York, USA.

Power, M.E. 1990. Effects of fish in river food webs. Science 250: 811-814.

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

Price, D.M. 1998. Multiscale habitat electivity and movement patterns by adult spring chinook salmon in seven river basins of northeast Oregon. Masters, Oregon State University, Corvallis, OR, USA. 77 pp.

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

Rahel, F.J. & W.A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120: 319-332.

Rieman, B.E. & J.B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9: 51-64.

Rieman, B.E., D.C. Lee & R.F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia and Klamath River basins. North American Journal of Fisheries Management 17: 1111-1125.

Rieman, B.E. & J.D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. pp. 37, United States Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Rodriguez, M.A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83: 1-13.

Ross, M.E. 1980. Stratigraphy, structure, and petrology of Columbia River Basalt in a portion of the Grande Ronde River-Blue Mounatins area of Oregon and Washington. Oregon Geology 42: 17-18.

Scalet, C.G. 1973. Stream movements and population density of the orangebelly darter, *Etheostoma radiosum cyanorum* (Osteichthys: Percidae). Southwest Naturalist 17: 381-387.

Schlosser, I.J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303: 71-81.

Schlosser, I.J. & P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17: 392-401.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

Scott, W.B. & E.J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184: 966.

Sheldon, A.L. 1968. Species diversity and longitudinal succession in stream fishes. Ecology 49: 193-198.

Shepard, B.B., K.L. Pratt & P.J. Graham. 1984. Life histories of westslope cutthroat trout and bull trout in the upper Flathead River basin, Montana. pp. 85, Environmental Protection Agency Region VIII, Water Division through the Flathead River Basin Environmental Impact Study, Denver, CO, USA.

Sinclair, A.R.E. & M. Norton-Griffiths. 1979. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, IL, USA.

Smith, R.J.F. 1985. The control of fish migration. Zoophysiology 17.

Smith, T.B. & S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annual Review of Ecology and Systematics 27: 111-133.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 30: 1-8.

Stalnaker, C.B., R.E. Gresswell & R.E. Siefert. 1974. Early life history and feeding of young mountain whitefish. pp. 46pp., Prepared for U.S. Environmental Protection Agency, Washington, D.C.

Stanford, J.A. & J.V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12: 48-60.

Swanberg, T.R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126: 735-746.

Swanson, D.A. & T.L. Wright. 1983. Geologic map of the Wenana-Tucannon Wilderness, Washington and Oregon, U.S. Geological Survey, Washington, D.C.

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

Taylor, C.M., M.R. Winston & W.J. Matthews. 1996. Temporal variation in tributary and mainstem fish assemblages in a Great Plains stream system. Copeia 2: 280-289.

Taylor, P.D., L. Fahrig, K. Henein & G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571-573.

Thompson, G.E. & R.W. Davies. 1976. Observations on the age, growth, reproduction, and feeding of mountain whitefish (*Prosopium williamsoni*) in the Sheep River, Alberta. Transactions of the American Fisheries Society: 208-219.

Thompson, R.N. & J.B. Haas. 1960. Environmental survey pertaining to salmon and steelhead in certain rivers of eastern Oregon and the Willamette River and its tributaries. Part I. Survey report of eastern Oregon streams. pp. 432, Research Division, Fish Commission of Oregon, Clackamas, Oregon, USA.

Thorpe, J.E. 1988. Salmon migration. Science Progress 72: 345-370.

Toretta, G. 1991. Wenaha River stream survey report, Pomeroy Ranger District, Umatilla National Forest, United States Forest Service, United States Department of Agriculture, Pomeroy, WA, USA.

Torgersen, C.E. 2002. A geographical framework for assessing longitudinal patterns in stream habitat and fish distribution. Ph.D., Oregon State University, Corvallis, OR, USA.

Torgersen, C.E., R.N. Faux, B.A. McIntosh, N.J. Poage & D.J. Norton. 2001. Airborne thermal remote sensing for water temperature assessment in rivers and streams. Remote Sensing of the Environment 76: 386-398.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8: 36-50.

Trippe, T.M. 1874. The migration of birds. The American Naturalist 8: 338-348.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20: 171-197.

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

Webster, J.R. & J.L. Meyer. 1997. Organic matter budgets for streams: a synthesis. Journal of the North American Benthological Society 16: 141-161.

Weiss, S.B., D.D. Murphy & R.R. White. 1988. Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69: 1486-1496.

Welcomme, R.L. 1985. River fisheries. Food and Agriculture Organization of the United Nations, Rome. 330 pp.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393-425.

Werner, R.G. 1979. Homing mechanism of spawning white suckers in Wolf Lake, New York. N.Y. Fish Game J. 26: 48-58.

White, G.C. & R.A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA, USA.

Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60: 331-367.

Winemiller, K.O. 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. pp. 298-312. *In:* G.A. Polis & K.O. Winemiller (ed.) Food webs: integration of patterns and dynamics, Chapman and Hall, New York.

Winemiller, K.O. & D.B. Jepsen. 1998. Effects of seasonality and fish movement on tropical river food webs. Journal of Fish Biology 53 (Supplement A): 267-296.

Winter, J.D. 1983. Underwater biotelemetry. pp. 371-395. *In:* L.A. Nielsen & D.L. Johnson (ed.) Fisheries Techniques, American Fisheries Society, Bethesda, MD, USA.

Wissmar, R.C., J.E. Smith, B.A. McIntosh, H.W. Li, G.H. Reeves & J.R. Sedell. 1994. A history of resource use and disturbance in riverine basins of eastern Oregon and Washington. Northwest Science 68: 1-35.

Wolanski, E., E. Gereta, M. Borner & S. Mduma. 1999. Water, migration and the Serengeti ecosystem. American Scientist 87: 526-533.

Wydoski, R.S. & R.R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle, WA, USA.

Zaret, T.M. & A.S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.