2000

Fish diversity behavior and microhabitat use in secondary channels of the Bitterroot River Montana

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Recommended Citation

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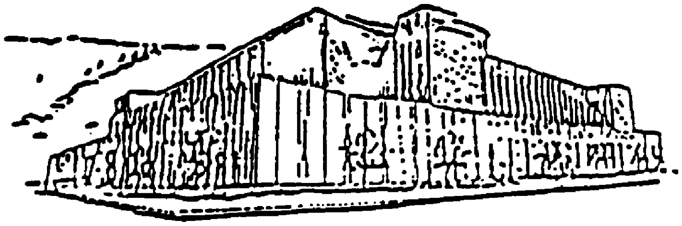

Fish diversity, behavior, and microhabitat use in secondary channels of the Bitterroot River, Montana

by

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B.S. University of California, Davis, 1996

Presented in partial fulfillment of the requirements
for the degree of Master of Science

The University of Montana
May 2000

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6-1-2000
Date

Brandt, Troy M., M.S., May 2000 Environmental Studies

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Advisor: Dr. Vicki J. Watson VW

The central Bitterroot River floodplain is characterized by a complex secondary channel network that provides a range of aquatic environments for native and nonnative fish. To better understand fish communities using these aquatic habitats, secondary channel habitat variation, fish community diversity, and fish microhabitat use were evaluated by snorkeling and backpack electrofishing in six secondary channels between August 1998 and September 1999. Secondary channels provide a range of habitats and microhabitats that are partially influenced by secondary channel proximity to the Bitterroot River, upwelling groundwater presence, and inchannel habitat complexity created by woody debris. Secondary channel morphologies generally remained stable over the year, although secondary channel water chemistry varied seasonally and in relation to the mainstem Bitterroot River. Fish community diversity was greatest in more-complex channel reaches and tended to decrease with distance from the Bitterroot River. Of the eight fish species that were commonly encountered, microhabitat use and day-night fish behavior patterns were apparent. Young-of-year and juvenile age classes exhibited similar microhabitat use and day-night behaviors. During the day, young fish primarily selected microhabitats associated with dense cover, while at night these fish moved into less protected, low water velocity microhabitats. Adult fish of larger species used different microhabitats than did young-of-year and juvenile fish. Adult fish occupied deeper microhabitats or were observed in microhabitats associated with large woody debris or overhead bank cover. However, these results were species-specific in many cases and were influenced by site-to-site differences in microhabitat availability. Bitterroot River secondary channels provide a variety of lateral floodplain habitats that are occupied by a diverse fish community. Managing human development on the Bitterroot River floodplain will be critical for maintaining secondary channel habitats that host numerous fish species and age classes.

Acknowledgements

I would like to thank many people who assisted me in completing this project, as well as my friends and family who supported me throughout graduate school. My committee members, Vicki Watson, Jon Graham, Chris Frissell, and Andrew Sheldon, provided equipment, valuable advice, and their individual expertise that improved both my project and my understanding of aquatic ecology. Dr. Jon Graham patiently answered my statistical questions, provided statistical insights, and encouraged a complete effort in his courses and for this project.

Chris Clancy with the Montana Department of Fish, Wildlife, and Parks, was generous with his time in discussing issues regarding Bitterroot River fish communities. Roger and Wendy Raynal allowed me to use valuable equipment throughout my project. Jim and Nancy Johnston invited me into their home after dark nights snorkeling in the Bitterroot. Several fellow students assisted me in the field, especially during portions of this project that required electrofishing. Marisa encouraged and motivated me to commit a complete effort and at the same time, stuck with me through the tedium. This project would have been impossible without the assistance of the aforementioned people, and many others who have contributed to my life. Without the backing and interest of my supportive family, my graduate school experience would have been far less rewarding.

This project is dedicated to Josie, without her I would not have made it this far.

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Chapter

2 **Bitterroot River Channel Formation and Floodplain Habitat Heterogeneity**

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Glossary

Adult fish: individuals that have experienced at least one winter and are reproductively active. Age class depends on species.

Alluvium: material eroded from upland areas, transported by streams, and deposited on the valley floor..

Anabranching River: a system of multiple channels characterized by vegetated or otherwise stable alluvial islands that divide flows at discharges up to nearly bankfull (see illustration below).

Avulsion: the relatively sudden and major shift in the position of a channel to a new part of the floodplain or the sudden reoccupation of an old channel on the floodplain (Nanson and Knighton 1996).

Bankfull Channel Depth: the maximum depth at a section measured at bankfull discharge.

Bankfull Discharge: the water surface is at floodplain level (top of channel banks) and the channel is flowing full. This discharge has a recurrence interval of approximately 1.5 years.

Bankfull Stage: the elevation of the water surface associated with the bankfull discharge.

Braided River: consists of flow separated by bars within the channel (Knighton and Nanson 1993).

Diel: pertaining to day and night.

Diurnal: pertaining to day-light hours.

Dynamic Equilibrium: a state that allows adjustment to changes of one, several, or all physical variables of a system (Heede and Rinne 1990).

Electivity: an organism's use of a resource relative to the resource's availability.

Floodplain: areas that are periodically inundated by the lateral overflow of river or lakes, and/or by direct precipitation or groundwater; the resulting physicochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic community structures (Junk et al. 1989).

Floodplain Channel: a subsidiary channel noted by groundwater or hyporheic water eruption onto the floodplain. The floodplain channel carries surface water during high flow. The channel connects with the mainstem channel (see illustration below).

Floodplain Tributary: a tributary channel influenced by upland lithology that traverses the floodplain and contributes water and sediment to the mainstem channel (see illustration below).

Fluvial: landforms or structures of, found in, or produced by a river or rivers.

Frequency of Use: a population's response to a resource or environmental variable (Baltz 1990).

Geomorphology: the study of the characteristics, origin, and development of land forms.

Glide: a wide uniform channel bottom with low to moderate velocities, lacking pronounced turbulence.

Habitat: is the kind or range of environments in which a species can live. These environments range in scale from microhabitat (substrate) to the watershed (Baltz 1990).

Hyporheic: Pertaining to the saturated zone beneath a river or stream consisting of substrate, such as sand, gravel, and rock, with water-filled interstitial pore.

Hydrograph: a plot of stream discharge over a period of time.

Juvenile fish: individuals that have experienced at least one winter but may not be reproductively active.

Microhabitat: fine scale habitat characteristics partially defined by water temperature, substrate, cover, and discharge in aquatic systems.

Microhabitat Use: an organism's selection of environmental conditions on a 10^0 m^2 scale.

Off-channel Habitats: aquatic habitats in the floodplain of a river that may or may not be connected to the mainstem channel.

Ontogenetic: pertaining to the development of an individual organism.

Resource Availability: resources that are assumed to be available to organisms based on their spatial occurrence in the environment.

Riffle: a swiftly flowing reach of turbulent water.

Run: a swiftly flowing reach with little surface agitation and no major flow obstructions.

Secondary Channel: subordinate channels to the river's channel that maintain aquatic habitats under varying discharges.

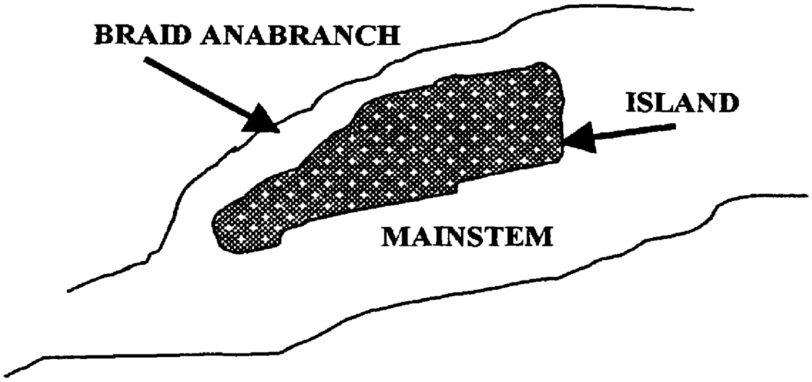
Species-age Class: a developmental life stage for a particular species of fish.

Tributary Channel: channels that arise at higher elevation terraces above the floodplain and ultimately discharge into the mainstem river.

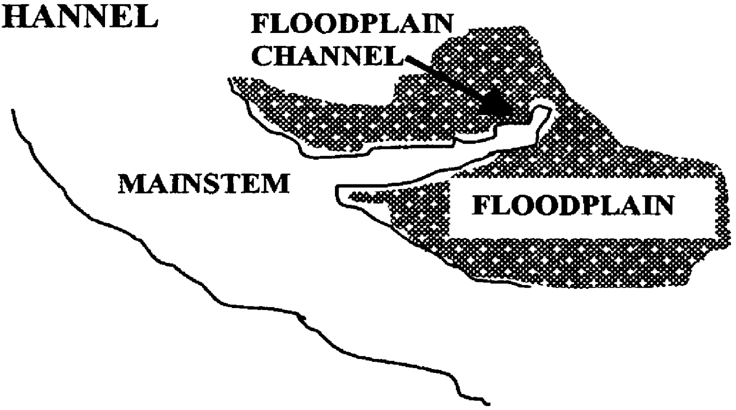
Young-of-year (YOY) fish: individual fish that have not experienced a winter since emergence.

CHANNEL ILLUSTRATIONS

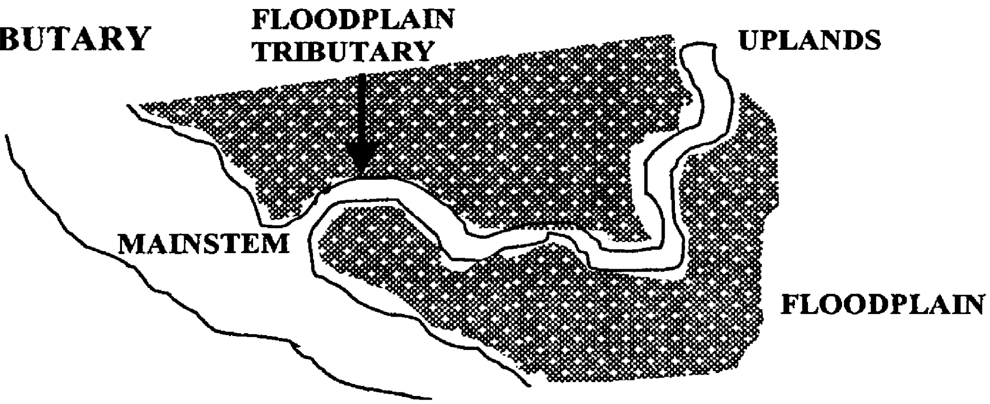
BRAID ANABRANCH



FLOODPLAIN CHANNEL



FLOODPLAIN TRIBUTARY



Chapter 1

An Introduction to Alluvial Rivers and Project Objectives

Understanding the roles of physical, chemical, and biological processes in creating floodplain aquatic habitats is paramount to understanding the linkage between a river, its floodplain, and the resident biotic communities. Valley topography, drainage geology, and regional climate define the physical processes that influence floodplain and river channel characteristics (Leopold et al. 1964). Basin geology, precipitation, floodplain vegetation, hyporheic influence, and groundwater intrusion partially govern the chemical constituents characterizing an aquatic system. While biological processes are generally limited to affecting the system's biological composition, woody debris and dense riparian vegetation also influence channel formation and affect both the physical and chemical processes that shape aquatic environments.

The importance of floodplain aquatic habitats to mainstem fish communities is likely dependent on the proximity of the floodplain habitat to the mainstem channel. Lateral habitats that are close to the mainstem are frequently inundated by the mainstem during high flows, maintain high mainstem connectivity over the hydrograph, and exhibit physicochemical conditions similar to the mainstem. Conversely, distant floodplain water bodies are influenced by other processes that are somewhat independent of the mainstem. Soil composition, upwelling from upland aquifers, and minimal surface water inputs may differentiate distant water bodies from the mainstem river.

In the semi-arid intermountain west, large alluvial floodplain rivers often display a range of channel types that are definable in four dimensions; longitudinal (downvalley), lateral (channel-floodplain), vertical (channel-hyporheic), and temporal (Ward 1989). In this region, many rivers can be described by their longitudinal progression. Mountain headwater reaches are confined to a single thread channel with a narrow floodplain and dense overhead riparian canopy. Groundwater infiltration through the thin soil layer to the channel contributes most of the inchannel flow. Water temperatures display minimal variability due to riparian shading and consistent groundwater inputs. Moving downvalley, the overhead canopy opens, the channel is less confined within the widening valley, and water temperatures are more influenced by the sun.

Fluvial processes erode and deposit the alluvial substrates that characterize the braided river reaches typical of this region (Ward and Stanford 1995). Stable well-vegetated bars dissect individual channels and lead to a more developed floodplain. Compared to the upstream headwater reaches, the braided river reach accesses an expansive floodplain comprised of diverse aquatic and riparian habitats. High habitat diversity is typical in this region due to the interactions among upwelling groundwater, surface water, and dynamic fluvial processes. In contrast to the main channel, secondary channels convey less water and follow more circuitous patterns on the flat floodplain. However, during high water periods, secondary channels may change dramatically as the primary channel inundates and transforms these overflow channels through rapid lateral erosion and channel avulsion. Over the remainder of the year, these secondary channels may become less connected to the mainstem as surface water levels drop. Upwelling water from the hyporheic zone and/or deeper aquifers that are supplied by valley runoff may continue to maintain these channels through the low water period. Thermal diversity is also prevalent in these floodplain reaches. Overhead riparian canopies and upwelling water in well-vegetated secondary channels maintain cool water temperatures during the summer and warmer water temperatures in the winter. Less shaded secondary channel reaches, or reaches without substantial upwelling, are more likely to have warmer water temperatures similar to the main channel during the summer in temperate streams. These environmental factors create a range of conditions that support diverse biological communities.

In the Bitterroot River, floodplain secondary channels are rarely sampled and little is known about their importance to mainstem fish populations. This study will improve our understanding of these habitats and the fish communities they support. The purpose of this project was to investigate floodplain secondary channel habitats and the fish communities using these habitats in the central Bitterroot River of southwestern Montana. This paper is divided into three subsequent chapters that describe different project objectives. Although each chapter will describe a different portion of the project, some of my ideas overlap among chapters as separating observations and interpretations was at times difficult.

Chapter 2 gives a detailed description of the diversity and complexity of secondary channel habitats sampled between August 1998 and September 1999. A proposed channel classification system is investigated and evaluated in the context of secondary channel habitat diversity and stability. This chapter explains the range of channel microhabitat conditions that will be referred to in later chapters regarding fish communities.

Chapter 3 presents information on fish community diversity, fish microhabitat use, and fish behavior. The purpose of this chapter was to identify patterns of fish presence/absence, microhabitat use, and behavior in secondary channel reaches connected to the Bitterroot River. These data were collected over seven sampling periods when I conducted day and night snorkeling. Microhabitat availability data described in Chapter 2 were used in this chapter to evaluate fish microhabitat use. Habitat complexity described in Chapter 2 is also referred to in this chapter.

Chapter 4 investigates fish communities inhabiting channel reaches at increasing distances from the Bitterroot River. Unlike Chapter 3 where microhabitat use and behavior were analyzed, Chapter 4 focuses more on fish community composition, possible microhabitat-fish community relationships, and fish length-frequency seasonal changes. The channel reaches sampled in Chapter 4 are separate from those surveyed in Chapter 3, although the reference names, Bell Crossing (BC) and Tucker Crossing (TC), are used to describe the secondary channels in both chapters. In Chapter 3, the sampled channels are referred to as BC1, BC2, BC3, TC1, TC2, and M1. In Chapter 4, the sampled channels are referred to as BCA, BCB, TCA, and TCB. The Bell Crossing channels are not related in the two chapters. The Tucker Crossing channels are the same in the two chapters, but the sampled reaches are different. Additionally, fish community diversity described in Chapter 3 refers to fish species diversity, were as fish diversity in Chapter 4 refers to fish species-size class diversity. Further explanations are included in each chapter. To reiterate, these two chapters are separate, and the data and observations therein should not be confused.

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Chapter 2

Bitterroot River Channel Formation and Floodplain Habitat Diversity

Introduction

Few free-flowing rivers remain in the intermountain western United States (Heede 1986). Harnessing rivers for flood control, power production, and irrigation has led to widespread alteration of once wild river systems in order to accommodate human needs (Stanford et al. 1996). This alteration has resulted in the extirpation of native species, simplified riparian habitats, less variable hydrographs, and modified river channel morphologies (Brown and Moyle 1981; Heede 1986; Richter et al. 1997; Ward and Stanford 1995; Kondolf 1997; Surian 1999; Dykaar and Wigington 2000). The remaining temperate broad alluvial floodplain rivers often exhibit high channel-floodplain connectivity critical for maintaining aquatic and riparian biodiversity (Junk et al. 1989; Triska et al. 1993; Bayley 1995; Poff et al. 1997). In these systems, physical and biological processes create a mosaic of complex floodplain habitats comprised of secondary channel networks. This floodplain diversity is enhanced by periodic overbank flows and less frequent abrupt channel avulsions that create new aquatic habitats (Power et al. 1995)

Lateral channel migration and subsequent secondary channel formation is limited in confined rivers that are restricted by narrow river valleys (Ward and Stanford 1995; Alabyan and Chalov 1998). Without a broad floodplain to disperse high flows, the narrow floodplain is maintained in a state of renewal by frequent scouring flows. Streamside riparian plant communities resemble upland communities, forming a narrow band of vegetation adjacent to the bank (Gregory et al. 1991). In contrast, alluvial rivers draining unconfined valley bottoms often have expansive floodplains. These floodplains are sculpted and otherwise influenced by braided or meandering mainstem channels and a continuum of secondary channels. Unconfined rivers displaying these characteristics are anabranching multichannel systems (Nanson and Knighton 1996). Anabranching channels are defined as "a system of multiple channels characterized by vegetated or otherwise stable alluvial islands that divide flows at discharges up to nearly bankfull" (Nanson and Knighton 1996). These multi-channel systems may arise from lateral erosion, channel avulsion, or meander cut-off and promote floodplain habitat diversity as well as enhance river-floodplain connectivity.

Channel morphologies are shaped during high water periods. Although catastrophic channel changes may occur during infrequent high magnitude floods (Knighton and Nanson 1993), efficient channel maintenance occurs at the channel's effective (channel-forming) discharge (Wolman and Miller 1960). This bankfull channel discharge has an approximate recurrence interval of 1.5 to 2 years (Leopold et al. 1964). In years when the river meets or exceeds its bankfull volume, fluvial processes entrain, sort, and redeposit floodplain sediments. Bank reaches lacking cohesive sediments and riparian vegetation may experience accelerated erosion rates and contribute sediment to the stream. Banks protected by woody debris (Piegay and Gurnell 1997), riparian vegetation (Hickin 1984), or comprised of less-erodable substrates are more resistant to degradation. Where bank stability varies and lateral erosion is prevalent, laterally migrating channels sculpt a wide floodplain hosting a diversity of secondary channels and other off-channel habitats of variable longevity (Nanson and Knighton 1993; Cavallo 1997; Alabyan and Chalov 1998).

In addition to lateral channel erosion, reaches with weak banks may become points of rapid channel adjustment caused by channel avulsions (Hickin and Nanson 1984; Brizga and Finlayson 1990; Nanson and Knighton 1996). These high-energy events contribute large quantities of sediment to the waterway as the river rapidly carves a new channel from the floodplain (Leopold et al. 1964) or reoccupies a previously abandoned channel (Nanson and Knighton 1996). The occurrence of such events may be accentuated in free-flowing rivers that convey substantial quantities of large woody debris (Hickin 1984; Piegay 1993). An accumulation of woody debris blocking the main channel may result in the rapid erosion of a nearby bank as flow is deflected by the obstruction towards the bank. As the river erodes or overtops the adjacent bank, the bank is degraded and the sediment transported. Channel avulsion magnitude is dependent on the channel gradient, floodplain material, stream power, and the presence of woody debris and ice jams that trigger rapid channel movement.

In places, flood flows overtop low-lying banks and interact with the floodplain without causing catastrophic channel avulsions or excessive lateral bank erosion. Woody debris, floodplain microtopography, and vegetation increase floodplain roughness and slow the advancing floodwater, causing sediment and debris deposition on the floodplain (Sparks 1995). Large woody debris aggregations on the floodplain and in backwaters provide cover for aquatic organisms and terrestrial animals.

A suite of variables including solar radiation, air temperature, groundwater properties, surface water properties, and stream geomorphology influence stream temperature (Sinokrat and Stefan 1993). In floodplain channels the influence of upwelling groundwater and hyporheic water is apparent. Groundwater discharging into floodplain channels creates living space for aquatic organisms during low water periods or where surface water is deficient. Influent stream reaches gaining water from subsurface sources, tend to have consistent water temperatures and channel discharge (Constantz 1998). These conditions provide persistent habitats and may be preferentially selected by aquatic organisms occupying floodplain channels (Cavallo 1997).

These fluvial processes create diverse secondary channels that spatially vary in relation to the mainstem channel (Schlosser 1991). Secondary channels are sometimes classified according to their location within the floodplain mosaic. Three channel classes investigated below include braid anabranches, floodplain channels, and floodplain tributaries. Braid anabranches are proximate to the mainstem channel and are separated from the mainstem by stable vegetated islands. These channels are generally connected at their upstream and downstream extents with the mainstem. Physicochemical characteristics and substrate sizes are similar between braid anabranches and the mainstem channel due to high channel connectivity.

Floodplain channels that arise within the floodplain boundary as avulsed or overflow channels comprise a second channel type. Channel discharge increases in a downstream direction by groundwater inputs or as other smaller channels contribute surface flow to the secondary channel. Since these channels originate and meander on the floodplain, they are affected by mainstem fluctuations especially during runoff. Although floodplain channels maintain connectivity at their downstream extent with the mainstem channel, flood water that overtops natural levees reconnects these floodplain channels at their upstream extent with the mainstem. Depending on floodplain channel location, other points of reconnection with the mainstem are possible as well.

A third channel class includes floodplain tributaries that begin above the valley floor and traverse the floodplain before connecting with the mainstem. During low water periods these channels may be more influenced chemically by upland lithology and groundwater upwelling from high terrace aquifers than by mainstem hyporheic upwelling. Mainstem hyporheic inputs increasingly influence the physicochemical conditions as the channel approaches the mainstem. Depending on channel location during the low water period, secondary channels may maintain water chemistry similar to upland aquifers. The mainstem may inundate the floodplain-portions of these tributary channels during high flow periods, homogenizing the floodplain's water chemistry.

From a biological perspective, multithread reaches provide a wide variety of critical aquatic habitats needed by fish at various life stages and seasons including; flow and thermal refugia, spawning and nursery habitats, feeding sites, and predator avoidance habitats. Additionally, secondary channels contribute to the system's complexity. Compared to a confined system with minimal lateral habitat complexity, alluvial floodplain rivers host diverse environments, potentially supporting a greater variety of aquatic organisms.

In subsequent chapters, the importance of floodplain secondary channels to fish community diversity will be discussed. The purpose of this chapter is to describe microhabitat characteristics of these three secondary channel classes in a Northern Rocky Mountain alluvial floodplain river, the Bitterroot River of southwestern Montana. The following questions will be addressed: 1) Do the measured variables support the proposed channel classification? 2) Can the above channel types be differentiated using the measured variables? 3) How do physical and chemical microhabitat conditions differ among braid anabranches, floodplain channels, floodplain tributaries and the mainstem Bitterroot River? Subsequent chapters will investigate fish diversity, behavior, and microhabitat use in the three channel types.

Methods and Materials

Study Site

The Bitterroot River in western Montana flows north from the confluence of the East and West Forks near Conner, Montana, to its confluence with the Clark Fork River, 8 km west of Missoula, Montana (Figure 1). Flowing approximately 134 km, the Bitterroot River drains a 7,288 km^2 (at Missoula USGS gauge) watershed, supporting agricultural land, pasture, rural and urban development, and upland forest systems. Tributaries originating in the Sapphire Mountains to the east, and the Bitterroot Mountains to the west, contribute much of the runoff that feeds the Bitterroot River.

Western tributaries to the Bitterroot River drain the heavily glaciated, high-relief Bitterroot Mountains. The Bitterroot Mountains form the eastern extent of the Idaho Batholith and are composed of granites, pre-Cambrian quartzites, and argillites of the Belt formation. Overlying soils range from shallow to very deep and have traces of volcanic ash, among other materials (Cartier 1984). Multiple glaciation events carved U-shaped valleys in the range front. These valleys are perpendicular to the Bitterroot River and head many of the tributaries that convey runoff to the river. High terraces that separate the front range from the floodplain are composed of glacial moraines and historic alluvial fans. Soils covering the high terrace alluvium are generally shallow and adequately drained, though clay lenses create pockets of poor drainage.

In contrast to the high relief Bitterroot Range, the Sapphire Mountains are more gradually sloped. Fluvial erosion and historic glaciation shaped the eastern boundary of the Bitterroot watershed. Soils 25-150 cm deep mantle metamorphosed sedimentary rocks of quartzite and calc-silicates of the Belt formation (NRCS 1995). East side soils on the high terraces are of Tertiary deposits ranging from clays to sand and gravels. Soils are generally very deep (25-100+ cm) and well drained where the soil is of loamy material over loose sand and gravel. Areas underlain by clay drain less efficiently.

The central and lower Bitterroot River is noted for its large, intricately channeled alluvial floodplain that is up to 5 km wide in places (Gaeuman 1997). Alluvial material deposited by historic glaciation and current fluvial processes reach depths of 3.2 km along the valley median. Several of the large lateral tributaries entering the Bitterroot floodplain from the valley margin contribute sediment to the Bitterroot River (Cartier 1984). Narrower floodplains occur where these channels enter the valley floor and overlap the primary Bitterroot floodplain. Within the floodplain, surface water drainage varies according to the distribution of loam and sand overlaying alluvial material. Although floodplain substrates are generally well drained, clays and silts result in locally elevated water tables within the river bottom area.

The *Populus trichocarpa/Cornus stolonifera* community type (Hansen et al. 1996) characterizes Bitterroot River floodplain vegetation consisting of a herbaceous and deciduous shrub understory with a mixed species overstory (Table 1). Riparian vegetation communities reflect the natural disturbance regime of this floodplain river. Black cottonwoods (*Populus trichocarpa*), dominate many of the mature multi-aged gallery forest stands bordering the river while moderately disturbed surfaces lying at and below the bankfull elevation are vegetated by flood-resistant willows and other flexible shrubs. Expansive, sparsely vegetated cobble bars predominate the braid belt during low water, suggesting the system's erosive power during spring runoff. Past and current agricultural practices on floodplain pastures have resulted in the replacement of native grasses with introduced grass species. Noxious weeds inhabit more-xeric surfaces, particularly substrates above the bankfull elevation. These invasive weed communities dominate areas impacted by frequent and persistent disturbance such as grazing and bank stabilization sites. Dense, mat-forming grasses, such as reed canary grass (*Phalaris arundinacea*), increase bank stability at the expense of less aggressive native species.

Cool summers and generally mild winters characterize the Bitterroot Valley's climate. Precipitation increases with elevation with annual averages ranging from 30 cm at the valley floor to 150 cm in the mountain elevations (National Climatic Data Center 1999). On average, runoff crests in May or June when 25% of the precipitation and 55% of the yearly discharge occurs. Discharge intensity and volume is dependent on snow pack depth, air temperature, and precipitation patterns during this period (Figure 2). Flooding may result from rain-on-snow events when large volumes of water enter the Bitterroot Valley over a short period of time. A network of overflow channels and a broad floodplain convey flood flows once water overtops the bankfull elevation and spills onto the low gradient floodplain. Due to the wide floodplain, the depth of flooding during a 100 year event is only slightly greater (15-30 cm) than for a 10-year event, although this more frequent event has 30% less discharge (NRCS 1995), indicating the floodplain's large capacity to disperse floodwater.

Landuse directly and indirectly influences the Bitterroot River. Extensive water development in the valley for irrigation, recreation, and municipal uses has impacted the river's natural flow regime and biological communities. Several irrigation districts and individual property owners divert water from both the Bitterroot River and its supporting tributary streams. Summer irrigation diversions desiccate tributaries before they reach the Bitterroot, isolating newly emerged young-of-year fish (age-0). Without summer tributary flow, summer river levels are maintained by groundwater discharging from the surrounding mountain ranges to the valley center (Finstick 1986; Uthman 1988). Water releases from Painted Rocks Reservoir above Darby augment inadequate summer flows and provide an emergency water source for water managers. Although the networks of irrigation ditches transport water away from tributaries and the Bitterroot River, ditch seepage recharges shallow aquifers on the valley floor and provides an important supply of late season water to the Bitterroot River (Finstick 1986; Uthman 1988).

Human development of the Bitterroot floodplain is rapidly increasing. As an example, permanent structures in the 100 year floodplain increased from 13 in 1936, to 146 in 1990 (Javorsky 1994). Accelerated development in the past decade has undoubtedly increased this figure. Road construction, land filling, bank stabilization, and residential construction continue to alter the floodplain. Floodplain development threatens both the integrity of the river and Bitterroot Valley residents' safety.

Sample Site Selection Criteria

The central and lower sections of the Bitterroot River are characterized by two channel patterns. The central Bitterroot between the towns of Hamilton and Stevensville is considered an anastomosing reach (Cartier 1984). Downstream of Stevensville the river follows a single meandering channel contained by the narrowing valley. Typical of an anastomosing river, the central reach is a network of secondary channels creating a diversity of aquatic habitats. Formed both historically and recently by lateral channel migration and avulsion, secondary channels are temporally and geographically variable. This variability is created during high water periods when the mainstem captures off-channel floodplain habitats and transports sediment into and out of these floodplain channels. The minimal stream power evident the remainder of the year does little to alter secondary channel geometry.

Sampling sites were selected based on four criteria: channel location, channel type, the channel's consistent connection with the Bitterroot River, and channel depth. The first criterion, location, was important for investigating the study's objectives. Sites were distributed over a reasonably long distance to increase the chance that all common habitats in the central reach were sampled. The most downstream site was selected to be geographically close to the Clark Fork River. The Clark Fork River likely supplies native and introduced fish species to the Bitterroot River. While the distribution of sites along a longitudinal distance was important, grouping sites within an access reach was necessary so sites could be sampled over a short time period. Considering these geographic stipulations, the study area was established between Tucker Crossing and Missoula.

A second criterion, having secondary channels in all three categories, was necessary for investigating whether resident fish populations respond differently to geomorphically different secondary channel types (See Chapter 3). Gaeuman's (1997) classification of Bitterroot River secondary channels relied on geomorphic channel characteristics mapped from historical and recent aerial photographs. Limited field surveys provided some information regarding physical differences among channels comprising the proposed channel continuum (See Gaeuman 1997 for complete description). Though concerned with how form and processes influence the evolution and persistence of channel stability, Gaeuman's classification did not consider a biotic component. Sampling biological communities inhabiting Bitterroot River secondary channels would help explain the possible biological importance of braid anabranches, floodplain channels and floodplain tributaries.

Third, each site had to be highly connected to the Bitterroot River so fish could access secondary channels throughout the year. In order to investigate fish use of connected secondary channel habitats (Chapter 3), a sample reach was defined as the first 70 m-100 m section of a secondary channel from the secondary channel's confluence with the Bitterroot River to an upstream geomorphic feature.

Lastly, each site had to be at least 0.3 m deep and wadable throughout the year to provide adequate fish habitat and survey accessibility. Three channels investigated during the receding limb of the 1998 hydrograph temporarily satisfied these depth requirements but were dry later in the summer and were eliminated from the data set. Six sites satisfying these four criteria were selected between Tucker Crossing and Missoula (Figure 1).

Selected Sample Sites

The six secondary channel sites included two braid anabranch channels, two floodplain channels, and two floodplain tributaries as classified previously (Table 2).

The first braid anabranch channel, BC1, was located approximately 3.4 km downstream from the Bell Crossing fishing access. Connected both upstream and downstream with the mainstem Bitterroot River, this channel was maintained by both surface water and subsurface river water discharging into the channel. Prior to the 1999 spring runoff, a shallow mobile sand bed and shallow depth characterized BC1. In spring 1999, the mainstem Bitterroot River flooded the braid anabranch and scoured a large volume of sediment. BC1 was transformed from a simple shallow reach to a deeper and more structurally complex channel. A second braid anabranch, termed M1, was located 15 km upstream of the Clark Fork confluence and south of Missoula. Similar to BC1, the Bitterroot River overtook this secondary channel during spring high water but effected only minor alterations on bank integrity and large woody debris distribution.

Two floodplain channel sites located at Tucker Crossing, termed TC1 and TC2, originate on an approximately 7 km-long island that divides the river into east and west channels. These channels were likely created over a long period of time by channel avulsions associated with Bitterroot River flood flows. A diverse array of channels and off-channel habitats suggests that Tucker Island is a highly avulsive landform. TC1 and TC2 are maintained by hyporheic water discharging into these floodplain channels. Secondary channel discharges rapidly increased during the 1999 spring runoff as the mainstem channel overtopped natural levees separating the Bitterroot River channel from the intra-island floodplain channels. Overbank flows during the 1999 spring runoff redistributed coarse woody debris and altered substrate composition within the floodplain channels.

The final two channels, BC2 and BC3, were classified as floodplain tributaries. Similar to the floodplain channels TC1 and TC2, BC2 and BC3 are part of a dynamic floodplain complex influenced by both surface water and subsurface discharge. The more downstream channel, BC3, consistently displayed specific conductance levels and water temperatures that deviated from Bitterroot River measurements. These differences suggest a greater influence of groundwater discharging from the Sapphire Range than from the Bitterroot River. Sapphire Mountain runoff is higher in dissolved ions than are other natural water sources in the Bitterroot Valley (Gaeuman 1997). Active springs along the channel margin appeared to influence local physiochemical characteristics. BC2, situated between BC3 and the Bitterroot River, represented intermediate conditions. Hyporheic exchange between BC3 and BC2 is likely due to their close proximity. Hyporheic discharge upwelled into the BC2 channel and surface water overtopped banks upstream of the sample reach during high water. Spring runoff also increased the discharge in BC3 but less drastically.

Sampling Design and Methods

Habitat Surveys

To investigate the study objectives pertaining to habitat differences among the six sampling sites, two sampling methods were employed. First, point sampling was used to obtain data from specific locations or where a few measurements were adequate to characterize a reach (temperature, specific conductance, and oxygen saturation). Secondly, point-transect sampling was used where conditions, such as depth, were expected to vary across a reach in a regular manner. Two measuring tapes were used to create a pseudo-lattice over the study area for the point-transect sampling. A 100 m tape was extended from each site's downstream to upstream extent. Eight to 12 transects were then regularly spaced perpendicular to the channel. Depth, substrate type, substrate cover, and water column cover were recorded every 1-2 m across the channel depending on channel width. Approximately 100 points were recorded for each secondary channel. Temperature was also recorded during the 1999 sampling. Depth was measured with a 1.5 m calibrated wading staff. The substrate was evaluated by picking up a single particle at each lattice point. The particle's secondary axis was used to group the particle according to one of six categories: silt (to touch), sand (<6mm), gravel (6<16 mm), pebble (17≤64 mm), cobble (65≤265 mm), boulder (>265 mm). Cover types included no cover, aquatic vegetation, overhanging bank, small woody debris (<1 m in length, <0.3 m in diameter), large woody debris (>1 m in length, >0.3 m in diameter), and boulder. Cover types were defined as either water column cover or substrate cover to account for material that may have provided cover high in the water column but not on the substrate, and vice versa. Water column cover exceeded at least 1/3 of the channel depth if it originated on the substrate. Other material, such as woody debris hanging into the water from the bank, was also considered a water column cover structure. Substrate cover was did not exceed 1/3 of the channel depth. Total coarse woody debris area and riffle surface area, were also estimated for each sample site.

A YSI Model 85 Handheld Dissolved Oxygen, Conductivity, Salinity and Temperature System was used to evaluate water parameters in the sample reaches and the adjacent Bitterroot River (YSI 1996). Instrument calibration and measurements were recorded before 0900 each sampling day to establish a consistent protocol and to minimize photosynthetic effects on oxygen saturation and oxygen concentration readings. Using this methodology, measurements were completed prior to direct sunlight reaching the sample site. Five to seven sets of measurements were recorded midchannel from upstream to downstream, at each sample site to assess within-site environmental variation. An additional three to five sets of measurements were recorded in the main channel in order to compare secondary channel and main channel water chemistry. A complete measurement set required under 20 minutes to complete.

One Onset Hobotemp continuous temperature recorder was deployed in each of the sample secondary channels and in the Bitterroot River to investigate annual water temperature patterns. Hobos were attached with steel airplane cable at a depth of 20 cm to large woody debris in a minimally exposed area of the site to reduce direct sunlight effects on recorded temperatures. Equipment loss and equipment malfunction resulted in incomplete data collections for four sites and the main channel. Year long temperatures were recorded for TC2 and BC3.

Data Analysis

Habitat variables (Table 3) were analyzed to: 1) determine their usefulness in explaining secondary channel variation, 2) compare and test the proposed secondary channel classification that was based on visual observation, 3) compare secondary channel habitat differences, and 4) investigate secondary channel-mainstem water chemistry differences. These investigations followed two separate procedures.

Habitat Variation and Site Classification

To determine the effectiveness of these variables in explaining secondary channel habitat variation, and to test the proposed secondary channel classification, principal components analysis (PCA) and discriminant function analysis (DFA) were used. PCA was used to reduce the set of physical habitat variables to several components comprised of descriptive variables. Prior to running the PCA, mean values and coefficients of variation for channel depth and width were calculated for each secondary channel sampling site on each sampling date and $\log_{10}(x+1)$ transformed for entry into the PCA. Values were transformed to improve normality and homogenize sample variance. Coefficients of variation were included to reflect within-site habitat variation during one period. Percent occurrence of each substratum type, water column cover type, and substrate cover type, was calculated, arcsine-square root transformed, and included in the PCA. Only principal components (PCs) with eigenvalues > 1.0 were retained for further analysis. Loadings ≥ 0.60 were considered important for individual components.

Descriptive discriminant function analysis seeks to exhibit differences among populations by means of linear combinations of the measured variables (Williams 1983; James and McCulloch 1990). The first five principal components from the PCA were used for the discriminant function variables since the first five components appeared to represent ecologically interpretable variables. A step-wise procedure was used to retain only important PC's in the DFA. The leave-one-out method was also used to cross-validate the predictions. With cross-validation, each case is classified by the functions derived from all cases other than that case. In this way, predictions are independent of the discriminant functions used to make these predictions. Euclidian distances were used to identify the two dimensional distances between points. The distance between two sites is the square root of the sum of the squared differences in values for each variable.

Secondary Channel Habitat Variation

To investigate environmental variable differences among secondary channels and sample dates, two-way factorial analysis of variance (ANOVA) was employed. Sample site was considered a fixed factor and date a random factor in an additive general linear model. Insufficient degrees of freedom disallowed interaction terms in the model. Multiple two-way ANOVA's, rather than a multivariate ANOVA (MANOVA), were executed to incorporate the sample date information since SPSS MANOVA's do not allow a random factor in the model. Ideally, a repeated measures ANOVA would have been employed for this analysis; however, inadequate sample sizes did not permit using the repeated measures model.

From the two-way ANOVA results, orthogonal contrasts were examined to determine if the proposed channel classifications were valid (Table 4). These tests were designed to test for significant differences among channel classifications and within channel classifications. Because BC1 was not sampled as consistently as the other five channels, its was not included in the orthogonal contrasts.

Secondary Channel-Mainstem Water Chemistry Variation

Comparisons between the secondary channel and mainstem water chemistry values were carried out using Wilcoxon rank sign paired samples tests. All data were maintained in Microsoft Excel (Microsoft Corporation, Microsoft Office 1997, 1996, unpubl.), and statistics were calculated using Statistical Package for the Social Sciences (SPSS Inc., Version 8 for Windows, Chicago, IL, 1997, unpubl.).

Table 4: Post hoc orthogonal contrasts for measured variables in the Bitterroot River secondary channels. Contrasts test for significant differences within and among classified channel groups.

Orthogonal Contrast	
$L1 = M1 - 0.25(TC1+TC2+BC2+BC3)$	Contrasts the Braid Anabranch with the Floodplain Channels and Floodplain Tributaries
$L2 = BC2 - BC3$	Contrasts the Floodplain Tributaries
$L3 = TC1 - TC2$	Contrasts the Floodplain Channels
$L4 = 0.5(TC1 + TC2) - 0.5(BC2 + BC3)$	Contrasts the Floodplain Channels with the Floodplain Tributaries

Results

Explaining Secondary Channel Variation and Site Prediction

The PCA reduced the measured variables to eight components with eigenvalues >1. These components accounted for 88% of the variation in the original measured variables (Table 5). Further discussion will only consider the first three components due to the difficulty in describing variable relationships beyond three spatial axes. The first PCA axis contrasts shallow sites that have minimal current, woody cover, sand substrata, and low specific conductance, with deeper sites characterized by faster currents, gravel substrata, higher specific conductance, and bank cover. The second PCA axis separated sites according to the aquatic vegetation and no cover categories. In a plot of the first and second PCA axes the sampled channels appeared to cluster similar to the three proposed channel classes (Figure 4a) except that BC1 clustered with the floodplain channels (TC1 and TC2) and M1 clustered better with the floodplain tributaries (BC2 and BC3). Euclidian distances were calculated to determine the two dimensional distances between sample sites for PCA I and PCA II scores (Table 6a). The third PCA axis compared average channel width and water oxygen concentrations. Because incorporating the third PCA axis complicated the interpretation of the scatterplot, PCA III was plotted with PCA I. The Euclidian distances were also calculated between samples sites for PCA I and PCA III scores (Figure 6b). The distribution of the channels changed slightly since BC1 was the widest of the six channels and most heavily weighted by PCA axis III (Table 6b). Again BC1 clustered with the floodplain channels and M1 clustered with the floodplain tributaries. The PCA I values for the other five secondary channels (excluding BC1) were more extreme than the PCA III values, so the PCA I values had more influence on the location of the channel within the two dimensional space.

The braid anabranches (M1 and BC1) were similarly described by PCA I and PCA II. These two channels had less extreme component values compared to the other two channel classifications. M1 was described by the no cover category, moderate current, coarser substrates, and greater water depth. PCA III described most of the variation in BC1 since this channel was the widest in the study. BC1 average oxygen concentrations were also higher probably since this channel was not sampled in August or September 1999, when the other channels exhibited higher average water temperatures and lower oxygen concentrations. BC1 and M1 were separated according to the available cover types, substrate distribution, and water depth.

The floodplain channels (TC1 and TC2) tended to be lentic and shallow with sand substrata. However, the channels differed by their dominant cover types. PCA I incorporating the woody debris cover variables, characterized the cover types describing TC1 while PCA axis II described the aquatic vegetation cover types that distinguished TC2. Vegetation was a prominent feature of TC2 especially during August and September sampling. The influence of vegetation cover on PCA II was apparent in the large negative coefficient of TC2 (-1.39). PCA axis III reflected the narrow channel of TC1; this component described little of the variation in TC2. BC1 was grouped with the floodplain channels since it was primarily characterized by a shallow, sand substrate channel with a large lentic area.

High specific conductance, moderate current speeds, coarser substrates, and deeper channels distinguished the floodplain tributaries (BC2 and BC3) and M1. PCA axis II described little of TC1's habitat variation since aquatic vegetation was less abundant relative to the total channel area in this site. As stated previously, PCA II described most of the variation in TC2. M1 was described by the no cover category and to a lesser extent by coarse substrates, moderate currents, deeper channel, and high specific conductance. The spatial relationship and relative locations of BC2 and BC3 changed minimally when PCA axis III was plotted against PCA axis I. M1 did not plot dramatically different when PCA axis III was plotted against PCA axis I. PCA axis III explained the intermediate channel width and moderate oxygen concentrations characterizing M1.

Discriminant function analysis retained the first five PCA components for predicting secondary channel group membership. The first two discriminant functions described 85.3% of the variation in the PCA components and clustered the site-date PCA scores (Figure 5). Again the floodplain channels (TC1 and TC2) clustered with BC1.

The floodplain tributaries BC3 grouped with M1, while BC2 plotted away from the other sample channels. Using the leave-one-out classification, the actual site-date samples were properly predicted 100% of the time.

Secondary Channel Habitat Variation

Two-way factorial ANOVAs were conducted for each measured variable and the first three PCA axes to determine if they varied among secondary channels and sample dates (Table 7). Physical variables displayed more variation among sites than among dates. Variables that significantly differed among sample dates were predominantly variables that varied seasonally such as water temperature, specific conductance, and average channel depth. Variables that were similar over time included the substrate categories, woody debris distributions, and measures of within-site variation for a single sampling period. PCA I scores differed significantly among the sample sites but not over time since this first component was primarily comprised of habitat variables that were temporally stable. Conversely, PCA II scores and PCA III scores varied significantly by site and date. Aquatic vegetation (PCA II scores) varied by sampling date as did the average channel width and water oxygen concentrations (PCA III scores).

Multiple orthogonal contrasts were also estimated to provide another test of the proposed channel classes. Results indicate high variability within and between the channel groups (Table 8a and Table 8b), since variable differences among groups (Contrasts 1 and 4) were only slightly greater than differences within groups (Contrast 2 and 3). Considering the four contrasts that were conducted, the floodplain channels (TC1 and TC2) and the floodplain tributaries were the most different from each other since 18 of the tested variables were significantly different ($P < 0.05$) between the two channel groups. Channels within a channel group were more similar to each other than to the other channel groups. For instance, only 13 variables were significantly different between BC2 and BC3 (the floodplain tributaries). Similarly, 17 variables were significantly different between TC1 and TC2. However, only 15 variables differed between the floodplain tributary-floodplain channel contrast group (BC2, BC3, TC1, and TC2) and the braid anabranch (M1). This result was less than expected and was mainly attributed to similarities between M1 and the floodplain tributaries. Comparing M1 to the grouped floodplain tributaries-floodplain channels weakened this contrast since M1 and BC2-BC3 shared similar channel characteristics. This comparison was necessary in order to meet the requirements of the orthogonal contrast model.

Several variables were significantly different over the four contrasts. Aquatic vegetation water column cover, channel average width, PC1, PC2, and PC3 were significantly different ($P < 0.05$) for all four contrasts. These five variables differentiated individual channels as well as the channel groups. Conversely, other variables such as channel length, intra-channel width variation, pebble substrate and shallow channel depths, did not significantly differ among channel groups or between channels. These variables were less important for describing channel variation and channel group similarity.

The sampling regime indicated that the sampled secondary channels were highly variable. However, the results of the principal components analysis and the orthogonal contrasts lend some credence to a channel classification system. To improve upon this model, more secondary channels would have to be sampled to improve channel sample size. This protocol would also rectify inter-period channel condition variation. By sampling more channels during one period, combined with sampling over several periods, channels could be more accurately classified since comparisons among channels could be made seasonally. This would alleviate some of the site-date variation found in these data.

Secondary Channel-Mainstem Water Chemistry Variation

Water chemical variables varied among the secondary channels and the Bitterroot River (Table 9). Using the Wilcoxon signed rank test, oxygen concentration levels were significantly greater in the secondary channels (BC2, BC3, TC1, and TC2, respectively) than in the Bitterroot River. Specific conductance was greater in BC2, BC3, and M1 than in the Bitterroot. However, water temperatures were not significantly different for any of the secondary channels compared to the Bitterroot. Comparisons were also performed for paired secondary channels (Table 10). For the floodplain tributaries, BC3 had significantly greater oxygen concentration (P = 0.046, 8.00 mg/L vs. 7.12 mg/L) and specific conductance (P = 0.028, 230.80 mS/cm vs. 160.20 mS/cm) than BC2. M1 had a significantly higher specific conductance (P = 0.028, 98.28 mS/cm vs. 64.92 mS/cm) than BC1. Water chemicals did not vary significantly between the floodplain channels, TC1 and TC2.

Discussion

A mobile primary channel and a mosaic of complementary secondary channels characterize the central Bitterroot River and its associated floodplain (Gaeuman 1997;

Clancy 1999). Physicochemical parameters measured in secondary channels and the Bitterroot River suggest high connectivity between the river and its floodplain, although some environmental conditions differ from channel to channel. The proposed channel classification based on geographic location of secondary channels relative to the mainstem, was supported by a principal components analysis and a discriminant function analysis incorporating geomorphic and chemical attributes of six secondary channels. The PCA separated the six channels into two channel groups rather than the proposed three groups. The braid anabranch BC1 was separated and placed with the floodplain channel group while M1 grouped with the floodplain tributaries. Orthogonal contrasts and Wilcoxon rank test results also indicated moderate variability among sites and sampling periods. The measured variability in secondary channel environmental conditions is indicative of an intact river-floodplain environment. High geographic and temporal environmental diversity among secondary channels is an important factor in sustaining biological communities in river floodplains (Ebersole et al. 1997).

A rapidly fluctuating river hydrograph and a broad, flat floodplain contribute to channel instability in the central Bitterroot River. Banks with minimal cohesion and large, infrequent flood events increase floodplain heterogeneity and promote complex interactions operating at the aquatic-terrestrial interface (Hickin and Nanson 1984; Brizga and Finlayson 1990; Nanson and Knighton 1996). This was evident in the presence of large woody debris in TC1 and M1. During high water, the Bitterroot River scours into the riparian fringe and removes trees from the forest community. Cottonwoods and Ponderosa pines are transported and eventually settle within the channel or close to it and provide transient channel complexity. Depending on subsequent floods, this material may be transported to other reaches of the river, thereby reducing channel complexity at one site and increasing complexity at another location.

In addition to variable habitats created by flood-driven fluvial processes, upwelling hyporheic water sustains a diverse secondary channel network during low flow periods and also augments surface water discharge in persistent channels. On the Bitterroot River floodplain, subsurface upwelling was deemed important for headcut advancement and capillary channel migration (Gaeuman 1997). Additionally, upwelling groundwater provides a consistent cold water source for aquatic organisms. Several cold water seeps were measured along channel margins in two of the sampled channels. The importance of hyporheic upwelling has been documented in other Northern Rocky Mountain drainages. In the Middle Flathead River, floodplain watercourse characteristics partially explained the resident fish communities (Cavallo 1997). These habitats varied according to their dependency on subsurface discharge and proximity to the mainstem.

Fluvial Processes and Channel Alteration

On the Bitterroot River, large intrachannel islands are formed by sediment deposition within the braid belt, and floodplain incision by channel avulsion. Cobble bars separating the M1 and BC1 braid anabranch channels from the Bitterroot River, likely originated from point bar aggradation (sediment deposition). Immature pioneer vegetation and minimal detritus accumulations suggest that the islands are relatively young and frequently disturbed by high flows. Dense vegetation patches and abundant woody debris on the islands increase bar roughness and sediment deposition during receding high flows (Malanson and Butler 1990; Abbe and Montgomery 1996).

Depending on annual discharge, continued growth of these sites is expected as vegetation colonizes annually deposited sediment (Malanson and Butler 1990).

Floodplain incision occurs during elevated discharge when overbank flows carve new channels from floodplain material. On the Bitterroot floodplain, avulsed channels such as TC1 and TC2 tend to be partially disconnected from the mainstem (except during high flows), convey subsurface flows, and experience channel scour when the Bitterroot River overtops natural levees and captures the secondary channel. Depending on the location and size of avulsed floodplain channels, portions of the floodplain may become intrachannel islands as channels surround the alluvial material.

Habitat diversity is enhanced by periodic flood flows responsible for altering floodplain environments. During this two year study, overbank flows were observed during the 1999 spring runoff (161% of the 13 year average peak). The effects of this flood on secondary channels varied by channel location and proximity to the mainstem. In some areas, overbank flows redistributed woody debris and deposited fine sediment on the floodplain. At other sites, fluvial processes altered floodplain surfaces by undercutting mature cottonwoods and mobilizing large volumes of sediment. Although floodplain vegetation, especially woody shrubs, improve bank integrity and reduce localized bank failure (Hickin 1984; Piegay and Gurnell 1997), even densely vegetated banks characterized by black cottonwood overstories and red osier dogwood shrub layers were eroded by the river during high water. This was apparent along the Tucker Crossing Island where several large cottonwoods fell into the river during the 1999 runoff. A broad low gradient area (~0.5 km^2) downstream of the Tucker Crossing secondary channels, contains large aggregations of fallen cottonwoods and Ponderosa pines transported by the river. These large tree rafts may accelerate localized channel scour and lateral channel widening as well as increase upstream sediment deposition during high water (Abbe and Montgomery 1996). High water velocities erode under and around these large woody debris aggregations, although such rafts may also create a damming effect that slows upstream discharge and causes localized sediment deposition (Abbe and Montgomery 1996).

Bankfull discharge channel scour was apparent in the BC1 channel after the recession of floodwaters. Prior to high water, the channel was primarily a migrating, unstable sand bed with water depths averaging 0.3 m to 0.5 m. During the 1999 high water, the Bitterroot River captured this braid anabranch and scoured it to depths in excess of 4 m. The altered channel geometry is now dominated by a cobble substrate. Hyporheic discharge into the channel has apparently increased judging by dense benthic algal blooms that now dominate the channel. In 1998, prior to channel scour, algal blooms were not observed in the reach. Complex fluvial processes operating at multiple spatial scales, transformed aquatic habitats, and lead to rapid channel adjustments and sediment mobilization throughout the study area.

Secondary Channel Variability

Braid anabranches, floodplain tributaries, and floodplain channels were similar for some environmental conditions, but these channel types were also distinguished by measured physicochemical variables. Secondary channels in the Bitterroot River provide diverse habitats that both resemble and contrast with main channel conditions. Channel diversity was greatest during moderate flow periods when secondary channels provide an array of riffle and pool habitats (personal observation). Groundwater upwelling and surface water flows mix to create a range of water temperatures that differ in magnitude and timing from the mainstem. Conversely, secondary channel habitats were less diverse during high and low flow periods compared to periods of intermediate flows. During low flow periods, channel areas contracted as water levels decreased. Although secondary channels remained connected to the Bitterroot River at their downstream ends, several sites (TC1, TC2, BC1, and BC2) shortened as upstream portions dried up during the low flow period.

Measured physicochemical properties suggest that environmental conditions varied both temporally and geographically for secondary channels. Water temperature, specific conductance, and oxygen saturation differentiated surveyed channels except during high water when the flooding Bitterroot River homogenized lateral secondary channels chemical conditions. During base flows, specific conductance and water temperatures separated BC2 and BC3 from the other channels in the survey. Elevated specific conductance levels suggest discharge from an upland aquifer rather than a hyporheic source. Similar stable water temperatures in the other channels suggest a common hyporheic water source or an overriding surface water influence since groundwater-dominated sites often have consistent water temperatures in other systems (Constantz 1998).

The physical structure of secondary channels also helped explain interchannel variation. Patchy aquatic environments should provide higher microhabitat diversity important for aquatic organisms. For example, coarse woody debris is an essential element for creating and maintaining complex pools preferred by some fish species. In

Bitterroot River secondary channels, patchy distributions of CWD influenced pool development with the deepest pools regularly corresponding with dense CWD aggregations. In a 25 km section of the Queets River in northwest Washington, the deepest surveyed pools were associated with CWD jams (Abbe and Montgomery 1996). Small stream geomorphology tends to be influenced by CWD since large pieces can extend the channel width.

Measured variables suggest many similarities exist among the sampled secondary channels. However, to rigorously test a channel classification system a larger sample size and more frequent sampling would be required. The distribution of the channels also influenced some of the measured variables. For instance, BC2 and BC3 were less than 300 m from one another and exhibited similar specific conductance and water temperatures. Nevertheless, relationships among the proposed channel groups revealed by the PCA and DFA illustrate the potential for a secondary channel classification system.

Floodplain Management

Using a 50 year aerial photograph record, Gaeuman (1997) determined that the length of the Bitterroot River has not significantly changed, although the current braid belt is wider and straighter than in the past. In managed watercourses of the western United States, rivers and riparian zones are often dramatically altered when rivers are diverted (Kondolf and Curry 1986), dammed (Suchomel 1994; Kondolf 1997), or laterally constrained by bank stabilization (Dykaar and Wigington 2000). Ultimately, rivers become less complex as the channel is decoupled from its associated floodplain by human activities (Sedell and Froggat 1984; Dykaar and Wigington 2000). As the river-floodplain relationship unravels, the importance of channel diversity becomes apparent. Dam construction and flow moderation in the Colorado River basin have simplified channel complexity and significantly affected the distribution of secondary channel spawning and nursery habitats utilized by Colorado pikeminnow (Van Steeter and Pitlick 1998a). Without periodic high discharge flows, vegetation establishment in secondary channels reduced the number of available backwaters and converted the water-riparian interface to a terrestrial environment (Van Steeter and Pitlick 1998b). A similar conversion of water to land ecosystems might be expected in the Bitterroot River as landowners increasingly develop floodplain properties and stabilize banks. Irrigation diversions could exacerbate this environmental transformation if the water table elevation recedes and groundwater discharge into floodplain channels is reduced. These processes would promote the displacement of hydric flora by more-xeric upland vegetation. Since numerous species and age classes of Bitterroot River fish use secondary channel habitats on multiple temporal scales (Chapters 3 and 4), managing floodplain development and river channel alterations will influence the dynamic interactions linking the central Bitterroot River, its floodplain, and the aquatic life that both support.

Conclusions

- Question 1 Results: The proposed channel classification was partially supported.
    - Based on water chemistry and physical microhabitat data, BC1 grouped with the floodplain channels and M1 grouped with the floodplain tributaries.

- Question 2 Results: The channel types were differentiated by the measured variables.
  - The principal components analysis explained 88% of the variation in the variables characterizing the sampled channels.
  - Discriminant function analysis explained 85.3% of the variation in the PCA scores and correctly grouped site-date samples according to the six secondary channels.
- Question 3 Results: Physical and chemical conditions differed among secondary channels and the Bitterroot River.
  - ANOVA and orthogonal contrasts suggested high microhabitat diversity within and among the proposed channel groups, and moderately variable conditions over time.
  - Water quality characteristics suggest that the floodplain channels (TC1 and TC2) and BC1 are influenced by the Bitterroot River perhaps due to their central floodplain locations. The other three channels appear to be more influenced by external conditions such as groundwater upwelling from upland aquifers.

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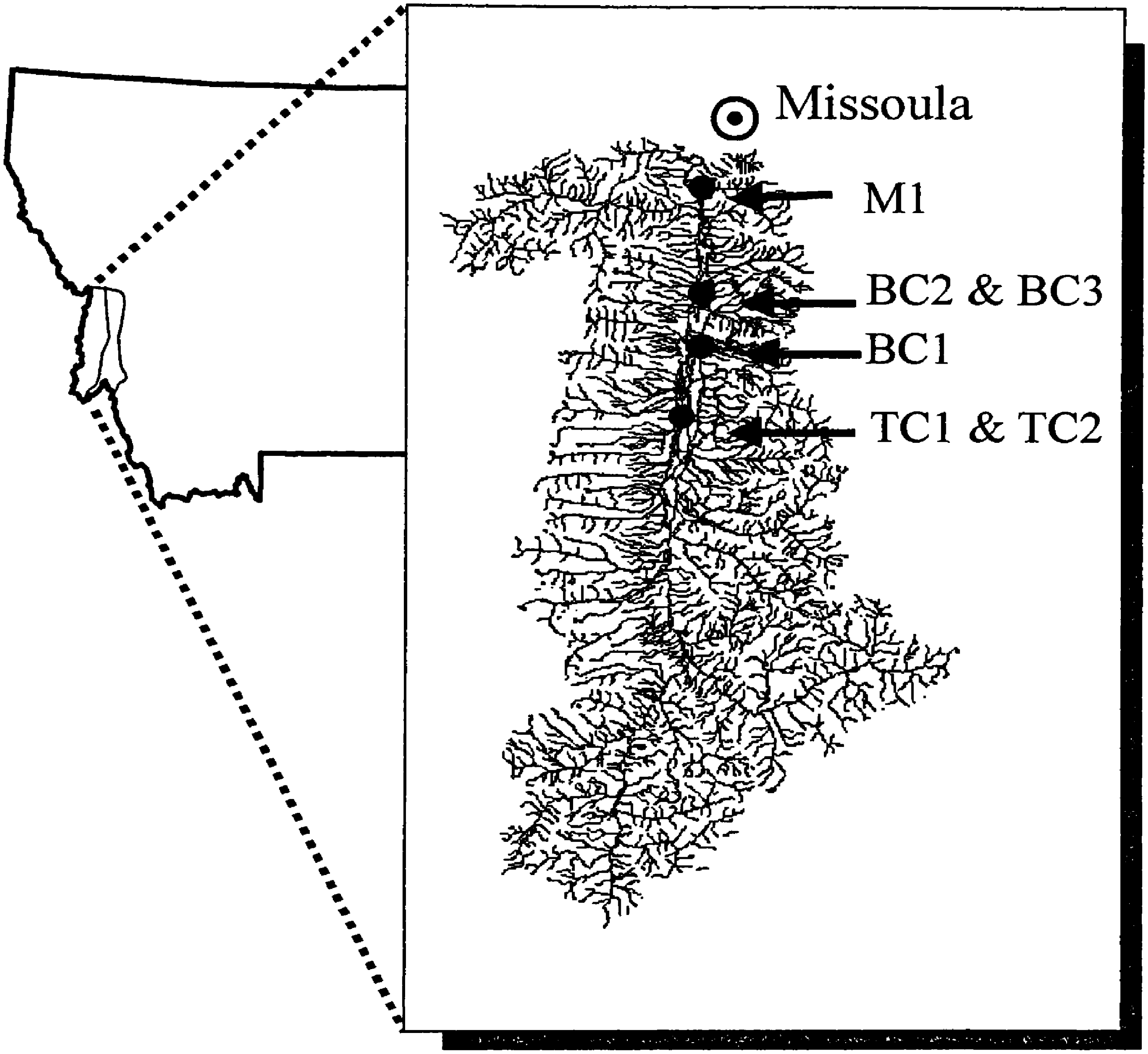

Figure 1: The Bitterroot River watershed and the secondary channel sample sites.

Table 1: Common vegetation found on the Bitterroot River floodplain.

Trees	Shrubs	Grasses and Forbs
Populus trichocarpa	*Cornus stolonifera*	*Phalaris arundinacea**
Populus tremuloides	*Crataegus douglasii*	*Centaurea maculosa**
Alnus incana	*Symphoricarpos albus*	*Tanacetum vulgare**
Pinus ponderosa	*Salix* spp.	*Poa pratensis*
Picea engelmannii	*Rosa* spp.	*Phleum pratense*
Larix occidentalis	*Ribes* spp.	*Carex* spp.

*: Denotes an introduced species

Table 2: Locations of sampled secondary channels relative to the most upstream sample site (Tucker Crossing 1).

Secondary Channel	Channel Type	Distance Downstream from Tucker Crossing 1
Tucker Crossing 1	Floodplain Channel	0 km
Tucker Crossing 2	Floodplain Channel	0.532 km
Bell Crossing 1	Braid Anabranch	12.5 km
Bell Crossing 2	Floodplain Tributary	15.5 km
Bell Crossing 3	Floodplain Tributary	15.8 km
Missoula 1	Braid Anabranch	102.0 km

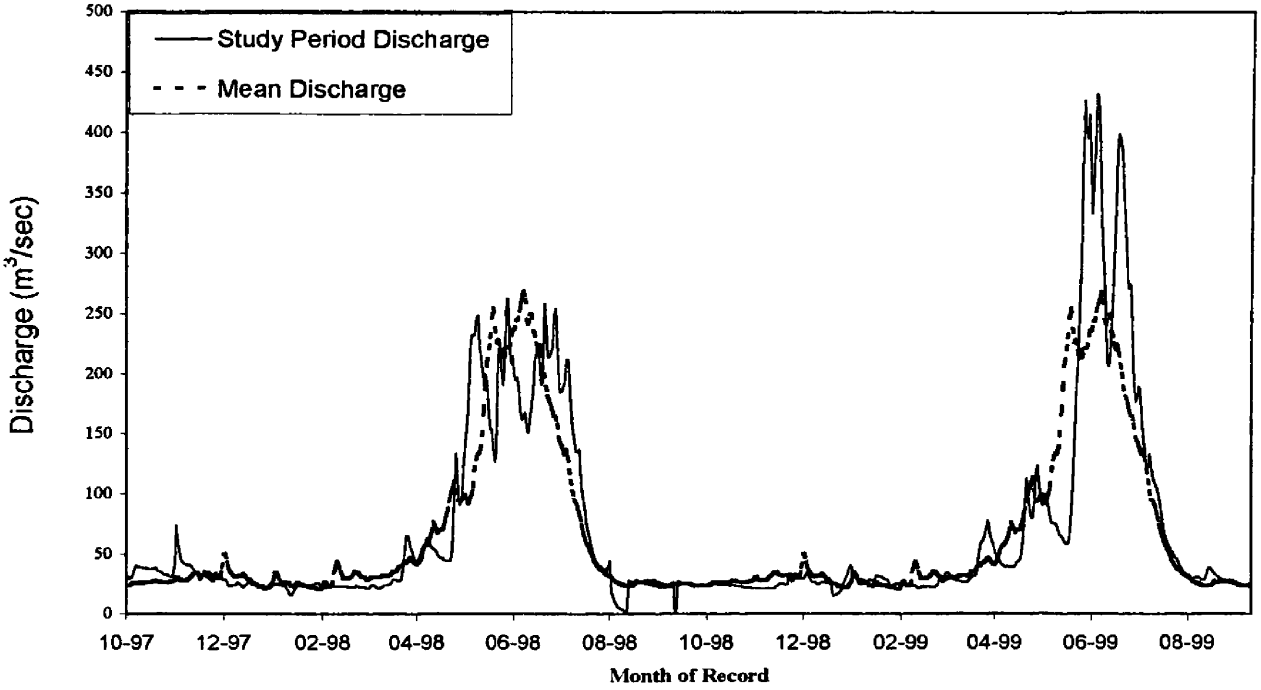

Figure 2: Bitterroot River average annual discharge measured over a thirteen year period and the discharge during the sampling period.

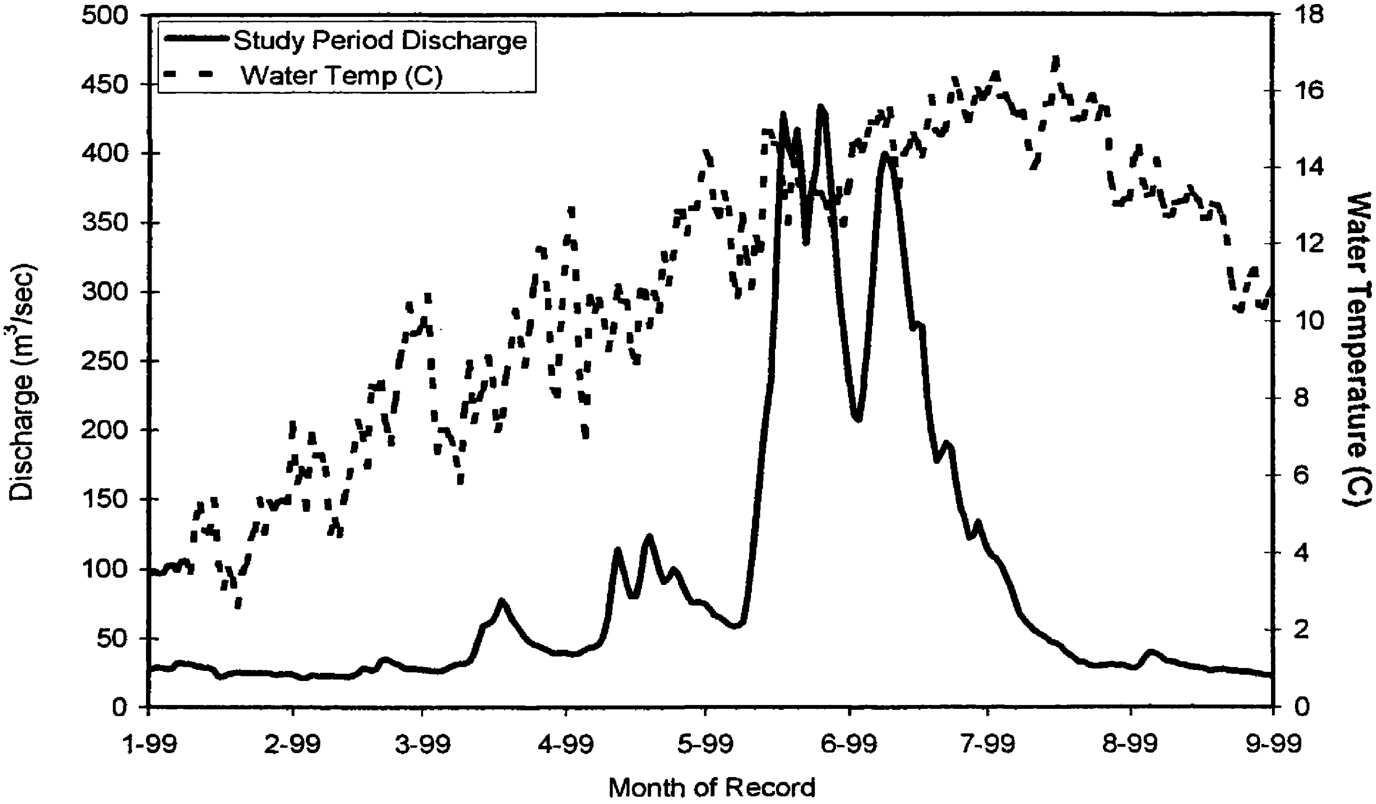

Figure 3: Bitterroot River discharge and water temperature measured over a portion of the sampling period.

Table 3: Physical and chemical variables that were measured or derived for Bitterroot River secondary channel sample sites. Variables were used to describe environmental variation among secondary channels. Percentages represent the number of times a value was sampled divided by the total number of samples that were measured using the point transect method.

Physical Variables[1]	Cover Types[1]	Water Chemistry Variables[2]
Glide Area (m^2)	Substrate Cover:	Water Temperature (°C)
Riffle Area (m^2)	% None	Specific Conductance (µS/L)
Substrate:	% Aquatic Vegetation	Oxygen Concentration (mg/L)
% Silt	% Bank	Oxygen Saturation (%)
% Sand	% Small Woody Debris	
% Gravel	% Large Woody Debris	
% Pebble	% Boulder	
% Cobble	Water Column Cover:	
% Boulder	% None	
Depth:	% Aquatic Vegetation	
% 0-0.49 m	% Bank	
% 0.5-0.99 m	% Small Woody Debris	
% 1.0-1.49 m	% Large Woody Debris	
% >1.50 m	% Boulder	
Site Depth (m) (mean and CV)	CWD Area (m^2)	
Site Width (m) (mean and CV)		
Greatest Site Width (m)		
Sample Reach Length (m)		

[1]: physical variables and cover type percentages collected using the point-transect method.

[2]: water chemistry variables based on the average of several points measured at midstream along the sample reach length.

Table 5: Loadings of environmental variables on components (PC) from the principal components analysis conducted on the habitat data describing the six secondary sites over all sampling periods.

	Component							
Environmental Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Glide Area	**0.87**	0.16	-0.30	0.02	-0.09	-0.07	0.03	-0.01
% Sand Substrate	**-0.85**	-0.13	-0.35	-0.05	0.23	0.10	-0.12	-0.05
Specific Conductivity	**0.85**	0.05	0.22	0.11	-0.34	-0.12	-0.02	0.05
Depth 1-1.49 m	**-0.80**	0.40	0.14	0.12	0.04	0.26	0.10	-0.18
CWD Area	**-0.77**	0.21	0.13	0.53	0.06	0.00	0.01	-0.11
% Gravel Substrate	**0.77**	0.34	0.42	0.07	-0.02	0.09	0.13	0.06
LWD Column Cover	**-0.75**	0.26	0.48	0.08	-0.07	-0.08	0.20	0.11
Bank Cover	**0.75**	-0.09	0.13	-0.49	0.07	0.03	-0.05	0.13
LWD Substrate Cover	**-0.71**	0.39	0.37	0.04	0.14	-0.21	0.17	0.05
SWD Column Cover	**-0.66**	-0.19	-0.24	0.20	0.09	0.16	0.15	0.05
Average Channel Depth	**-0.63**	0.13	0.09	0.09	-0.59	0.29	-0.01	0.00
SWD Substrate Cover	**-0.62**	0.33	-0.18	-0.12	0.19	0.38	-0.14	0.19
Aquatic Veg. Sub. Cover	0.09	**-0.78**	-0.01	0.43	0.37	-0.04	-0.02	0.11
Aquatic Veg. Col. Cover	0.29	**-0.71**	0.29	0.48	0.03	-0.07	0.15	0.00
No Substrate Cover	0.27	**0.70**	-0.12	-0.36	-0.42	0.00	0.10	-0.24
No Column Cover	0.13	**0.62**	-0.47	-0.44	-0.02	0.12	-0.19	-0.14
Average Channel Width	0.53	0.07	**-0.69**	0.06	0.19	0.23	0.10	-0.07
Oxygen Concentration	0.25	0.54	**-0.60**	0.26	-0.05	-0.16	0.18	0.26
% Boulder Substrate	0.47	0.29	0.35	**0.65**	0.01	0.11	0.21	-0.01
Riffle Area	0.50	0.39	0.26	**0.63**	0.01	0.17	0.22	-0.02
Depth 0.5-0.99 m	-0.14	-0.38	-0.31	0.15	**-0.66**	0.39	0.23	0.16
% Cobble Substrate	0.47	-0.13	0.46	-0.12	**-0.60**	-0.22	0.07	-0.13
Depth 0-0.49 m	0.53	0.14	0.12	-0.08	**0.60**	-0.43	-0.23	-0.10
Water Temperature	0.17	-0.21	0.57	-0.05	-0.02	0.26	-0.03	**-0.62**
Depth > 1.5 m	-0.56	0.29	0.34	-0.20	-0.07	-0.34	0.04	0.31
Channel Depth CV	-0.26	0.47	0.34	0.00	0.55	-0.02	0.39	-0.13
Channel Width CV	0.05	-0.20	0.26	-0.52	0.48	0.13	0.43	0.09
% Silt Substrate	0.15	-0.25	-0.52	0.56	-0.12	-0.29	0.18	-0.04
Boulder Column Cover	0.36	0.33	0.25	0.51	0.15	0.31	-0.47	0.11
Oxygen Saturation	0.39	0.56	-0.42	0.28	-0.02	-0.10	0.23	-0.03
Boulder Substrate Cover	0.39	0.34	0.27	0.52	0.22	0.32	-0.38	0.14
Channel Length	0.42	-0.36	0.26	-0.37	0.04	0.55	0.17	0.14
Greatest Channel Width	0.54	-0.02	-0.49	-0.10	0.45	0.28	0.30	-0.12
% Pebble Substrate	0.55	0.24	0.48	-0.37	0.00	0.14	0.07	0.36
Eigenvalue	10.03	4.63	4.35	3.81	2.95	1.85	1.39	1.03
% Total Variation	29.50	13.62	12.81	11.21	8.69	5.44	4.08	3.04

Only eigenvalues > 1 were retained. Values with loadings ≥ \|0.6\| are in bold.

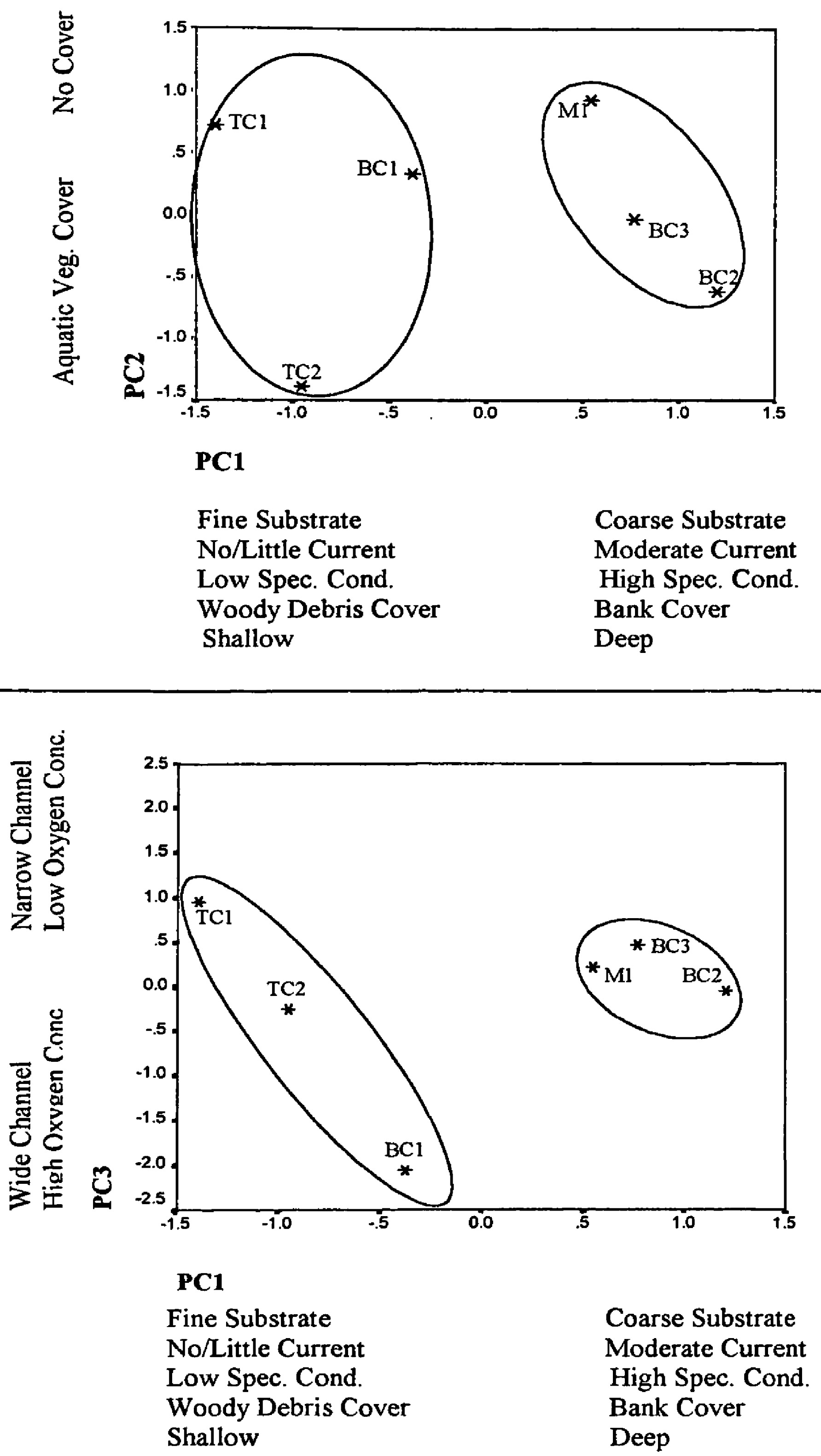

Figure 4: Scatterplot of principal component scores with elipses encircling a priori groupings of sample sites. PC1 and PC2 are at top and PC1 and PC3 are plotted at bottom.

Table 6a: Proximity matrix for the PCA axis I vs. PCA axis II scatterplot. For each secondary channel, the nearest neighbor secondary channel is in bold. The Euclidian distance is the square root of the sum of the squared differences between the PCA axis I and PCA axis II scores for each secondary channel.

Euclidian Distances

	TC1	TC2	BC1	BC2	BC3	M1
TC1		2.161	**1.087**	2.925	2.298	1.954
TC2	2.161		1.825	2.293	2.199	2.767
BC1	**1.087**	**1.825**		1.850	1.212	1.099
BC2	2.925	2.293	1.850		**0.726**	1.683
BC3	2.298	2.199	1.212	**0.726**		**0.991**
M1	1.954	2.767	1.099	1.683	0.991	

Table 6b: Proximity matrix for the PCA axis I vs. PCA axis III scatterplot. For each secondary channel, the nearest neighbor secondary channel is in bold. The Euclidian distance is the square root of the sum of the squared differences between the PCA axis I and PCA axis III scores for each secondary channel.

Euclidian Distances

	TC1	TC2	BC1	BC2	BC3	M1
TC1		**1.282**	3.194	2.790	2.225	2.081
TC2	**1.282**		**1.913**	2.167	1.868	1.569
BC1	3.194	1.913		2.562	2.784	2.462
BC2	2.790	2.167	2.562		0.675	0.710
BC3	2.225	1.868	2.784	**0.675**		**0.340**
M1	2.081	1.569	2.462	0.710	**0.340**	

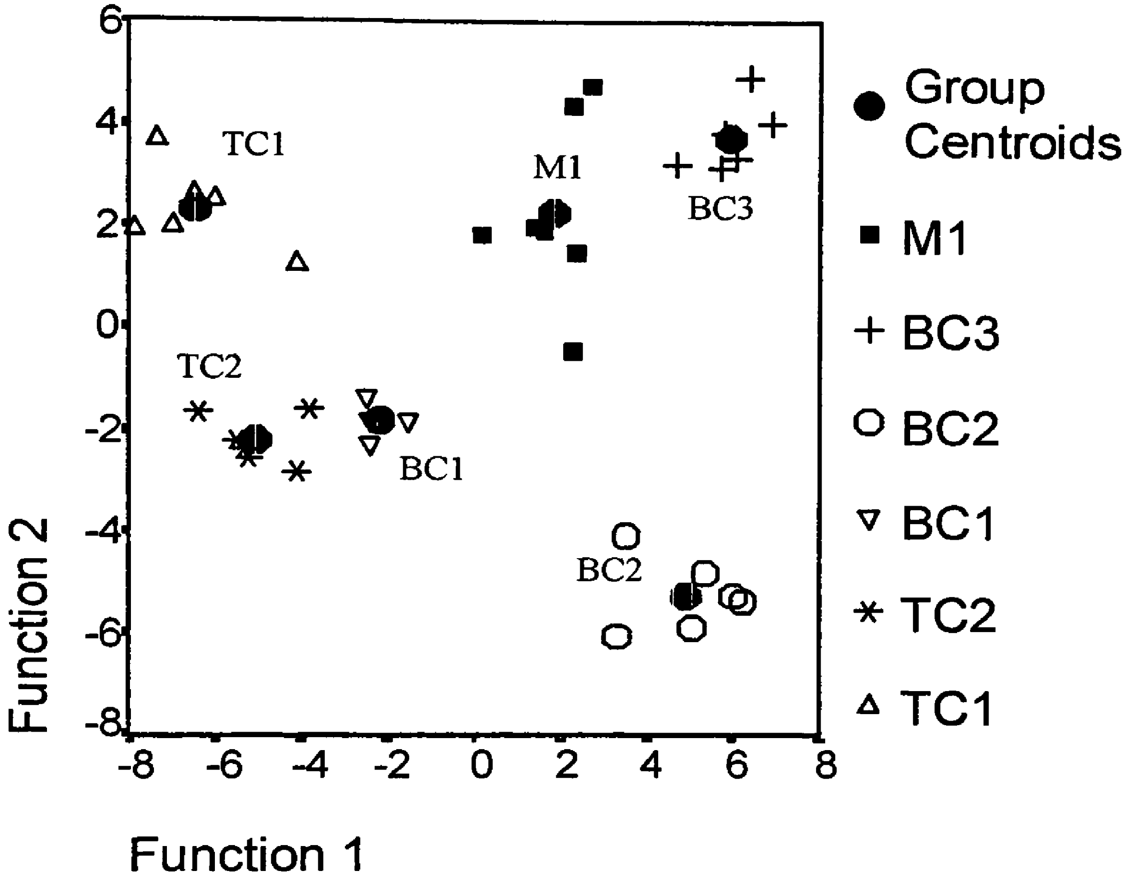

Figure 5: Discriminant function analysis results for the first two discriminant functions. The first five PCA scores were used to create the two discriminant functions. Similar to the PCA scatterplots, BC1 plotted with the floodplain channels (TC1 and TC2) while M1 plotted with the floodplain tributaries (BC2 and BC3).

Table 7: Results from factorial ANOVA with Site as the fixed factor, Date the random factor, and Variable as the response. BC1 was excluded from the analysis due to incomplete data. Glide Area, Riffle Area, and CWD Area not included due to low variability within sites over time. The variables Depth >1.5 and Boulder Column Cover were not included due to low frequencies. Measured variables were analyzed by secondary channel (Site) and sampling period (Date). For example, the % Sand Substrate varied by secondary channel although the amount of sand substrata in secondary channels did not change over time. Conversely, specific conductance varied significantly among secondary channels and was also significantly different over time. Results were used to conduct multiple contrasts. Bold figures indicate variable measurements were significantly different at the $P < 0.05$ level.

Variable	Site	Date
% Sand Substrate	**<0.0001**	0.864
Specific Conductance	**<0.0001**	**<0.0001**
Depth 1-1.49 m	**<0.0001**	0.277
% Gravel Substrate	**<0.0001**	0.404
LWD Column Cover	**<0.0001**	0.635
Bank Cover*	**0.049**	0.264
LWD Substrate Cover	**<0.0001**	0.475
SWD Column Cover	**0.004**	0.177
Average Channel Depth	**0.001**	**0.032**
SWD Substrate Cover	**0.002**	0.053
Aquatic Veg. Sub. Cover*	**<0.0001**	**0.060**
Aquatic Veg. Col. Cover	**<0.0001**	**<0.0001**
No Substrate Cover	**<0.0001**	**0.023**
No Column Cover	**0.012**	**0.001**
Average Channel Width	**<0.0001**	0.141
Oxygen Concentration	**0.004**	**0.001**
% Boulder Substrate*	**0.039**	0.135
Depth 0.5-0.99 m*	**0.003**	0.478
% Cobble Substrate	**<0.0001**	**0.037**
Depth 0-0.49 m*	**0.003**	0.255
Water Temperature	0.348	**<0.0001**
Channel Depth CV	**<0.0001**	0.071
Channel Width CV*	**<0.0001**	0.212
% Silt Substrate	**<0.0001**	**0.001**
Oxygen Saturation	**0.002**	**0.025**
Boulder Substrate Cover*	0.685	0.884
Channel Length*	**<0.0001**	**0.012**
Greatest Channel Width	**<0.0001**	0.292
% Pebble Substrate*	**<0.0001**	0.846
PC1	**<0.0001**	0.547
PC2	**<0.0001**	**<0.0001**
PC3	**<0.0001**	**<0.0001**

*: Transformed variables were also weighted to meet the assumption of variance homogeneity required by ANOVA. Weight equaled $\mu_x/(1/\mathrm{var}(X))$.

Table 8a: Multiple contrasts for secondary channel physicochemical variables. Secondary channel BC1 was not included for the analysis due to incomplete data. The table includes variables that were significantly different among sites, but did not change significantly over time. See text for contrast equations. Channel comparisons denote multiple contrast results. For a particular variable, a significant contrast represents a statistically significant difference in the values of that variable measured at the contrasted secondary channels. For example, M1 had a significantly greater average channel width ($P < 0.0001$) than did TC1 and TC2 for Contrast 1. Bold figures indicate contrasts significant at the $P < 0.05$ level.

					Channel Comparisons			
Physicochemical Variable	Contrast 1 P-values	Contrast 2 P-values	Contrast 3 P-values	Contrast 4 P-values	Contrast 1 Results	Contrast 2 Results	Contrast 3 Results	Contrast 4 Results
% Sand Substrate	0.0608	0.1313	**0.0087**	**<0.0001**			TC2 > TC1	TC1, TC2 > BC2, BC3
% Gravel Substrate	**<0.0001**	0.4615	**0.0002**	**<0.0001**	M1 > TC1, TC2, BC2, BC3		TC1 > TC2	BC2, BC3 > TC1, TC2
LWD Column Cover	0.0800	**0.0006**	**<0.0001**	**<0.0001**		BC3 > BC2	TC1 > TC2	TC1, TC2 > BC2, BC3
LWD Substrate Cover	0.9817	**0.0343**	**<0.0001**	**<0.0001**		BC2 > BC3	TC1 > TC2	TC1, TC2 > BC2, BC3
SWD Column Cover	**0.0355**	0.4409	0.0706	**<0.0001**	TC1, TC2, BC2, BC3 > M1			TC1, TC2 > BC2, BC3
Channel Average Width	**<0.0001**	**0.0052**	**0.0001**	**0.0012**	M1 > TC1, TC2, BC2, BC3	BC2 > BC3	TC2 > TC1	BC2, BC3 > TC1, TC2
Depth 0.5-0.99 m	0.7621	0.9031	0.7618	0.8894				
Depth 0-0.49 m	0.8083	0.8838	0.9490	0.8927				
Channel Width CV	0.5856	0.5705	0.9706	0.5470				
Channel Greatest Width	**<0.0001**	**<0.0001**	**<0.0001**	0.3484	TC1, TC2, BC2, BC3 > M1	BC2 > BC3	TC2 > TC1	
% Pebble Substrate	0.6983	0.6118	0.6605	0.5268				
Aquatic Veg. Sub. Cover	0.6321	0.7685	**0.0523**	0.9838			TC2 > TC1	
PC1	**<0.0001**	**0.0099**	**0.0082**	**<0.0001**	M1 > TC1, TC2, BC2, BC3	BC2 > BC3	TC2 > TC1	BC2, BC3 > TC1, TC2

Table 8b: Multiple contrasts for secondary channel physicochemical variables. Secondary channel BC1 was not included for the analysis due to incomplete data. The table includes variables that were significantly different among sites and over time. See text for contrast equations. Channel comparisons denote multiple contrast results. For a particular variable, a significant contrast represents a statistically significant difference in the values of that variable measured at the contrasted secondary channels. For example, M1 had a significantly greater average oxygen saturation ($P = 0.0049$) than did TC1 and TC2 for Contrast 1. Bold figures indicate contrasts significant at the $P < 0.05$ level.

					Channel Comparisons			
Physicochemical Variable	Contrast 1 P-values	Contrast 2 P-values	Contrast 3 P-values	Contrast 4 P-values	Contrast 1 Results	Contrast 2 Results	Contrast 3 Results	Contrast 4 Results
Channel Depth CV	**<0.0001**	0.8076	**<0.0001**	**<0.0001**	M1 > TC1, TC2, BC2, BC3		TC1 > TC2	TC1, TC2 > BC2, BC3
O2 Saturation	**0.0378**	0.3214	0.3214	0.0892	M1 > TC1, TC2, BC2, BC3			
Channel Ave. Depth	**0.0030**	**0.0144**	**0.0503**	0.9293	TC1, TC2, BC2, BC3 > M1	BC3 >BC2	TC1 > TC2	
Water Temp	0.0576	0.3333	0.3912	**<0.0001**				BC2, BC3 > TC1, TC2
O2 Concentration	**0.0191**	0.1928	0.3437	0.3801	M1 > TC1, TC2, BC2, BC3			
Specific Conductance	0.0843	**0.0029**	0.4179	**<0.0001**		BC3 >BC2		BC2, BC3 > TC1, TC2
SWD Substrate Cover	0.7312	0.4115	0.6885	**<0.0001**				TC1, TC2 > BC2, BC3
% Silt Substrate	0.3286	**0.0003**	**0.0007**	**0.0037**		BC3 >BC2	TC2 > TC1	BC2, BC3 > TC1, TC2
% Cobble Substrate	**0.0001**	0.3477	**0.0238**	**<0.0001**	TC1, TC2, BC2, BC3 > M1		TC1 > TC2	BC2, BC3 > TC1, TC2
Depth 1-1.49 m	0.1490	**0.0027**	**0.0033**	**<0.0001**		BC3 >BC2	TC1 > TC2	TC1, TC2 > BC2, BC3
No Substrate Cover	**0.0117**	0.5835	**0.0001**	**0.0017**	M1 > TC1, TC2, BC2, BC3		TC1 > TC2	BC2, BC3 > TC1, TC2
No Column Cover	**0.0010**	**0.0249**	0.0948	0.6440	M1 > TC1, TC2, BC2, BC3	BC2 > BC3		
Channel Length	0.9284	0.9137	0.9424	0.9914				
Aquatic Veg. Col. Cover	**0.0009**	**0.0024**	**<0.0001**	**<0.0001**	TC1, TC2, BC2, BC3 > M1	BC3 >BC2	TC2 > TC1	BC2, BC3 > TC1, TC2
PC2	**<0.0001**	**0.0017**	**<0.0001**	**0.0174**	M1 > TC1, TC2, BC2, BC3	BC3 >BC2	TC1 > TC2	BC2, BC3 > TC1, TC2
PC3	**0.0048**	**0.0119**	**<0.0001**	**0.0203**	TC1, TC2, BC2, BC3 > M1	BC3 >BC2	TC1 > TC2	BC2, BC3 > TC1, TC2

Table 9: Mean physicochemical variables measured at secondary channel sample sites and an adjacent location on the Bitterroot River. Mean values were compared across all paired sampling periods using Wilcoxon signed rank tests (Z-statistic). Bold *P*-values represent significant differences between secondary channel values and paired Bitterroot River values at the $P < 0.05$ level.

Secondary Channel Sample Sites

	Floodplain Tributaries				Braid Anabranches				Floodplain Channels			
Variable	Bitterroot River	BC2 (n=6)	Bitterroot River	BC3 (n=5)	Bitterroot River	M1 (n=6)	Bitterroot River	BC1 (n=4)	Bitterroot River	TC1 (n=6)	Bitterroot River	TC2 (n=6)
Water Temp. (°C)												
mean	11.19	11.02	10.59	10.36	10.32	10.27	5.75	5.81	10.13	10.63	9.05	9.22
SD	4.18	3.61	4.26	3.27	5.20	5.17	3.25	3.77	5.13	4.06	4.79	2.58
Range	4.7 - 15.9	5.3 - 15.1	4.8 - 16.1	5.4 - 13.9	5 - 17.7	4.9 - 17.6	1.8 - 10.2	1.9 - 10.3	2.4-15.8	4.7-14.6	1.9-15.8	5.7-13.0
Z		-0.734		-0.405		-0.135		-0.730		-0.734		-0.507
P		0.463		0.686		0.893		0.465		0.463		0.612
Oxygen Conc. (mg/L)												
mean	8.08	7.12	8.59	8.08	8.91	8.92	9.95	10.38	8.70	6.74	9.39	6.0
SD	1.61	1.52	1.16	1.52	1.79	1.73	0.84	1.64	2.79	2.39	2.51	1.81
Range	5.5 - 10.2	5.2 - 8.9	7.3 - 10.4	6.9 - 10.4	8.1 - 12.2	7.2 - 12	8.8 - 10.8	8.72 - 12.9	4.7-12.4	4.3-9.4	7.1-13.7	4.5 - 9.5
Z		-2.201		-2.023		-0.674		-0.365		-2.201		-2.366
P		**0.028**		**0.043**		0.500		0.715		**0.028**		**0.018**
Specific Cond. (mS/cm)												
mean	86.23	163.51	76.40	232.42	98.35	102.04	58.23	58.32	64.45	58.79	63.99	55.44
SD	35.13	65.69	34.37	29.50	27.5	26.27	19.36	19.21	19.95	14.88	19.39	12.91
Range	28.5-139.1	30.9-205.1	33.8-121.6	188.2-239.3	52.2-134.6	60.13-138.5	26.7-78.5	27.0-78.6	9.7-12.4	31.0-73.5	30.7-87.7	32.4-75.6
Z		-2.201		-2.023		-2.201		-0.730		-1.572		-1.859
P		**0.028**		**0.043**		**0.028**		0.465		0.116		0.063

Table 10: Mean physicochemical variables measured at paired secondary channel sample sites. Mean values were compared across all paired periods using Wilcoxon signed rank tests (Z-statistic). Bold *P*-values represent significant differences between compared values at the $P < 0.05$ level.

	Secondary Channel Sample Sites					
Variable	BC2 (n=5)	BC3 (n=5)	BC1(n=4)	M1 (n=4)	TC1 (n=6)	TC2 (n=6)
Water Temperature (°C)						
Mean	11.343	11.075	7.698	9.156	11.442	9.813
SD	4.002	3.405	5.335	4.793	5.307	2.250
Range	5.3 – 16.1	5.4 – 14.7	1.9 – 15.3	4.9 – 16.4	4.7 – 19.5	6.7 – 13.0
Z		-0.524		-1.782		-0.943
P		0.600		0.075		0.345
Oxygen Saturation (%)						
Mean	64.765	72.583	75.956	77.006	63.317	52.657
SD	11.893	10.948	5.668	12.068	15.070	16.531
Range	52.3 – 75.6	58.7 – 84.6	66.0 – 79.9	64.5 – 94.9	44.0 – 80.7	40.1 – 82.7
Z		-2.201		-0.314		-1.782
P		**0.028**		0.753		0.075
Oxygen Conc. (mg/L)						
Mean	7.120	8.002	9.628	8.992	7.053	5.970
SD	1.512	1.370	2.352	2.069	2.109	1.981
Range	5.2 – 8.9	6.9 – 10.4	6.6 – 12.9	6.3 – 12.0	4.6 – 9.3	4.4 – 9.5
Z		-1.992		-1.363		-1.572
P		**0.046**		0.173		0.116
Specific Cond. (mS/cm)						
Mean	160.202	230.798	64.922	98.280	57.478	52.085
SD	64.934	26.683	24.233	26.712	13.617	10.264
Range	30.9 – 205	188.2 – 260.1	27.0 – 91.4	60.1 – 133.6	31.0 – 66.2	32.4 – 60.3
Z		-2.201		-2.201		-1.572
P		**0.028**		**0.028**		0.116

Chapter 3

Bitterroot River Secondary Channel Fish Community Diversity, Behavior, and Microhabitat Use

Introduction

Resource partitioning by stream fishes has long garnered interest among aquatic ecologists. Schoener (1974) is often credited as the first to review species habitat requirements described in the terrestrial literature. A groundswell of studies in the last twenty years has investigated the importance of habitat use in aquatic systems. For many species, these investigations are essential to understanding the studied organism's life history and microhabitat needs. With increasing human development and related alteration of aquatic systems, researchers are now called upon to describe microhabitat use to conserve aquatic habitats that may be critical for maintaining ecologically important or threatened fish populations (Moyle and Baltz 1985; Baltz et al. 1987; Lobb and Orth 1991; Sabo and Orth 1994; Gido and Propst 1999).

Secondary channels provide diverse microhabitats near the mainstem river channel that are often used by fishes to avoid environmental extremes (Kwak 1988; Gido et al. 1997; Allouche et al. 1999). Additionally, these sites may be critical nursery areas for young-of-year (yoy) and juvenile fish requiring a range of shallow, low velocity habitats with protective cover (Sedell et al. 1990; Cavallo 1997; Gido et al. 1997; Gadomski and Barfoot 1998). Understanding the distribution of native and nonnative fish species using secondary channel microhabitats provides insight to microhabitat partitioning, microhabitat use overlap, and competition among species and age classes (species-age classes).

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The goal of a microhabitat requirement study is to better understand a species' niche, or the fine-scale resources that a species selects or avoids at a point in time (See Baltz 1990). The frequency of a species-age class in space suggests a preference for the particular variables characterizing that microhabitat. Since individuals belonging to a species-age class are likely to require similar environmental conditions for growth and reproduction, they will likely select similar microhabitats. To unravel the complex ecology of fish microhabitat use, experiments are carried out both in the field and in the laboratory. Field observations provide a glimpse of fish behavior in their natural surroundings while laboratory experiments allow the researcher to control the organism's environment (Baltz 1990). Water temperature (Baltz et al. 1982; Bonneau and Scarnecchia 1996), water velocity (Moyle and Baltz 1985), food supply (Greenberg 1991), competitive interactions (Dunham et al. 1999), and available microhabitat characteristics (i.e. depth and cover) (Baltz and Moyle 1984; Grossman and de Sostoa 1994) affect microhabitat selection. Although controllable in laboratory experiments, these variables are generally beyond the field researcher's manipulation. Combining field observations and laboratory research leads to a better understanding of organism behavior and resource requirements.

The distribution of fish within and among microhabitats is often related to an individual's life history stage (Baltz and Moyle 1984; Näslund et al. 1998; Snodgrass and Meffe 1999). Young-of-year and juvenile age classes generally require habitats with low velocity refuges, high productivity, and ample cover. Optimal nursery sites are diverse environments that provide a range of microhabitats beneficial to young fish as their requirements for food and protection change (Sabo and Orth 1994). As fish grow, their swimming ability improves, potential prey sizes increase, and their vulnerability to predation decreases. Considering these ontogenetic shifts in resource requirements, adult fish generally use a different suite of habitats and microhabitats compared to juveniles. For adult fish, deep pools and complex cover provide refuge from terrestrial predators as well as environmental extremes. Depending on the individual's developmental stage and available habitat, microhabitat selection by species-age classes may vary considerably across aquatic environments.

Microhabitat use and behavior may also vary by time of day. Day-night (diel) movements within and among microhabitats provide insights regarding fish resource needs. During the day, juvenile fish often prefer dense cover to avoid piscivores (Lima 1998). Juveniles may then move into shallower water at night when fewer avian and terrestrial predators are active but aquatic predators continue to feed. Such movements may reflect species-age class site selection for predator avoidance, foraging, competitive release, or thermal preference to optimize growth.

Organism behavioral observations often overlap with microhabitat preference studies since microhabitat selection can be a reflection of behavioral requirements (Fausch and White 1981; Noakes and Baylis 1990). For example, stream salmonids maintain different feeding and resting locations. Feeding positions are characterized by low velocity water adjacent to faster currents. Fish maximize energy consumption by making active forays into the current to capture invertebrate drift and then return to lower velocity locations to minimize metabolic energy expenditure (Fausch and White 1981). Resting positions may be associated with stable overhead structure that provides protective cover from predators.

The purpose of the following section is to describe composition and microhabitat use of fish communities inhabiting Bitterroot River secondary channels. The following questions will be addressed: 1) Which fish species-age classes use the selected secondary channels? 2) Do species-age classes exhibit substantially different microhabitat preferences? 3) How does diel behavior vary among species-age classes?

Methods and Materials

Study Site

The Bitterroot River in western Montana flows north from the confluence of the East and West Forks near Conner, Montana, to its confluence with the Clark Fork River, 8 km west of Missoula, Montana. Flowing approximately 134 km, the Bitterroot River drains a 7,288 km^2 (at Missoula USGS gauge) watershed, supporting agricultural land, pasture, rural and urban development, and upland forest systems. Tributaries originating in the Sapphire Mountains to the east, and the Bitterroot Mountains to the west, contribute much of the runoff that feeds the Bitterroot River.

The central Bitterroot River extends from Hamilton to Stevensville. An expansive alluvial floodplain created by a network of abandoned and active river channels typifies this section of the river. Braided channel reaches and sections of anastomosis reflect the transitory relationship between river discharge and sediment transport in the central Bitterroot River. The resulting floodplain mosaic provides a diversity of secondary channel habitats that vary by hydrology, channel morphology, water temperature regime, and mainstem influence. Floodplain channels are sites of groundwater surfacing during periods of low water and are conduits for high flows during spring runoff. A mobile bedload and rapid hydrographic fluctuations during spring runoff contribute to the instability that characterizes the central Bitterroot River.

Single-channel reaches and occasional areas of anastomosis mark the channel pattern of the lower valley that extends from Stevensville to Missoula. As the Bitterroot River nears its confluence with the Clark Fork River, the channel assumes a meandering single channel pattern, confined by the narrowing of the lower Bitterroot Valley and extensive channel stabilization projects. Through this reach the river follows a more predictable course (See Chapter 2 for a complete site description).

Sample Site Selection Criteria

The central and lower sections of the Bitterroot River are characterized by single and multiple channel reaches. Typical of an anastomosing river, the central Bitterroot is a network of braided channels creating a diversity of aquatic habitats. Secondary channels formed both historically and recently by the meandering of the Bitterroot River, vary in morphology and seasonal flow pattern. This variability is created during high water periods when the primary Bitterroot River captures off-channel floodplain habitats. Fluvial processes shape channel geometry by scouring and depositing sediment and organic material relative to the channel. Although created during the brief high water period, the affected floodplain channels reflect these geomorphic changes until the next runoff period.

Numerous secondary channels in the central Bitterroot Valley permitted the selection of sample secondary channel reaches based on four specific criteria. The first criterion, location, required that sites be distributed over a reasonably large area in order to sample a variety of habitats and species, but over an area small enough to permit sampling all sites within seven days. Hypothetically, the most downstream site would host more fish species than the most upstream site based on the species-area theory (Sheldon 1968; Gorman and Karr 1978; Horwitz 1978; Angermeier and Schlosser 1989). Additionally, the most downstream site is geographically closest to the Clark Fork River, a source of native and introduced fish species to the Bitterroot River fish assemblage. These geographic stipulations resulted in the establishment of the designated study area between Tucker Crossing and Missoula.

Second, in order to investigate whether geomorphically different secondary channel types elicit dissimilar biological responses with respect to resident fish populations, the study area needed to include several distinct secondary channel types. Gaeuman's (1997) classification of Bitterroot River secondary channels relied on geomorphic channel characteristics (See Chapter 2). Though concerned with how form and processes influence the evolution and persistence of channel stability, Gaeuman's classification did not consider a biological component. By grouping secondary channels as braid anabranches, floodplain channels and floodplain tributaries, fish sampling results may provide insights regarding the distribution of species and age classes using these different types of secondary channels.

Third, each site had to be highly connected to the Bitterroot River so fish could access secondary channels throughout the year. In order to investigate fish use of secondary channel habitats, a sample reach was defined as the first 70 m-100 m section of a secondary channel from the secondary channel's confluence with the Bitterroot River to an upstream geomorphic feature.

Fourth, each site had to be at least 0.3 m deep and wadable throughout the year to provide adequate fish habitat and survey accessibility. Following these four criteria, six secondary channel sample sites selected between Tucker Crossing and Missoula by August 1998 (Figure 1).

Selected Sample Sites

See Chapter 2 for complete sample site descriptions.

Sampling Design and Methods

Snorkeling Surveys

Snorkeling surveys were conducted to investigate fish species-age classes using Bitterroot River secondary channels (Table 1). Snorkeling is less costly and more accurate than other methods of sampling fish when fish are not disturbed prior to observation (Baltz 1990; Nielsen 1998; Mullner et al. 1999). Snorkeling is also more effective than backpack electrofishing when the habitat contains deep water. Sample secondary channel reaches were snorkeled seven times between July 1998 and September 1999. Sampling effort was concentrated from July through September when conditions were most conducive to sampling (low water, high clarity). Sites were also snorkeled during winter and prior to spring runoff to investigate seasonal fish habitat use. Most sample reaches were snorkeled at least once during each of the sampling periods. Day and night snorkeling were conducted to investigate diel microhabitat use and fish behavior. Day surveys were completed at least two hours before sunset while night surveys commenced at least one hour after the onset of darkness. A Princeton Tec dive light and headlamp were used for night snorkeling surveys.

For each survey, the snorkeler investigated all habitats within the sample reach. To ensure a consistent level of effort among sampling dates and sites, snorkeling routes were established for each sample reach. Although snorkeling effort varied by diel period, sample period, and sample reach, snorkeling effort usually lasted 45 to 60 minutes. The number of fish encountered, water temperature, and water clarity affected sampling effort. Water clarity in the secondary channels was generally good (visibility > 3 m), though clarity varied by sample period and among sites.

The snorkeler moved in an upstream direction to minimize fish disturbance (Baltz 1990). The locations of encountered fish were marked with a flagged and numbered steel washer. The location of fish found in close proximity to one another (< 0.5 m) and using the same microhabitat features were marked with a single washer. For each washer the following variables were recorded with a grease pencil on a PVC tablet worn on the snorkeler's left arm; ring number, fish species, number of individuals, size of individuals, and the individual's activity. The PVC tablet was organized with a ruler at the bottom, a list of the common species' abbreviations in a row across the top, and five total length size classes listed down the tablet's side. The length of observed fish was estimated relative to the ruled PVC tablet. Size classes included 50-74 mm, 75-99 mm, 100-149 mm, 150-199 mm, and 200+ mm. Fish smaller than 50 mm were not recorded due to their great abundance and the difficulty in identifying age-0 individuals of some species. A vertical or horizontal line drawn adjacent to the ring number on the tablet denoted fish activity. Activity levels included feeding (line preceding the number), swimming (line following the number), resting (line below number), or holding (line above number). A resting fish was quiescent near the substrate or in the water column. A resting fish may also be feeding opportunistically by limiting their energy expenditure until a prey item is encountered. However, because identifying this feeding mechanism was beyond the scope of this study, an encountered fish that was resting was considered to be a fish exerting minimal energy. Holding fish were active but maintained a consistent position in the water column.

To minimize disturbance to the resident fish assemblage, microhabitat use for all surveys was mostly measured the following day. A 400 cm^2 area located around each ring was evaluated as the microhabitat used by the fish (Grossman and Freeman 1987). Variables including water depth, velocity at 60% total depth, substrate types, substrate cover, water column cover, and water temperature were measured in the 400 cm^2 area. Initially, water velocity was classified as "flowing" or "non-flowing". Non-flowing or minimal flow habitats such as depositional pools were registered with a "1". Habitats with greater flows typifying erosive glides and riffles were recorded as a "2". A Marsh-McBirney Model 2000 Flow-Mate portable flowmeter was later used to measure flow velocities. Similarly, an Atkins digital thermocouple thermometer was used to measure point temperatures for surveys conducted after December 1998.

Habitat Surveys

To compare microhabitat availability and microhabitat use, two sampling procedures were instituted. First, point sampling was used to obtain data from specific locations or where a few measurements were adequate to characterize a reach (temperature, specific conductance, and oxygen saturation). Secondly, point-transect sampling was used where conditions, such as depth, were expected to vary across a reach in a regular manner. Two measuring tapes were used to create a psuedo-lattice over the study area for the point-transect sampling. A 100 m tape was extended from each site's downstream to upstream extent. Eight to 12 transects were then regularly spaced perpendicular to the channel. Depth, substrate type, substrate cover, and water column cover were recorded every 1-2 m across the channel depending on channel width. Approximately 100 points were recorded for each secondary channel. Temperature was also recorded during the 1999 sampling. Depth was measured with a 1.5 m calibrated wading staff. The substrate was evaluated by picking up a single particle at each lattice point. The particle's secondary axis was used to group the particle according to one of six categories: silt (to touch), sand (<6mm), gravel (6<16 mm), pebble (17≤64 mm), cobble (65≤265 mm), boulder (>265 mm). Cover types included no cover, aquatic vegetation, bank, small woody debris (<1 m in length, <0.3 m in diameter), large woody debris (>1 m in length, >0.3 m in diameter), and boulder. Cover types were defined as either water column cover or substrate cover to account for material that may have provided cover high in the water column but not on the substrate, and vice versa. Water column cover exceeded at least 1/3 of the channel depth if it originated on the substrate. Other material, such as woody debris hanging into the water from the bank, was also considered a water column cover structure. Total coarse woody debris area and riffle surface area, were also estimated for each sample site.

A YSI Model 85 Handheld Dissolved Oxygen, Conductivity, Salinity and Temperature System was used to evaluate water parameters in the sample reaches and the adjacent Bitterroot River (YSI 1996). Instrument calibration and measurements were recorded before 0900 each sampling day to establish a consistent protocol and to minimize photosynthetic effects on oxygen saturation and oxygen concentration readings. Using this methodology, measurements were completed prior to direct sunlight reaching the sample site. Five to seven sets of measurements were recorded for each sample site to assess within-site environmental variation. An additional three to five sets of measurements were recorded in the main channel in order to compare secondary channel and main channel water chemistry. A complete measurement set required under 20 minutes to complete.

One Onset Hobotemp continuous temperature recorder was deployed in each of the sample secondary channels and in the Bitterroot River to investigate annual water temperature patterns. Hobos were attached with steel airplane cable at a depth of 20 cm to large woody debris in a minimally exposed area of the site to reduce direct sunlight effects on recorded temperatures. Equipment loss and equipment malfunction resulted in incomplete data collections for four sites and the main channel. Year long temperatures were recorded for TC2 and BC3.

Data Analysis

Fish Community Diversity

Species richness and the Shannon-Weaver diversity index (H') were used to compare fish richness and evenness among the secondary channels and channel groups (Figure 2) (Shannon and Weaver 1949). Species richness is a simple count of species in a reach while evenness measures the distribution of individuals among species. The Shannon-Weaver index gives less weight to rare species than to common ones, and is one of several indices that are useful for comparing biological communities (Ricklefs 1990; Kohler and Hubert 1993).

Since H is roughly proportional to the logarithm of the number of species in the sampled community, it will be expressed as e^H, which is proportional to the number of species in the sample (Ricklefs 1990). For example, when each sampled species is equally abundant (evenness), e^H will equal the number of species in the sample (Ricklefs 1990).

$$H = -\sum_{i=1}^{S} p_\mathrm{i} \ln p_\mathrm{i}$$

e^H is proportional to the number of species

Where: p_i is the frequency of a species i in a sample
S is the number of species in a sample
H is the Shannon information coefficient

Figure 2: The Shannon-Weaver Diversity Index measures species richness and evenness based on the frequency of individual species in a sample.

Microhabitat Use

An electivity index was used to evaluate microhabitat use by fish species-age classes inhabiting Bitterroot River secondary channels. The electivity index provides a measure of an organism's preference, avoidance, or indifference relative to an environmental variable such as microhabitat depth (Baltz 1990). Electivities are calculated by determining an organism's use of a resource relative to the resource's availability. Electivities for water depth, substrate type, water column cover, and substrate cover were calculated using Jacobs' (1974) formula as presented in Moyle and Baltz (1985) (Figure 3). Microhabitat use data from the summer sampling periods (August and September, 1998 and 1999) were utilized in the analysis to limit inter-season variability. To generate the microhabitat electivities, variables corresponding to "used" microhabitats were measured where a fish was located. The point sampling data comprised the range of "available" microhabitats that fish could occupy. All microhabitats measured in a space were assumed to be available to the organism.

Available microhabitats were averaged over the sites and summer sample periods for each individual species-age class. Thus, available microhabitats varied depending on where and when a fish species-age class was sampled. The nonparametric chi-square test was used to test for distributional differences among used and available microhabitat variables. Chi-square test use was limited by small sample sizes and by the low availability of some microhabitats in the sampled channels. Differences between used and available microhabitats were considered to be significant at the $P < 0.05$ level.

To identify environmental variables describing microhabitat use variation among fish species-age classes, stepwise discriminant function analysis was employed.

$$D = \frac{r - p}{(r + p) - 2rp}$$

Where: r is the proportion of the resource used by a species-age class
p is the proportion of the resource available in the environment
D is the electivity coefficient

Figure 3: The microhabitat electivity coefficient calculated to determine microhabitat preferential use by secondary channel fish species-age classes.

Descriptive discriminant function analysis seeks to exhibit differences among populations by means of linear combinations of the measured variables (Williams 1983; James and McCulloch 1990). This analysis has been used to classify fish use of secondary channel habitats (Gido and Propst 1999) and stream microhabitats (Baker and Ross 1981; Baltz et al. 1987). For this comparison, species were categorized into two age classes (age-0 and age-0+) to account for age-related shifts in microhabitat use. Leave-one-out classification was used to determine which of the measured environmental variables accounted for the greatest amount of variation among species-age class microhabitat use. Species-age classes with less than 1% (6 fish) of the total number of fish sampled were dropped from the analysis. Depth was $\log_{10}(x+1)$ transformed while substrate percentages were arcsine-square-root transformed to better meet the model's normality assumptions. The categorical variables, dominant substrate, water column cover, and substrate cover were converted to dummy variables for the model. Only variables that were significant ($P < 0.05$) were retained in the model. All statistics were calculated using Statistical Package for the Social Sciences (SPSS Inc., Version 8 for Windows, Chicago, IL, 1997, unpubl.).

Fish Behavior

Fish behavior was determined by observing encountered fish for a period of time while snorkeling. Fish were observed until they were disturbed by the snorkeler's presence or until the snorkeler was confident of the fish's behavior. Fish behavior was categorized as resting, holding, swimming, and feeding. "Resting" fish appeared to be inactive although this behavior may represent opportunistic feeding. A "resting" fish might be minimizing metabolic losses while using its sensory organ (lateral line) to detect prey items. Swimming and feeding fish displayed active movement. Behavior was evaluated for species-age classes that were commonly sampled. Species-age classes that were infrequently encountered were not evaluated since minimal information can be derived from small sample sizes. Histograms comparing the frequency of fish displaying the four evaluated behaviors were produced to compare species-age class behavioral differences qualitatively.

Results

Habitat Availability

The availability data for water depth, substrate, water chemistry, and cover types, indicate that a wide range of habitats were available in each secondary channel. Primary differences among channels include channel discharge, cover type and abundance, substrate distribution, and channel size (See Chapter 2). The braid anabranch and floodplain tributaries were characterized by moderate flows while the Tucker Crossing floodplain channels were lentic environments. TC1, TC2, and M1 contained similar amounts of CWD cover, whereas cover in the BC2 and BC3 channels was mainly aquatic vegetation and bank cover. BC1 had minimal cover in the study area. Substrata distribution varied by channel as well as within individual channels. Sand substrate was most common in TC2 and BC1. M1 and BC2 had a range of sediments while BC3 and TC1 had coarser substrates. The braid anabranch channels were the widest of the studied channel types. Mean total depths were similar for the channels though the distribution of depth categories varied. TC1 exhibited the deepest habitat (>1.5 m) over the sampling period while M1 and BC2 had similar average depths.

Within-channel habitat and microhabitat differences were also apparent. Water velocities were variable in four of the six sites. Surface water in TC1 and TC2 lacked measurable velocity. Conversely, BC1, BC2, and M1 had a range of water velocities associated with low gradient riffles, glides, and channel margin pools. BC3 was a nearly continuous riffle-glide with minimal pocket water associated with a midchannel island. Patchy distributions of stable CWD provided fixed cover while aquatic vegetation and small woody debris varied seasonally and provided more transient cover. Water chemistry differed among channels while water temperatures were similar among sites in a given period.

Fish Community Composition

Night snorkeling results were used to compare species composition for each channel and period since more fish were generally observed during night surveys than during day surveys (Table 2). Fish community composition varied both by channel and channel groups although trends in presence and abundance patterns were difficult to detect (Table 3). Species diversity was greatest in TC1 (e^H, range: 3.87, 3.30-4.22) and peaked during the September sampling periods (Table 4). Species diversity was greatest in the floodplain channel group and least in the floodplain tributaries, while braid anabranches exhibited intermediate species diversity, although none of these results were significantly different. Diversity was lowest during the winter sampling, perhaps due to reduced sampling effort or behavioral changes by fishes during winter.

Microhabitat Electivities

Depth, substrate, and cover use by the native and introduced fish species can be generalized as follows. (1) Species-age classes utilized a wide range of conditions depending on microhabitat availability and diel period. (2) YOY and juvenile fish occupied shallower, lower velocity microhabitats at night than did adult fish of the same species (Figure 4). (3) Adult salmonids preferentially selected deeper microhabitats (relative to available depths) usually associated with woody debris or overhanging bank cover. (4) Adult salmonids occurred in a range of water velocities depending on activity level and available microhabitat. (5) Interspecific overlap in microhabitat use was common, though intraspecific microhabitat use differences were apparent among age classes.

Diel microhabitat use differed for some species-age classes sampled in the secondary channels. Adult salmonids observed during both day and night snorkeling selected similar microhabitat depths. Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) strongly selected bank and large woody debris cover (Figure 4a and Figure 4b). Brown trout and rainbow trout also used a range of substrates though gravel and cobble were strongly selected.

Mountain whitefish (*Prosopium williamsoni*), displayed distinct diel microhabitat use. During the day, YOY fish inhabited moderately deep microhabitats (40-90 cm) characterized by coarse substrates and minimal CWD cover (Figure 5a). At night, YOY fish were commonly observed in shallow riffles and riffle margins but rarely in deep sites (Figure 5b). At night, YOY fish did not select the measured cover categories although overhead broken water and substrate intersticies seemed to be adequate cover sources. Age-1+ mountain whitefish were found in deeper microhabitats (80-110 cm) with several substrate types. Similar to the YOY fish, older mountain whitefish selected LWD substrate cover during the day but did not select cover structure at night.

Redside shiner (*Richardsonius balteatus*), a small cyprinid species found in lentic habitats, selected shallow microhabitats associated with a range of substrates and cover structure. Diurnally, redside shiner predominantly selected sand and pebble substrates near aquatic vegetation, banks, and CWD (Figure 6a). At night, fish occupied silt substrate sites with CWD (Figure 6b). Fewer fish used dense cover at night compared to day locations.

The second cyprinid inhabiting the Bitterroot was the northern pikeminnow (*Ptychocheilus oregonensis*). YOY fish were not recorded due to their small size although they were extremely abundant in the TC1 and M1 channels. On some day dives, northern pikeminnow used complex CWD in TC1 but was also found midchannel and away from cover on other day dives (Figure 7a). This species preferred finer substrates especially at night when age-1 (juvenile) fish inhabited silt-bottomed shallow channel margins (Figure 7b). Juvenile and adult fish varied cover use during the sampling periods. At night adults of this species inhabited the middle portion of the water column in moderately deep pools while detectable YOY and juvenile fish preferred channel margins with woody debris cover.

Two catostomids comprised the last two commonly encountered species. Longnose suckers (*Catostomus catostomus*) and largescale suckers (*C. macrocheilus)* were secretive during the day and inhabited dense woody debris aggregations. At night, YOY and juvenile suckers moved into shallow channel margins characterized by fine substrates and patchy woody debris (Figure 8). Alternatively, adult fish preferred deeper microhabitats primarily away from cover. Largescale suckers were seen most often in TC1, M1 and BC2. Longnose suckers are less populous than largescale suckers in the Bitterroot River and were not encountered as frequently during snorkeling (Figure 9). The few fish that were encountered appeared to select microhabitats similar to selected by largescale suckers.

Discriminant Analysis and Microhabitat Use

Stepwise discriminant function analysis indicated that four of the ten variables that were entered into the model significantly contributed toward discriminating microhabitat use among the eleven species-age classes (Table 5). The first two axes accounted for 76.4% of the variation in microhabitat use among the species-age classes. Depth and substrate cover presence/absence were most strongly associated with Axis I and Axis II, respectively. Adult microhabitat use was most strongly explained by the depth variable (Axis I) (Figure 10). YOY and juvenile fish separation was explained similarly by both axes. Using the leave-one-out classification, the model correctly predicted the proper species-age class 39% of the time. This result is comparable to other studies that successfully classified fish groups 23.4% (Gido and Propst 1999) and 62% (Baker and Ross 1981) of the time, respectively.

Diel Fish Behavior

When observing fish in their natural environment it is often difficult to determine if they are behaving naturally or if their activity level reflects the presence of the snorkeler. Fish that were resting at night were easily approached. Other fish that swam in a small area or held position in the water column may have been reacting to the observer. Also, some fish such as mountain whitefish were at times attracted to the snorekeler's dive light during nocturnal dives. Efforts were made to limit influencing the observed fish's behavior though the snorkeler's presence likely affected some fish.

Diel behavioral differences varied by species and age classes (Figures 11-15). Nocturnal activity was limited for most species although adult mountain whitefish and rainbow trout frequently fed during both diurnal and nocturnal periods. During the day, YOY and juvenile fish often inhabited areas of thick cover and exhibited minimal activity. As stated previously, few largescale suckers were observed during the day because they inhabited complex cover. At night, most individuals were found "resting" either close to the substrate or in the lower third of the water column. Mountain whitefish YOY exhibited the greatest behavioral differences between nocturnal and diurnal periods with most fish feeding during the day and resting at night.

Discussion

Secondary Channel Habitat Use

The importance of secondary channels in floodplain rivers is increasingly apparent as ecologists investigate lateral channel habitat use by riverine fish communities

(Kwak 1998; Cavallo 1997; Gido and Propst 1999). Extensive studies in both the temperate and tropical regions (Welcomme 1979; Allouche and Teugels 1998; Merigoux et al. 1999) have elucidated the use of lateral floodplain channels as spawning sites, nursery habitats, and high water refugia for fish inhabiting the primary river channel. In highly connected river-floodplain systems, species exchange between the primary channel and off-channel habitats may occur at multiple temporal scales (Gido and Propst 1999).

At the diel level, fish move from the mainstem into secondary channels to exploit feeding sites or to occupy low velocity resting locations. Seasonally, fish may utilize these secondary channels to minimize exposure to suboptimal mainstem conditions. Periods of elevated runoff (Gido and Propst 1999) or unfavorable water temperatures may promote migrations into secondary channels until mainstem conditions improve.

Secondary channels may also be critical for fish to complete their life histories. In central Bitterroot River secondary channels, fish communities observed during snorkeling surveys were often represented by abundant populations of YOY fish, but relatively few adult fish. This differentiation was most pronounced with native species. However, for introduced brown trout and rainbow trout, adults were frequently encountered although YOY fish were rarely seen during snorkeling. Aside from mountain whitefish, YOY salmonids were rarely found in highly connected secondary channel reaches; however, YOY brook trout (*Salvelinus fontinalis)* and brown trout were sampled in upstream reaches of four secondary channels, especially TC2 (See Chapter 4). The absence of complex CWD in the TC2 snorkeling reach may have limited the downstream range of YOY fish particularly when large piscivorous adult brown trout and brook trout were present.

The distribution of native species-age classes suggests that highly connected secondary channels are used as nursery habitats by YOY fish while older fish emigrate from these sites into other habitats while the secondary channels and the Bitterroot River are connected. Snodgrass and Meffe (1999) observed a similar absence of adult fish in relation to abundant YOY fish in blackwater stream fish assemblages utilizing beaver ponds. In the Colorado River basin, YOY Colorado pikeminnow used shallow ephemeral backwaters as nursery habitats after being transported from emergence areas while adults selected alternative habitats (Tyus and McAda 1984). Similarly, Gido et al. (1997) found that adults of abundant San Juan River fish species utilized mainstem habitats for spawning, while juvenile and subadult fish mainly occupied secondary channel habitats. The authors further speculated that secondary channel fish communities are influenced by fish movement between secondary channels and the primary channel (Gido et al. 1997).

Spawning also occurs in secondary channels. Fall movement of brown trout is pronounced in the BC2 and BC3 channels (J. Johnston, *personal communication*) as fish leave the Bitterroot and migrate to upstream floodplain tributary springs. One spawning redd was seen in TC2. Abundant age-0 brook trout downstream of the spawning redd the following spring suggested that the redd was produced by brook trout.

Secondary Channel Fish Communities

Complex interactions among fish community members complicate the understanding of individual species-age class microhabitat preferences and behavior. Native fish assemblages of the Northern Rocky Mountain region, less species diverse than assemblages inhabiting rivers east of the Continental Divide, usually contain morphologically diverse species. Native trout (*Salmo*, *Salvelinus*, or *Oncorhynchus*), sucker (*Catostomus*), sculpin (*Cottus*), and dace (*Rhinichthys*) often constitute assemblages inhabiting North American coldwater streams (Moyle and Vondracek 1985). In the Bitterroot River, three additional cyprinids complete the native fish community. In addition to the native assemblage, introduced brown trout, brook trout, and rainbow trout successfully inhabit a range of environments in both the mainstem and floodplain channels and have likely displaced westslope cutthroat trout (*O. clarki lewisi*) from some habitats (See Chapter 4). Other introduced fishes, including yellow perch (*Perca flavascens*), northern pike (*Esox lucius*), pumpkinseed (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), and black bullhead (*Ictaluras melas*) inhabit less-connected Bitterroot River floodplain aquatic habitats (Jones 1990), although these species were infrequently encountered in highly connected secondary channels that I sampled.

Secondary channel fish communities are a reflection of fish movement between lateral channel and mainstem habitats as well as the habitat quality of the secondary channel. If the mainstem contains more preferred habitat and plentiful food resources than a secondary channel, then a fish would be expected to remain in the mainstem and not inhabit secondary channels. Conversely, if secondary channels provided more optimal conditions than the mainstem, fish may be expected to occupy the secondary channels as opposed to the mainstem. Since each sampled reach appeared to be similarly connected to the Bitterroot River, secondary fish community variation was more likely influenced by secondary channel environmental conditions than channel accessibility. Mainstem habitat characteristics in the vicinity of particular secondary channels and perhaps the composition of the local fish assemblage would also influence the fish community occupying a specific secondary channel. These presumptions are supported by differences between paired secondary channels that were geographically close to each other and similarly connected to the Bitterroot River, but were environmentally dissimilar. For example, deeper pools and complex CWD aggregations differentiated TC1 from the more simplified TC2 channel. TC2 was primarily a sand channel with intermittent aquatic vegetation cover. Patchy woody debris provided cover for resident salmonids but a uniform channel and lack of complex rootwads may have influenced the infrequent presence of YOY and small species. In comparison, TC1 maintained the highest community diversity of the six channels.

Similar to the TC1 and TC2 channel comparison, BC2 and BC3 exhibited a similar dichotomy. BC2 had a variety of habitats dominated by an expansive riffle/glide as well as a ~400 m^2 lentic area. BC2 maintained a diverse community represented by numerous species and age classes. In comparison, the BC3 channel was a uniform glide with minimal pocket water and overhead cover. The BC3 fish community mainly contained rainbow trout and mountain whitefish, species that tend to prefer lotic environments. Infrequent brown trout and redside shiner occupied the few slow water patches.

Identifiable trends in fish community variation over the year were not obvious. However, the sample period's brevity may have precluded detecting community-level changes and/or trends. Less species diverse communities and low population abundance suggest that microhabitat availability may limit species inclusion in some secondary channel communities. Less diverse communities were consistently sampled in the less-habitat diverse TC2 and BC3 compared to other more-habitat diverse secondary channels such as TC1 and M1.

Diel Microhabitat Use and Microhabitat Electivity

Microhabitat use is a reflection of resource availability, resource requirements, competitive interactions, and predator avoidance by individual fish. Because microhabitat variables are often highly correlated, unraveling specific microhabitat variable preferences for a species-age class is difficult in field observations. As an example, in Bitterroot River secondary channels, silt substrates were mainly associated with shallow, low velocity microhabitats. Likewise, microhabitats associated with riffles and glides had faster water velocities and less cover than complex pools. Determining a single critical variable explaining fish microhabitat use is a difficult proposition. The patchy distribution of fish within the channel matrix is a response to multiple variables rather than a single variable.

In addition to the abiotic environmental variables that makeup microhabitat variation, predator presence and abundance and other biotic variables also influence the distribution of species-age classes (Schlosser 1987). Predator effects influence day-night differences in microhabitat use among species-age classes. Power et al. (1989) proposed that small species and juvenile age classes of larger species are limited from using deep water by aquatic piscivores while adults of large species avoid shallow water to avoid terrestrial and avian predators. This phenomenon was expressed by fish assemblages occupying Bitterroot River secondary channels. Day-night shifts in microhabitat use were apparent for smaller fishes. YOY and juvenile fish used dense cover during the day and were rarely observed away from such structure. At night these fish were distributed in shallow channel margins and were distant from cover structure. The fish community inhabiting TC1 regularly displayed this behavior. In TC1, large brown trout inhabited deeper pools during both day and night snorkeling, while juvenile cyprinids and catostomids (potential prey) clustered within rootwad interstices during the day but primarily inhabited shallow channel margins at night. Brown and Moyle (1991) found that when Sacramento pikeminnow larger than 15 cm were present in a habitat, small fish were forced into pool margins. In the absence of these predators, small fish did not show strong selection for these microhabitats. Juvenile rainbow trout carried out day-night inshore-offshore migrations to maximize food acquisition (offshore) and minimize predation exposure (inshore) in Lake Tahoe (Tabor and Wurtsbaugh 1991). In the Bitterroot River, the threat of predation by large piscivores on smaller fish resulted in high interspecific microhabitat overlap among small individuals, but reduced intraspecific interactions between large and small fish inhabiting secondary channels.

In Bitterroot River secondary channels, large fish selected similar microhabitats during the day and night. Adult brown trout and rainbow trout, were commonly encountered in the TC1 site. Brown trout and rainbow trout remained in deep water around complex CWD cover during both day and night snorkeling. When disturbed these fish moved to downstream pools with broken surface water. The frequency of large brown trout in low frequency, deep, and complex cover habitats may be typical of brown trout (Clapp et al. 1990; Young 1995). Brown trout in a southern Wyoming stream tended to occupy deep water close to overhead cover (Young 1995). As was the case in many of the Bitterroot River brown trout microhabitats, Young found that most brown trout microhabitats had minimal water velocity and were well sheltered under banks or other cover. Clapp et al. (1990) observed similar use of low velocity, deep habitats with overhanging cover by large (> 400 mm TL) brown trout.

Microhabitat use in secondary channels by fish at different developmental stages was also apparent. Largescale sucker and mountain whitefish used a range of channel depths depending on lifecycle stage. YOY mountain whitefish primarily inhabited riffles or riffle margins during both day and night snorkeling. At night, quiescent fish occupied dead water riffle margins while fish inhabiting riffles positioned themselves against the downstream side of substrate particles. This behavior minimized displacement by turbulent forces and allowed fish to avoid predators inhabiting deeper habitats. During the day, YOY mountain whitefish used slightly deeper habitats but were again primarily associated with shallow riffle habitats. This species-age class also strongly selected for CWD cover during the day whereas at night, fish were generally not associated with complex cover structure. Similar substrate-cover-seeking behavior has been observed in Atlantic salmon parr during winter when parr compressed against substrates in shallow riffles at night (Whalen and Parrish 1999). Shallow riffles in Bitterroot River secondary channels afford young mountain whitefish protection from predators and reduce interspecific competitive interactions with juveniles of other species.

Adult mountain whitefish selected deeper microhabitats than YOY fish especially during the day, and used a wider range of depths at night. Adults similarly preferred woody debris cover during the day and selected microhabitats lacking cover at night. Adult occupation of deeper day microhabitats suggests less risk of predation on larger mountain whitefish than YOY fish.

A similar dichotomy was observed for YOY and adult largescale sucker during night surveys. YOY fish inhabited shallow microhabitats far from large brown trout occupying deep channel areas. Adult fish selected deeper habitats proximate to large brown trout. The larger adult fish were at less risk of predation compared to the YOY fish. However, YOY and adult largescale sucker inhabited similar diurnal locations associated with complex woody structure along deeper channel margins. Diurnal terrestrial and avian predators may influence the location of largescale sucker to a greater extent than aquatic piscivores.

Day-Night Fish Behavioral Changes

Intraspecific behavior may be highly variable depending on a fish's environment. Predators, microhabitat availability, resource requirements, and life stage are a few of the conditions affecting fish behavior. For this study, fish were observed during snorkeling and their behaviors classified into one of four groups. Although some species-age classes behaved similarly during day and night periods, others displayed distinctly different behaviors between the two periods.

Fish microhabitat use and behavior are intertwined. An YOY fish resides in dense cover during the day to minimize the risk of predation and moves into shallow water at night to exploit more productive channel margins (feeding), reduce competitive interactions, and to rest. Largescale suckers perhaps best exemplified behavioral differences in diel microhabitats. During the day fish held position in complex CWD high in the water column. At night these fish moved into shallow habitats where they were quiescent. In Lake Tahoe, juvenile rainbow trout displayed a similar behavior in the shallow littoral zone of Lake Tahoe as they vacated complex cover and occupied open microhabitats (Tabor and Wurtsbaugh 1991). This behavior may be a response to low predator densities at night or an absence of nocturnal predators in a reach.

Conversely, adult brown trout exhibited similar day-night behavior and habitat selection. Large brown trout (>300 mm) inhabited the same territories over time and were rarely seen actively feeding. Although these fish did not actively pursue prey, they may have been selectively foraging. By resting, these fish minimize their energy expenditure and then may opportunistically feed on unwary prey that venture too close to the predator's position. This feeding technique increases the amount of energy devoted to growth compared to the energy spent on metabolism (Moyle and Cech 1988). Telemetry studies indicate brown trout behavior is highly variable. Studies have documented brown trout feeding at night (Clapp et al. 1990; McIntosh and Townsend 1995) while others indicate these fish are daytime predators. Bunnell et al. (1998) found brown trout movement varied seasonally and occurred at different times of the day depending on the season. Fish located in a particular location over several sampling visits may suggest an optimal feeding position.

Behavior differences between YOY fish of multiple species and adult brown trout suggest the importance of diurnal predation in Bitterroot River secondary channels. Young fish seek complex cover during the day when they are vulnerable to aquatic and terrestrial predators. These fish then occupy shallow margins at night when terrestrial predators are inactive and aquatic predators remain in deeper microhabitats. Because large brown trout (> 300 mm) were infrequently sampled in this study and the large fish that were observed rarely actively foraged, small fish may be able to minimize their exposure to predators by inhabiting microhabitats unfavorable to large piscivores. An absence of small fish in the vicinity of large brown trout and an abundance of small fish in areas not inhabited by large brown trout, suggest that small fish avoid inhabiting deeper sites occupied by large piscivores in favor of shallow microhabitats that rarely contained predators.

Fisheries Management Implications

The proliferation of nonnative salmonids and absence of native fish in Bitterroot River secondary channels should be a cause of concern for fisheries managers. Historically, westslope cutthroat trout and perhaps bull trout used these lateral channels both seasonally to avoid mainstem environmental extremes, and preferentially during portions of their life histories. Gido et al. (1997) concluded that native fish likely used secondary channels as foraging areas and as flow refugia during high flows while juvenile and subadult fish used the sites as nursery areas. Similar utilization would be expected in the Bitterroot River sites since the ecological niche once occupied by westslope cutthroat trout is now filled by rainbow trout, brown trout, and brook trout, depending on site location, channel habitat characteristics, a fish developmental stage. These competing introduced species are primarily insectivorous, require low water temperatures, and utilize microhabitats similar to the westslope cutthroat trout. Gido et al. (1997) described a similar competitive interaction among native and introduced fish species. Prior to introductions, native YOY fish were likely abundant in San Juan River secondary channels. The proliferation of introduced salmonids in the Bitterroot River is apparent in the seasonal domination of secondary channel fish communities by several nonnative species (See Chapter 4) and the absence of native salmonids. The ecological niches of the native species may now be restricted by the nonnative species' abundance.

Comparison of secondary channel fish communities with mainstem communities was not possible since data on non-salmonid gamefish species are not collected by Montana Fish, Wildlife and Parks. However, biannual population estimates for rainbow trout, westslope cutthroat trout, and brown trout are generated for selected reaches of the Bitterroot River (Clancy 1998). In the Bell Crossing reach (includes the BC1-BC3 area), rainbow trout constitute 50+% of the salmonid assemblage, brown trout comprise 40-50%, and westslope cutthroat trout account for <10% of the trout caught. Montana Fish, Wildlife and Parks' fish population estimates are limited to mainstem populations and do not incorporate non-salmonid species. Sampling salmonids and non-salmonids in off-channel habitats would provide fisheries managers with a broader picture of fish assemblages inhabiting the Bitterroot River and associated secondary channels.

Diverse fish communities using secondary channels suggest these sites are important habitats for multiple species at different developmental stages. Because tributaries to the Bitterroot River are affected by dewatering during the summer irrigation season, the importance of secondary channels as nursery habitats may be accentuated. Managing floodplain development will be essential to control the alteration of the Bitterroot River channel and floodplain. Large portions of the central Bitterroot River are already constrained by extensive bank stabilization projects that limit the lateral movement of the river channel and sites of channel avulsion. Restricting or eliminating these two fluvial processes will likely limit secondary channel formation and the subsequent creation of environments I have found to be used by diverse fish communities. Providing mainstem instream flows and managing floodplain alteration will protect diverse floodplain habitats necessary for maintaining buffer populations of native and nonnative fishes to the Bitterroot River.

Conclusions

- Question 1 Results: Numerous species-age classes used the sampled secondary channels. Greater fish community diversity was found in more complex channels and during the summer samplings.
- Question 2 Results: Species-age classes used different microhabitats
  - Fish used a range of microhabitats depending on microhabitat availability and diel period.
  - YOY and juvenile fish selected shallower microhabitats than did adults.
  - All fish tended to use deeper microhabitats during the day than at night.
  - Interspecific overlap was common, though intraspecific microhabitat use differences were apparent among age classes.
- Question 3 Results: Fish behavior varied between day and night periods.
  - Most species-age classes were more active during the day than at night.
  - YOY and juvenile fish selected complex cover structure (where available) during the day but were found in shallow, open water areas at night.
  - Adult rainbow trout and mountain whitefish actively foraged at night and during the day.
  - "Resting" fish may have been opportunistically feeding at night (especially large piscivorous brown trout).

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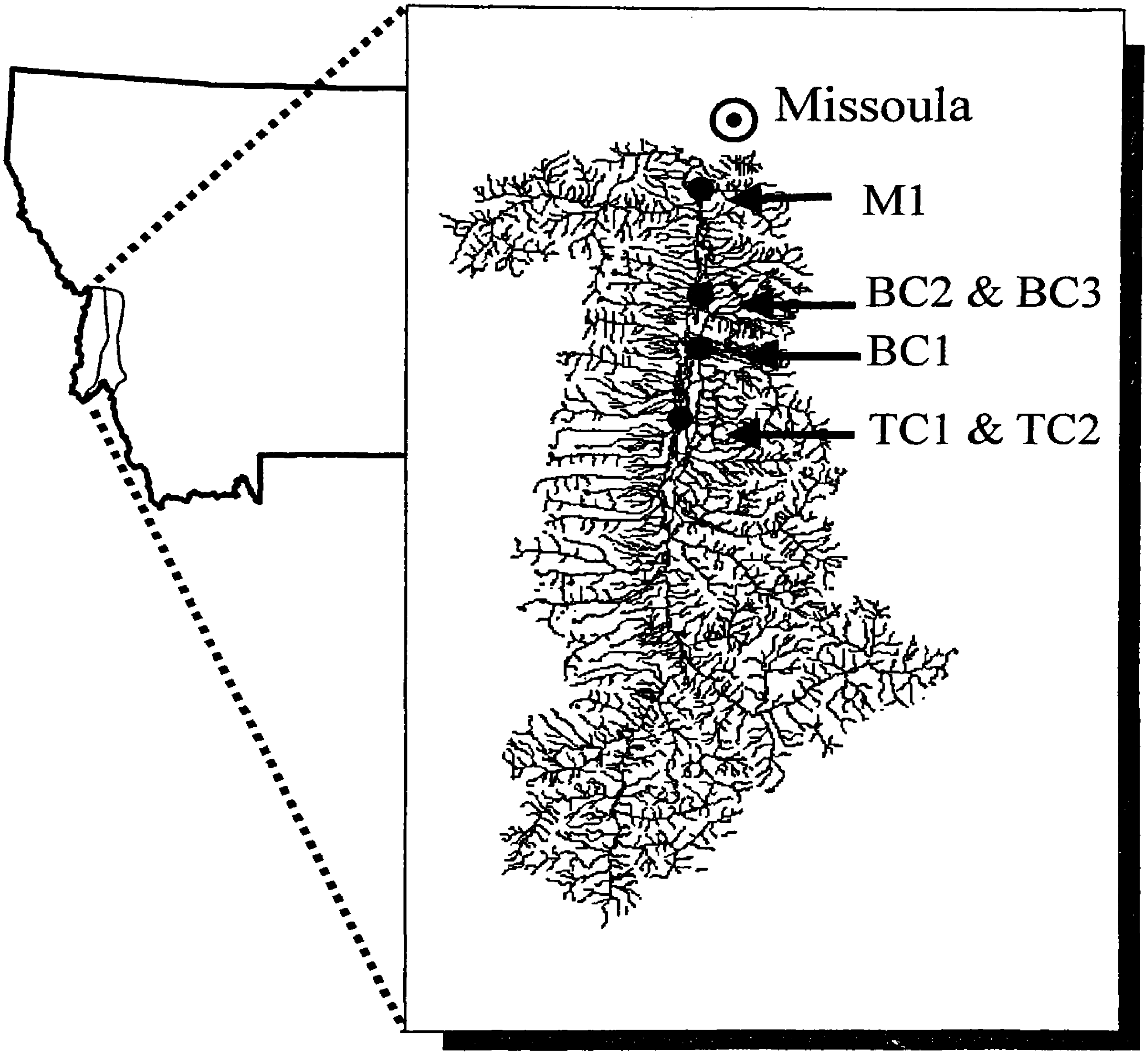


Figure 1: The Bitterroot River watershed and the secondary channel sample sites.

Table 1: Fish species that occur in the Bitterroot River drainage.

Fish Species	Common Name
Native Fish Species	
*Catostomus catostomus**	Longnose Sucker
*Catostomus macrocheilus**	Largescale Sucker
*Richardsonius balteatus**	Redside Shiner
*Rhinichthys cataractae**	Longnose Dace
*Ptychocheilus oregonensis**	Northern Pikeminnow
Mylocheilus caurinus	Peamouth
*Prosopium williamsoni**	Mountain Whitefish
Oncorhynchus clarki lewisi	Westslope Cutthroat Trout
Salvelinus confluentus	Bull Trout
*Cottus cognatus**	Slimy Sculpin
Introduced Fish Species	
*Salvelinus fontinalis**	Eastern Brook Trout
*Salmo trutta**	Brown Trout
*Oncorhynchus mykiss**	Rainbow Trout
*Micropterus salmoides**	Largemouth Bass
*Perca flavascens**	Yellow Perch
*Lepomis gibbosus**	Pumpkinseed
*Esox lucius**	Northern Pike
Ictalurus melas	Black Bullhead Catfish

*: Fish species that were sampled in central Bitterroot River secondary channels.

Table 2: Fish species inhabiting Bitterroot River secondary channels sampled during night snorkeling.

Secondary Channel	August 1998	September 1998	October 1998	December 1998	April 1999	August 1999	September 1999
TC1	Rainbow trout Brown trout Mountain whitefish	Rainbow trout Brown trout Mountain whitefish Redside shiner Largescale sucker Longnose sucker Northern pikeminnow	Brown trout Redside shiner Largescale sucker Longnose sucker Northern pikeminnow	Brown trout Mountain whitefish Redside shiner Largescale sucker Longnose sucker Northern pikeminnow		Rainbow trout Brown trout Mountain whitefish Redside shiner Largescale sucker Northern pikeminnow	Rainbow trout Brown trout Redside shiner Largescale sucker Longnose sucker Northern pikeminnow
TC2	Rainbow trout Brook trout Mountain whitefish Longnose sucker Northern pikeminnow	Rainbow trout Brook trout Brown trout Mountain whitefish	Rainbow trout Brook trout Brown trout Mountain whitefish			Rainbow trout Brown trout Brook trout	Rainbow trout Brown trout Mountain whitefish
BC1	Rainbow trout Brown trout Mountain whitefish Longnose sucker Redside shiner Northern pikeminnow	Rainbow trout Brown trout Mountain whitefish Largescale sucker Northern pikeminnow	Rainbow trout Brown trout Mountain whitefish Largescale sucker Longnose sucker Redside shiner Northern pikeminnow	Rainbow trout Mountain whitefish	Rainbow trout Brown trout Mountain whitefish Redside shiner Northern pikeminnow		
BC2	Brown trout Redside shner Longnose sucker Mountain whitefish	Brown trout Mountain whitefish	Rainbow trout Brown trout Mountain whitefish Largescale sucker Longnose sucker Redside shiner Northern pikeminnow		Mountain whitefish Longnose sucker	Mountain whitefish Largescale sucker Longnose sucker	Rainbow trout Brown trout Mountain whitefish Largescale sucker Redside shiner
BC3		Rainbow trout Brown trout Mountain whitefish Redside shiner	Rainbow trout Mountain whitefish			Rainbow trout Mountain whitefish Redside shiner	Rainbow trout Brown trout Mountain whitefish
M1	Redside shiner Largescale sucker Mountain whitefish Northern Pikeminnow	Rainbow trout Mountain whitefish Largemouth bass Redside shiner Largescale sucker Northern pikeminnow	Rainbow trout Mountain whitefish Northern pikeminnow Largescale sucker Redside shiner Yellow perch	Rainbow trout Mountain whitefish Yellow perch	Rainbow trout Brown trout Mountain whitefish Redside shiner	Rainbow trout Mountain whitefish Redside shiner Northern pikeminnow	Rainbow trout Mountain whitefish Redside shiner Northern pikeminnow

Table 3: Species richness and Shannon-Weaver diversity information for the Bitterroot River secondary channels and channel groups. Richness and Shannon-Weaver information were averaged for each secondary channel measured over the sampling periods.

	Richness	Range	Shannon	Range
TC1	5.80	(5 - 7)	3.87	(3.30 - 4.22)
TC2	3.40	(2 - 4)	2.43	(1.65 - 3.75)
BC1	5.00	(2 - 6)	2.63	(1.75 - 3.79)
BC2	3.80	(2 - 6)	2.82	(1.82 - 5.00)
BC3	3.33	(3 - 4)	2.38	(1.75 - 3.40)
M1	4.43	(3 - 6)	3.02	(1.37 - 4.83)
Floodplain Channels (TC1 & TC2)	4.60	(2 - 7)	3.07	(1.65 - 4.22)
Braid Anabranches (BC1 & M1)	4.70	(2 - 6)	2.85	(1.37 - 4.83)
Floodplain Tributaries (BC2 & BC3)	3.60	(2 - 6)	2.62	(1.75 - 5.00)

Table 4: Species richness and Shannon-Weaver diversity information for the sampling periods. Richness and Shannon-Weaver information were averaged over the secondary channels for each of the sampling periods.

	Richness	Range	Shannon	Range
August 1998	4.3	(4 - 5)	2.90	(1.95 - 3.75)
September 1998	5.4	(4 - 7)	3.82	(3.46 - 4.35)
October 1998	5.4	(4 - 6)	2.95	(1.81 - 4.83)
December 1998	3.8	(2 - 6)	2.08	(1.37 - 3.75)
April 1999	4.0	(2 - 6)	2.61	(1.82 - 3.79)
August 1999	3.4	(2 - 5)	2.36	(1.65 - 4.18)
September 1999	4	(2 - 6)	3.07	(2.20 - 3.97)

Table 5: Fish age classes used to categorize Bitterroot River fish sampled during snorkeling. a) Fish species are separated into two groups depending on the number of age classes that were discernable from snorkeling results. TL refers to fish total length that was measured from the tip of the fish's nose to the end of the tail. b) Species approximate average total lengths (mm) for Montana as suggested by Brown (1971).

a)

	Fish Age Class	
Fish Species	Age-0	Age-1+
O. mykiss	TL ≤ 100 mm	100 mm < TL
S. trutta	TL ≤ 100 mm	100 mm < TL
P. williamsoni	TL ≤ 100 mm	100 mm < TL
C. catostomus	TL ≤ 75 mm	75 mm < TL

		Fish Age Class	
Fish Species	Age-0	Age-1+	Age-2+
R. balteatus		50 mm	50 mm < TL
P. oregonensis	TL ≤ 75 mm	75 mm < TL ≤ 100 mm	100 mm < TL
C. macrocheilus	TL ≤ 75 mm	75 mm < TL ≤ 100 mm	100 mm < TL

b)

			Fish Age Class		
Fish Species	Age-0	Age-1	Age-2	Age-3	Age-4
P. williamsoni	101 mm	203 mm	279 mm	330 mm	355 mm
O. mykiss	76 mm	203 mm	279 mm	330 mm	406 mm
S. trutta	101 mm	203 mm	305 mm	355 mm	406 mm
S. fontinalis	76 mm	152 mm	203 mm	254 mm	304 mm
R. balteatus	20 mm	43 mm	69 mm	102 mm	
P. oregonensis	50 mm	89 mm	114 mm	152 mm	177 mm
C. macrocheilus	50 mm	89 mm	140 mm	190 mm	254 mm
C. catostomus	76 mm	140 mm	216 mm	266 mm	317 mm

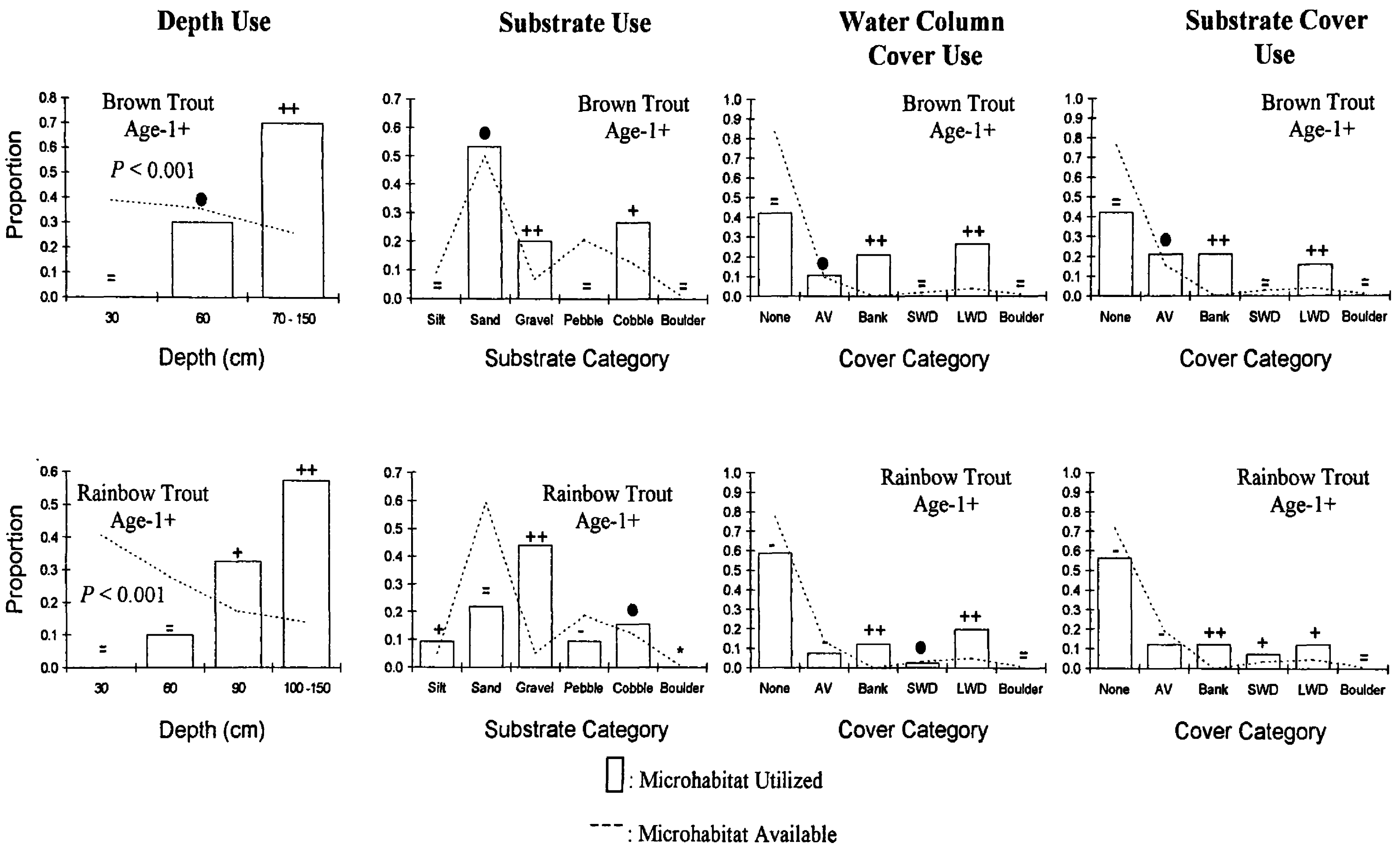


Figure 4a: Daytime microhabitat use by age-1+ (n = 20) brown trout and rainbow trout (n = 40) in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Due to small sample sizes, only microhabitat depth was tested using the chi-square test.

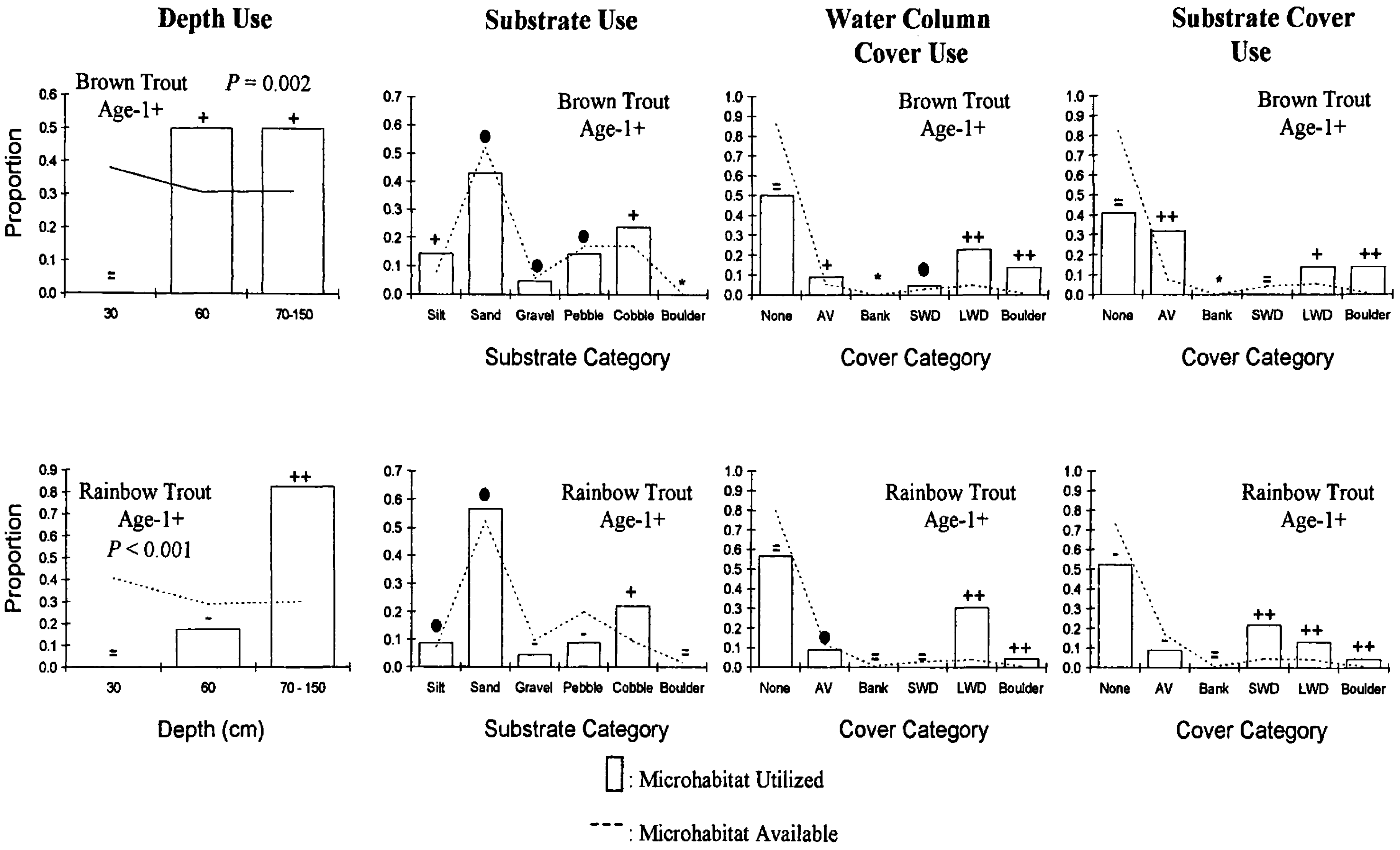


Figure 4b: Nighttime microhabitat use by age-1+ brown trout (n = 22) and rainbow trout (n = 23) in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Due to small sample sizes, only microhabitat depth was tested using the chi-square test.

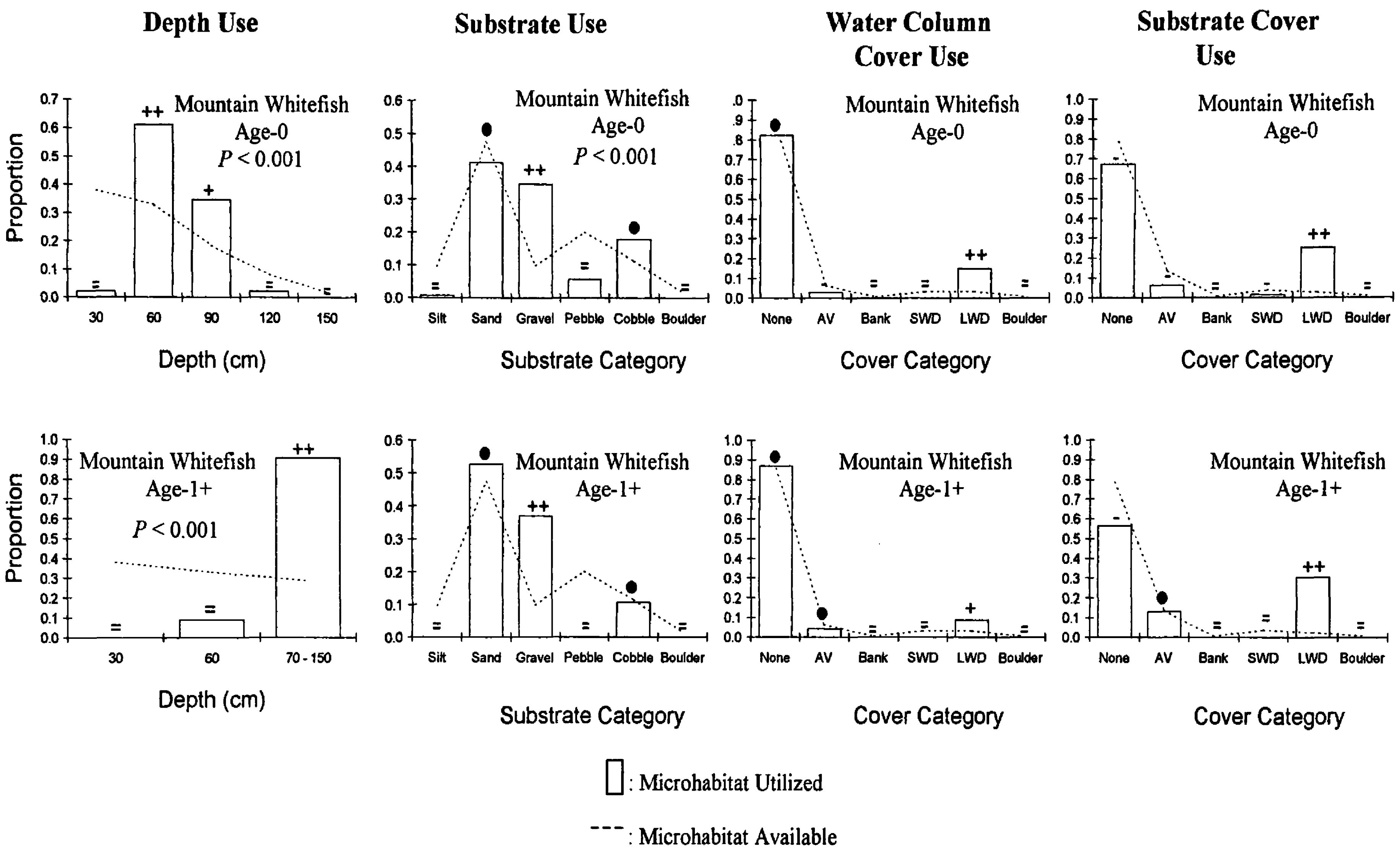


Figure 5a: Daytime microhabitat use by age-0 (n = 144) and age-1+ (n = 23) mountain whitefish in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ (0.50 ≤ *d*, strong preference), + (0.25 ≤ *d* < 0.5, moderate preference), • (-0.25 ≤ *d* < 0.25 no preference), - (-0.50 ≤ *d* < -0.25), and = (*d* < -0.50, strong avoidance) (Moyle and Baltz 1985). *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-0 water column cover use and substrate cover use were not tested due to low availability of multiple categories. Age-1+ mountain whitefish were not tested due to low sample size (except for depth use).

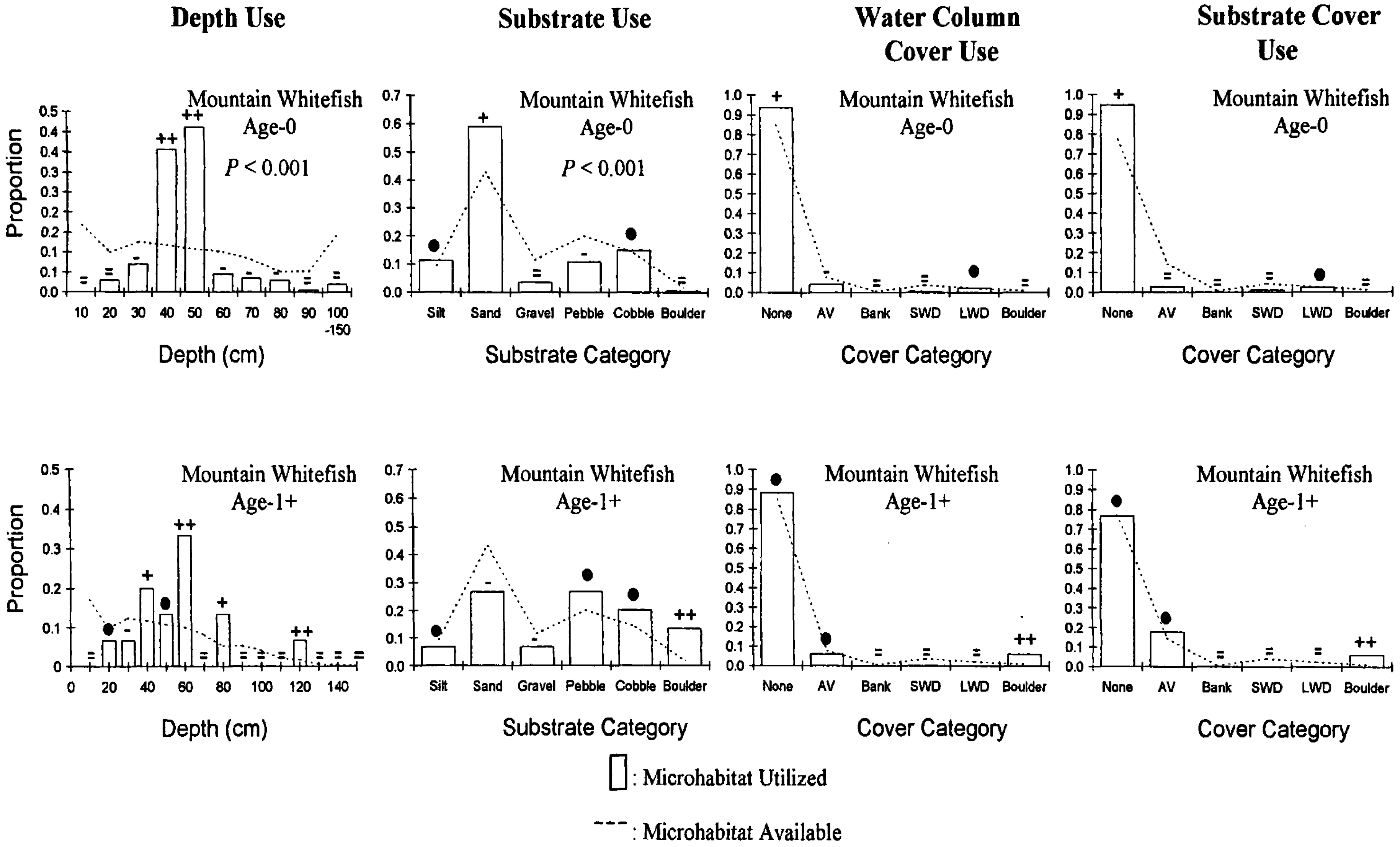


Figure 5b: Nighttime microhabitat use by age-0 (n = 202) and age-1+ (n = 15) mountain whitefish in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-0 water column cover use and substrate cover use were not tested due to low availability of multiple categories. Age-1+ mountain whitefish microhabitat use was not tested due to low sample size.

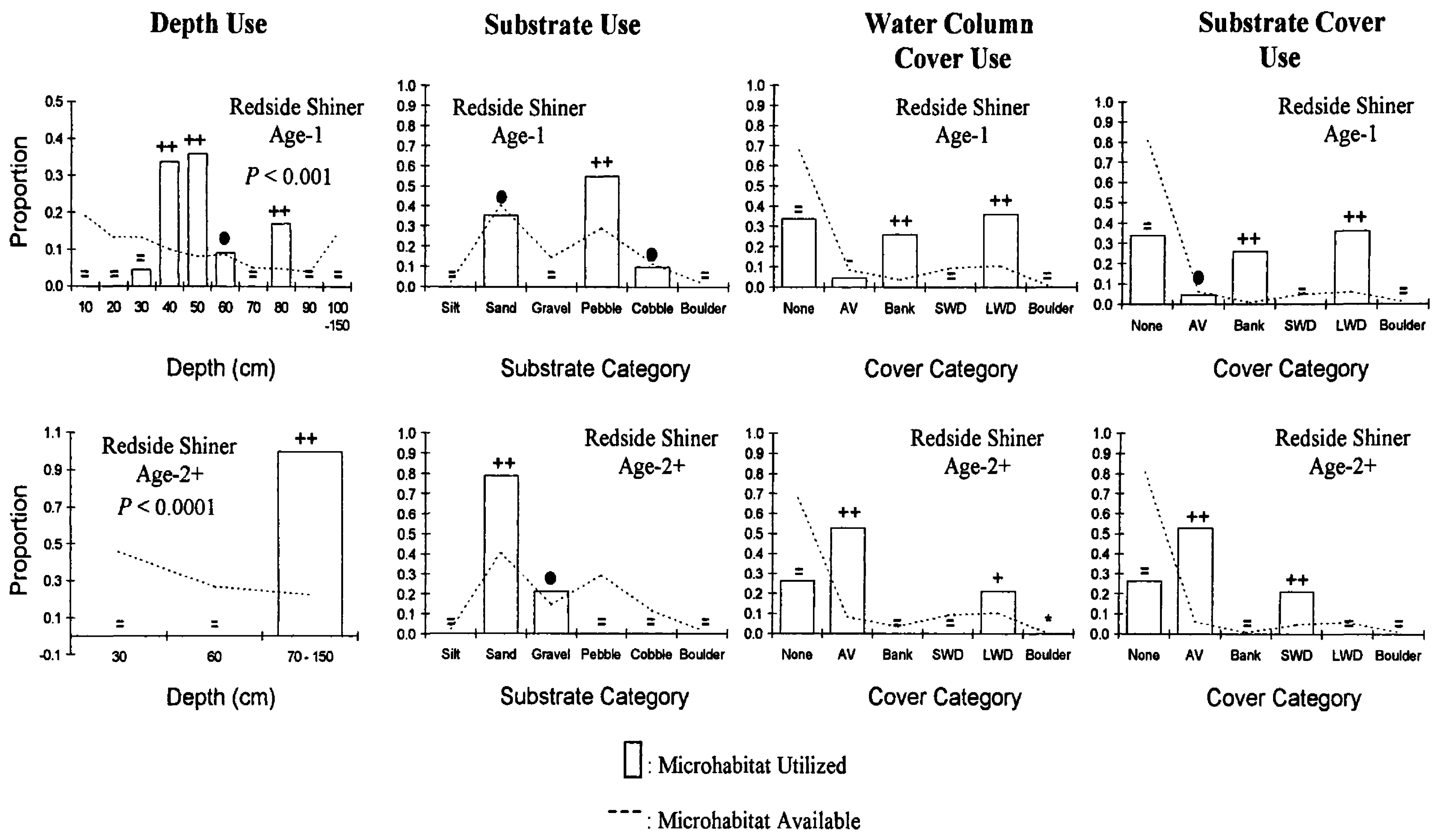


Figure 6a: Daytime microhabitat use by age-1 (n = 89) and age-2+ (n = 19) redside shiner in Bitterroot River secondary channels. Electivities (d) compare used and available microhabitats and are indicated by ++ ($0.50 \le d$, strong preference), + ($0.25 \le d < 0.5$, moderate preference), • ($-0.25 \le d < 0.25$ no preference), - ($-0.50 \le d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. P-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-1 substrate use, water column cover use, and substrate cover use were not tested due to low availability of multiple categories. Only age-2+ depth use was tested due to low sample sizes for the other microhabitat variables.

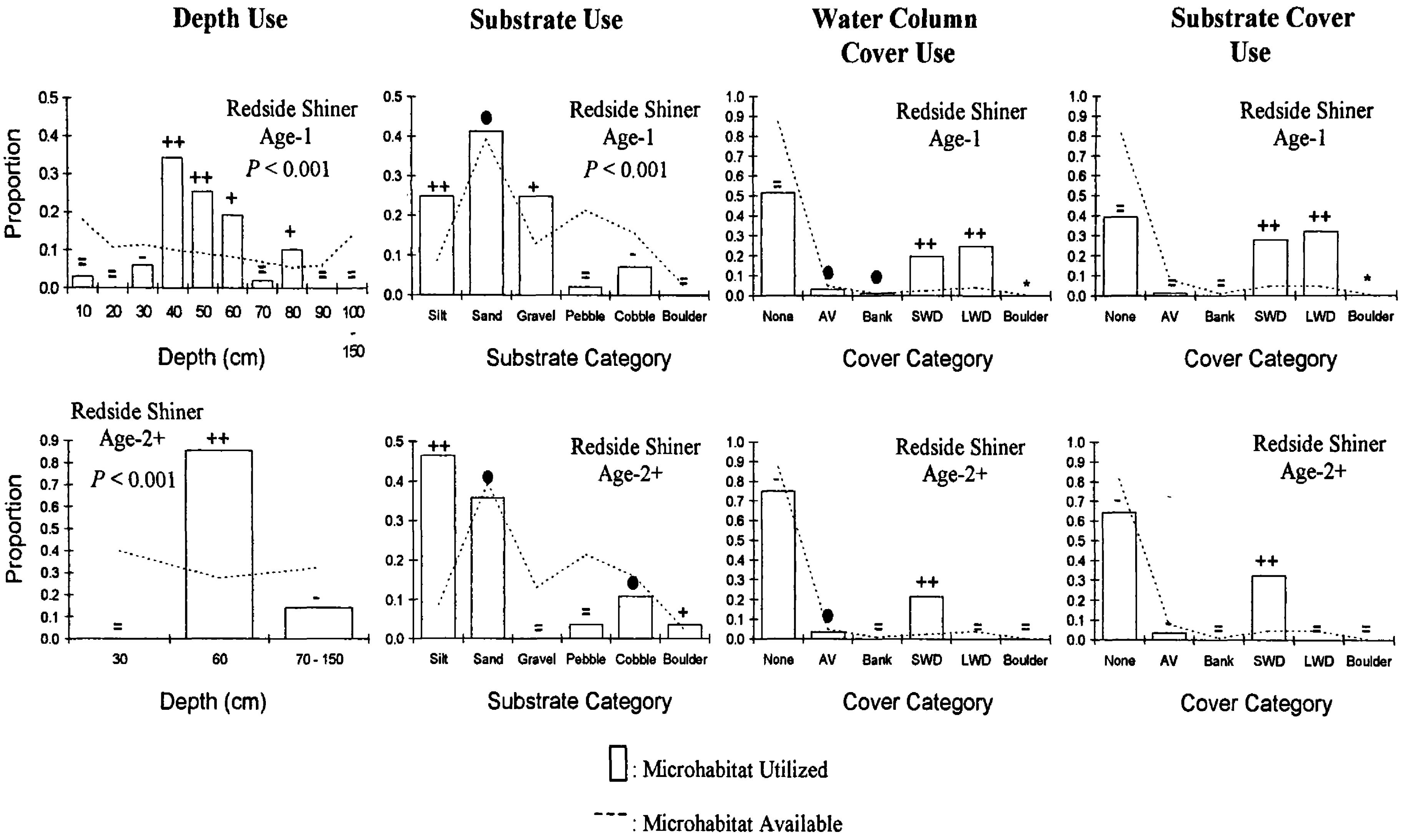


Figure 6b: Nighttime microhabitat use by age-1 (n = 99) and age-2+ (n = 28) redside shiner in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-1 water column cover use and substrate cover use were not tested due to low availability of multiple categories. Only age-2+ depth use was tested due to low sample sizes for the other microhabitat variables.

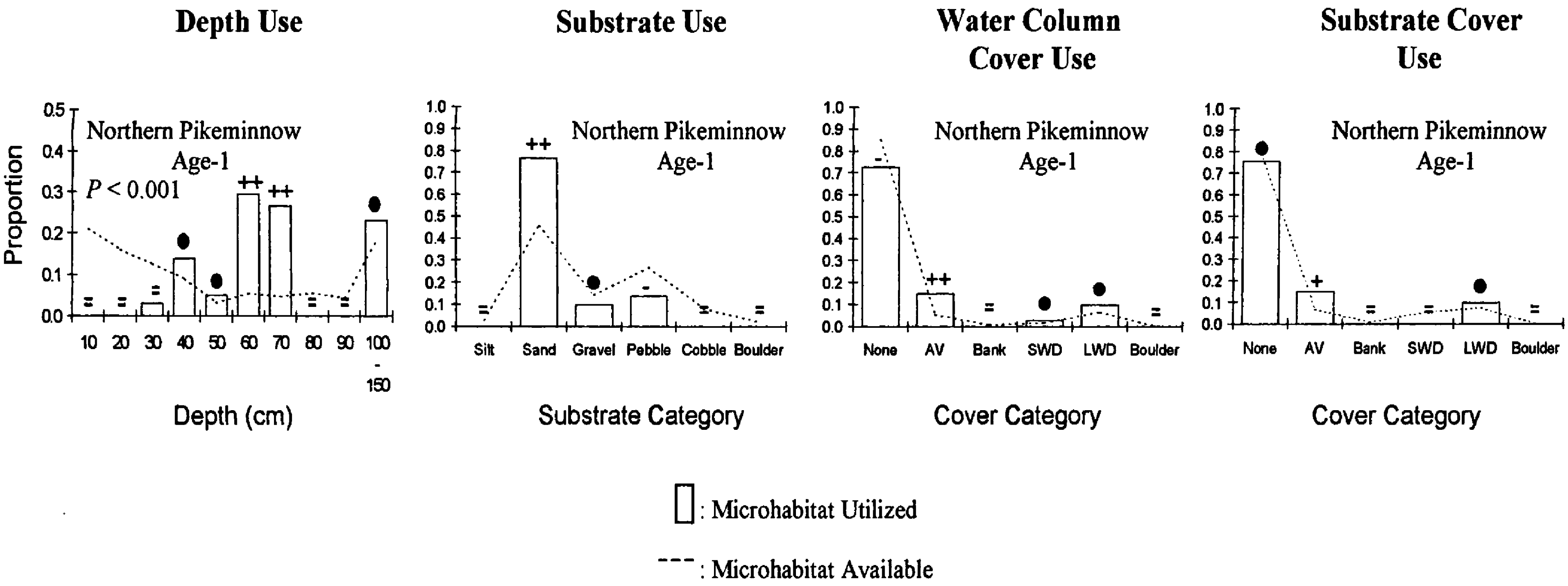


Figure 7a: Daytime microhabitat use by age-1 northern pikeminnow (n = 102) in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-1 substrate use, water column cover use, and substrate cover use were not tested due to low availability of multiple categories.

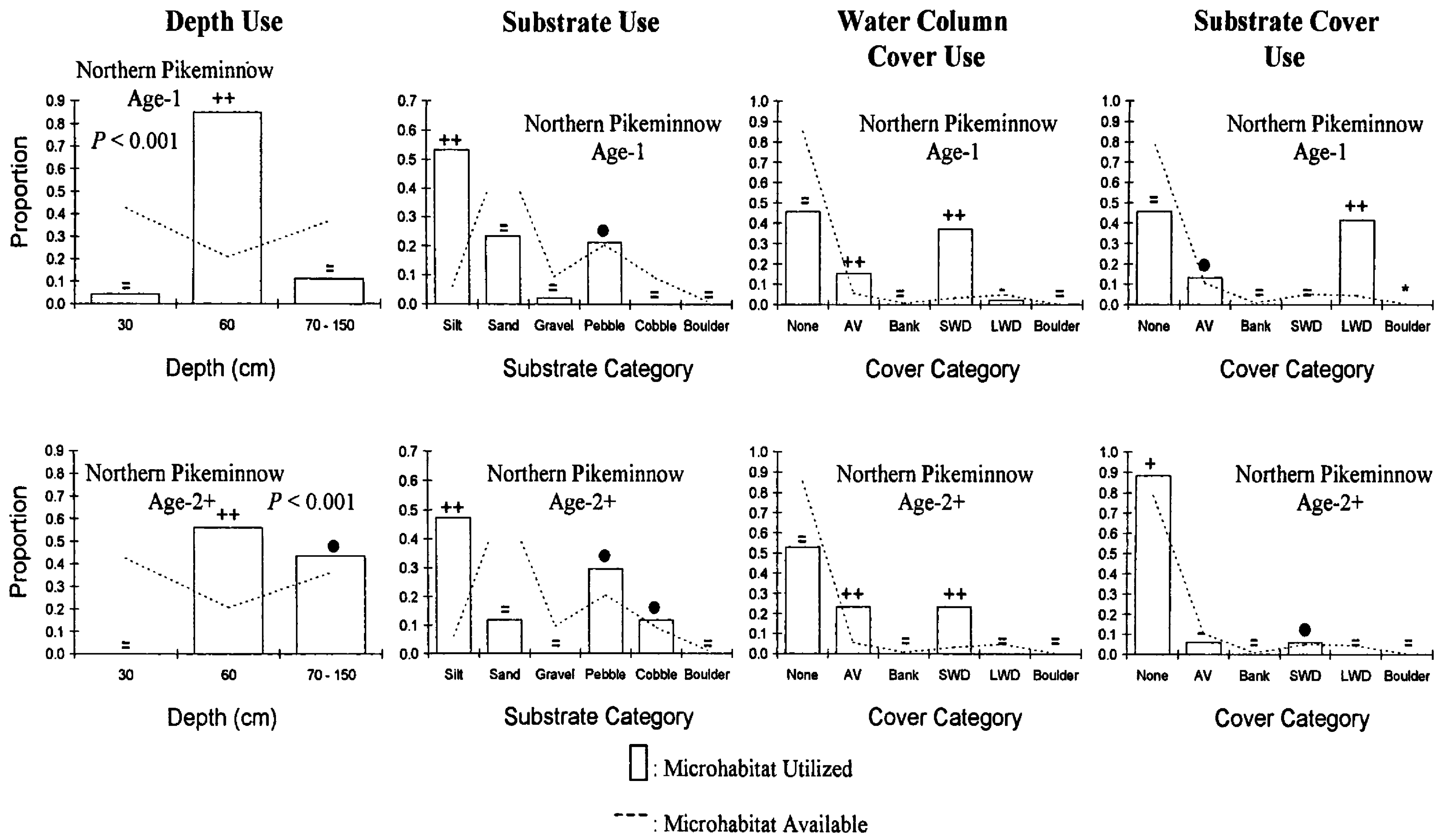


Figure 7b: Nighttime microhabitat use by age-1 (n = 46) and age-2+ (n = 16) northern pikeminnow in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-1 substrate use, water column cover use, and substrate cover use were not tested due to low availability of multiple categories. Only age-2+ depth use was tested due to small sample size.

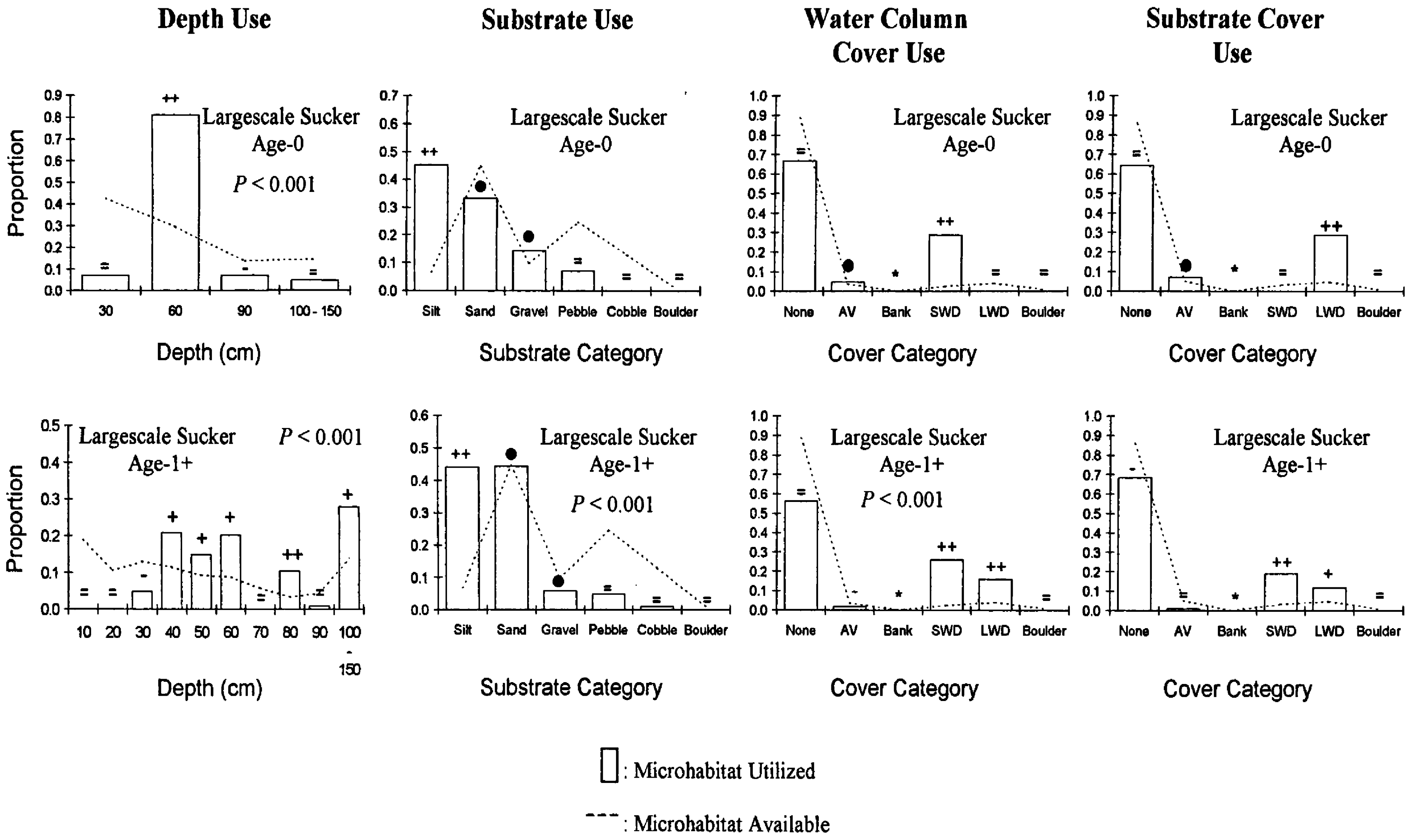


Figure 8: Nighttime microhabitat use by age-0 (n = 42) and age-1+ (n = 106) largescale sucker in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-0 substrate use, water column cover use, and substrate cover use were not tested due to low availability of multiple categories. Only age-1+ depth use and substrate use were tested due to low availability of the other microhabitat variables.

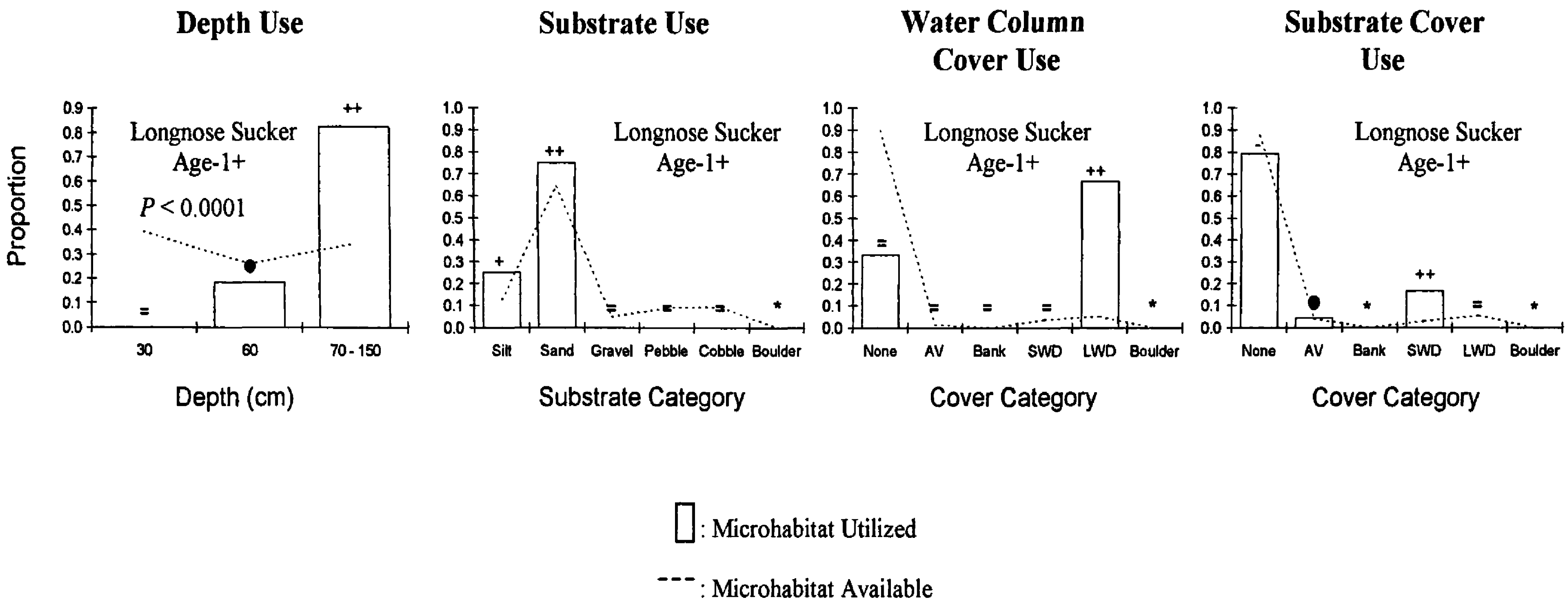


Figure 9: Nighttime microhabitat use by age-1+ longnose sucker (n = 22) in Bitterroot River secondary channels. Electivities (*d*) compare used and available microhabitats and are indicated by ++ ($0.50 \leq d$, strong preference), + ($0.25 \leq d < 0.5$, moderate preference), • ($-0.25 \leq d < 0.25$ no preference), - ($-0.50 \leq d < -0.25$), and = ($d < -0.50$, strong avoidance) (Moyle and Baltz 1985). Asterisks indicate lack of availability data and undefined electivity. *P*-values represent significant differences between used microhabitat values and available microhabitat values using the chi-square test. Age-1+ substrate use, water column cover use, and substrate cover use were not tested due to small sample sizes.

Table 6: Eigenvalues, percent variance explained, and discriminant function coefficients for microhabitat variables selected from a stepwise discriminant analysis used to separate microhabitat use by eleven species and age classes of fish in Bitterroot River secondary channels. Microhabitat data were measured during night snorkeling.

Axis	I	II	III	IV
Eigenvalue	0.550	0.257	0.155	0.095
% of Variance	52.1	24.3	14.7	9.0
Habitat Variables				
Silt	0.363	-0.116	0.968	-0.027
Pebble	0.045	-0.152	0.271	0.989
Depth	0.905	-0.273	-0.354	0.023
Substrate Cover	0.370	0.911	-0.128	0.233

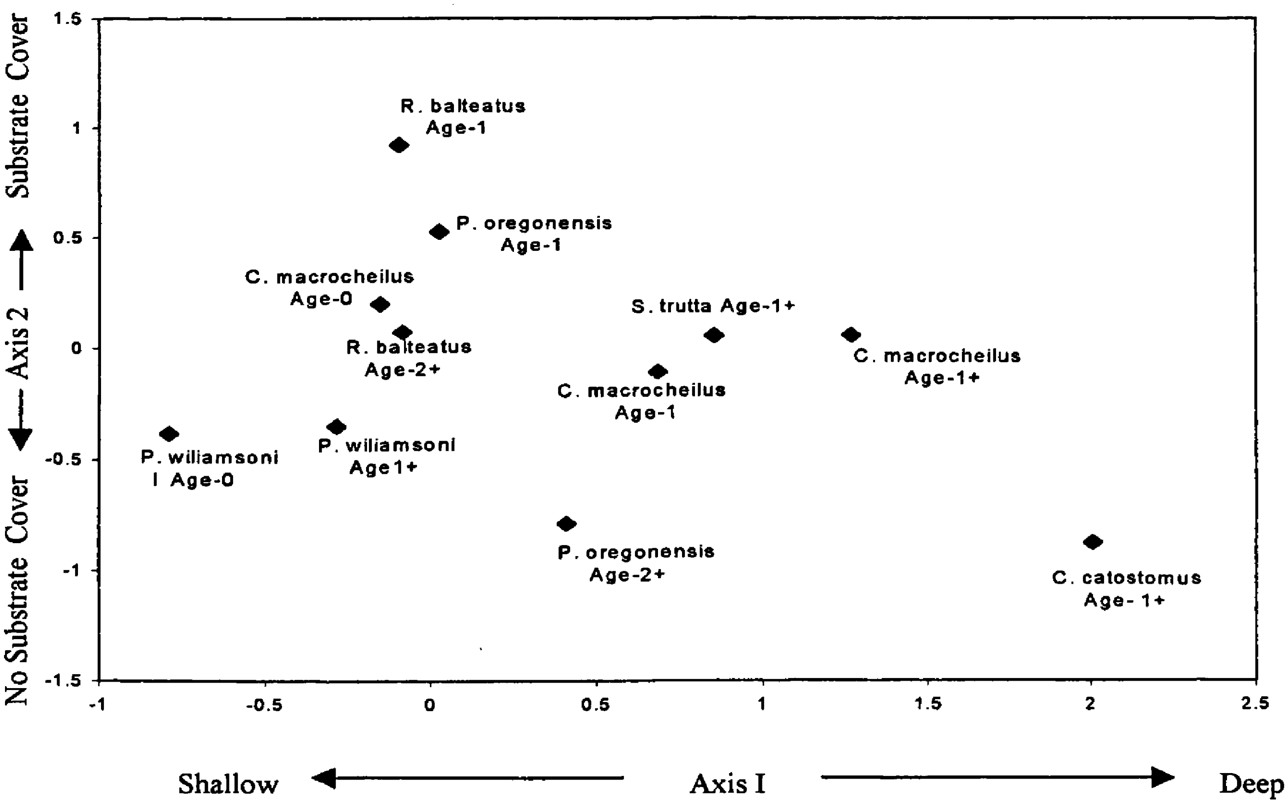
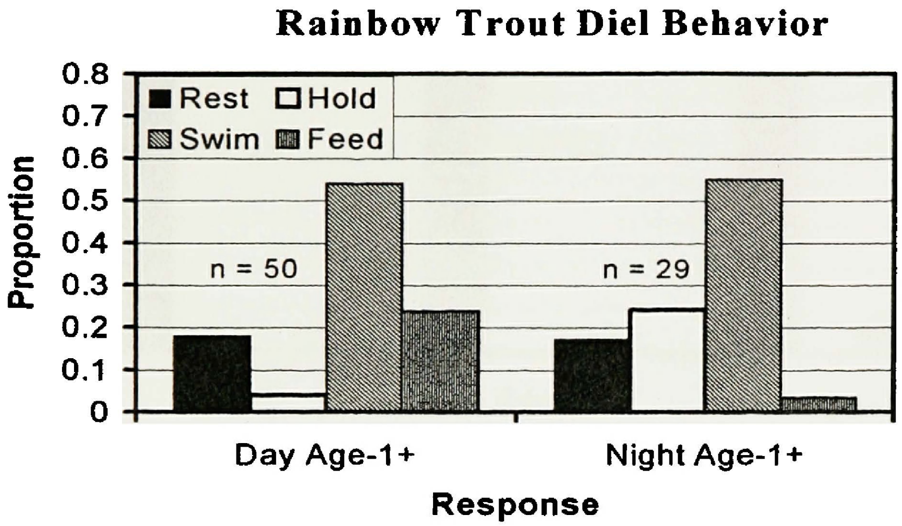


Figure 10: Plot of species-age class centroids on the first two axes derived from a discriminant function analysis to classify species-age classes by microhabitat associations. Microhabitat data were measured during night snorkeling.



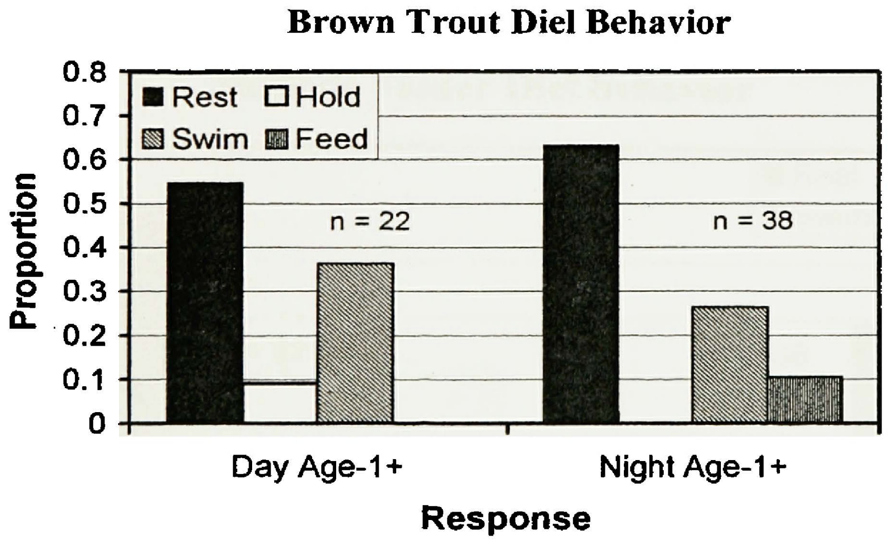


Figure 11: Rainbow trout and brown trout age-1+ diel behavior in Bitterroot River secondary channels.

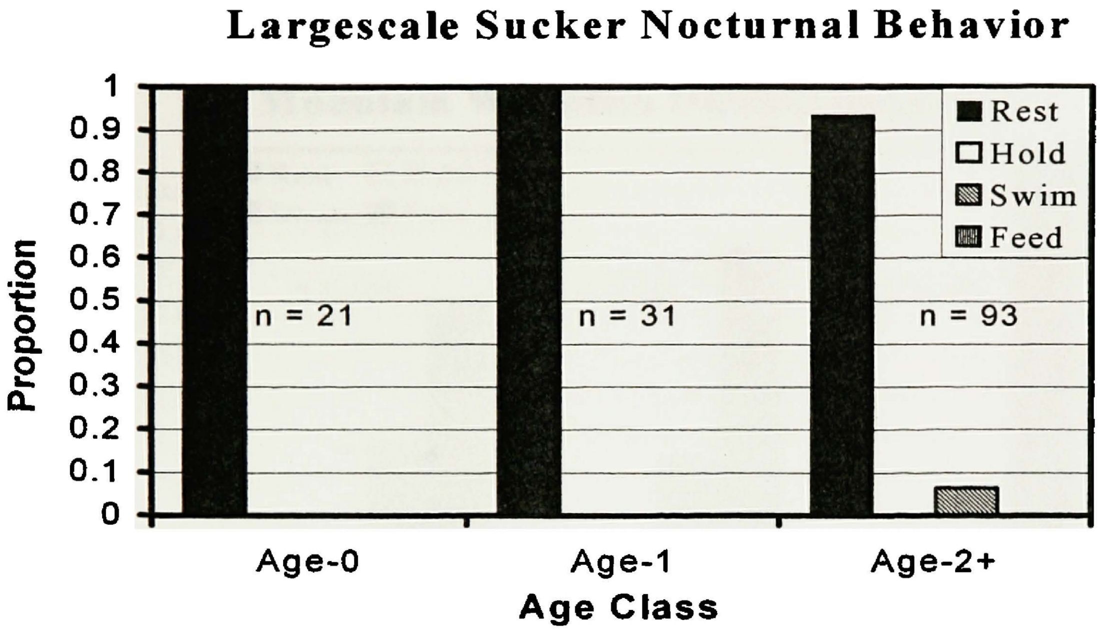


Figure 12: Largescale sucker diel behavior in Bitterroot River secondary channels. Diurnal behavior was not included due to low sample size.

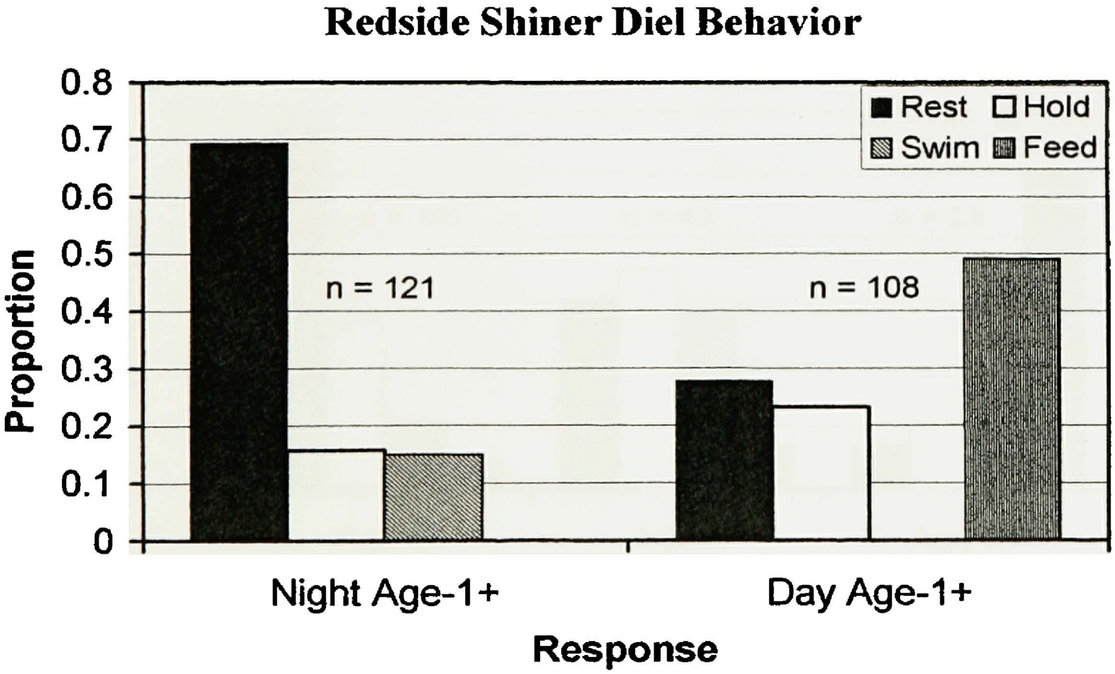
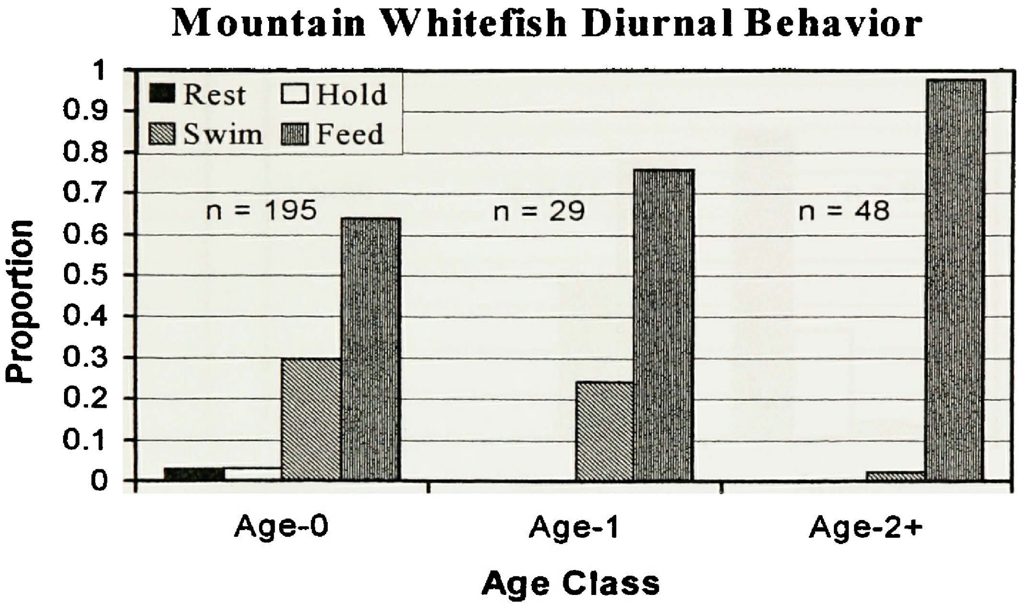


Figure 13: Redside shiner age-1+ diel behavior in Bitterroot River secondary channels.



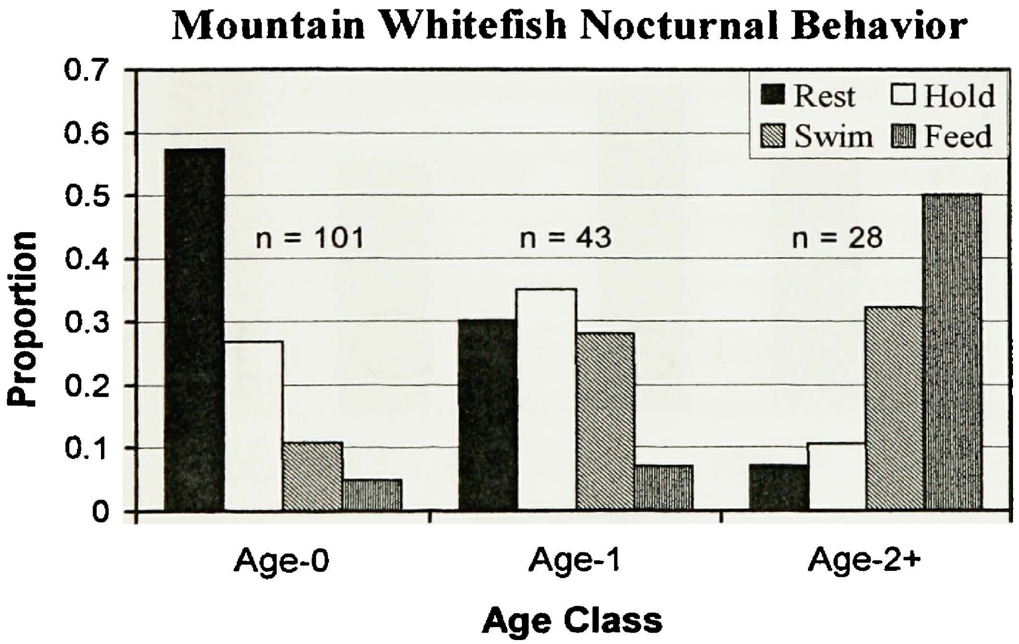
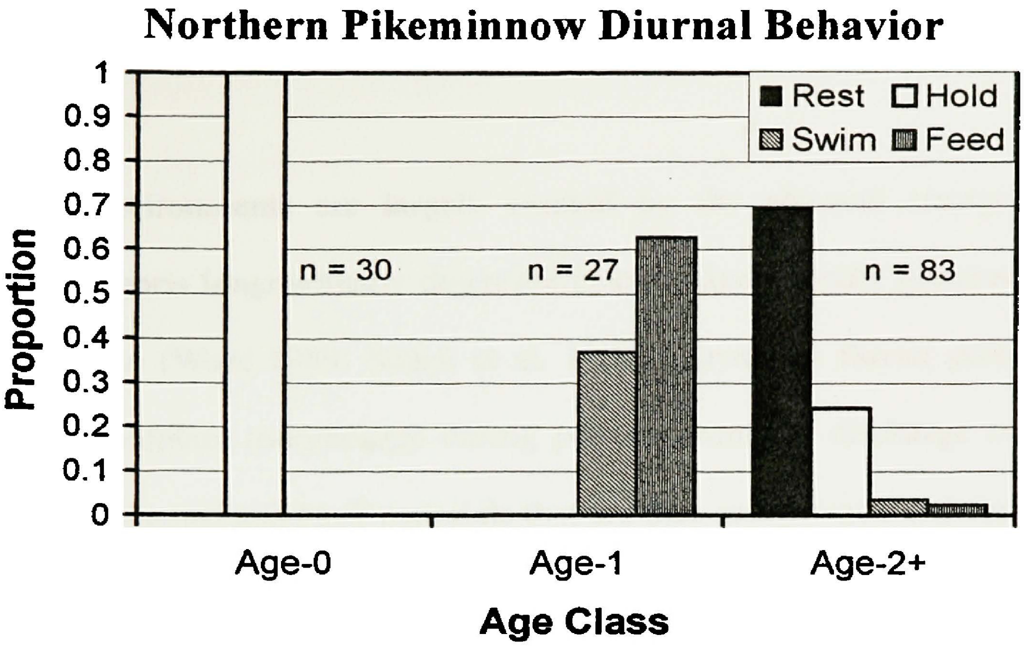


Figure 14: Mountain whitefish diel behavior in Bitterroot River secondary channels.



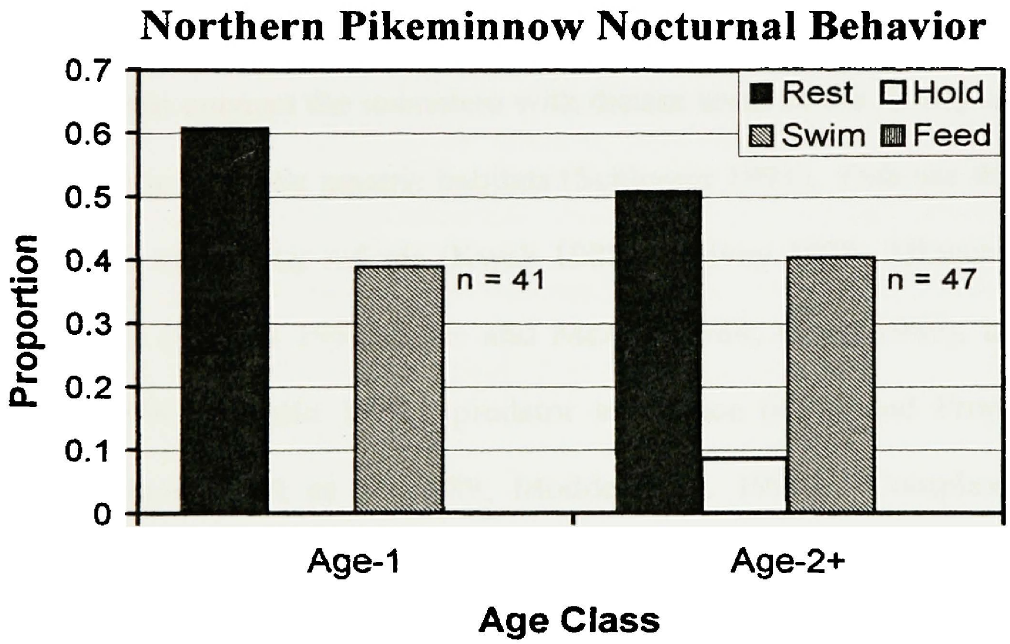


Figure 15: Northern pikeminnow diel behavior in Bitterroot River secondary channels.

Chapter 4

Bitterroot River Floodplain Channel Fish Community Diversity

Introduction

River environments are largely created by the physical transport of water, sediment, and debris longitudinally down the channel and laterally between the channel and its floodplain (Ward 1989; Sedell et al. 1990). Dynamic fluvial processes modify channel and floodplain morphology during periodic bankfull discharge events. These flows mobilize channel and bank materials that are then reorganized and deposited within the channel or on the adjacent floodplain (Ward and Stanford 1995). Depending on the river's flow regime and interaction with its associated floodplain, floodplain channels are created, shaped, or filled annually (Brunke and Gonser 1997; Poff et al. 1997). Persistent floodplain channels connect the mainstem with distant areas of the floodplain which offer a diversity of lentic and lotic aquatic habitats (Schlosser 1991). Fish use these floodplain environments for high water refugia (Kwak 1988; McEvoy 1998; Allouche et al. 1999), spawning habitat (Starrett 1951; Tyus and McAda 1984; Copp 1989), nursery habitat (Sedell et al. 1990; Cavallo 1997), predator avoidance (Gido and Propst 1999), and resource acquisition (Junk et al. 1989; Modde et al. 1996). Complex physical and biological processes couple the river and its floodplain, affecting the composition of aquatic communities inhabiting these floodplain environments (Ward and Stanford 1995).

Within these floodplain environments, stream channels form a continuum of habitats that vary according to their degree of mainstem hydrologic connectivity (Triska et al. 1993; Brunke and Gonser 1997), geographic location (Junk et al. 1989), period of inundation (Welcomme 1979), and geomorphic characteristics (Copp 1989). Habitats that are proximate to the mainstem are expected to display characteristics more-similar to the mainstem's conditions than would habitats that are at a distance from the mainstem. Within this framework of physical habitat characteristics, habitats closer to the mainstem are influenced by the mainstem's hydrograph, fluvial processes, and upwelling ground water sources. Conversely, habitats at a greater distance from the mainstem channel would likely be more influenced by conditions that are somewhat independent of primary channel processes (Copp 1989). Distant habitats are little influenced by mainstem surface water except during high flow periods. Floodplain channel geomorphic properties are less similar to the mainstem, and are more reflective of stratified vertical and horizontal floodplain soils created by historical flood events (Amoros et al. 1986). Because surface water sources are less available, both upland runoff and riverine groundwater sources influence floodplain channel water chemistry (Heiler et al. 1995; Brunke and Gosner 1997). Within this context, persistent channels maintained by cold groundwater discharge provide essential juvenile fish rearing habitat within the floodplain matrix (Frissell 1999). Additionally, physicochemical characteristics such as oxygen saturation, reflect both biological processes (i.e. autochthonous production and organic decomposition) and physical processes (sedimentation and groundwater upwelling) that may be of differing importance to biological communities inhabiting lentic backwater areas. Considering these conditions, habitats distant from the mainstem may be more hospitable and preferred by some aquatic organisms, especially tolerant species capable of surviving warmer, low oxygen conditions (Copp 1989). Conversely, these habitats may be avoided by other species that prefer mainstem conditions or are intolerant of lower oxygen levels (Welcomme 1995). However, since most species have complex life histories, floodplain habitats likely provide an important environment for both fish types during at least part of their lifecycles (Moyle and Cech 1988).

Changes in fish community diversity in a river system reflect the lifehistories of the constituent species as well as the range of available habitats in the aquatic environment, among other things. Fish community diversity in rivers and streams has been found to increase in a downstream continuum from basin headwaters to low gradient reaches (Sheldon 1968; Gorman and Karr 1978; Horwitz 1978; Angermeier and Schlosser 1989). In these lotic systems, downstream habitats are characterized by larger habitat patches, greater pool volume, proximity to potential source populations, and greater environmental stability (Horwitz 1978; Schlosser 1987; Angermeier and Schlosser 1989; Taylor 1997; but see Cross 1985). The species-area hypothesis investigates the relationship between these habitat conditions and fish community diversity. While this theory has been supported in larger systems, its application to floodplain channels is untested.

To investigate the downstream distribution and abundance of fish communities using floodplain channels, fish communities inhabiting Bitterroot River floodplain channels were sampled during the spring and summer of 1999. The objectives for this project were to; 1) characterize fish communities using floodplain habitats at increasing distances from the Bitterroot River, and 2) identify changes in community structure over the sampling period.

Methods and Materials

Study Site

The Bitterroot River in western Montana flows north from the confluence of the East and West Forks near Conner, Montana, to its confluence with the Clark Fork River, 8 km west of Missoula, Montana. Flowing approximately 134 km, the Bitterroot River drains a 7,288 km^2 (at Missoula USGS gauge) watershed, supporting agricultural land, pasture, rural and urban development, and upland forest systems. Tributaries originating in the Sapphire Mountains to the east, and the Bitterroot Mountains to the west, contribute much of the runoff that feeds the Bitterroot River.

The central Bitterroot River extends from Hamilton to Stevensville. An expansive alluvial floodplain created by a network of abandoned and active river channels typifies this section of the river. Braided channel reaches and sections of anastomosis reflect the transitory relationship between river discharge and sediment transport in the central Bitterroot River. The resulting floodplain mosaic is a diversity of secondary channel habitats that vary by hydrology, channel morphology, water temperature regime, and mainstem influence. Floodplain channels are sites of groundwater surfacing during low water periods and are conduits for high flows during spring runoff. A mobile bedload and rapid hydrographic fluctuations during spring runoff contribute to the instability that characterizes the central Bitterroot River.

Single-channel reaches and occasional areas of anastomosis mark the channel pattern of the lower valley that extends from Stevensville to Missoula (Gaueman 1997). As the Bitterroot River nears its confluence with the Clark Fork River, the channel assumes a meandering single channel pattern, confined by the narrowing of the lower

Bitterroot Valley and extensive channel stabilization projects (riprap). Through this reach the river follows a more predictable course (See Chapter 2 for a complete site description).

Selected Sample Sites

The bankfull floodplain is a topographically-flat area adjacent to a watercourse that is inundated by floodwaters approximately every two out of three years. For this discussion, the "floodplain" includes the mainstem and the river bottom area up to the first terrace. To investigate fish habitat use in floodplain channels, two channel complexes were selected in March 1999. Floodplain channel complexes located at Bell Crossing (BC) and Tucker Crossing (TC), host multiple channels that vary by volume, physical complexity, amount of subsurface groundwater discharge, and distance from the mainstem Bitterroot River. On the floodplain, the largest secondary channels are maintained by groundwater discharge throughout the year and also convey surface water during spring runoff. Intermittent channels only convey water during spring runoff. In the persistent channels selected for this study, discharge increases in a downstream direction as additional groundwater sources surface into the floodplain channels. Bitterroot River flows that are greater than the bankfull elevation reconnect floodplain channels at both their upstream and downstream ends with the primary Bitterroot River and may completely inundate channels within the bankfull channel width. Coarse woody debris (CWD) aggregations on the topographically varied braid belt and adjacent floodplain attest to the extent of high flows throughout these areas.

The two TC floodplain channels flow across a large floodplain island that divides the Bitterroot River into east and west channels. At the BC floodplain complex, one channel is within the bankfull width while the second channel is fed by the Big Creek tributary and an irrigation channel during high water. All four channels maintain connectivity with the Bitterroot River at their downstream ends during low water. Two or three study reaches were selected in each floodplain channel. For a given channel, the first study reach was located at the floodplain channel's downstream end near the channel's confluence with the Bitterroot River. A second study reach was established at the approximate midpoint of the floodplain channel length. A third reach was marked at the upstream channel origin where groundwater surfaced into the channel. Selected study reaches were representative of the floodplain channel and usually included both riffle and pool habitats where available. The downstream and middle reaches originated and terminated at definable geomorphic features, usually a riffle or other gradient break.

Floodplain Channels: Tucker Crossing

The TC channels, termed TCA and TCB, originate on a 7 km-long island (Tucker Island) that divides the river into east and west channels (See Figure 8). Tucker Island is a stable landform hosting diverse vegetation including decadent black cottonwoods (*Populus trichocarpa*) and Ponderosa pine (*Pinus ponderosa*). From July through May, subsurface river water discharges into these two floodplain channels. Channel discharge grew rapidly during the May 1999 spring runoff as groundwater discharge increased and the Bitterroot River overtopped natural levees and inundated the intra-island floodplain channels. Overbank flows during the 1999 spring runoff redistributed coarse woody debris and altered substrates within the TC channels. Both TC channels discharge directly into the mainstem Bitterroot River within 300 m of each other.

Bank structure and materials are similar in TCA and TCB due to their common alluvial origin. Upstream reaches are incised with substrates and banks primarily composed of pebbles and cobbles. Downstream substrata and banks are mainly sand. Channel structure is enhanced by abundant in-channel CWD aggregations and dense overhanging riparian vegetation patches. Land use adjacent to the TC channels is predominantly summer cattle grazing. Bank erosion caused by bank trampling and riparian vegetation removal has led to bank chiseling and channel widening.

Floodplain Channels: Bell Crossing

The BC channels, termed BCA and BCB, traverse an expansive floodplain complex bordering the Bitterroot River's western boundary (see Figures 8 & 9). From July through May, subsurface water discharges into these two floodplain channels. The Bitterroot River captured BCA before the river reached bankfull-level flows in May 1999. Channel discharge rapidly increased as the primary channel overflowed low-lying cobble bars upstream of the sample site. Compared to BCA, the more-westerly BCB is less influenced by Bitterroot River discharge since it is farther from the river. High water conveyed by Big Creek and the irrigation channel flowed into BCB above the upstream sample reach. Both floodplain channels discharge into two larger channels (>20 m wetted width), that subsequently join the primary Bitterroot River.

Bank structure varies between BCA and BCB. BCA lies within the Bitterroot's bankfull channel. While the floodplain channel's western bank is steeply sloped and averages 2 m in height in the study area, the eastern bank is below the river's bankfull elevation. Substrate composition is similar between BCA and BCB. Upstream reach substrates are mainly pebble and cobble. The lower reaches of BCA are primarily sand substrate while nearly the entire BCB channel is pebble and cobble. Unlike the TC channels, in-channel CWD in the BC channels is sparse. Aquatic vegetation and overhanging banks provided in-channel cover structure. Low density livestock grazing typifies land use adjacent to the BC channels. Livestock are restricted from the channel thereby reducing their effects on channel geometry and adjacent riparian vegetation.

Sampling Design

Fish Sampling

To investigate fish communities using floodplain channel habitats at distances from the Bitterroot River, floodplain channels were electrofished three times during 1999. The first sampling commenced in March 1999 at floodplain channel ice out, but low conductivity and high water precluded efficient sampling between June and July 1999. Sampling was again conducted in August and September 1999.

A Smith-Root 15-D POW backpack electrofishing unit was used for fish sampling. Block nets (13 mm mesh openings) were installed at the upstream and downstream ends of each reach prior to electrofishing. Block nets were not used for sites isolated by steep gradients or dry channel expanses. All reaches were two-pass depletion electrofished (300 – 600 Volts) by a two-person crew fishing in an upstream direction. Captured trout were placed in a bucket carried by the backpack operator. At the end of each pass, captured fish were placed in separate baskets. At the culmination of the sampling effort, fish were anesthetized 40 mg/L of clove oil and 90% ethanol mixed with river water in a 40 L bucket (Anderson et al. 1997). Upon losing equilibrium each fish was identified, measured to the nearest millimeter total length and standard length (nose to end of spine), weighed to the nearest 0.1 g using an Ohaus LS 200 portable scale, and placed in a recovery bucket. Active fish were returned to the channel within fifteen minutes of being placed in the recovery bucket. Although all habitats were thoroughly sampled, electrofishing effort was concentrated along reach banks and cover structures. Sampling effort per pass was recorded from the electrofishing unit's digital counter.

Habitat Surveys

To investigate habitat availability and differences in the channel's physical characteristics, a point-transect methodology was employed to survey sample sites following the last electrofishing date. Available habitat was similar throughout the survey period although channel connectivity decreased in TCA and TCB over the sampling period as water levels dropped and stretches of wetted channel were interrupted by short dry cobble reaches. For the transect sampling, two measuring tapes were used to create a pseudo-lattice over the study area. A 100 m tape was extended from each site's downstream to upstream ends. Eight to ten regularly spaced transects were then established perpendicular to the channel. Depth, substrate type, substrate cover, water column cover, and temperature were recorded for each of the approximately 100 points comprising the pseudo-lattice (See Chapter 2 for complete methods). Total CWD area and riffle area were also recorded for each sample site.

An adjustable stadia rod and a Marsh-McBirney Model 2000 Flow-Mate portable flowmeter were used to measure water velocities at 60% total depth at random points within each reach to characterize water velocity variability.

A Trimble (Trimble Navigation Limited) global positioning system (GPS) was used to map the study area and to measure the distance of each sampled reach from the mainstem Bitterroot River (refer to Figures 7-9).

Data Analysis

Descriptive statistics (mean and standard deviation) were used to characterize the physical habitat of the eleven study reaches. To investigate the fish communities utilizing each floodplain channel reach during each of the three sampling periods, fish sampled in the two electrofishing passes were considered as a single sample. Due to the low fish densities measured during each of the three sample periods, fish collections were pooled over the three sampling periods in order to identify species-channel reach relationships. Total number of individuals, species-size class groups (richness), and the Shannon-Weaver diversity index coefficient (H) were calculated for each channel reach. Species richness is a simple count of species in a reach. For species-size class richness, fish were grouped by size (explained below). The Shannon-Weaver index, developed from information theory, evaluates the proportion of individuals of each species relative to the total number of individuals in the sample (Figure 2) (Shannon and Weaver 1949). The Shannon-Weaver index gives less weight to rare species than to common ones, and is one of several indices that are useful for comparing communities. When comparing diversity values for two sites that were similarly sampled, the site with the higher diversity value has either more species, more individuals of a species, or both than the site with the lower diversity value (Ricklefs 1990; Kohler and Hubert 1993).

Since H is roughly proportional to the logarithm of the number of species in the sampled community, it will be expressed as e^H, which is proportional to the number of species in the sample (Ricklefs 1990). For example, when each sampled species is equally abundant (evenness), e^H will equal the number of species in the sample (Ricklefs 1990).

Because some sampled reaches contained juveniles of a particular species but few adults, and other sites contained many adults of a species but few juveniles, the sampled communities were partitioned into two size groups (hereafter species-length group), (fish < 120 mm) and (fish ≥ 120 mm), to capture size-related community diversity differences. This length was selected by analyzing the length-frequency histograms from the sampled communities and after consulting the suggested age-size classes in the literature (Brown 1971; Wydoski and Whitney 1979). For most species there was a break in the range of sizes, as well as the number of sampled fish, around 120 mm. This classification separates large and small fish of "large" species such as the rainbow trout. However, for "small" species such as the redside shiner, all fish were included in the < 120 mm size class. Some information is lost using this methodology since multiple age classes were grouped to form the small and large length groups. For example, the adult group might include fish representing age-2, age-3, and age-3+ age classes, as was the case for brown trout. However, with the numerous species and age-classes sampled, this protocol simplified the analysis of size-related fish presence in floodplain channel reaches. For instance, an abundance of <120 mm (YOY and juvenile) fish in a reach combined with an absence of adult >120 mm (adult) fish would suggest the importance of the reach as a nursery habitat.

Pie charts were created to illustrate the abundance of species-length classes represented by at least three individuals in each sampled reach to improve pie chart clarity (although the e^H values include all recorded fish).

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

e^H is proportional to the number of species-length classes

Where: p_i is the frequency of a species-length class i in a sample
S is the number of species-length classes in a sample
H is the Shannon information coefficient

Figure 2: The Shannon-Weaver Diversity Index was adjusted to measure species-length class diversity based on the frequency of individual species-length classes in a sample.

Kendall's rank correlation coefficient was used to test the strength of relationships between the electrofishing fish abundance-diversity data and the channel attribute data. The Kendall's rank correlation coefficient is a widely used nonparametric test useful for analyzing the importance of such relationships (Noether 1991). Channel variables included the reach distance to the Bitterroot River (m), reach channel area (m^2), depth diversity, substrate diversity and water column cover diversity. Depth diversity, substrate diversity and water column cover diversity were calculated using the Shannon-Weaver diversity index.

Moving from diversity information to species' length-frequency data, length frequencies for common species were plotted for each sample period. Species that were infrequently sampled (< 5 individuals) during a sampling period were not plotted. Length frequencies for seasonal samplings illustrate fish community changes primarily associated with fish growth and the appearance of young-of-year (YOY) individuals in the reach. The nonparametric Kruskal-Wallace procedure or the Mann-Whitney U test was used to identify changes in species lengths among the channels and sampling periods (Noether 1991). Differences in species' lengths among the sample reaches would again suggest the importance of reaches for particular developmental stages of the sampled fish. Average total length and average weight were also calculated for the five most abundant species sampled for reference.

Results

Floodplain Channel Habitat Characteristics

Measured prior to high water, floodplain channel length extended from the point of groundwater surfacing downstream to the floodplain channel's confluence with the Bitterroot River (Table 1). The lengths of individual sampled floodplain channel reaches varied (from 63 m to 135 m) and fluctuated slightly over the three sampling periods. The Shannon-Weaver index was used to characterize the complexity of the measured channel variables. Channel depth diversity (Table 2) and mean channel depth (Figure 3), were similar among the eleven reaches and did not show a downstream trend within a particular channel. Except for TCB-R2 and BCA-R3, few reaches had depths greater than 1 m. In these two reaches the deeper pools comprised less than 5% of the total reach area.

Channel discharge differed within and among the sampled floodplain channels. The two BC channels were primarily lentic habitats except for periodic low gradient riffles and glides. Riffle sections were noted by a narrowing of the channel and an increase in water velocity compared to glide and pool habitats.

Substrates were also similar for the four floodplain channels except for the downstream reaches of BCA and TCB, which were dominated by sand substrate (Figure 4). Substrate diversity was consistent among the four channels with most reaches fairly evenly represented by at least four substrate classes.

Cover structures in the four channels varied by both material type and abundance. Aquatic vegetation was the most common of the cover structures (Figure 5), while CWD was less common (Figure 6), but was frequently used by sampled fish. Tucker Crossing CWD was primarily complex log aggregations and rootwads. In comparison, the BC channels were largely devoid of CWD except for BCB-R2. Cover diversity did not increase in a downstream direction. Changes in cover diversity were primarily influenced by changes in the abundance of aquatic vegetation (BC channels) and woody debris (TC channels).

Fish Species Distribution

Over the three sampling periods, 469 individuals representing five age classes and ten of the eighteen fish species known to reside in the Bitterroot drainage were sampled in the selected floodplain channel reaches (Table 3). Age classes were determined by comparing fish total lengths with size estimates provided in the literature (Brown 1971; Wydoski and Whitney 1979). Although these species were commonly encountered when considering all of the sampled reaches, species richness and Shannon diversity varied by channel as well as by reach location.

Total individuals and species-length group richness increased in a downstream direction in three of the four channels. Richness was highest at the upstream site in TCB although more individuals were sampled at the downstream site. Total individuals per reach was significantly correlated with downstream distance to the Bitterroot River (Kendall's τ, $P = 0.001$) (Figure 7). Species-length group richness and Shannon diversity varied among reaches and were not significantly correlated with the tested channel variables. The TC channels had more diverse fish communities than the BC channels with TCB having the highest average Shannon index (Figure 8) of the four sampled channels. BCA and BCB each hosted eleven species-length groups in their downstream reaches while TCA hosted ten species-length groups. Compared to the middle and downstream reaches, fewer individuals and species-length groups inhabited upstream sites. The upstream BCA-R3 and BCB-R3 reaches generally contained YOY individuals.

Introduced salmonid species comprised a predominant portion of the sampled fish communities. Brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) were abundant in TCA and TCB relative to other species. Conversely, brook trout were rare in the BC channels where only one individual was sampled (Figure 9 and Figure 10). In the BC sites, YOY brown trout comprised the dominant salmonid species-size class followed, by juvenile rainbow trout (*Oncorhynchus mykiss*). Other species that were commonly sampled included mountain whitefish (*Prosopium williamsoni*), largescale sucker (*Catostomus macrocheilus*), longnose sucker (C. catostomus), redside shiner (*Richardsonius balteatus*), and slimy sculpin (*Cottus cognatus*).

Species' Length Frequencies

In order to identify how fish community composition varied by floodplain channel, sampled fish lengths were compared among channels and sampling dates. Brown trout were significantly smaller in BCA and BCB during two of the three sample periods (August: $P < 0.0001$, 3 df; September: $P < 0.0001$, 3 df) than in the deeper and more complex TCA and TCB (August) and TCB (September) which hosted adult brown trout. Similarly, longnose suckers were significantly larger in TCB than in BCA and BCB (September: $P < 0.008$, 3 df). However, significantly larger longnose sucker utilized BCB ($P < 0.042$, 1 df) compared to longnose sucker utilizing the BCA channel during the March sampling.

Intraspecific length differences for YOY brown trout and brook trout (Figures 11 and 12) were apparent between the August and September sampling. Other species such as rainbow trout (Figure 13) and largescale sucker (Figure 14) were not common enough to merit growth comparisons. The length of YOY brown trout in all channels was significantly different ($P < 0.001$) between August (median total length = 65 mm), and September (median total length = 87 mm). The length of YOY brook trout in TCA and TCB was significantly different ($P = 0.033$) between August (median total length = 75 mm), and September (median total length = 86 mm) (Table 4).

The structure of fish communities utilizing the floodplain channels varied over the sample period as YOY fish matured and older fish migrated from the sample reach or were removed by predators. For most species, juvenile fish were most abundant in the

March sampling. A few infrequently encountered older individuals represented the adults in the sampled fish communities.

Depending on the time of spawning for a particular species, YOY in fish used floodplain channels by August and/or September. The juvenile fish that were apparent in the initial sampling were more dispersed by late summer, reflected in the capture of fewer large fish during August and September sampling. The YOY fish that were sampled in August had generally increased in size by September. Older age classes sampled in August, were less numerous than the YOY of the same species in September likely due to mortality.

Discussion

Floodplain Channel Habitat Diversity

The variability in physicochemical habitat characteristics displayed by floodplain channels in the central Bitterroot Valley can be represented on a number of spatial scales, including 1) between floodplain complexes, 2) between channels within a complex, and 3) among reaches within a channel. Floodplain channel habitats are shaped by fluvial processes during periods of high water when the Bitterroot River captures large portions of the four study channels. The river overtops natural levees and inundates intra-island channels comprising the TC complex. CWD is transported both within the channel and on the adjacent floodplain. Sediment and CWD are redistributed and deposited within the floodplain channel, elsewhere on the floodplain, or in the mainstem Bitterroot River. The BC complex undergoes a similar transformation. BCA is completely inundated and scoured as the river crests the low-lying braid belt. Minimal inchannel CWD and simple channel morphology suggest efficient transport of both sediment and material to the Bitterroot River. Similar to the TC channels, the BCB channel conveyed floodflows within channel during the high water period. Although channel morphology did not change relative to pre-flood conditions, the channel's wetted width increased with a rise in the flood flows. Low gradient riffles, that during low water were a barrier to adult fish passage, were sufficiently deep at high water for migrating fish to move upstream. Over the remainder of the hydrograph, persistent upwelling groundwater provided off-channel habitat in both floodplain complexes.

Sites with deep, complex pools would be expected to hold more fish and maintain higher species richness (Gorman and Karr 1978; Angermeier and Schlosser 1989; Taylor 1997). CWD abundance often influences pool complexity and stability. Channel reaches with stable and intricate woody debris (root wads or large aggregations) contain a wider range of habitats than reaches lacking such complex structures. CWD and dense riparian vegetation were common features in the TC channels with each of the TC reaches containing at least a moderate amount of CWD (> 30 m^2). In comparison, relatively little woody debris was found in the BC channels, even though the surrounding floodplain hosted plentiful aggregations of CWD. The difference in deep pool and CWD frequency between the two floodplain complexes was likely an important factor defining the fish communities using these sites (Sedell et al. 1990; Townsend and Hildrew 1994). Pearsons et al. (1992) found that stream reaches with complex CWD maintained higher fish densities following scouring flashfloods than did reaches that lacked stable CWD. After seasonal flashfloods, fish densities in complex isolated pools in Great Plains streams remained higher than fish densities in more-simplified pools that lacked complex pools (Fausch and Bramblett 1991). In BCA, adult fish were not encountered in the sample reaches possibly due to a lack of deep, complex pools. In another portion of BCA (a non-sampling area), 8-12 adult brown trout and largescale suckers occupied a deep pool (>1.5 m) with overhead woody debris cover on three occasions. Multiple adult fish using CWD in other portions of BCA suggests both the presence of adult fish in the channel and the importance of patchy overhead cover. The absence of adult fish in BCA sample reaches may indicate the low retention of fish in this channel due to few deep pools and minimal CWD.

In contrast to the BC channels, the TC channels exhibited greater habitat complexity measured by the prevalence of deep pools and abundant CWD. Although portions of the TC channels were isolated late in the summer due to channel dewatering, persistent groundwater sources and riparian shading ensured hospitable environments for the resident fish. Where dewatering would have been catastrophic for fishes in the shallow BC channels, lower water levels were less detrimental to the TC channels' deep pools. The abundance of adult salmonids suggested that the oxygen levels were adequate to support late season low fish densities.

In addition to physical habitat, water temperature and thermal complexity at both the microhabitat (Bonneau and Scarnecchia 1996; Cavallo 1997) and reach scales (Rahel and Hubert 1991; Swanberg 1997; Dunham et al. 1999) influence species assemblage composition and species distribution in river and creek systems. Cavallo (1997) found that geographically different floodplain channel types exhibited dissimilar temperature signatures. Unlike the findings of other workers (see Cavallo 1997, p. 34) describing the importance of cold water in limiting the distribution of introduced species, invasive brook trout were found throughout the range of sampled channel types and water temperatures (Cavallo 1997). Cavallo's rare observations of bull trout and westslope cutthroat trout suggested to him that brook trout exclude native salmonids from at least a portion of their habitat. In the Bitterroot River, the presence of temperature-tolerant brown trout and brook trout in floodplain channels likely reflects a similar phenomenon of introduced species competitively excluding native congeners. Native westslope cutthroat may be less aggressive feeders than introduced species or may incapable of displacing introduced fish from quality feeding locations. Larger brown trout and more aggressive brook trout likely displace natives from the sampled floodplain springbrooks. Prior to the introduction of these two species, native westslope cutthroat trout likely used these sites in a manner similar to these two nonnatives.

Longitudinal Habitat Complexity

One intent of this study was to investigate the species-area hypothesis. This hypothesis has been applied to longitudinal gradients on many spatial scales ranging from streams (Sheldon 1968; Angermeier and Schlosser 1989; Rahel and Hubert 1991) to individual habitat units (Taylor 1997). The hypothesis predicts that downstream reaches will contain larger habitat units capable of supporting larger and more diverse fish communities than upstream reaches that have less developed by fluvial processes. Floodplain channels may provide a more tenuous test for this hypothesis. Unlike tributaries where channel size is coupled with discharge magnitude, floodplain channels represent semi-independent systems that are accessed by the primary river during high water periods. On the Bitterroot River, the mainstem inundates subsidiary channels during high water events. The Bitterroot River can erode or deposit substantially more material from or into these channels than would be expected if these channels were independent of the Bitterroot River and drained their own scaled watersheds. Perhaps more succinctly, these floodplain channels are conduits for the Bitterroot River during high water, but the channels appear to be oversized for the upwelling water they discharge the remainder of the year. This dichotomy in flows partially explains the wide channels and abundance of bare cobbles. With this in mind, the relatively short lengths of these channels and similar high water flow intensity over the channel length, may limit the longitudinal channel development described by Angermeier and Schlosser (1989). In tributaries and small streams, downstream habitats tend to be deeper and more complex than habitats in headwater reaches. This downstream increase in channel size is attributed to inputs from feeder streams and a greater cumulative drainage area. In contrast to this phenomenon, Bitterroot River floodplain channel discharge slightly increased in a downstream direction during the low water period and the entire channel conveyed surface water during high water events.

I did not find any significant relationships between a reach's distance from the Bitterroot River and channel variable diversity. Personal observation supported this finding as the location of the most complex reaches varied by floodplain channel. For these reasons, the longitudinal increase in habitat area found in other systems was not supported in the floodplain channels I sampled.

Fish Community Comparisons

Fish community composition and fish abundance also differed between the different floodplain channels. Fish species-length class richness was greatest in the downstream sites in each of the sampled channels, although the intermediate site, TCA-R2, had the highest richness of all the sites. Richness increased downstream with the fewest number of species-length classes inhabiting the upstream channel origin reaches. Total fish abundance followed a similar pattern. The Shannon diversity coefficient was more variable for the sampled reaches. However, compared to the upstream sites, downstream sites had greater Shannon diversity except for the TCB channel. Unlike the findings of Angermeier and Schlosser (1989), fish diversity did not increase in a downstream direction as expected perhaps because sampled reaches did not significantly differ in a downstream direction. In another system, habitat loss in downstream areas led to lower habitat diversity that partially explained lower fish diversity (Cross 1985). In the Bitterroot River floodplain channels, the relationship between fish diversity and habitat area seems a bit tenuous. Because fish abundance was low, sampling more sites over a longer period would be required to thoroughly address the species-area issue in floodplain channels.

The overall high species-length class diversity but low abundance of fish using floodplain channels was somewhat surprising. Since channel connectivity fluctuates according to the Bitterroot River hydrograph, fish may select sites during high water but are then isolated when surface flows decline. The number of individuals and species inhabiting these sites is likely a reflection of the channel's connectivity with the Bitterroot River as well as the quality of the site for maintaining community members.

Recruitment in these channels occurs through immigration from the mainstem and YOY emergence within the floodplain channel. Water levels drop through the summer until some reaches are isolated. Fish remaining in these reaches contend with low water conditions and predation. Individuals that survive these conditions until the next high water will then be able to select another environment to occupy.

Considering these processes, reasons for community diversity differences can be hypothesized. Since only weak relationships were found between the fish community variables and the measured channel habitat variables (except for fish abundance and reach distance), other biotic or abiotic factors likely influence fish community structure. Two possible explanations include; (1) the composition of the fish community, and (2) the source-distance effect. Species occurrence patterns may depend on the dispersal ability of the fish in the community. For example, the adult fish that were sampled in deeper reaches may be resident fish that remain in the floodplain channel throughout the year. These fish favor floodplain channel conditions and may not disperse from the floodplain channels to the river. Conversely, YOY and juvenile fish may only inhabit the floodplain channels during the early part of their life and then move to the mainstem Bitterroot River in seek of more optimal conditions. This would especially be expected if dominant adult fish already occupy preferred positions in the floodplain channels.

Some speculation has also been garnered concerning the lifehistories of some fish species. As there are resident, fluvial, and adfluvial forms of some species (i.e. bull trout, brown trout, and rainbow trout), perhaps there is a segment of the fish community that remains in floodplain channels (C. Frissell, *personal communication*). This resident group would prefer the more stable environment afforded by floodplain springbrooks in contrast to the more fluctuating mainstem conditions. The transient members of the community might migrate from floodplain channels to the mainstem in search of more-hospitable habitat, optimal feeding conditions, less competition, or for reproductive purposes.

Secondly, the source-distance effect evaluates the distance a fish would have to migrate from a source body to the sampling location. Unlike headwater streams where the only migrant source is from downstream reaches, the Bitterroot River floodplain channels could receive migrants over a large portion of their channel length during high water events when the Bitterroot River partially inundates the subsidiary channels. Fish could into the floodplain channels at their downstream, upstream, or lateral points of connection with the Bitterroot River. This characteristic of floodplain channels vastly differs from tributaries in that there are more potential migrant sources for floodplain channels. For this reason, fish may only have to move a short lateral distance between the mainstem and the floodplain channel during high flow periods as opposed to swimming upstream a great distance from the confluence of the secondary channel and the mainstem. The transient vs. resident population effect and the source-distance effect may help explain the fish community differences found in the floodplain channels.

Seasonal Fish Use

Bitterroot River floodplain channels are seasonally valuable habitats for river fish species and age classes. Considering the abundance of YOY fish of at least six species, these floodplain channels likely provide important nursery habitats. In addition to using low gradient riffles and channel margin CWD, YOY fish inhabited shallow, temporary channel margins during the receding limb of the hydrograph. Warmer water temperatures and isolation from aquatic predators (Power et al. 1995; Brown and Moyle 1991) likely result in increased juvenile growth rates and survival. In a literature review, Sedell et al. (1990) found diverse backwater habitats to be integral nursery areas for a number of river fish species. Off-channel habitats were selectively utilized by adult Colorado pikeminnow (*Ptychocheilus lucius*), for spawning, while the YOY population also used these sites as nursery habitats (Tyus and McAda 1984). YOY brown trout inhabited pool, riffle, and backwater margins during late summer when most of the fishes' growth occurred (LaVoie and Hubert 1996). Similarly, more YOY brown trout were observed in shallow riffles than in the deeper runs inhabited by adults (Näslund et al. 1998). Killgore and Baker (1996) observed that YOY abundance in a floodplain channel actually increased with distance from the river channel, particularly when resources were exploitable in the surrounding flooded hardwood forest.

Prominent upwelling groundwater sources and heterogeneous substrates in the floodplain channels are important for over-wintering success. Surfacing groundwater moderates water temperatures and reduces ice formation. In Bitterroot River floodplain channels, juvenile fish were often seen positioned between pebbles and cobbles and swimming under surface ice when the channel perimeter was disturbed. Over-winter survival by juvenile fishes in floodplain channels not only creates diverse floodplain communities, but also creates a source of migrants for the primary channel.

As late season water temperatures rise, temperature intolerant species may select floodplain environments buffered by upwelling groundwater and riparian shading. These channels provide thermal refugia critical during the late season when mainstem environments are affected by solar warming. Brown trout population densities in southern Sweden were positively related to water temperature (Eklöv et al. 1999) that was regulated by abundant vegetation shading, although in that particular study, temperature was correlated negatively to the amount of shading.

One final purpose for sampling Bitterroot River floodplain channels was to investigate the prevalence of introduced non-salmonid species. Most introduced species have some undesirable effects on native species assemblages via competition or predation (Ross 1991). Introduced fish species success often depends on abiotic and biotic processes characterizing the aquatic habitat and the existing fish community (Moyle and Vondracek 1985; Baltz and Moyle 1993). Jones (1990) noted the presence of large mouth bass (*Micropterus salmoides*), pumpkinseed (*Lepomis gibbosus*), black bullhead catfish (*Ictaluras melas*), yellow perch (*Perca flavascens*), and northern pike (*Esox lucius*) in several lentic floodplain water bodies disconnected from the Bitterroot River except during infrequent high flow events. Jones' investigation indicated that these floodplain habitats supported introduced fish assemblages but were not extensively inhabited by salmonids. Although a lack of salmonids may have indicated biased sampling methods, these more environmentally stable (flows, moderate water temperature) habitats provide relatively benign habitats for nonnative fishes compared to the more fluctuating mainstem conditions. Although pumpkinseed and largemouth bass are known to populate off-channel lentic habitats in the Bitterroot Valley, including the sites sampled by Jones (1990), they were infrequently encountered in floodplain channels sampled in this study. A single pumpkinseed was sampled on two separate occasions in TCBR1. Cold upwelling groundwater and natural flow variation in floodplain channels may exclude the successful reproduction and population growth of these species that tend to prefer less fluctuating lentic environments. While introduced salmonids appear to exclude native trout from floodplain channels, introduced non-salmonid species only comprised a small proportion of fish communities inhabiting highly connected floodplain channels. Nonetheless, management of these introduced species may be imperative to preserving native fish populations.

Results of this study suggest that Bitterroot River floodplain channels offer a continuum of habitats that vary geographically, geomorphically, chemically, biologically, and temporally. The distribution of species and age classes inhabiting these floodplain channels indicate the importance of these sites both as nursery habitats for juvenile rearing as well as sites occupied by adults of several species. The proliferation of introduced salmonid species in these groundwater fed systems may be problematic for native westslope cutthroat which likely used these habitat types prior to nonnative salmonid introductions.

These sample channels may act as an important fish source for the primary Bitterroot River. Species inhabiting these sites may be flushed into the mainstem during high water periods or migrate between the mainstem and floodplain channels while these habitats are connected. As semi-independent systems, floodplain environments improve biological diversity and fish community stability (Sedell et al. 1990; Townsend and Hildrew 1994). Catastrophic mainstem events that diminish the standing fish stock may not affect more isolated backwater channels traversing the floodplain. Conversely, extended droughts that lower the floodplain aquifer elevation could diminish river-floodplain connectivity. Excessive surface water diversions on the central Bitterroot

River during the 1980's resulted in the desiccation of mainstem reaches between Tucker Crossing and Bell Crossing. If similar events occur in the future, floodplain channel fish communities would likely recover with the return of high water as mainstem fish seek high water refugia in secondary channel habitats. These interactions exemplify the importance of complex intact floodplains to river dynamics and associated biological communities.

Further research is necessary to identify the factors that define fish community structure in Bitterroot River floodplain habitats. Investigating the importance of these sites during high water periods would provide insights concerning the recolonization and recruitment of fish into floodplain channels.

Conclusions

- Objective 1 Results: Fish species-size classes using floodplain habitats were characterized.
  - Fish community richness and Shannon diversity tended to increase in a downstream direction although trends were not significant.
  - Floodplain channel fish communities included members of the native assemblage and introduced trout species. Native westslope cutthroat trout and bull trout were not sampled in the floodplain channels. Introduced non-salmonid fish were rare.
  - YOY and juvenile fish were more common than adults of large species such as rainbow trout and brown trout.
  - Large adult fish were excluded from some reaches due to shallow depths. These same reaches were often inhabited by abundant YOY (i.e. BCA-R2 and BCB-R1).

- Objective 2 Results: Floodplain channel fish communities changed over time as YOY fish emerged and older fish either migrated from sampled reaches or experienced mortality.
    - Brown trout and brook trout YOY displayed significant growth from August to September.
    - Fish communities may contain resident and transient fish. Some adult fish were sampled on multiple occasions.
    - The abundance of YOY fish and few adult fish suggest the importance of floodplain channel reaches as YOY and juvenile nursery areas.

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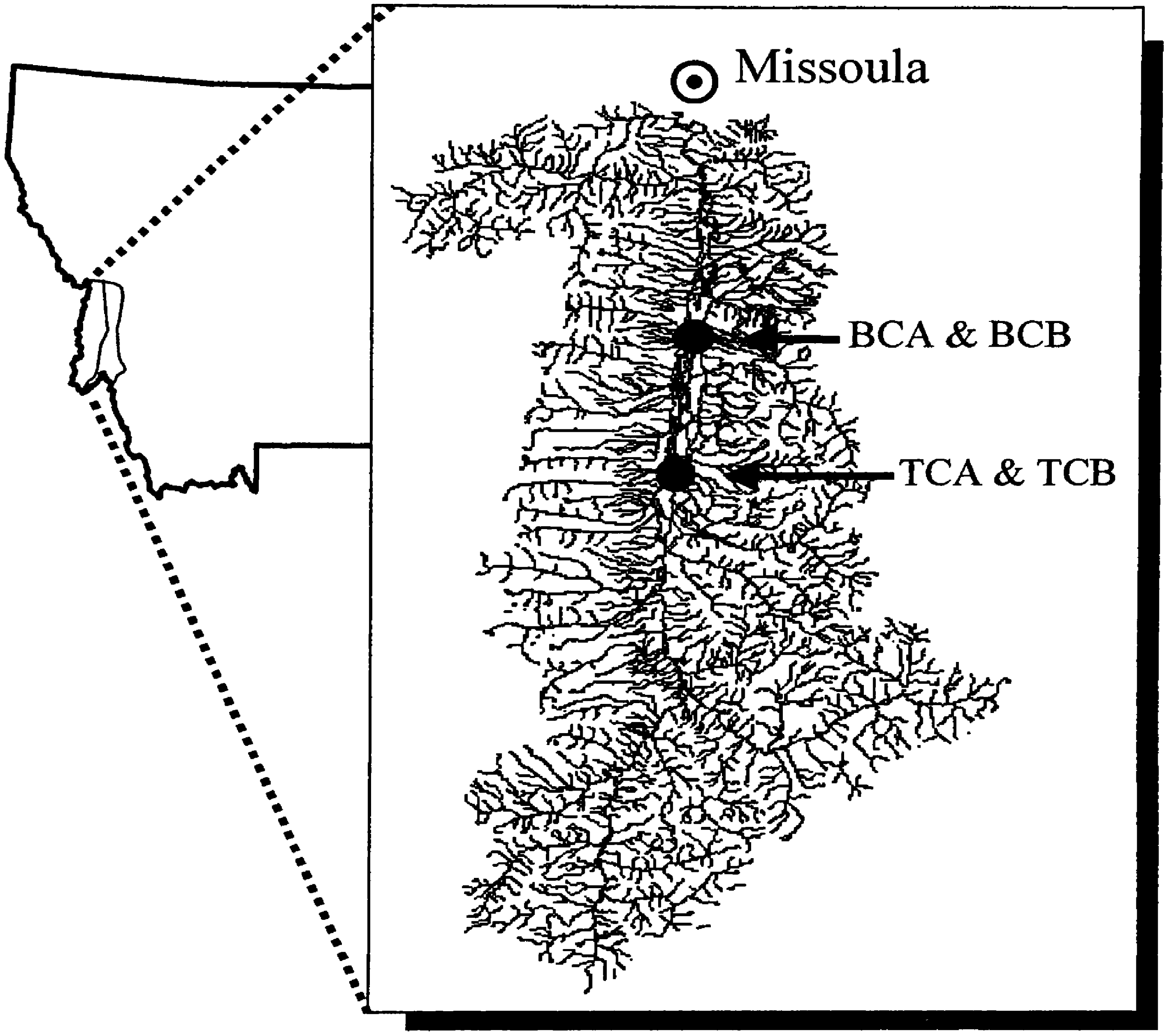


Figure 1: The Bitterroot River watershed and the Tucker Crossing and Bell Crossing sample sites.

Table 1: Physical habitat data for the sampled floodplain channel reaches.

		Floodplain Channel Reaches										
		TCA-R1	TCA-R2	TCA-R3	TCB-R1	TCB-R2	BCA-R1	BCA-R2	BCA-R3	BCB-R1	BCB-R2	BCB-R3
Distance to Bitterroot (m)*		129	998	1465	145	1146	18	348	541	42	515	842
Reach Area (m^2)		1037	472	266	560	947	744	380	866	905	813	740
Reach Volume (m^3)		331	128	40	108	295	187	83	307	141	270	191
Reach Width (m)	Average	10	8	3	6	7	7	5	7	7	8	8
	SD	3	2	1	2	2	2	3	3	4	3	3
Reach Depth (m)	Average	0.32	0.27	0.15	0.19	0.31	0.25	0.22	0.36	0.16	0.33	0.26
	SD	0.27	0.24	0.14	0.17	0.26	0.18	0.13	0.27	0.08	0.20	0.17
Depth Categories	0-0.3 m	63%	68%	87%	82%	56%	67%	72%	56%	98%	48%	69%
(% Coverage)	0.31 - 0.6 m	25%	23%	13%	15%	33%	32%	28%	29%	2%	48%	28%
	0.61 - 0.9 m	9%	9%	0%	3%	9%	1%	0%	12%	0%	4%	3%
	> 0.9 m	3%	0%	0%	0%	2%	0%	0%	3%	0%	0%	0%
Reach Substrate	Silt	0%	2%	0%	7%	0%	11%	0%	0%	0%	40%	44%
(% Coverage)	Sand	15%	18%	51%	68%	28%	75%	69%	29%	22%	3%	10%
	Gravel	10%	11%	6%	1%	16%	7%	4%	1%	4%	5%	4%
	Pebble	44%	42%	28%	13%	39%	4%	18%	32%	28%	20%	16%
	Cobble	30%	27%	16%	11%	18%	3%	9%	39%	47%	32%	26%
Substrate Cover	No Cover	60%	67%	91%	55%	85%	28%	27%	33%	32%	42%	52%
(% Coverage)	Aquatic Vegetation	30%	26%	0%	36%	6%	72%	73%	57%	68%	35%	39%
	Boulder	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	Small Woody Debris	2%	3%	0%	4%	5%	0%	0%	2%	0%	10%	8%
	Large Woody Debris	8%	5%	9%	5%	4%	0%	0%	4%	0%	13%	1%
	Bank	0%	0%	0%	0%	0%	0%	0%	4%	0%	0%	0%
Water Column Cover	No Cover	80%	76%	93%	77%	80%	26%	38%	59%	47%	50%	55%
(% Coverage)	Aquatic Vegetation	8%	15%	0%	15%	3%	72%	62%	33%	52%	29%	38%
	Boulder	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	Small Woody Debris	2%	3%	0%	2%	8%	1%	0%	2%	0%	10%	6%
	Large Woody Debris	8%	5%	7%	6%	8%	1%	0%	3%	0%	11%	1%
	Bank	1%	2%	0%	0%	1%	0%	0%	2%	0%	0%	0%

*: Distance to the Bitterroot River was measured from the downstream extent of each reach to the Bitterroot River.

Table 2: Channel diversity variables calculated using the Shannon-Weaver diversity index. Sites with a higher value for a particular variable are more diverse for that variable than a site with a low diversity score.

Channel Reach	Depth Diversity	Substrate Diversity	Substrate Cover Diversity	Column Cover Diversity
BCA-R1	1.97	2.38	1.82	1.98
BCA-R2	1.81	2.50	1.79	1.94
BCA-R3	2.84	3.09	2.74	2.57
BCB-R1	1.12	3.22	1.87	2.01
BCB-R2	2.32	3.74	3.40	3.24
BCB-R3	2.07	3.95	2.48	2.61
TCA-R1	2.61	3.46	2.60	2.08
TCA-R2	2.26	3.78	2.38	2.24
TCA-R3	1.47	3.18	1.34	1.30
TCB-R1	1.74	2.75	2.63	2.10
TCB-R2	2.66	3.75	1.80	2.07

Table 3: Electrofishing results for the sampled floodplain channel reaches.

Channel Reach	Total Individuals	Species-Length Class Richness	Shannon Diversity*
BCA-R1	74	11	8.94
BCA-R2	47	5	3.31
BCA-R3	31	4	3.44
BCB-R1	78	11	6.26
BCB-R2	33	8	5.24
BCB-R3	23	4	3.01
TCA-R1	57	10	6.99
TCA-R2	27	13	7.94
TCA-R3	26	5	3.80
TCB-R1	42	5	3.86
TCB-R2	31	9	6.82

*: Shannon diversity is based on species-length classes.

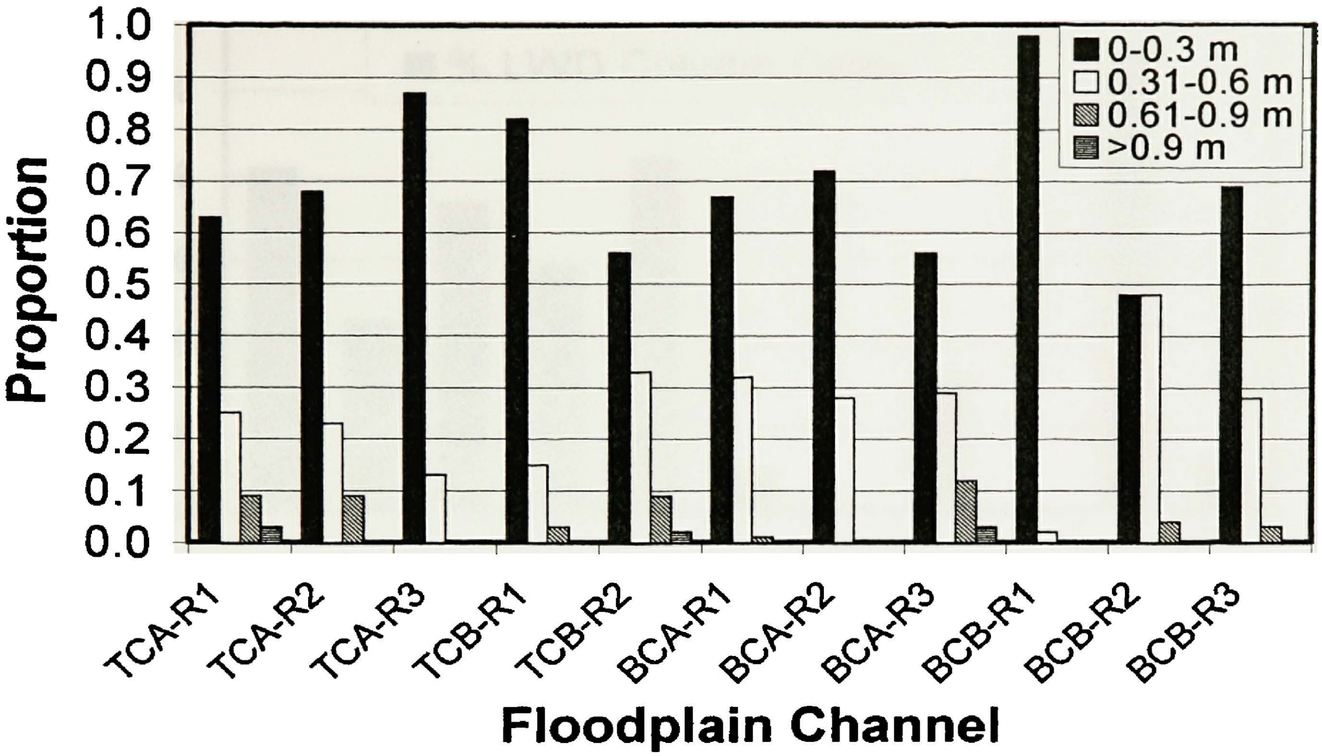


Figure 3: Depth classes measured in the Tucker Crossing and Bell Crossing floodplain channels.

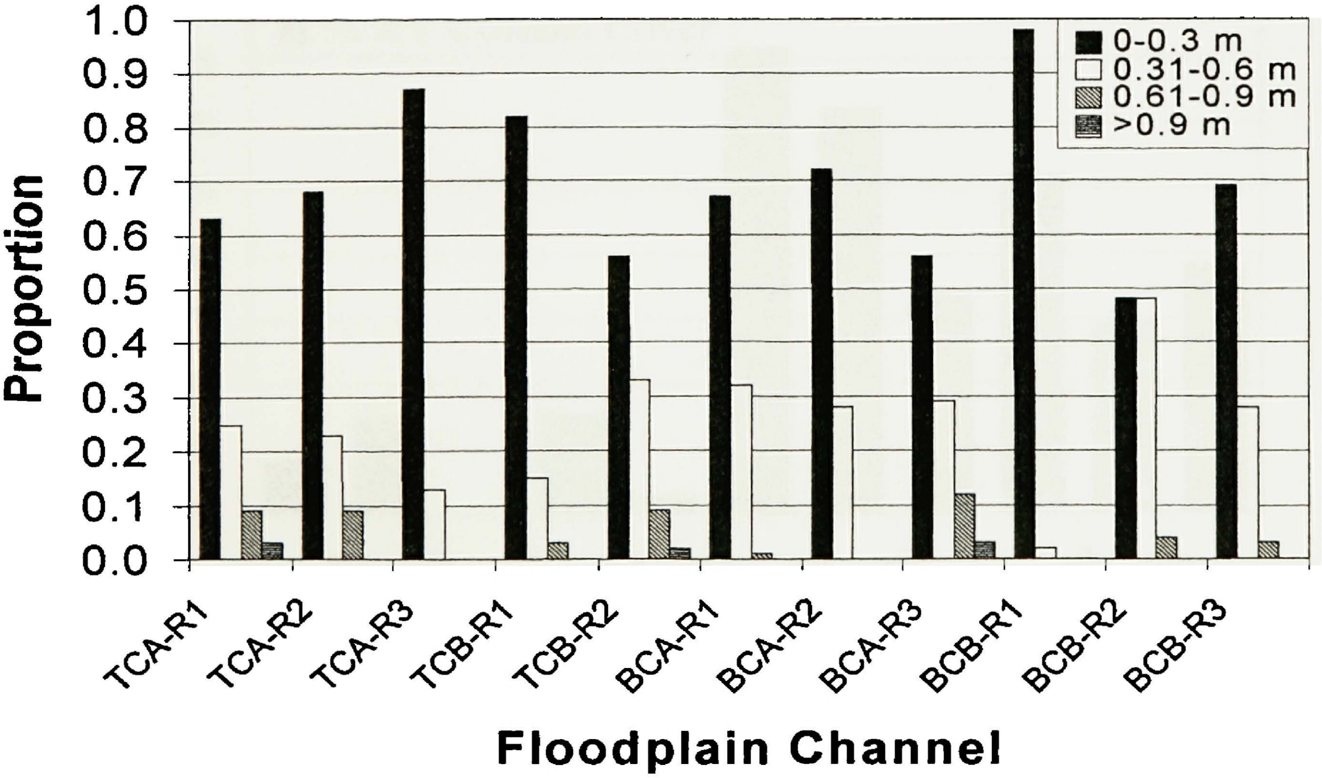


Figure 4: Substrate composition in the Tucker Crossing and Bell Crossing floodplain channels.

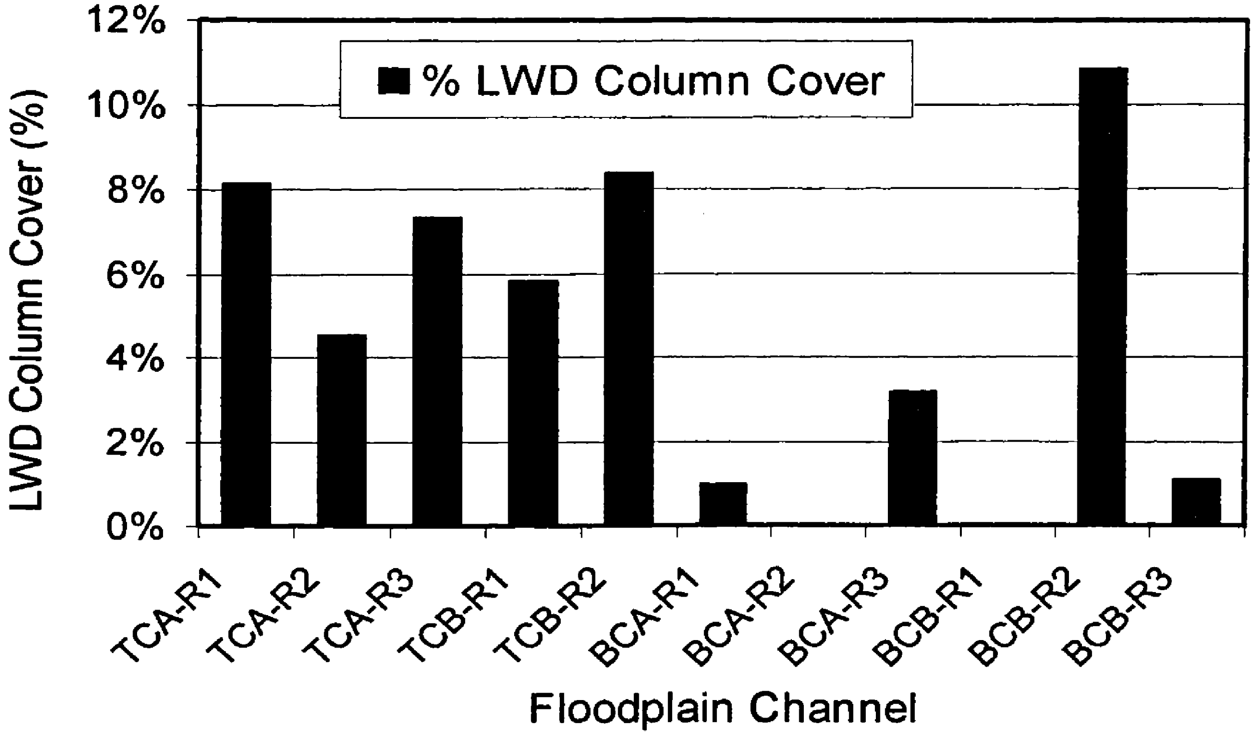


Figure 5: The distribution of large woody debris water column cover in the floodplain channels. Percentage represents the number of points that were sampled that included large woody debris cover.

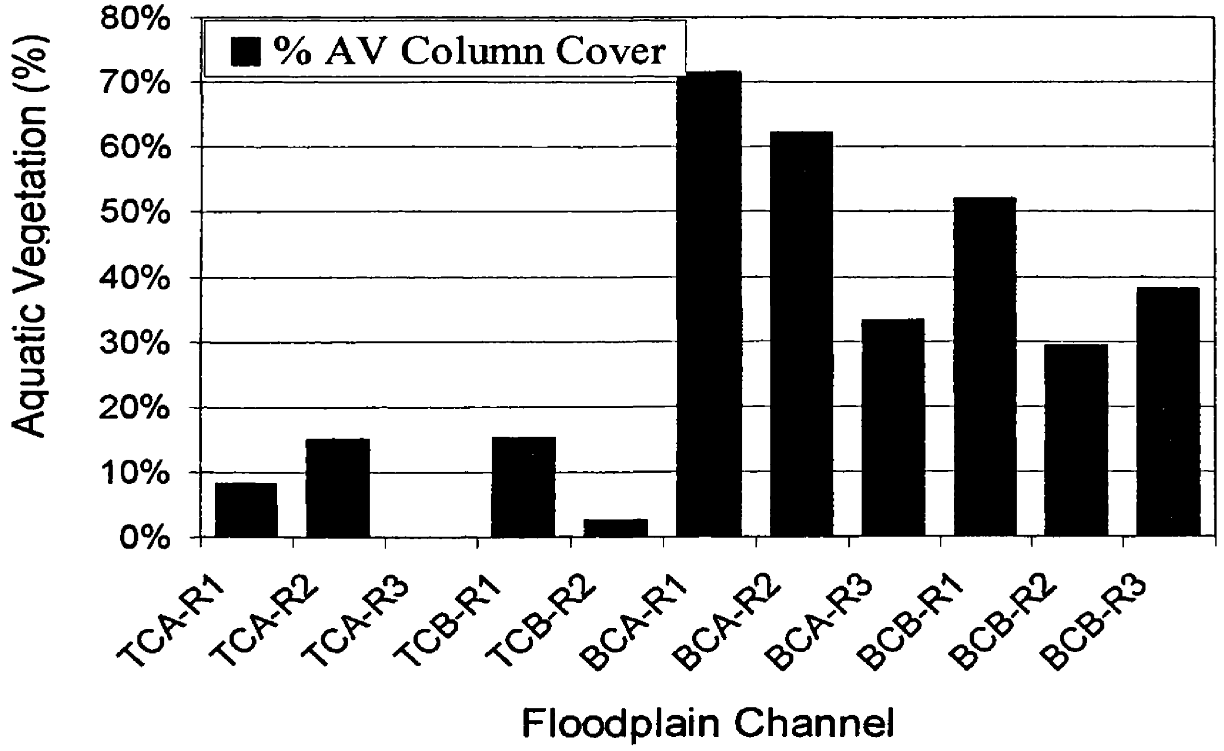


Figure 6: The distribution of aquatic vegetation water column cover in the floodplain channels. Percentage represents the number of points that were sampled that included aquatic vegetation cover.

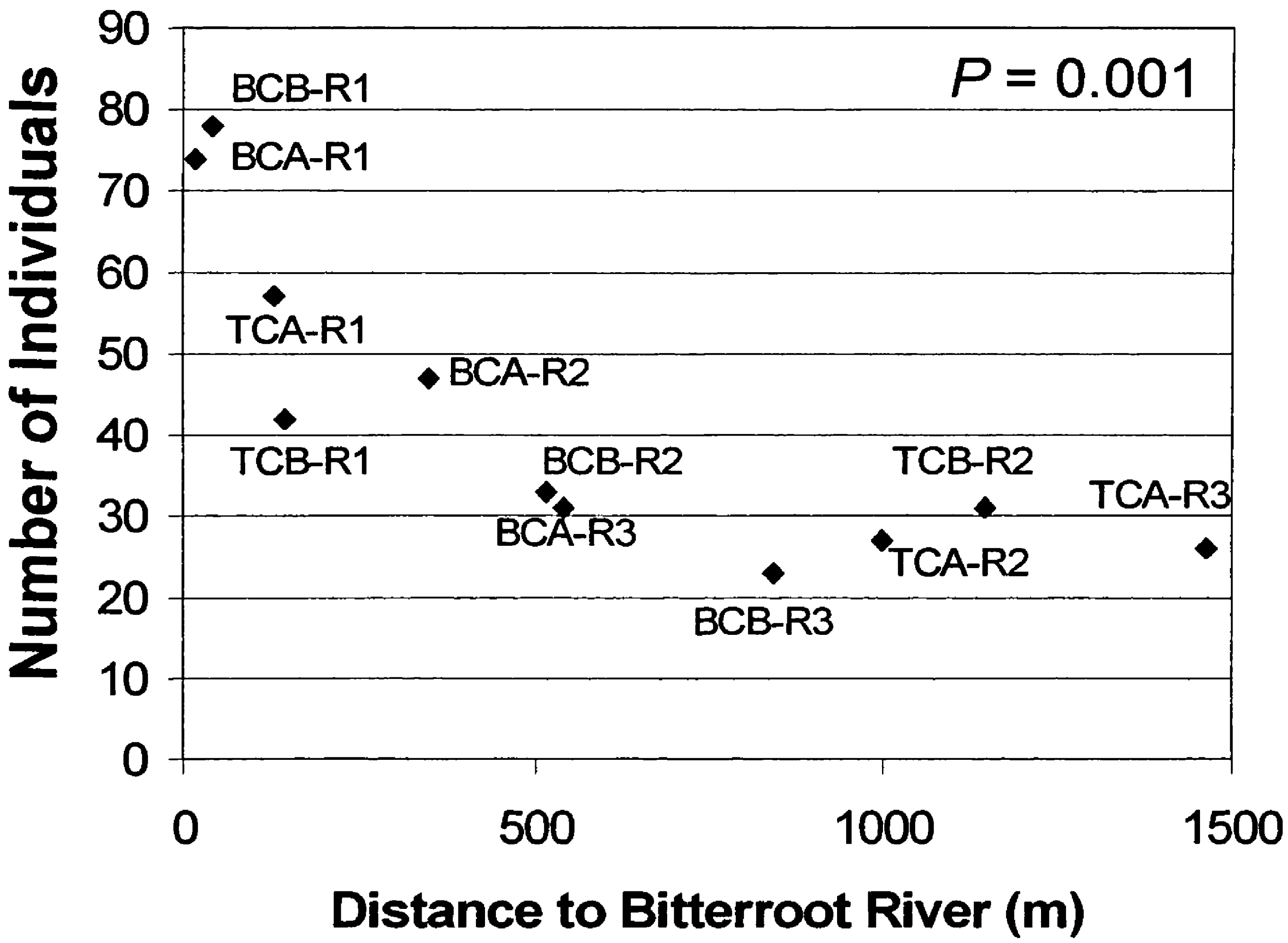


Figure 7: Scatterplot of the number of individuals sampled in floodplain channel reaches vs. reach distance to the Bitterroot River. Reaches closer to the Bitterroot River maintained larger fish communities (Kendall's tau, $P = 0.001$)

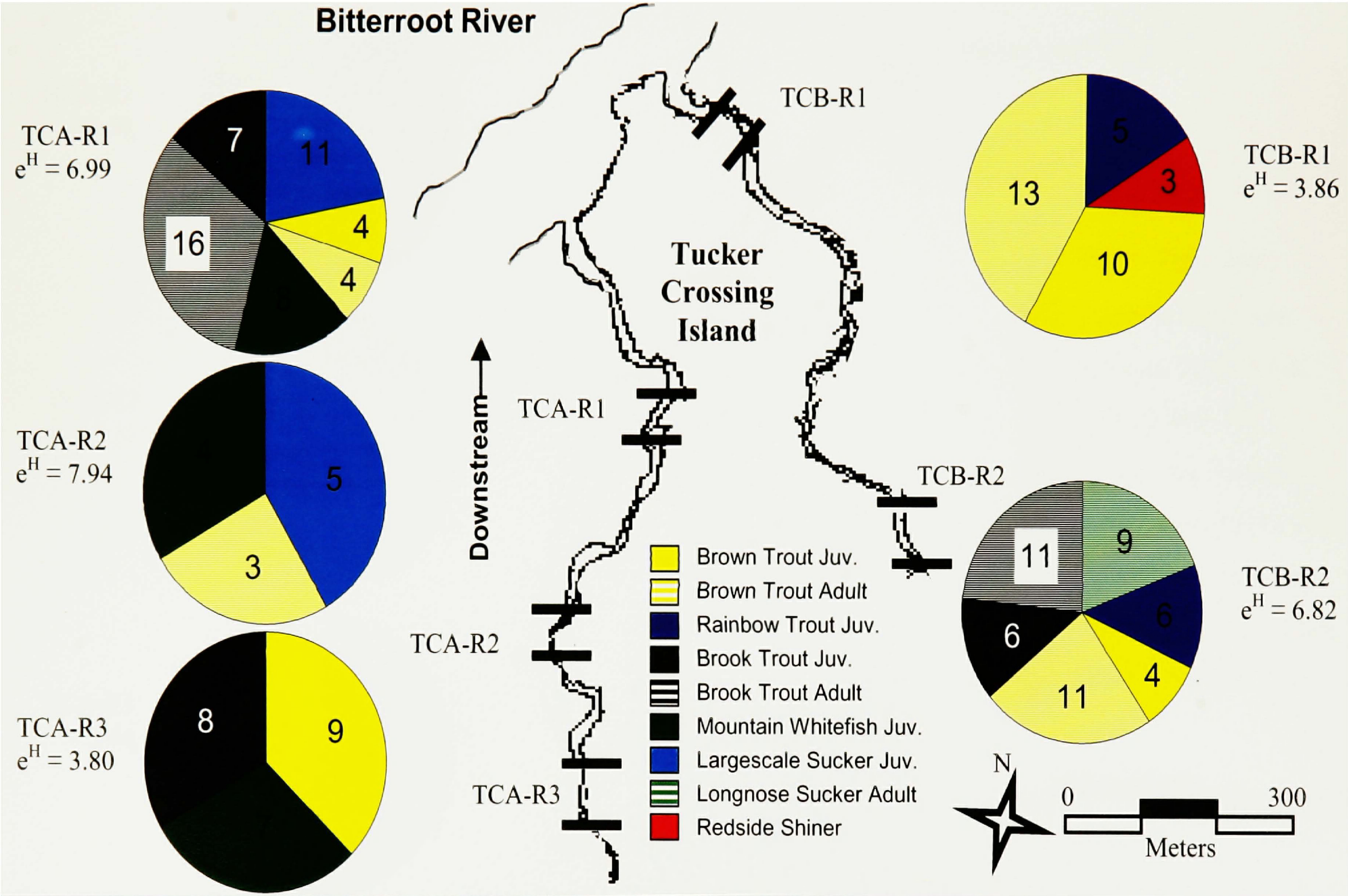


Figure 8: Distribution and abundance of fish species-length classes sampled in Tucker Crossing Channel A and Channel B. Data are pooled over three sampling periods due to low numbers of individual fish. Pie charts illustrate sampled species-length classes that were represented by at least three individuals. Numbers in the pie charts represent the number of individuals of each species-length class. The e^H refers to the Shannon-Weaver diversity index coefficient. The e^H includes rare species-length classes (< 3 individuals) that are not incorporated in the pie charts.

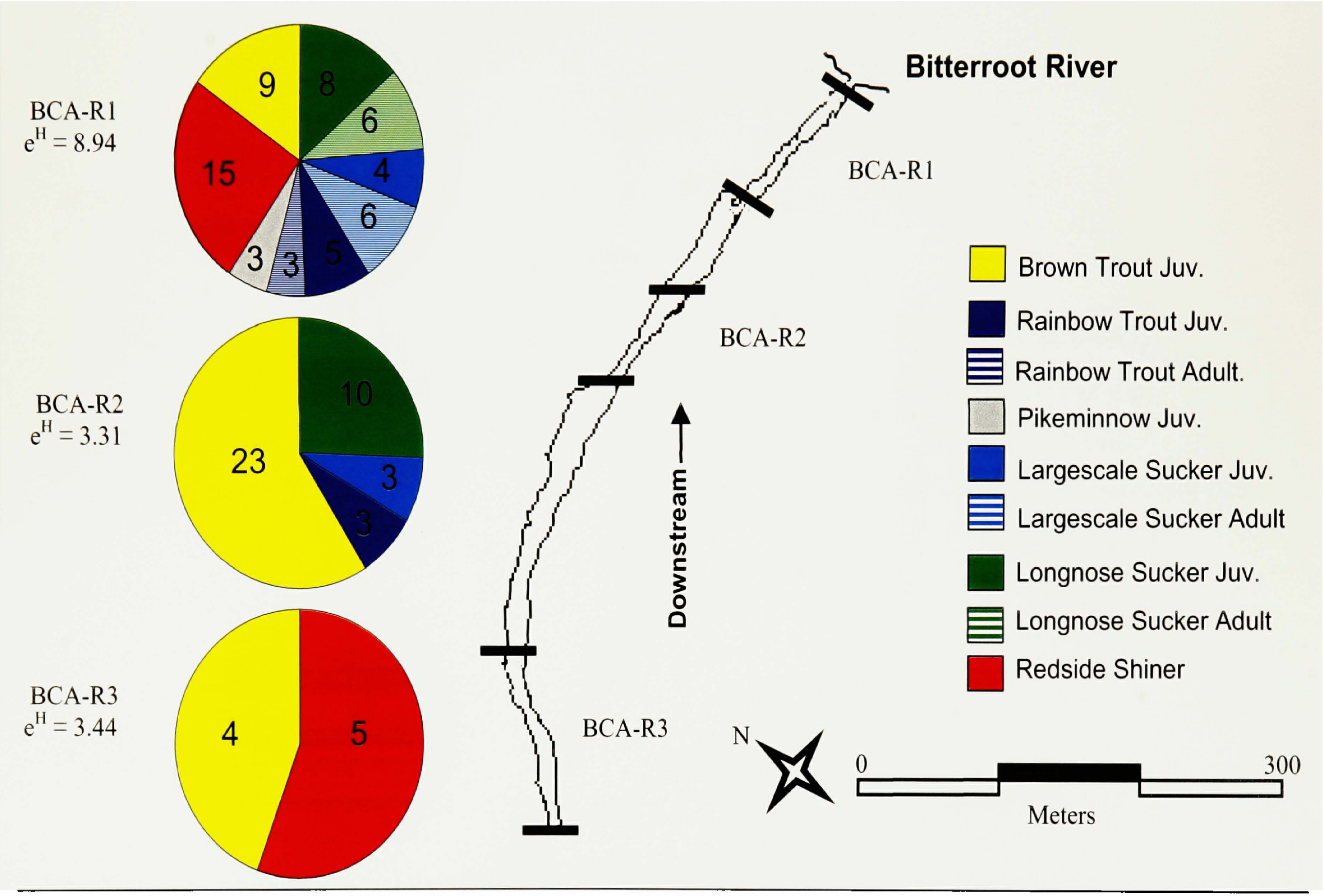


Figure 9: Distribution and abundance of fish species-length classes sampled in Bell Crossing Channel A. Data are pooled over three sampling periods due to low numbers of individual fish. Pie charts illustrate sampled species-length classes that were represented by at least three individuals. Numbers in the pie charts represent the number of individuals of each species-length class. The e^H refers to the Shannon-Weaver diversity index coefficient. The e^H includes rare species-length classes (< 3 individuals) that are not incorporated in the pie charts.

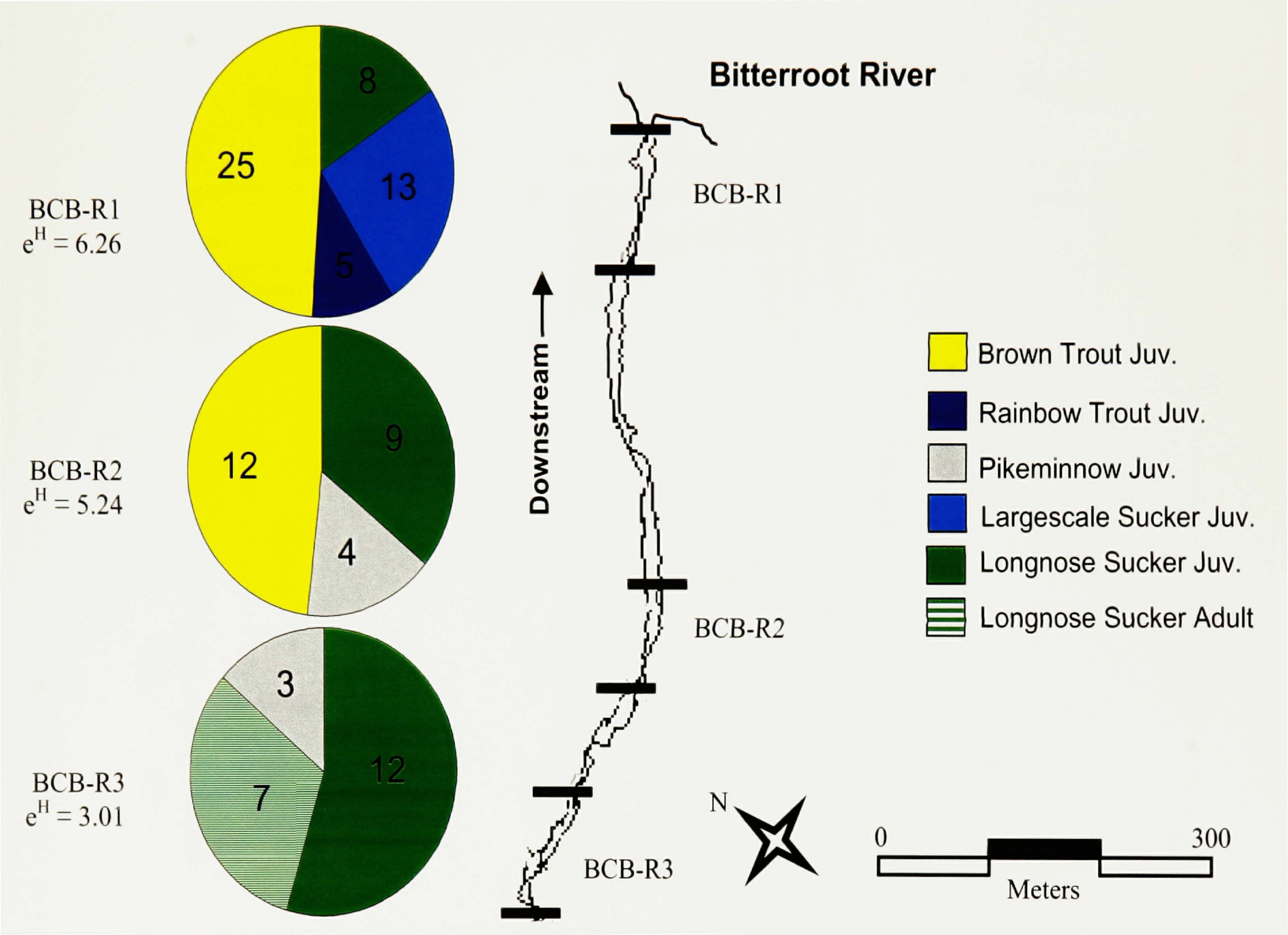
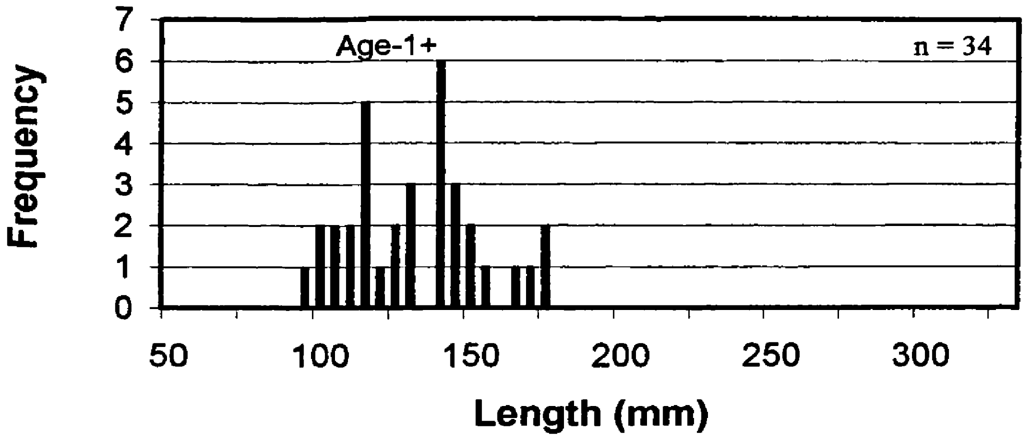
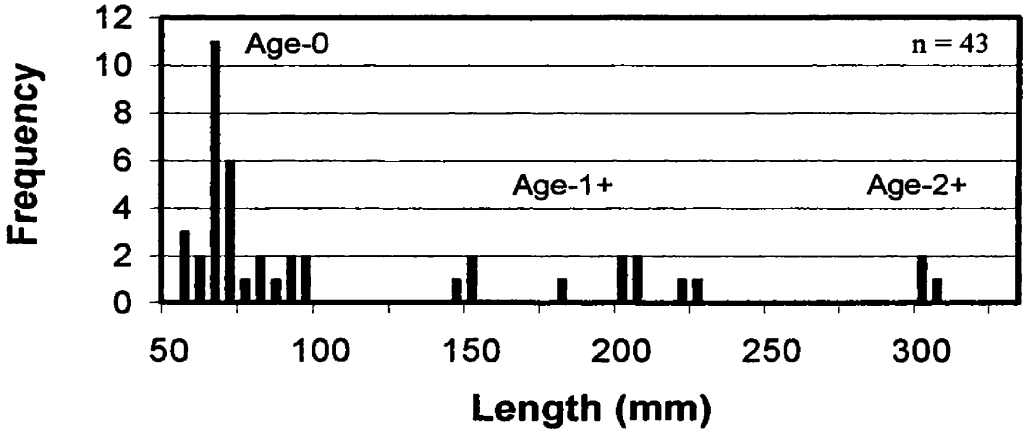


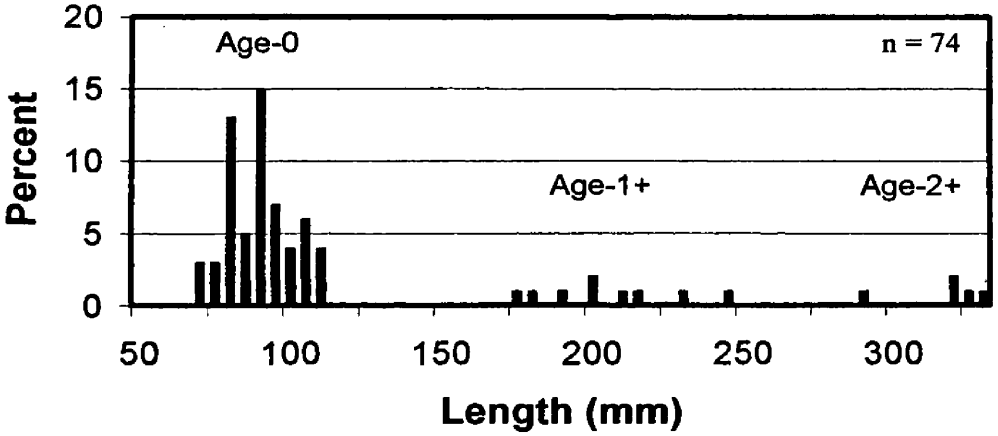
Figure 10: Distribution and abundance of fish species-length classes sampled in Bell Crossing Channel B. Data are pooled over three sampling periods due to low numbers of individual fish. Pie charts illustrate sampled species-length classes that were represented by at least three individuals. Numbers in the pie charts represent the number of individuals of each species-length class. The e^H refers to the Shannon-Weaver diversity index coefficient. The e^H includes rare species-length classes (< 3 individuals) that are not incorporated in the pie charts.

a) March 1999



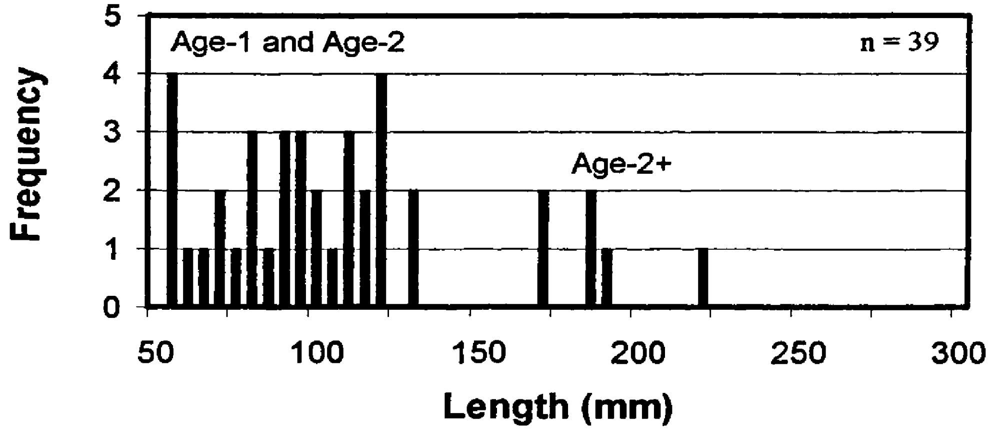
c) September 1999





igure 11: Length frequencies for brown trout sampled in Bitterroot River floodplain channels between March nd September 1999. Three distinct age groups are apparent in the August and September samplings. Young-of-ear fish (age-0) were significantly larger ($P < 0.001$) in September than in August 1999.

a) March 1999



b) September 1999

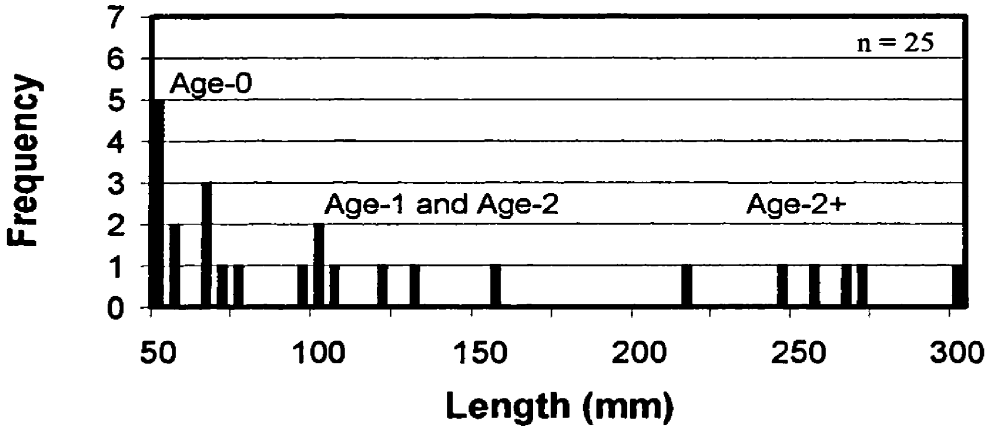
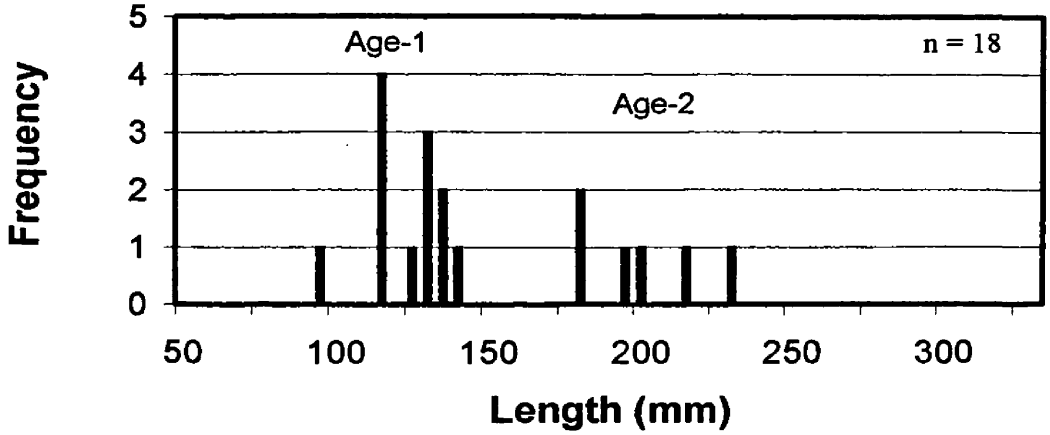
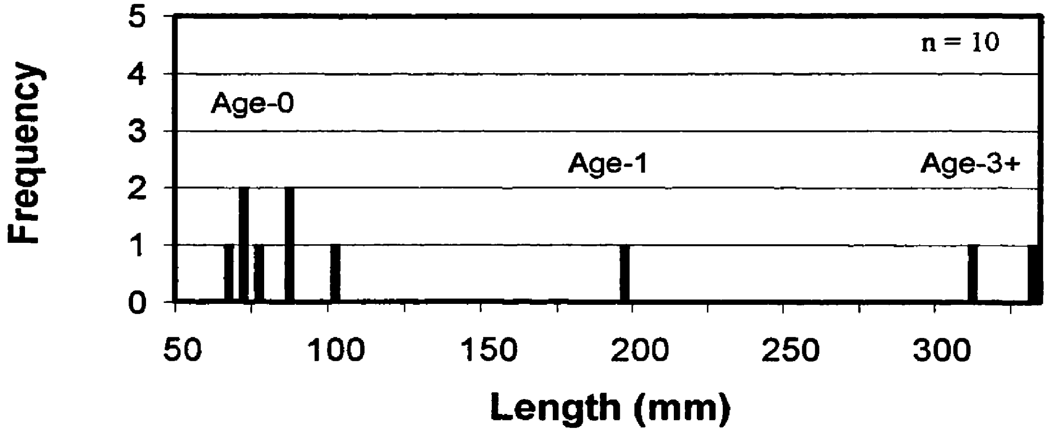


Figure 12: Length frequencies for longnose suckers sampled in Bitterroot River floodplain channels in March and September 1999. The March sampling displays an influx of young-of-year individuals into the floodplain channels.

a) March 1999



b) August 1999



c) September 1999

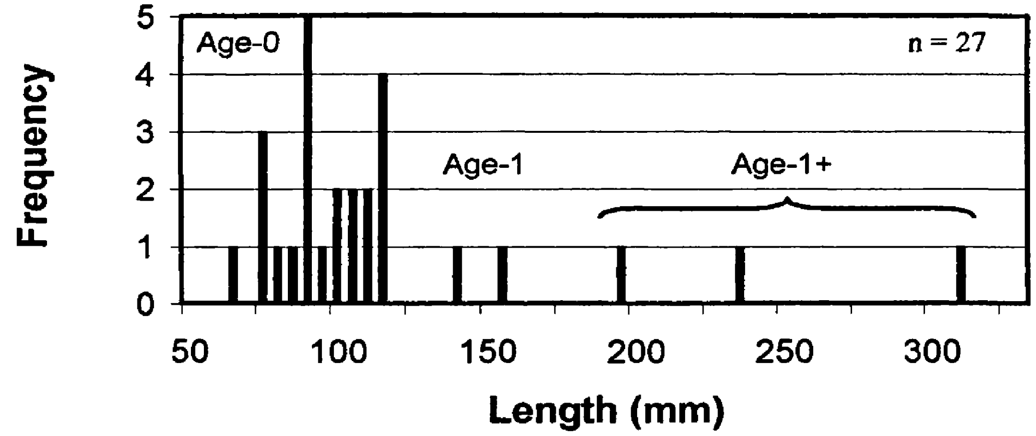
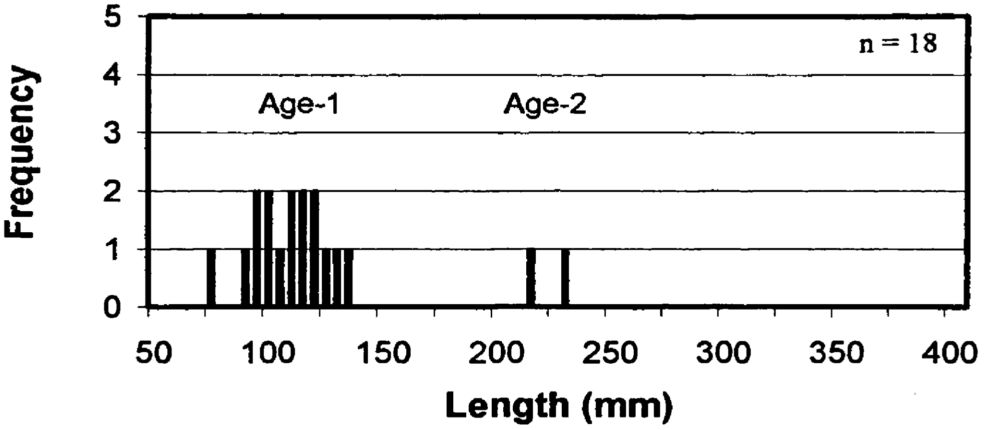


Figure 13: Length frequencies for brook trout sampled in Bitterroot River floodplain channels between March and September 1999. An influx of young-of-year fish is apparent in the September sampling. Young-of-year fish were significantly larger ($P = 0.033$) in September than in August 1999.

a) March 1999



b) September 1999

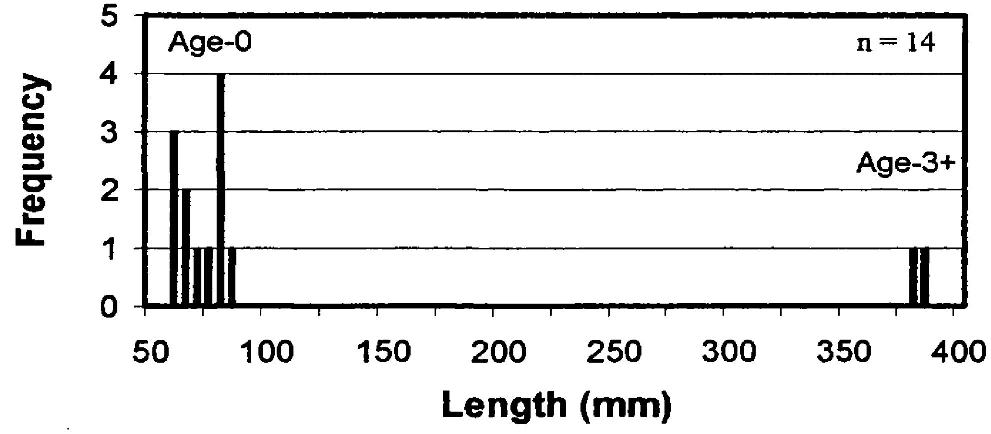
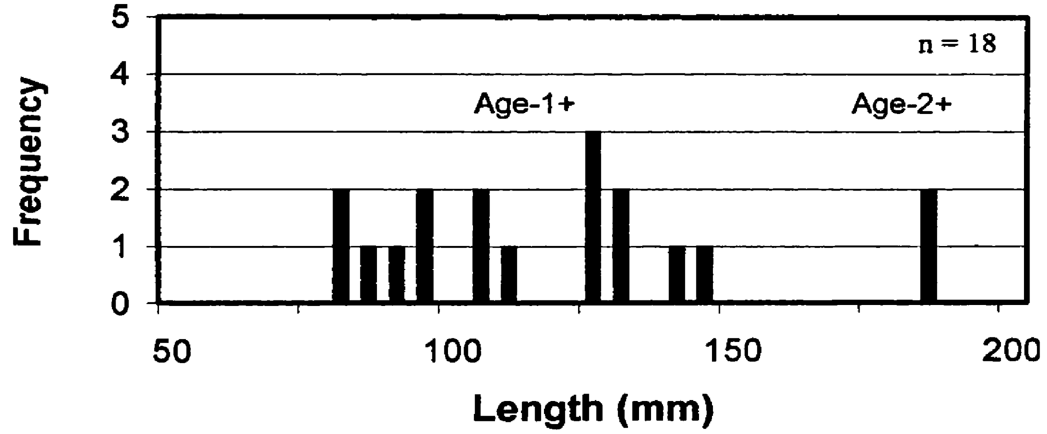


Figure 14: Length frequencies for rainbow trout sampled in Bitterroot River floodplain channels between March and September 1999. The September sampling displays an influx of young-of-year individuals into the floodplain channels.

a) March 1999



b) September 1999

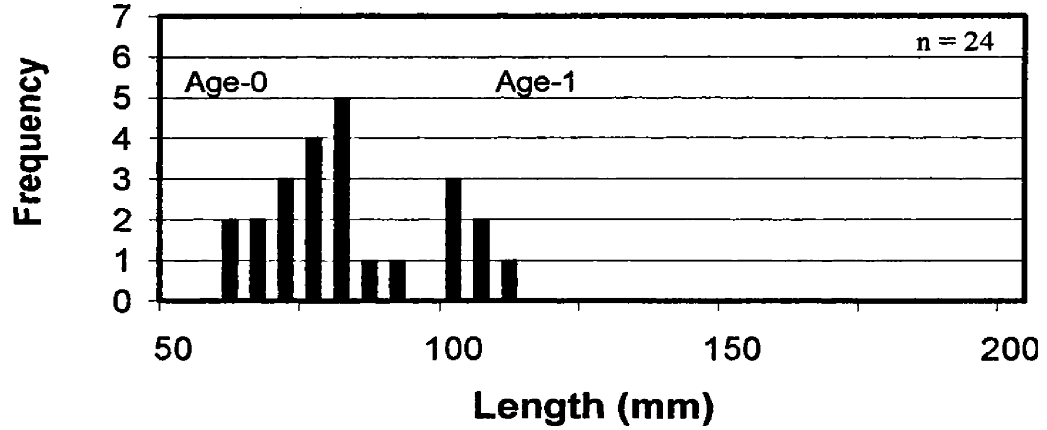


Figure 15: Length frequencies for largescale suckers sampled in Bitterroot River floodplain channels between March and September 1999. The September sampling displays an influx of young-of-year individuals into the floodplain channels.

Table 4: Total length and weight for commonly sampled species in Bitterroot River floodplain channels. Values are averages with one standard deviation in parentheses.

Date	Fish Species	n	Total Length (mm)	Weight (g)
03-99	Brown Trout	34	146.67 (14.01)	28.07 (9.81)
	Rainbow Trout	18	120.28 (40.36)	22.71 (32.52)
	Brook Trout	18	147.06 (40.81)	32.37 (32.01)
	Longnose Sucker	39	105.05 (41.77)	16.66 (24.14)
	Largescale Sucker	18	116.67 (30.62)	16.37 (15.71)
08-99	Brown Trout	43	112.19 (73.73)	20.3 (33.28)
	Brook Trout	10	138 (103.51)	12.06 (20.76)
09-99	Brown Trout	74	121.68 (76.99)	25.13 (46.58)
	Rainbow Trout	14	114.43 (113.92)	31.7 (71.31)
	Brook Trout	27	114 (53.75)	23.94 (44.36)
	Longnose Sucker	25	120.40 (83.34)	30.45 (55.64)
	Largescale Sucker	24	79.54 (14.67)	4.85 (2.72)