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Bradley J. Cavallo
The University of Montana

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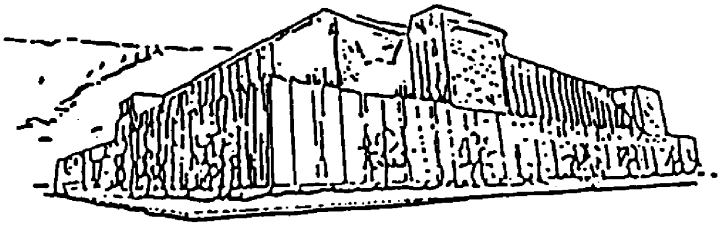

FLOODPLAIN HABITAT HETEROGENEITY AND THE DISTRIBUTION, ABUNDANCE, AND BEHAVIOR OF FISHES AND AMPHIBIANS IN THE MIDDLE FORK FLATHEAD RIVER BASIN, MONTANA

by

Bradley J. Cavallo

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Approved by:

Chairperson

Dean, Graduate School

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Floodplain habitat heterogeneity and the distribution, abundance, and behavior of fishes and amphibians in the Middle Fork Flathead River basin, Montana

Advisor: Christopher A. Frissell CAF

Main river channel branches, isolated floodplain ponds, and low-gradient springbrooks, through the mixing of surface water and groundwater, create a mosaic of thermal habitats different from those of surface-fed tributaries and laterally confined rivers. I quantified thermal variation and other physical habitat variables between reaches, and studied the influence of this habitat template on distribution and behavior of fishes and amphibians. From summer of 1994 through summer of 1996 I conducted regular habitat and temperature surveys of main channel anabranches, floodplain ponds and springbrooks and observed aquatic vertebrate distribution in day and night snorkel surveys.

Floodplain habitat types expressed relatively distinct assemblages and densities of aquatic vertebrate species-age classes, reflecting different physical conditions characterizing reach types. Young-of-the-year longnose suckers *Catostomus catostomus*, mountain whitefish *Prosopium williamsoni*, and boreal toad tadpoles *Bufo boreas* dominated pond assemblages where they exhibited varying associations with warm, shallow edge microhabitats. Springbrook reaches had the lowest diversity and were dominated by nonnative brook trout *Salvelinus fontinalis* of all age classes. Main channel assemblages exhibited high diversity and evenness, but densities of salmonids were generally higher in off-channel habitats.

Nocturnal activity was common in all reaches among some species (adult and subadult bull trout *Salvelinus confluentus*, brook trout, longnose suckers), but was especially prevalent in springbrooks reaches. A springbrook sampled on McDonald Creek was occupied by densities and size distributions of nocturnal westslope cutthroat trout (*Oncorhynchus clarki lewisi*) nearly identical to those of brook trout observed in the Middle Fork. These observations suggest cutthroat trout have been excluded from the Middle Fork springbrook by brook trout, and conflict with evidence supporting cold waters as habitats providing refugia for native salmonids. Innate physiological traits determining efficiency of nocturnal foraging could profoundly influence the outcome of species interactions where nocturnalism is an important behavioral mode (e.g. springbrooks). Relative thermal and hydrologic stability may also render groundwater influenced habitats more invasible, compromising floodplain habitats as reproductive or winter refugia for native species such as westslope cutthroat trout and bull trout.

Acknowledgments

Many thanks to the staff of the Flathead Lake Biological Station, and to my friends and fellow graduate students for their camaraderie and occasional, sometimes reluctant, but always much appreciated assistance with field work. My committee members (Jack Stanford, Vicki Watson and Chris Frissell) were smart, responsive and quick to offer suggestions, and for this I am grateful. Chris Frissell in particular, has been a source of inspiration, ideas and encouragement from the beginning; a wayward graduate student couldn't hope for a better major advisor. Special thanks also to Geoff Poole for his plentiful (and reasonably priced) contributions to this study. I shudder to think what this all might look like without the guidance and labors of those two. Much is owed also to my family (Mom, Dad, Greg) and to the affable and lovely Carrie Ann Ingram (girlfriend). Without them this whole experience certainly would have resulted in my withdrawal from society, and eventual purchase of a small cabin where I could manufacture mail bombs at my leisure. On that note, I'd also like to offer some heartfelt ingratitude to select curmudgeons of the DBS faculty whose mistrust and pettiness was a source of recurrent annoyance. Funding was provided by the Environmental Protection Agency and the National Science Foundation EPSCoR project.

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CHAPTER 1

AN INTRODUCTION TO: FLOODPLAIN HABITAT HETEROGENEITY AND THE DISTRIBUTION, ABUNDANCE, AND BEHAVIOR OF FISHES AND AMPHIBIANS IN THE MIDDLE FORK FLATHEAD RIVER BASIN, MONTANA

Floodplains are widely recognized as integral components of riverine ecosystems, and in recent decades stream ecologists have come to recognize the significance of the land-water interface, and hence the folly of "divorcing the stream from its valley" (Hynes 1975). In large rivers, connections between river channel, riparian zone and floodplain create transverse habitat heterogeneity over larger scales than in small streams, or laterally confined rivers (Decamps et al. 1988; Naiman et al. 1988; Pinay et al. 1990). Connectivity and interactions along the vertical dimension, between surface water and groundwaters, also are increasingly recognized as significant drivers of riverine process and function (Gilbert et al. 1990; Stanford and Ward 1993; Brunke and Gonser 1997).

Natural, functioning floodplains benefit fishes by providing increased food base, spawning and rearing habitat, and refuge from flooding or other environmental extremes (Welcomme 1979). In large tropical and temperate rivers, the ecology of fluvial fishes in relation to floodplains has been the subject of numerous investigations (reviews in Lowe-McConnell 1975; Welcomme 1979; Copp 1989). Less studied are the intermountain floodplains of gravel-bed rivers, common in glaciated regions worldwide (Rosenshein 1988). These floodplains typically occur repeatedly as aggraded river segments followed and preceded by confined river segments (Stanford and Ward 1993). Like other floodplains, intermountain floodplain surfaces display a diverse array of aquatic habitats, but differ in that these habitats are profoundly influenced by the emergence and downwelling of large volumes of groundwater.

Groundwater upwelling on floodplain surfaces can create thermal complexity at a range of spatial scales. Localized seepage in pools or side channels can result in small scale thermal patches (Ozaki 1988), while discrete upwelling along the river bed can produce longitudinal temperature patterns for many kilometers downstream (Beschta et al. 1987; Sullivan et al. 1990). In previous research, Stanford and Ward (1988, 1992, 1993), have characterized some patterns of surficial eruption of hyporheic flows. Effluent groundwaters may enter mainstem channels directly where they are subjected to immediate mixing with surfaces waters. Off-channel habitats, such as floodplain springbrooks, occur in abandoned river channels and exhibit seasonally dynamic hydrographs controlled by the intrusion of surface waters during flood events, and the supply of groundwater from the hyporheic. Small and ephemeral springbrooks are common on low terrace paleochannels and in abandoned active channels with weak sources of hyporheic flow. Such active channel seepages often form hydrologically dynamic floodplain ponds as they feed into and out of flood filled scour pools. Large, perennial springbrooks with stable and consistent hydrographs occur in relict mainstem channels. These springbrook channels are typically blocked at the upstream end by alluvial deposits, woody debris and riparian vegetation. As a result, the are subjected to surface flows only during severe flooding. All of these habitats are to a greater or lesser extent influenced by cool groundwaters and warming due to solar radiation, resulting in a mosaic of heterogeneous aquatic habitats exhibiting a diversity thermal gradients.

In aquatic ecosystems, the structure of biotic communities as well as the persistence of populations and species, may be directly or indirectly regulated by the diversity of habitats and thermal gradients available (Frissell et al. 1986; Pringle et al. 1988; Stanford and Ward 1988; Cech et al. 1990). Life history events of locally adapted fishes are closely adapted to prevailing thermal regimes (Beacham and Murray 1987; Holtby 1988; Hartman and Scrivener 1990). The availability of a diverse array of thermal habitats in an aquatic ecosystem provides fishes and other ectothermic organisms the opportunity to thermoregulate and optimize energy intake relative to metabolic costs (Brett 1971; Medvick et al. 1981; Smith and Li 1983; Berman and Quinn 1991; Hall et al. 1992; Snucins and Gunn 1995). Among coldwater, riverine fishes water temperature can also be an important factor influencing diel activity patterns (e.g. Fraser et al. 1993; Riehle and Griffith 1993). In warmer climates, coldwater-dependent fishes may persist by seeking refuge in groundwater-cooled habitats (Meisner 1990; Nielsen 1991; Li and Moyle 1993). Floodplain springbrooks and other groundwater-warmed habitats can also be important in providing habitat for spawning, egg incubation, rearing and shelter from adverse flow and ice conditions in the main channel during winter months (Craig and Poulin 1975; Cunjak and Power 1986; Sedell et al. 1990; Stanford and Ward 1992).

Water temperature also becomes ecologically significant through its potential mediation of biotic interactions such as competition and predation (Magnuson et al. 1979; Baltz et al. 1982; Reeves et al. 1987; Hill and Magnuson 1990; Vigg and Burley 1991). In some cases, organisms are known to actively seek thermal patches serving as refugia from predation (Fraser and Cerri 1982) or competition (Gehlbach et al. 1978; Magnuson et al. 1979). Habitat diversity and thermal complexity may decrease the incidence and severity of such interactions by allowing increased opportunities for interspecific partitioning.

Nonnative fishes, because they are not coevolved with natives, present special and serious threats as competitors and predators of native species. The impact of nonnatives is heightened in many systems by their proliferation and success in aquatic habitats altered by human activities (Li et al. 1987). Despite the widespread threat and impact of nonnative fishes no studies to date have examined the role of thermal habitat complexity in mediating interactions between native and introduced fishes, although several sources have mentioned the potential importance of such phenomena (e.g. Li et al. 1987; Nielsen 1991; Moyle and Leidy 1992; Li and Moyle 1993). Two native, coldwater-dependent species occurring in our study area, bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarki lewisi*, appear most resistant to invasion by introduced salmonids in headwaters or spring-fed streams, which ostensibly function as coldwater refugia (Howell and Buchanan 1992; De Staso and Rahel 1994; Young 1995). However, no previous studies have examined how the presence of introduced species such as brook trout, affects the utilization of groundwater influenced habitats, or the extent to which such impacts may contribute to the decline and local extirpation of native salmonids.

Despite the habitat diversity and environmental gradients characteristic of floodplains, few studies have holistically addressed how these complexities direct species distribution and assemblage structure of aquatic vertebrates. The complex thermal and physical factors structuring aquatic floodplain habitats also provide an excellent setting in which to evaluate the influence of temperature on the distribution, behavior and potential for interactions among native and nonnative species. Information on the ecological affinity and relative productivity of different floodplain habitats is valuable in that it may help anticipate losses in biological diversity or productivity which may result from anthropogneic disturbances such as river regulation, channelization or the introduction of exotic species. In my study I addressed the following questions: What thermal regimes, spatial thermal complexities and physical habitat variables characterize floodplain habitat types including springbrooks, floodplain ponds and main channel anabranches? How are fish species-age classes distributed among floodplain reach types (macrohabitats) and within reach types (microhabitats)? Do fishes utilize floodplain springbrooks as seasonal refugia from harsh mainstem conditions? How do diel activity patterns and movements differ seasonally and among floodplain habitats? What is the role of groundwater influenced floodplain habitats in buffering native species from displacement by invading non-natives? And what is the relative contribution of off-channel habitats to the overall productivity of the river system?

Chapter 2 provides an overview on the distribution and abundance of aquatic vertebrates in the study areas as influenced by a heterogeneous habitat template strongly structured by relatively large-scale groundwater upwelling and complexly branched and shifting river channels in a functioning, natural floodplain. The necessity for accurate estimates of abundance and data on activity patterns among fishes required that I conduct biological surveys during both day and night hours. Chapter 3 describes my findings of diel activity patterns among fishes in the Nyack floodplain, and assesses the potential implications and significance of nocturnalism as they relate to sampling methods and understanding of coldwater, riverine fish ecology. Chapter 4 focuses on the patterns and significance of nonnative brook trout invasion and exclusion of native salmonids form cold, low gradient and hydrologically stable floodplain springbrooks.

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CHAPTER 2

DISTRIBUTION AND ABUNDANCE OF FISHES AND AMPHIBIANS IN HETEROGENEOUS AQUATIC HABITATS OF THE NYACK FLOODPLAIN

Introduction

In recent decades stream ecologists have come to recognize the significance of the land-water interface, and hence the folly of "divorcing the stream from its valley" (Hynes 1975). In large rivers, connections between river channel, riparian zone and floodplain create transverse habitat heterogeneity over larger scales than in small streams, or laterally confined rivers (Decamps et al. 1988; Naiman et al. 1988; Pinay et al. 1990). Connectivity and interactions along the vertical dimension, between surface water and groundwaters, also are increasingly recognized as significant drivers of riverine process and function (Gilbert et al. 1990; Stanford and Ward 1993; Brunke and Gonser 1997).

Natural, functioning floodplains benefit fishes by providing increased food base, spawning and rearing habitat, and refuge from flooding or other environmental extremes (Welcomme 1979). In large tropical and temperate rivers, the ecology of fluvial fishes in relation to floodplains has been the subject of numerous investigations (reviews in Lowe-McConnell 1975; Welcomme 1979; Copp 1989). Less studied are the intermountain floodplains of gravel-bed rivers, common in glaciated regions worldwide (Rosenshein 1988). These floodplains typically occur repeatedly as aggraded river segments followed and preceded by confined river segments (Stanford and Ward 1993). Like other floodplains, intermountain floodplain surfaces display a diverse array of aquatic habitats, but differ in that these habitats are profoundly influenced by the emergence and downwelling of large volumes of groundwater.

Groundwater upwelling on floodplain surfaces can create thermal complexity at a range of spatial scales. Localized seepage in pools or side channels can result in small scale thermal patches (Ozaki 1988), while discrete upwelling along the river bed can produce longitudinal temperature patterns for many kilometers downstream (Beschta et al. 1987; Sullivan et al. 1990). In previous research, Stanford and Ward (1988, 1992, 1993), have characterized some patterns of surficial eruption of hyporheic flows. Effluent groundwaters may enter mainstem channels directly where they are subjected to immediate mixing with surfaces waters. Off-channel habitats, such as floodplain springbrooks, occur in abandoned river channels and exhibit seasonally dynamic hydrographs controlled by the intrusion of surface waters during flood events, and the supply of groundwater from the hyporheic. Small and ephemeral springbrooks are common on low terrace paleochannels and in abandoned active channels with weak sources of hyporheic flow. Such active channel seepages often form hydrologically dynamic floodplain ponds as they feed into and out of flood filled scour pools. Large, perennial springbrooks with stable and consistent hydrographs occur in relict mainstem channels. These springbrook channels are typically blocked at the upstream end by alluvial deposits, woody debris and riparian vegetation. As a result, the are subjected to surface flows only during severe flooding. All of these habitats are to a greater or lesser extent influenced by cool groundwaters and warming due to solar radiation, resulting in a mosaic of heterogeneous aquatic habitats exhibiting a diversity thermal gradients.

In aquatic ecosystems, the structure of biotic communities as well as the persistence of populations and species, may be directly or indirectly regulated by the diversity of habitats and thermal gradients available (Frissell et al. 1986; Pringle et al. 1988; Stanford and Ward 1988; Cech et al. 1990). Life history events of locally adapted fishes are closely adapted to prevailing thermal regimes (Beacham and Murray 1987; Holtby 1988; Hartman and Scrivener 1990). The availability of a diverse array of thermal habitats in an aquatic ecosystem provides fishes and other ectothermic organisms the opportunity to thermoregulate and optimize energy intake relative to metabolic costs (Brett 1971; Medvick et al. 1981; Smith and Li 1983; Berman and Quinn 1991; Hall et al. 1992; Snucins and Gunn 1995). In warmer climates, coldwater-dependent fishes may persist by seeking refuge in groundwater-cooled habitats (Meisner 1990; Nielsen 1991; Li and Moyle 1993). While evidence is scarce, many researchers have speculated that floodplain springbrooks and other groundwater-warmed habitats are used by fishes during winter months for spawning, egg incubation, rearing and shelter from adverse flow and ice conditions in the main channel (Craig and Poulin 1975; Cunjak and Power 1986; Sedell et al. 1990; Stanford and Ward 1992).

Water temperature also becomes ecologically significant through its potential mediation of biotic interactions such as competition and predation (Magnuson et al. 1979; Baltz et al. 1982; Reeves et al. 1987; Hill and Magnuson 1990; Vigg and Burley 1991). In some cases, organisms are known to actively seek thermal patches serving as refugia from predation (Fraser and Cerri 1982) or competition (Gehlbach et al. 1978; Magnuson et al. 1979). Habitat diversity and thermal complexity may decrease the incidence and severity of such interactions by allowing increased opportunities for interspecific partitioning. Nonnative fishes, because they are not coevolved with natives, present special and serious threats as competitors and predators of native species. The impact of nonnatives is heightened in many systems by their proliferation and success in aquatic habitats altered by human activities (Li et al. 1987). Despite the widespread threat and impact of nonnative fishes no studies to date have examined the role of thermal habitat complexity in mediating interactions between native and introduced fishes, although several sources have mentioned the potential importance of such phenomena (e.g. (Li et al. 1987; Nielsen 1991; Moyle and Leidy 1992; Li and Moyle 1993). Two native, coldwater-dependent species occurring in my study area, bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarki lewisi*, appear most resistant to invasion by introduced salmonids in headwaters or spring-fed streams, which ostensibly function as coldwater refugia (Howell and Buchanan 1992; De Staso and Rahel 1994; Young 1995). However, no previous studies have examined how the presence of introduced species such as brook trout, affects the utilization of groundwater influenced habitats, or the extent to which such impacts may contribute to the decline and local extirpation of native salmonids.

Despite the habitat diversity and environmental gradients characteristic of floodplains, few studies have addressed how these complexities direct species distribution and assemblage structure of aquatic vertebrates. Furthermore, while riverine habitats are increasingly recognized as existing at several, spatially nested scales (Frissell et al. 1986), few studies have addressed how organisms may respond to multi-scale habitat heterogeneity (Poizat and Pont 1996). Information on the ecological affinity and relative productivity of different floodplain habitats is valuable in that it may help anticipate losses in biological diversity or productivity which may result from anthropogneic disturbances such as river regulation, channelization or the introduction of exotic species. The unique thermal properties of floodplain habitats (e.g. springbrooks) also provide an excellent setting in which to evaluate the influence of temperature on the distribution, behavior and potential for interactions among native and nonnative species. Specifically, the purpose of my study was to describe, at two spatial scales, how fishes and amphibians exploit a heterogeneous habitat template strongly structured by relatively large-scale groundwater upwelling and complexly branched and shifting river channels in a functioning, natural floodplain. I addressed the following questions: What thermal regimes, spatial thermal complexities and physical habitat variables characterize floodplain habitat types including springbrooks, floodplain ponds and main channel anabranches? How are fish species-age classes distributed among floodplain reach types (macrohabitats) and within reach types (microhabitats)? Do fishes utilize floodplain springbrooks as seasonal refugia from harsh mainstem conditions? What is the role of groundwater influenced floodplain habitats in buffering native species from displacement by invading non-natives? And what is the relative contribution of off-channel habitats to the overall aquatic vertebrate productivity and diversity in the river system?

Study site

The study was conducted on Nyack floodplain of the Middle Fork Flathead River, at the southern boundary of Glacier National Park, Montana (Figure 1). This alluvial intermountain river segment, bounded upstream and downstream by narrow canyons, is about 7 km long and 1-2 km wide. The middle fork is a 5th order river with a catchment approximating 3200 km^2 in area. It drains heavily glaciated, high-relief terrain underlain by uplifted sedimentary and metasedimentary rocks of the Belt series. Thick deposits of glacial and periglacial origin mantle the valley floors and many side slopes. The valley fill is dominated by well-sorted cobble- and gravel-sized deposits, with local interbeds of finer sands and extensive overbank deposits of sand, silt and organic matter on floodplain surfaces that are frequently occupied by standing water during peak flows. The main river channel traverses or inundates a swath of the valley floor between 300 and 700 m wide; within this band lies a dynamic mosaic of low flow channels, recently abandoned channels, and coarse gravel bars with early successional herbaceous and shrub vegetation. Channel patterns range from meandering to braided, fluctuating from reach to reach and year to year. This annually active zone is nested within a broader zone comprising an anastmosed network of active and relict channels (Figure 2). Most of the lower surfaces in this zone are inundated or reoccupied by the river during high flow events on an apparently decadal time frame. Topography and vegetation suggest branches of the main river channel occupied this zone in previous decades or centuries (Figure 2). During high flow stages, some surfaces are typically occupied by overflow from river sources, others are inundated by groundwater that emerges at the surface when the water table is raised during high river stages. Most valley surfaces (away from the active channel) appear to have been historically covered by mixed deciduous and coniferous forests, dominated by overstories of black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*) and Englemann spruce (*Picea engelmanni*), and possibly other conifers. Some large patches of forest cover have been removed for logging, grazing, and construction and maintenance of a railroad and highway corridor that traverse the south side of the valley (away from the river). The selected study reaches have seen limited direct impact by these alterations, and appear to remain largely dominated by natural riverine successional processes.

The upstream portion of the Nyack segment is known to be strongly downwelling, with net loss of about 20 percent of the river's flow in the first 2 kilometers (Stanford et al. unpublished). This flow deficit is reportedly regained through upwelling of groundwater into surface waters before the river exits into a canyon downstream. Off-channel habitats such as springbrooks and floodplain ponds, many maintaining strong perennial flow, erupt in some abandoned channels and are a common and distinct component of aquatic habitats in the floodplain (Stanford and Ward 1993). Springbrooks emerge on the floodplain surface and are disconnected from surface water at the upstream end, except during extreme flood events, and flow downvalley for distances of hundreds of meters to several kilometers before converging with the main river channel. Floodplain ponds are variably influenced by groundwater seepage, and are typically connected to surface waters annually or at higher frequencies.

Methods

Reach selection

I designated nine reaches which included the diversity of aquatic biotopes present on the floodplain surface. Three study reaches were relegated to each aquatic habitat type: springbrook, floodplain pond and main channel anabranches. One of the springbrook reaches (lower) was later found to exhibit main channel-like physical characteristics, and was grouped with mainchannel reaches for subsequent analyzes. Springbrook and main channel reaches were paired as upper, middle and lower beginning at the upstream end of the valley and running northwest downstream (Figure 1). By necessity, floodplain pond sites were clustered across from the confluence of a major tributary, Nyack Creek. This portion of the floodplain is highly unstable and avulsive, and thus a favored site for the formation of ponds. Springbrook and main channel reaches consisted of at least three consecutive pool-riffle sequences and included such lateral habitats as backwaters and side channels, if present. Floodplain pond reaches consisted of a single, surface water isolated pond. The general physical characteristics of floodplain reach types is further summarized in Table 1.

Sampling design

In the summer of 1994 detailed physical surveys were initially conducted on each of the study reaches. Utilizing measuring tape, Sonin® electronic distance meter and compass, I constructed two-dimensional maps for all study reaches. Maps included location of woody debris, overhanging vegetation, wetted area, and boundaries of within-reach habitat units such as riffles, pools, and backwaters. Depth, substrate, velocity categories were designated to reflect the relevant physical attributes observed within the study area. Habitat variables were recorded on these maps every 2-5m^2 of wetted area, the scale depending on the size of the study reach. Finer resolutions (2m^2) were utilized in smaller study reaches (e.g. 300m^2 floodplain pond) while coarsest resolution was applied in largest study units (e.g. 9000m^2 main channel reach). Physical habitat surveys and maps were repeated when reach habitat conditions changed. All mainchannel and pond reaches were resurveyed in summer 1995 as a result of channel changes which occurred in the spring run-off of 1995. Springbrook reaches were stable throughout the study period and did not require repeated surveys. In reaches that were surveyed twice, habitat variables were largely consistent between survey dates.

Temperatures were monitored by a network of Onset StowAway® and Hobo® thermistor devices throughout the study period. Initially, at least two temperature recorders were placed in each study reach to continuously monitor ambient temperatures. The harsh physical conditions of main channel reaches resulted in the loss of several data loggers and fewer devices were operating in these reaches by the 1995 field season. Spatial thermal complexity was quantified recording water temperatures for each microhabitat cell of a reach (see below). Spatial thermal surveys were conducted by wading and probing study reaches with an Atkins® digital thermocouple thermometer and sounding probe attached to a 1.5 m wading staff. These surveys took place at or within one week of biological surveys and were conducted from 13:00 to 2 hours before darkness.

Beginning in the summer of 1994 and continuing through winter 1996 in some cases, study reaches were surveyed for aquatic vertebrates every 2 to 4 months except during winter and spring when ice and poor visibility precluded sampling of some main channel reaches and floodplain ponds. Water clarity was typically excellent in all study reaches (visibility ≥ 5 m), and all surveys were conducted by visual observations of divers and bank observers. As required by reach width, 1 or 2 snorkelers swam slowly, zigzagging upstream through the reach. Divers searched intensively by regularly overturning rocks and exploring under banks and woody debris with dive lights. Bank observers (1 or 2) followed close behind to check shallow edges and lateral habitats, and to record notes on fish observations. Only day surveys were conducted during the summer/fall 1994, but thereafter most surveys were conducted during day and night. Day surveys took place between 13:00 and 2 hours before darkness. Night surveys utilizing dive lights began 1 hour after sunset and were completed before 01:00. The time required to complete each surveyed varied depending on the number of fish observed, and the size of the reach. All fish and amphibian species were identified and their total length estimated to the nearest centimeter. Individuals were periodically captured by hand net to verify length estimates and species identification. The position of each individual observed was recorded on the corresponding reach map, or in the case of night surveys, was marked with a colored washer, and the position recorded the following day.

I studied seasonal upstream and downstream movement patterns in Beaver springbrook by utilizing two, double-weir stations. The design of these weirs was similar to that of Hall (1972), except that I used 1/8 inch hardware cloth to construct barrier fences instead of tightly spaced horizontal steel shafts. The first weir was located at the upstream end of Beaver springbrook , just downstream from the upper springbrook reach (Figure 1), and was operated from July 1995 through February 1996. The second weir was located upstream from the lower springbrook reach (Figure 1) and was operated from September 1995 through January 1996. Weirs were operated for five days of each month, during which traps were checked twice daily. Fish captured in weirs were measured, recorded and marked, either with a coded anchor tag (fish total length > 10 cm) or an adipose fin clip (fish < 10 cm), and then were released beyond the weir in their original direction of movement.

Data analysis

Fish observations were summarized in terms of density (#/100 m^2 of total reach surface area) and total counts for survey dates, times and reaches (Appendix). To simplify analysis and discussion, data presented in this paper is restricted to summer and early fall, unless otherwise stated. Estimates for fish species were used to break down species into year class categories based on my own length frequency data and other published sources (Brown 1971). Species-age classes provided a convenient way to address independently the ontogenical changes in distribution, abundance and behavior which are commonly observed within age classes of a species (Polis 1984). In all, 18 species-age classes of fishes and amphibians were encountered in my study (Table 2). Sculpins were generally abundant in surveys, but were not included in my analysis because of low confidence in sampling effectiveness for these benthic fishes. Computation of availability and usage of microhabitats and within reach habitat units was accomplished by breaking down reach maps into grid cells ranging in size from 2 to 5 m^2. All physical and biological data were recorded into the corresponding cell based on the reach map position onto which data were recorded in the field. The large relational database which resulted from this approach allowed us to consider habitat associations or other distributional patterns at a range of spatial scales and with various levels of sampling effort.

Data was analyzed at two spatial scales: reach (10^2 m^2) and microhabitat (10^0 m^2). I quantified reach abundance by calculating densities for each species-age class observed in a survey (Appendix). Density estimates differed vastly between day and night surveys, usually with higher densities and more species-age classes being detected during night surveys especially in springbrook and mainchannel reaches (see Chapter 3). Data were utilized from survey times (day or night) which provided the best estimate for each species-age class within each reach type. Differences in physical conditions led us to expect different assemblages among reach types; I tested this by classifying reaches in a table arrangement and through hierarchical cluster analysis (Gauch 1982). Microhabitat data was analyzed by contrasting availability and utilization of temperature, depth, substrate, velocity, woody debris and edge microhabitats for each species-age class. I expected some covariance in microhabitat variables and tested for this by constructing a two-way matrix contrasting each possible pair of microhabitat variables.

I analyzed weir data by calculating mean number of fish captured per day in each month of operation for upstream movement and downstream movement, or both directions combined. In order to avoid bias associated with 'trap happy' individuals, fishes recaptured within any sampling month were not included in analysis.

Results

Physical reach characteristics

Temporal and spatial thermal patterns varied between floodplain habitat types, but also among reaches within habitat types. Springbrook reaches showed the least diel and seasonal variation in temperature (Figure 3). Upper and middle springbrook temperatures fluxed roughly between 5 and 10 °C throughout the study period, with peak temperatures occurring in mid-Fall. The thermal regime of lower Beaver springbrook was however, more similar to that observed in mainchannel reaches (Figure 3). Spatial thermal surveys indicate that the lower springbrook reach receives limited groundwater inputs (Figure 5), and demonstrates that groundwater fed thermal signatures may attenuate rapidly as they acclimatize to effects of air temperature and solar radiation. Floodplain pond temperatures showed high seasonal thermal variability, but typically remained warmer during winter months than main channel sites. However, floodplain pond thermographs do not present a complete picture of the thermal complexities characteristic of these habitats, since only bottom temperatures were monitored. During warm summer months, ponds often stratified vertically (Figure 4) at which time they displayed high temperatures along shallow edges and surface waters (22-30 °C), and cooler temperatures in deep areas or near groundwater seeps (11-14 °C). Mainchannel temperatures were characterized by high diel variation, moderate summer temperatures (12-16 °C) and extreme cold during winter months (Figure 3).

Spatial thermal complexity also differed dramatically between floodplain habitats (Figure 5). Springbrook reaches display a downstream pattern which parallels thermograph data. During late-summer, thermal surveys in upper Beaver springbrook show cold temperatures relative to other habitats and high spatial thermal complexity (Figure 5). Thermal complexity of the upper springbrook reach is a result of numerous groundwater seeps which feed into this site. Middle Beaver Springbrook exhibits slightly higher median temperatures (presumably an effect of rapid warming due to solar radiation) and dampened spatial thermal variation. The lower springbrook reach is most similar to mainchannel reaches in having warmer temperatures and little spatial thermal complexity relative to other springbrook reaches. In floodplain ponds, thermal stratification makes these reaches the warmest, and with groundwater influences, the most thermally heterogeneous of all floodplain habitats (Figure 5). Thermal complexity was typically minimal in mainchannel reaches, but shallow, warm backwaters resulted in some thermal complexity (Figure 5).

Besides temperature, floodplain reach types differed in a number of other physical habitat variables. Floodplain ponds are essentially lentic habitats, and as a result were composed mostly of low velocity pools with fine substrates (Table 1). Ponds were generally deeper than mainchannel or springbrook reaches, but had more woody debris and edge habitats. Mainchannel and springbrook reaches displayed similar proportions of reach scale habitat units (e.g. pools, riffles), substrate types, and woody debris. Springbrooks were generally more shallow and had slower water velocities than mainchannel reaches (Table 1).

Reach scale distribution and abundance

I observed a total of 28,858 individual aquatic vertebrate individuals in my surveys, representing 8 species and 18 species-age classes (Table 2). Assemblages of aquatic vertebrates encountered in surveys were distinct and consistent among floodplain reach types. Hierarchical cluster analysis of study reaches found that springbrook, pond and main channel reaches grouped well, and expressed the most parsimonious classification of aquatic vertebrate assemblage structure (Figure 6). Two mainchannel reaches ('my' and 'mu') however, did fall out away from other mainchannel reaches (Figure 6). These relatively poor groupings resulted in part from high, but variable diversity and abundance, characteristic of mainchannel reaches (Figure 7). Reach 'mu' for example, grouped closest to pond reaches because this mainchannel reach had backwater habitats that were often occupied by age-0 longnose suckers and toad tadpoles, species-age classes otherwise restricted to floodplain pond sites.

Assemblages of springbrook, pond and mainchannel reaches were characterized by relatively distinctive species-age class communities. Only ≥age-1 brook trout, age-0 mountain whitefish and sculpins (*Cottus sp.*) occurred regularly in all study reaches. Springbrook reaches expressed relatively low diversity, their ichthyofauna dominated by brook trout of all age classes and moderate densities of age-0 mountain whitefish (Figure 7). Bull trout, cutthroat trout, and longnose suckers occurred in springbrook reaches but were uncommon and transient. Floodplain pond sites were characterized by exceptionally high densities of boreal toad tadpoles, age-0 longnose suckers and age-0 mountain whitefish characterized (Figure 7). Brook trout of all age classes and ≥ age-1 longnose suckers were also common and abundant. Bull trout were rare and cutthroat trout absent from floodplain ponds. By comparison, peak densities were lower in mainchannel reaches than in springbrooks or floodplain ponds, but mainchannel reaches appeared to support more species-age classes at higher densities than other reach types (Figure 7). The most abundant species occurring in mainchannel reaches were age-0 mountain whitefish and brook trout of all age classes. Boreal toad tadpoles and age-0 longnose suckers were also abundant, but variable because they occurred only sporadically in reaches with suitable backwater habitats. The remaining assemblage of mainchannel reaches was defined by moderate densities of ≥ age-2 bull trout, ≥ age-1 longnose suckers, ≥ age-1 cutthroat trout, and ≥ age-1 mountain whitefish (Figure 7).

Microhabitat distribution

Most species-age classes exhibited fairly distinctive patterns of fine scale habitat selection relative to overall availability of floodplain microhabitats. Many physical variables characterized floodplain reach types, but when viewed at the microhabitat scale a few variables (2-3) could be distinguished as driving most observed distribution patterns. Temperature appeared to be a strong determinant of habitat selection for many species-age classes. Age-0 brook trout selected cold water temperatures relative to their availability (Figure 8). Conversely, age-0 longnose suckers, age-0 mountain whitefish and boreal toad tadpoles preferentially selected warm water habitats (Figures 9 and 10). Most age-0 aquatic vertebrates preferentially selected shallow, low velocity, edge microhabitats, but because of covariance in these variables (i.e. edge habitats tend to be shallow) it is difficult to distinguish the dominant factor driving microhabitat distribution (Figure 11). However, boreal toad tadpoles shifted their microhabitat distribution between day and night (Figure 12), suggesting warmer water temperatures characteristic of shallow floodplain pond margins may drive daytime microhabitat selection for these species-age classes. Age-0 mountain whitefish, unlike other young-of-the-year species, did not select shallow edge habitat (Figure 9), but instead were often observed cruising in warm, midwaters of floodplain ponds.

The microhabitat selection of fishes older than age-0 was largely consistent with expectations. Brook trout, cutthroat trout and mountain whitefish ≥ 2 typically selected deeper microhabitats than younger age classes of the same species (Figures 8, 9). Brook trout and bull trout tended to select lower velocity habitats compared to ≥ age-1 cutthroat trout and mountain whitefish (Figures 8, 9). Adult and subadult salmonids also showed a preference for microhabitats associated with woody debris. Most species-age classes showed little evidence for selection of specific substrates classes. Mountain whitefish ≥ age-1 were most often associated with coarse substrates (Figure 9) while age-0 longnose suckers and boreal toad tadpoles utilized finer substrates (Figures 9, 10). However, these patterns may largely be driven by strong covariance between substrate class and water velocity (Figure 11).

Seasonal movement and abundance in springbrook reaches

I observed few seasonal changes in assemblage composition among springbrook reaches. Brook trout dominated springbrook reaches throughout the year, although relative densities did show some seasonality. Age-0 brook trout began to emerge from spawning gravel in February and reached highest densities in June (Figure 13). Brook trout ≥ age-1 were most abundant in October surveys when they moved into groundwater fed springbrook habitats for spawning. A fall influx of adult brook trout was also indicated by the weir capture of large numbers of fish migrating upstream into heavily groundwater influenced habitats (Figure 14). Winter densities of adult brook trout in the springbrook were low (Figure 13), suggesting that these fish moved out of springbrook reaches after spawning. Native salmonids such as bull trout, cutthroat trout and mountain whitefish were present in springbrook habitats, but occurred sporadically and at low densities (Figures 7, 13). Weir data indicate that native salmonids are at least making exploratory movements into springbrook reaches (Figure 15), even though they rarely establish residence or reproduce. Besides the influx of fall spawning brook trout, weir data and reach surveys provide little evidence for seasonal, refuge-seeking migration into springbrook reaches.

Discussion

Floodplain pond, springbrook and mainchannel reaches were distinguished by distinct physical conditions and environmental gradients. A total of 18 species-age classes were observed in my study, and, when viewed on a simple presence/absence basis, many were cosmopolitan in their overall floodplain distribution. However, very few species-age classes were abundant in all three floodplain reach types, and when densities are taken into account, three relatively discrete assemblages of fish and amphibian species-age classes are revealed (Figures 6, 7). Patterns of species-age class diversity also differed among floodplain reach types. Springbrook reaches expressed relatively low diversity, their ichthyofauna dominated by brook trout of all age classes (Figure 7). By comparison, mainchannel sites generally supported more species-age classes at moderate densities (more evenness) than other reach types. Among invertebrates, high abundance and low diversity at sources of groundwater emergence is a common pattern (Minshall 1968; Ward and Dufford 1979), but similar patterns have not previously been documented among fishes. Low diversity in springs may result from physiological stress associated with cold, constant temperatures, and from exclusion through biotic interactions (exacerbated by environmental stability) of species not suited to such environments (Ward and Dufford 1979). Linkages of mainstem channels with floodplain ponds, springbrooks, and tributaries may explain in part, diversity and evenness observed in mainchannel reaches (e.g. Osborne and Wiley 1992).

The organisms composing assemblages in springbrooks, ponds and mainchannels appear in large part directed by the unique habitat variables which characterize different reach types. Age-0 longnose suckers for example, occurred in all reach types but were only super abundant in floodplain ponds. However, the scale at which organisms respond to habitat heterogeneity affects perceived distribution patterns, and is a critical ecological issue (Wiens 1989; Poizat and Pont 1996). Small scale habitat selection may be constrained by large scale habitat selection, or fine-scale requirements may direct distribution of species at larger scales (Wiens 1989; Bayley and Li 1992). Viewing the age-0 longnose suckers example at the microhabitat scale demonstrates that this species-age class is selecting microhabitats (warm, shallow, low velocity) which constrain and direct distribution patterns at higher scales. In my study, restricting analysis to reach scale distribution patterns elucidates gross macrohabitat associations, but obscures fine-scale patterns which appear in large part to regulate observed distributions and species-age class assemblages at the reach scale. Visual assessment of microhabitat utilization for all species-age classes suggests that temperature, depth and velocity are in general, important variables structuring microhabitat distributions (Figures 8, 9, 10). Most of the age-1 and older salmonids also demonstrated a fairly distinctive association with woody debris, which is consistent with other published accounts (reviews in Bryant 1983; Harmon et al. 1986). Microhabitat variables for the most part, did not show significant covariation (Figure 11). However, the fact that some variables were correlated (i.e. velocity x substrate), and the fact that species-age classes are undoubtedly responding to multiple environmental factors makes interpreting the relative importance of physical variables highly speculative.

In the case of boreal toad tadpoles, differences in day and night distribution suggest that water temperature alone may profoundly influence microhabitat selection. During daytime, toad tadpoles strongly selected shallow, edge habitats (Figure 12) which also tended to be warmer (Figure 10). After nightfall, when margins of ponds and backwaters rapidly began to cool (personal observation), tadpoles moved away from edges and into deeper habitats (Figure 12). However, predation risk can also influence behavior and habitat selection. For example, armored catfish shift depth selection between day and night relative to predation risk from aerial predators and piscivorous fishes (Power 1984), and predation by large centrarchid predators and avoidance of these predators can restrict small fishes to shallow water refugia (Power and Matthews 1983; Schlosser 1987). The extent to which fish predation pressure in ponds influences microhabitat selection of small fishes and larval amphibians is uncertain. Small brook trout (< 30 cm) were the dominant predatory species encountered in these habitats. During the day they were typically aggregated, sometimes feeding on surface insects, in deep areas, close to cover of woody debris; hence they appear not to present a high predation risk. Threat of predation for small fishes and tadpoles might actually be higher at night, when subadult bull trout sometimes emerged from daytime concealment (Chapter 3) and when brook trout often moved into shallower areas to forage (personal observation). However, the extent to which fishes feed on toad tadpoles is unknown, and I observed no such predation during my numerous surveys. Birds and diving beetles on the other hand, are known to prey on toad tadpoles (Kruse 1983; Hews 1988). Interestingly, daytime selection of shallow margin habitats by boreal toad tadpoles would appear to increase exposure to these predators, strengthening the argument that temperature can be a primary variable directing the daytime selection of shallow, marginal microhabitats (although unmeasured physiochemical variables or food availability may also be important). In contrast, age-0 longnose suckers, which utilized microhabitats similar to toad tadpoles (although slightly deeper), exhibited no diel shift in habitat use

(Figure 12), suggesting that in this case, temperature is only among a suite of factors influencing habitat selection. The fact that some species-age classes are responding strongly to temperature in microhabitat selection is not surprising. My findings are significant in that spatial thermal complexity is rarely considered explicitly in microhabitat studies, despite its obvious consequence to ectothermic organisms.

More than any other species, brook trout were ubiquitous across all floodplain reach types (Figure 7). This observation is significant in that the upper Flathead Basin is considered one of the last strongholds for native westslope cutthroat trout (Liknes and Graham 1988). Brook trout are now widely distributed through out the Rocky Mountains, but the present status of brook trout invasion in the Middle Fork Flathead River is unknown. Reports from the early 1980s (Weaver et al. 1982) relative to my findings suggest that brook trout may have considerably expanded their range and abundance in the last decade.

The existence of thermal complexity, especially in the form coldwater reaches are thought to play a role in mediating interactions between native and introduced fishes (Li et al. 1987; Nielsen 1991; Moyle and Leidy 1992; Li and Moyle 1993). Evidence of bull trout and westslope cutthroat trout persisting in headwater or spring-fed refuges when subject to intrusion of nonnative salmonids (Howell and Buchanan 1992; Young 1995), and in demonstrating enhanced competitive abilities at cold water temperatures (De Staso and Rahel 1994), seem to support this hypothesis. However, I found that nonnative brook trout dominated in groundwater influenced, thermally complex, off-channel habitats (ponds and springbrook reaches) which might otherwise have been expected to serve as refugia for native salmonids. Bull trout and westslope cutthroat trout certainly had access to these habitats and were occasionally observed , but the fact that they were not more abundant suggests that brook trout may functionally exclude native salmonids from these habitats. This argument is strengthened by other observations in the Flathead basin, where westslope cutthroat trout successfully utilize springbrooks in the absence of brook trout. Significantly, natives appear to utilize the springbrooks much the same as brook trout do in the Nyack floodplain (see Chapter 4).

Many researchers have speculated that floodplain springbrooks and other groundwater-fed habitats are utilized by fishes during winter months for spawning, egg incubation, rearing and shelter from adverse flow and ice conditions in the main channel (Craig and Poulin 1975; Cunjak and Power 1986; Sedell et al. 1990; Stanford and Ward 1992). Among temperate warmwater fishes, Peterson and Rabeni (1996) found large concentrations of adult fish in spring branches during the coldwater period. However, besides the short-lived influx of fall spawning brook trout I found no evidence that springbrooks were utilized by any species as winter refugia. The extent to which brook trout dominance in springbrooks may compromise these habitats as winter refugia for native fishes is unknown, but seems a distinct possibility.

While the value of off-channel habitats in contributing to fish productivity is understood among many large, lowland rivers (reviews in Lowe-McConnel 1975, Welcomme 1979), the significance of such habitats is generally less recognized among cold water fish assemblages in temperate, alluvial rivers (but see Peterson and Reid 1984; Swales et al. 1986; Hartman and Brown 1987; Murphy et al. 1989). Off-channel habitats such as backwaters, braids, sloughs, ponds, down-valley terrace tributaries and springbrooks represent significant heterogeneity in habitat and environmental gradients which facilitate productivity and diversity of aquatic vertebrates. In the Taku River, Alaska, these off-channel habitats compose only 5% of the rivers total area, yet contain 39 and 83% of juvenile sockeye and coho salmon populations, respectively (Murphy et al. 1989). In the Nyack floodplain, springbrooks and ponds together represent 27% of the available aquatic habitat, but match mainchannel reaches in their total salmonid population (Figure 16). Springbrooks and floodplain ponds appear especially important in serving as breeding and nursery areas for young-of-the-year fishes and toad tadpoles.

The functional integrity of aquatic floodplain habitats and their significance to native aquatic vertebrate communities are impacted by several, often interacting, human activities. In many western rivers, non-native species have been introduced into off-channel floodplain habitats. Species introduced into the Bitterroot River, Montana floodplain for example, include bullfrog *Rana catesbeiana*, northern pike *Essox lucius*, rainbow trout *O. mykiss*, brown trout *Salmo trutta*, brook trout, sunfishes *Lepomis* spp., yellow perch *Perca flavescens*, largemouth bass *Micropterus salmoides*, and black bullhead *Ictalurus melas* (Jones 1990). Because many off-channel habitats are essentially lentic (backwaters, sloughs, ponds) and are buffered from environmental extremes, they are susceptible to colonization by nonnatives not otherwise adapted to regional climatic conditions. Introductions are often rationalized as improvements to 'underexploited' habitats or vacant niches (Moyle et al. 1986), and are promoted by fisheries managers viewing these off-channel habitats as disconnected from the mainstem river and assuming they make no significant contribution to productivity, diversity or resilience of native species. Unfortunately, this is often a self-fulfilling prophecy; by the time research is conducted, native species have already been displaced. Jones (1990) for example, after finding sloughs and ponds dominated by northern pike and other nonnative fishes, brazenly concluded that, "pike do not pose a serious threat to other species in the river system" and that, "use of backwaters of in the Bitterrot River by salmonids is probably not important." A similar situation exists in the Flathead River near Kalispell, where programs to enhance fisheries for pike, bass and crappie, continue with little consideration of impacts (historic or current) such practices may have on imperiled native bull trout and westslope cutthroat trout. In the Nyack floodplain, nonnative brook trout have in particular capitalized on the productivity and favorable conditions of off-channel habitats. I speculate that prior to the invasion of brook trout, bull trout and westslope cutthroat trout utilized off-channel habitats to a similar capacity.

Human activities can also directly threaten the ecological integrity of floodplain habitats by disrupting hydrologic exchange and fluvial geomorphological processes. Flow regulation, channelization and bank stabilization eliminate natural disturbance regimes, truncate environmental gradients and severe lateral (river channel, off-channel, riparian) and vertical (groundwater, surface water) connectivity (Ward 1996) (Stanford et al. 1996).

Any of these anthropogneic alterations can result in reduced productivity and diversity of aquatic vertebrates (Guillory 1979; Halyk and Balon 1983; Junk et al. 1989; Turner et al. 1994; Stanford et al. 1996; Ward 1996). Often, the negative effects of human encroachment are linked to and exacerbated by the introduction of nonnative species (Li et al. 1987).

Incremental degradation and exotic species proliferation in off-channel habitats appear particularly insidious because species diversity may not decline rapidly, if it all, and losses in productivity may also be masked by lagged responses. In my study, while certain species-age classes were super abundant and showed definite affinities for certain off-channel habitats, virtually all species-age classes were represented in mainchannel reaches. Thus if ponds and springbrooks were eliminated altogether the native biological diversity of the floodplain segment might not decline at all, and similarly, losses in productivity contributed by high recruitment of salmonids, suckers and boreal toads would likely go unnoticed, especially in the absence of historical abundance data.

Since aquatic floodplain habitats are not homogeneous with respect to environmental conditions or assemblage composition, successful conservation or restoration efforts should rely on the natural capacity of river systems to develop complex habitats (Ebersole et al. 1997), rather than on the preservation of single habitat types thought to be most important. However, the fact that off-channel habitats appear prone to colonization by undesirable nonnative species (e.g. brook trout) should not serve as a basis for eliminating or disconnecting these habitats. Rather, since removal of established nonnative fishes is not practical nor likely to be successful, management efforts should focus on preventing continued introductions, and on maintaining or restoring connectivity and natural hydrologic regimes which will favor native species and potentially drive out maladapted exotic fishes. Ultimately meeting these goals will require management strategies integrating principles of river ecology which recognize mainstem channels, floodplains and groundwaters as interconnected components of riverine ecosystems, and that, "are based on sustaining, rather than suppressing, environmental heterogeneity" (Ward 1996).

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		Reach type		
		Floodplain pond	Main channel	Springbrook
Reach scale habitats	backwater	0.33 (0.8)	3.0 (2.7)	1.33 (1.5)
	pool	99.7 (0.8)	56.8 (18.7)	71 (1.7)
	riffle	0.0	27.2 (11.6)	22.3 (8.1)
	side pool	0.0	10.3 (13.1)	4.3 (5.1)
	side riffle	0.0	2.7 (2.5)	1.0 (1.7)
Depth classes (cm)	1-10	10.3 (4.5)	10.0 (4.2)	13.0 (3.0)
	11-25	29.3 (6.6)	32.0 (7.7)	35.7 (5.9)
	26-50	22.0 (9.8)	28.3 (4.1)	33.3 (4.0)
	51-100	31.0 (6.0)	24.2 (7.8)	16.3 (5.1)
	100+	7.2 (3.3)	5.3 (2.6)	1.3 (2.3)
Substrate classes	sand-silt	43.3 (18.9)	16.7 (10.5)	11.7 (4.6)
	gravel	38.0 (10.7)	62.0 (13.1)	66.7 (18.4)
	cobble	18.7 (17.8)	21.2 (10.6)	21.7 (14.5)
Velocity classes (cm/s)	0.0-4.9	99.3 (1.0)	4.2 (2.6)	2.7 (4.6)
	5.0-10.9	0.7 (0.0)	30.3 (10.3)	40.3 (16.5)
	11.0-24.9	0	21.3 (10.3)	39.0 (16.5)
	25.0-47.4	0	24.0 (9.4)	17.0 (11.5)
	47.5-77.4	0	17.8 (16.8)	1.0 (1.0)
	77.5+	0	2.2 (2.6)	0
Edge	present	57.8 (5.6)	45.0 (3.2)	51.7 (11.9)
	absent	42.3 (5.6)	55.0 (3.2)	48.3 (11.9)
Woody debris	present	28.3 (9.1)	14.0 (8.9)	16.0 (13.8)
	absent	71.7 (9.1)	86.0 (8.9)	84.0 (13.8)
Groundwater influence		medium-low	low	high
Surface water influence		seasonal	continuous	infrequent

Table 1. Summary of habitat characteristics of floodplain reach types. Data for each habitat variable class are mean percent of reach area, SD in parenthesis.

Species	Size class	Observations
Brook trout[a]	0	1534
Salvelinus fontinalis	1	619
	≥2	365
Westslope cutthroat trout	0	3
Oncorhynchus clarki lewisi	1	7
	≥2	16
Bull trout	≥2	18
Salvelinus confluentus		
Mountain whitefish	0	1619
Prosipium williamsoni	1	86
	≥2	50
Longnose/Largescale suckers[b]	0	7674
Catostomus catostomus	1	16
Catostomus macrocheilus	≥2	25
Boreal toad	tadpole	16771
Bufo boreas	toadlet	17
	adult	23
Spotted frog	adult	14
Rana pretiosa		
Tailed frog	tadpole	1
Ascaphus truei		

[a] nonnative species

[b] only longnose suckers were positively identified, age-0 largescale suckers my have been present, but are difficult to distinguish

Table 2. Common and scientific names for all aquatic vertebrate species observed in the study area. The total number of individuals observed in each species-age class category is also listed.

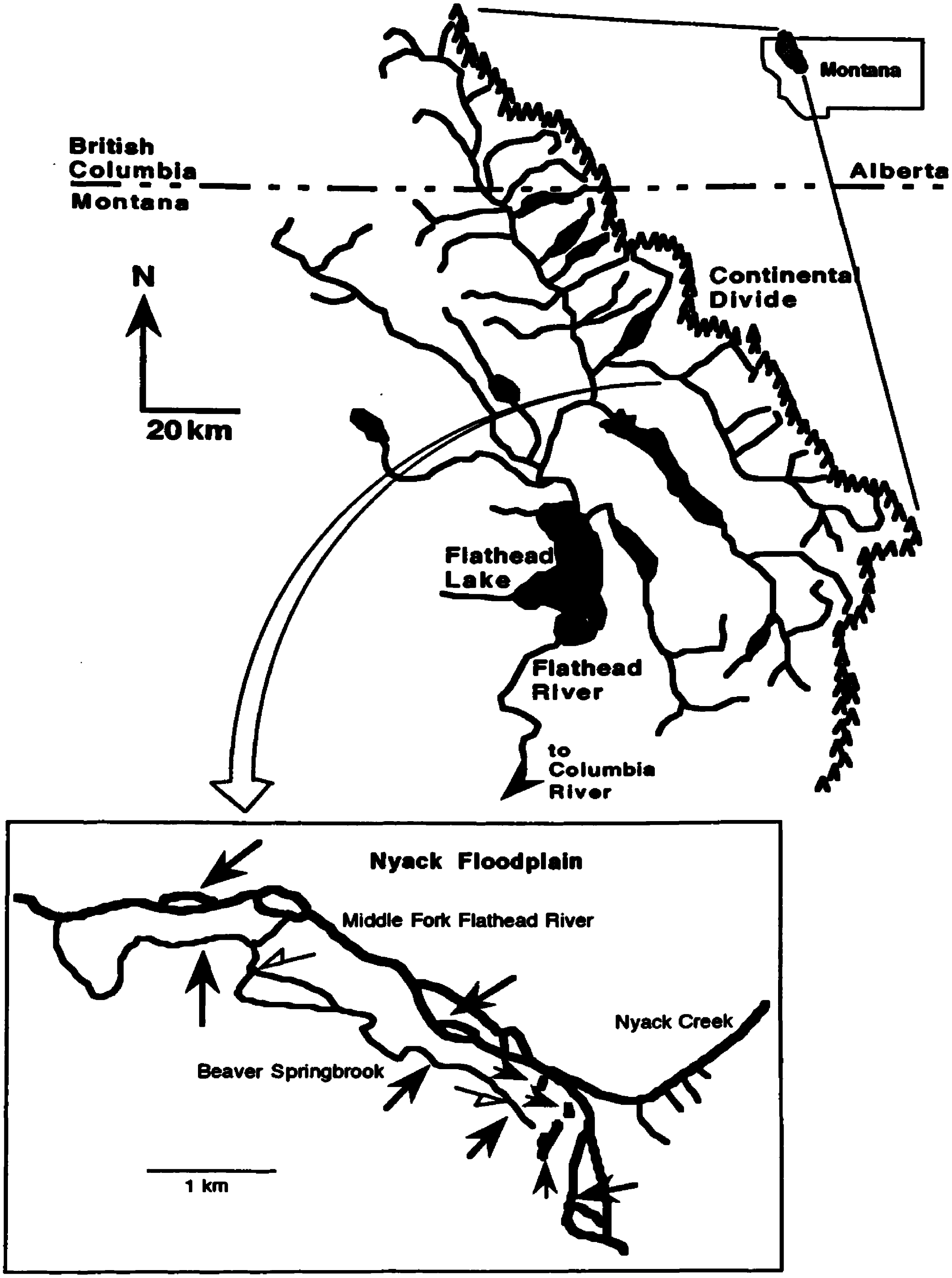

Figure 1: Map of study area on the Middle Fork Flathead River, Montana. Dark arrows designate study reaches, open arrows designate weir locations.

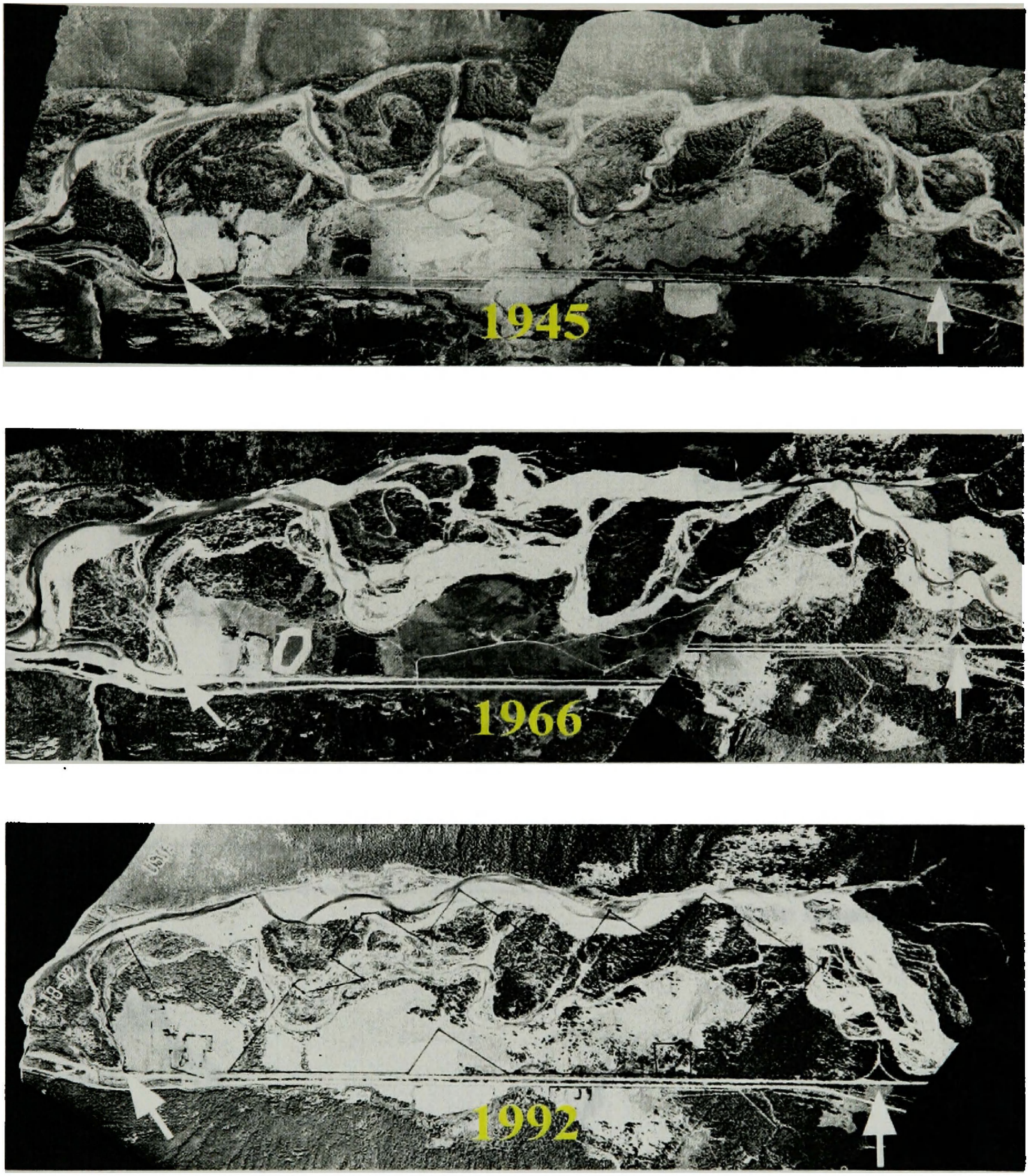

Figure 2: Aerial photographs of the Nyack floodplain from 1945, 1966, and 1993. In 1945 the main river channel was located in the valley center, flowing through what is now Beaver sprinbrook. By 1992 the river mainstem had shifted to the North side of the valley. White arrows designate common points of orientation since the photographs are at slightly different scales.

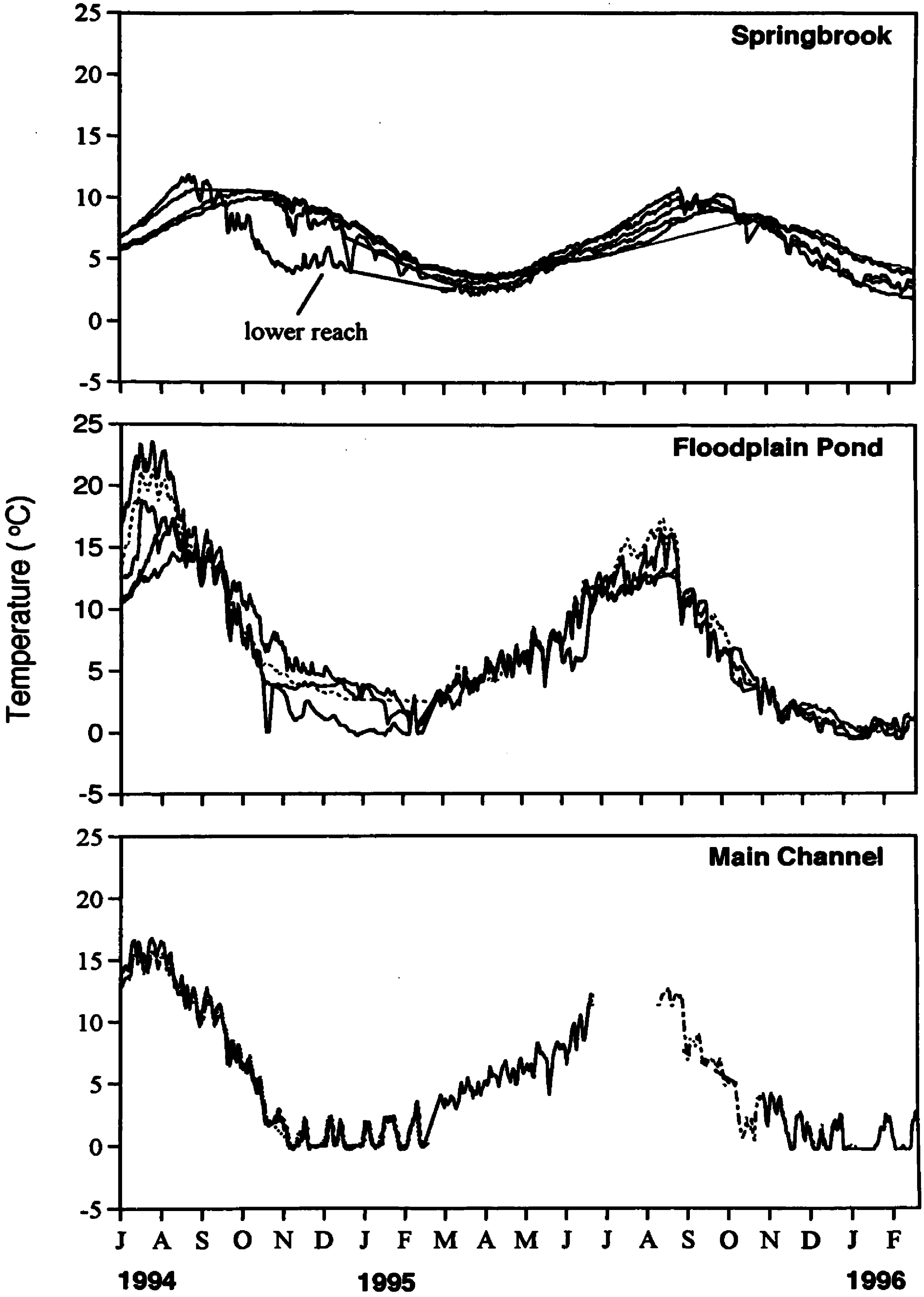

Figure 3: Thermal regimes of floodplain reach types summarized as mean daily temperatures. Data plotted are from multiple thermistors located within each reach type. Missing mainchannel data for summer 1995 resulted from Fall flooding and loss of thermistors.

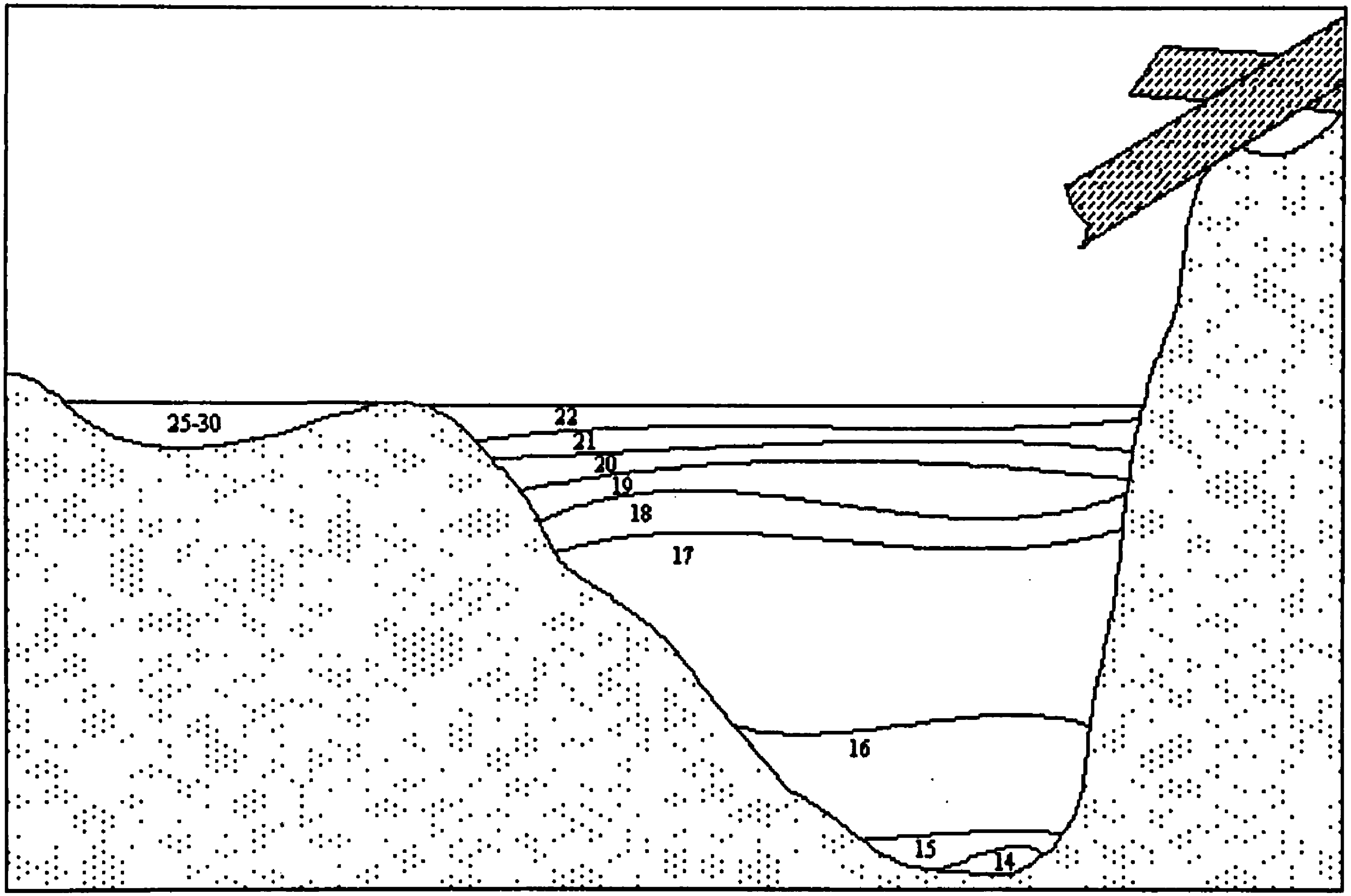

Figure 4: Cross section of a floodplain pond in summer showing vertical stratification and warming along shallow margins.

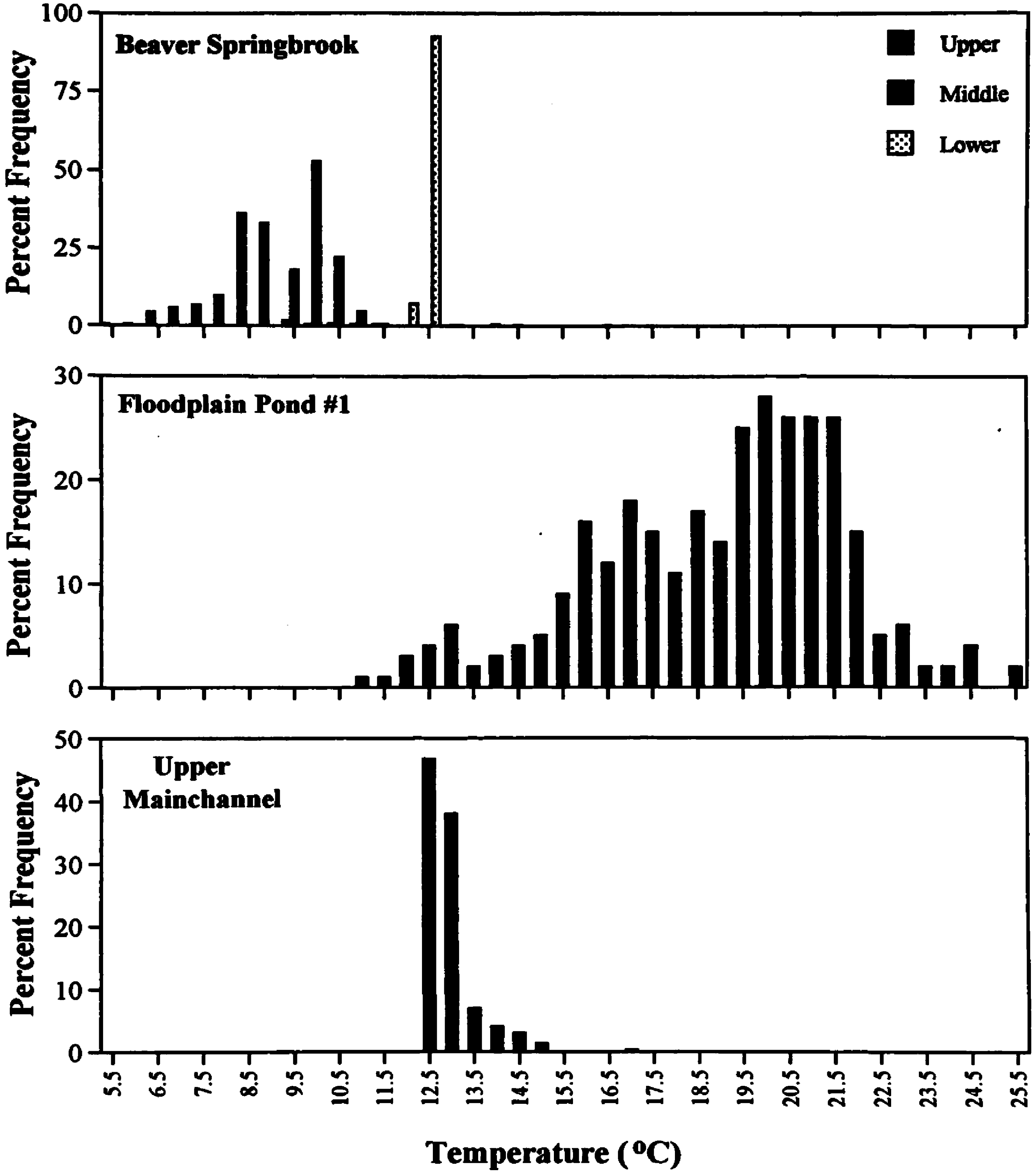

Figure 5: Temperature frequency distributions for floodplain reach types from spatial thermal surveys conducted in early August 1995. Floodplain pond frequencies are a comosite of surface and bottom temperatures.

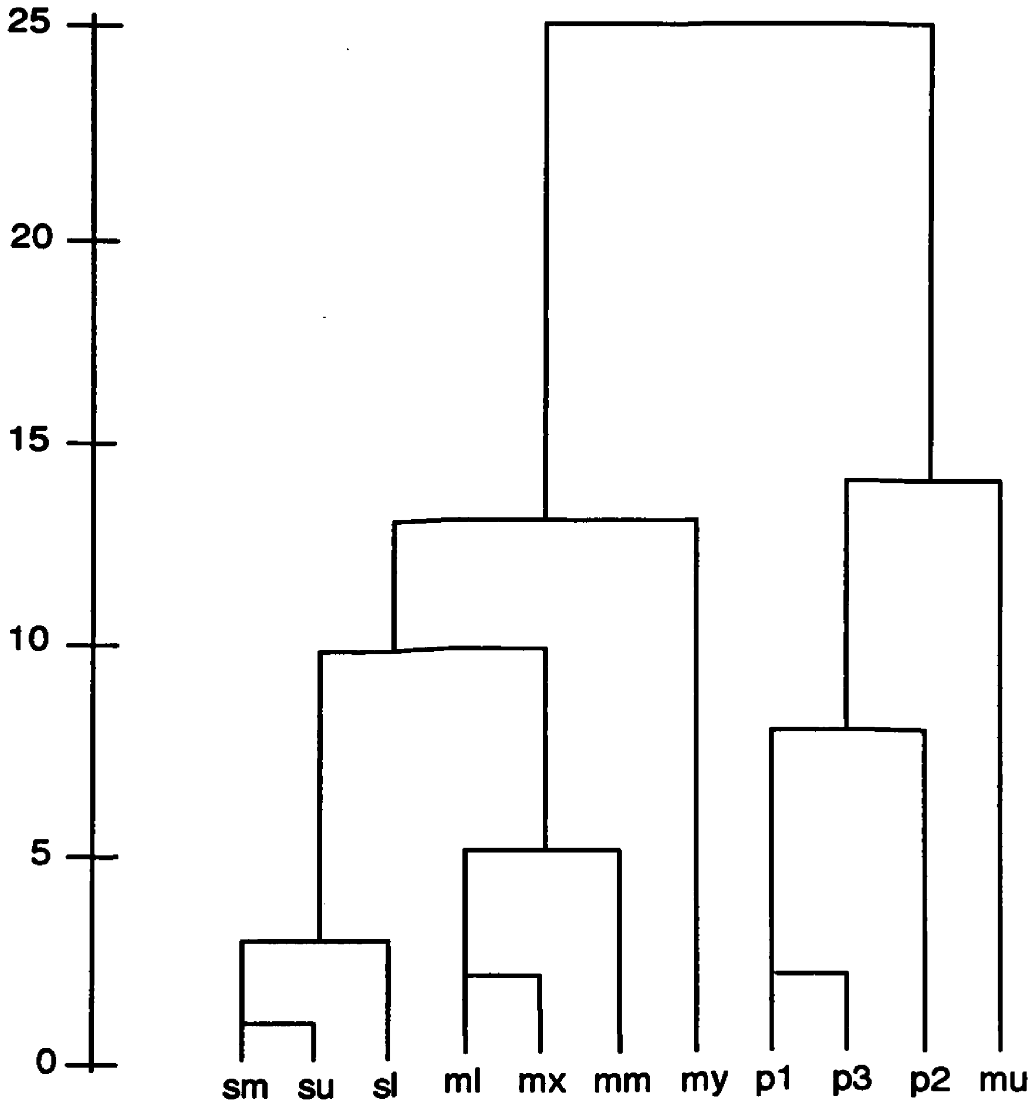

Figure 6: Dendrogram based on average linkage between groups, derived from Fig. 7 data converted to octave values (see Gauch 1982). Two-letter labels beginning with s, m and p are springbrook, mainchannel and pond reaches, respectively.

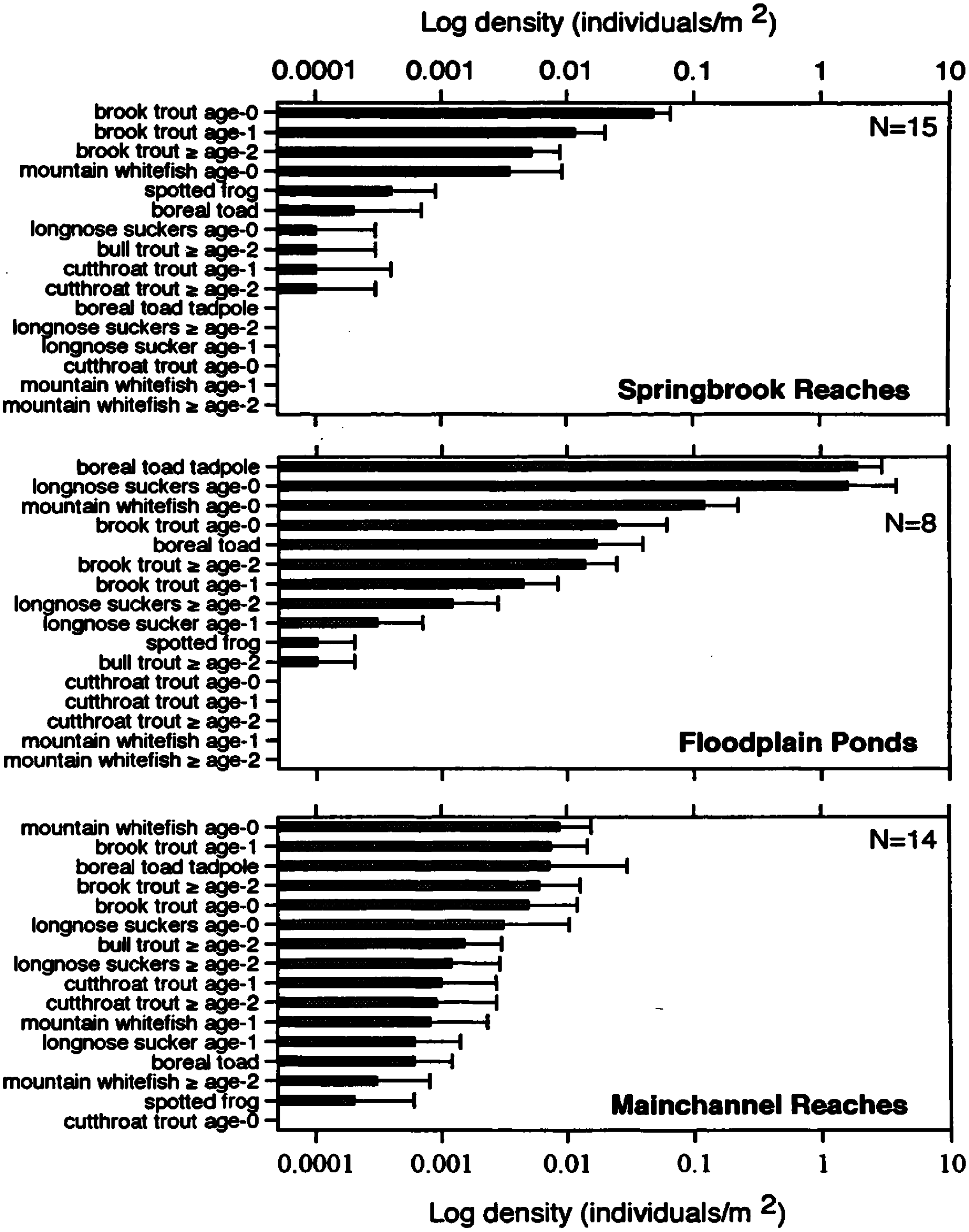

Figure 7: Assemblages of species-age classes observed in springbrooks, floodplain ponds and mainchannel reaches during summer/fall surveys. Horizontal bars are mean densities with SD. Note logarithmic scale.

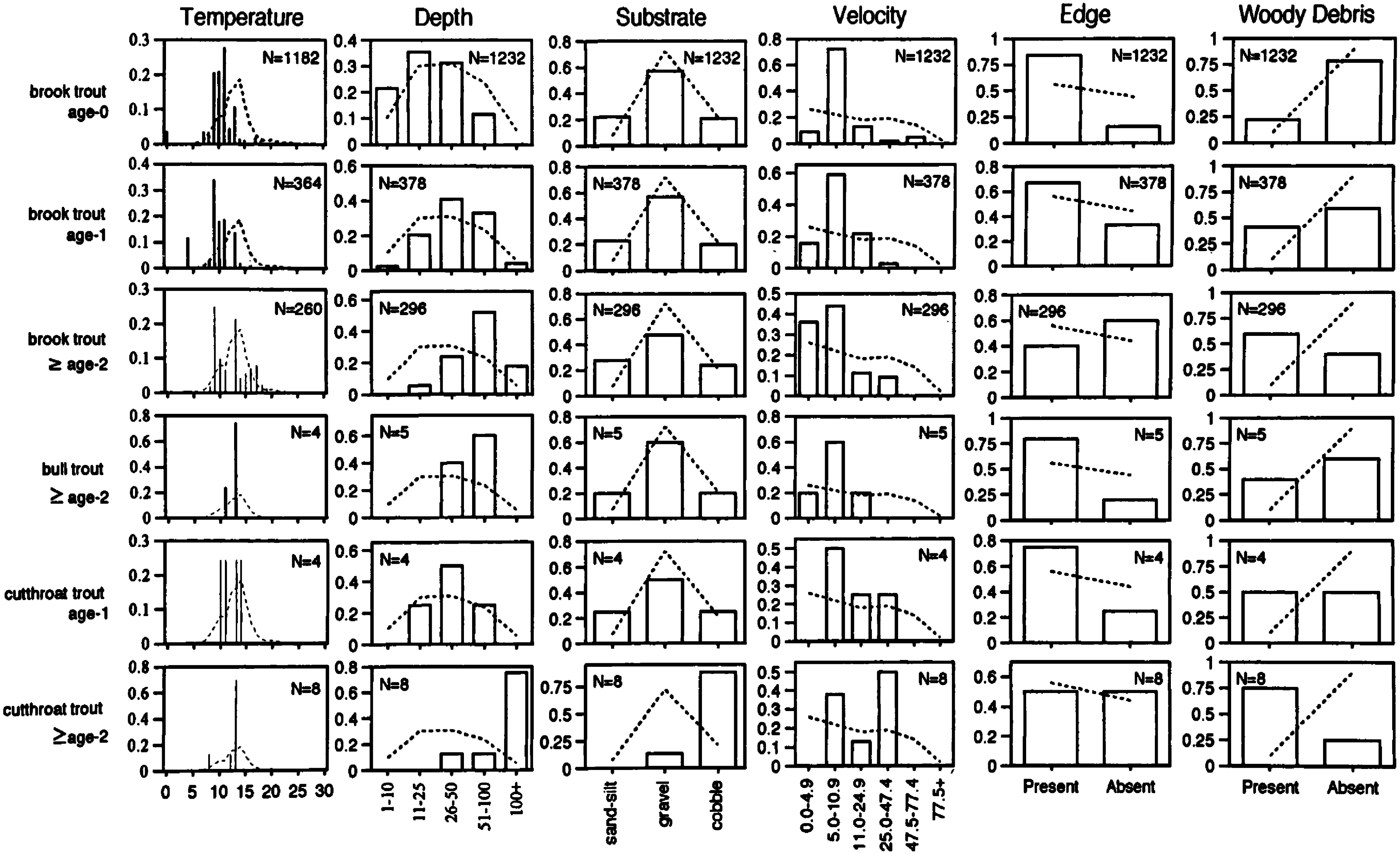

Figure 8: Summer and fall microhabitat distributions for trout species-age classes across all reach types. Vertical bars represent percent utilization, dotted lines represent percent availability.

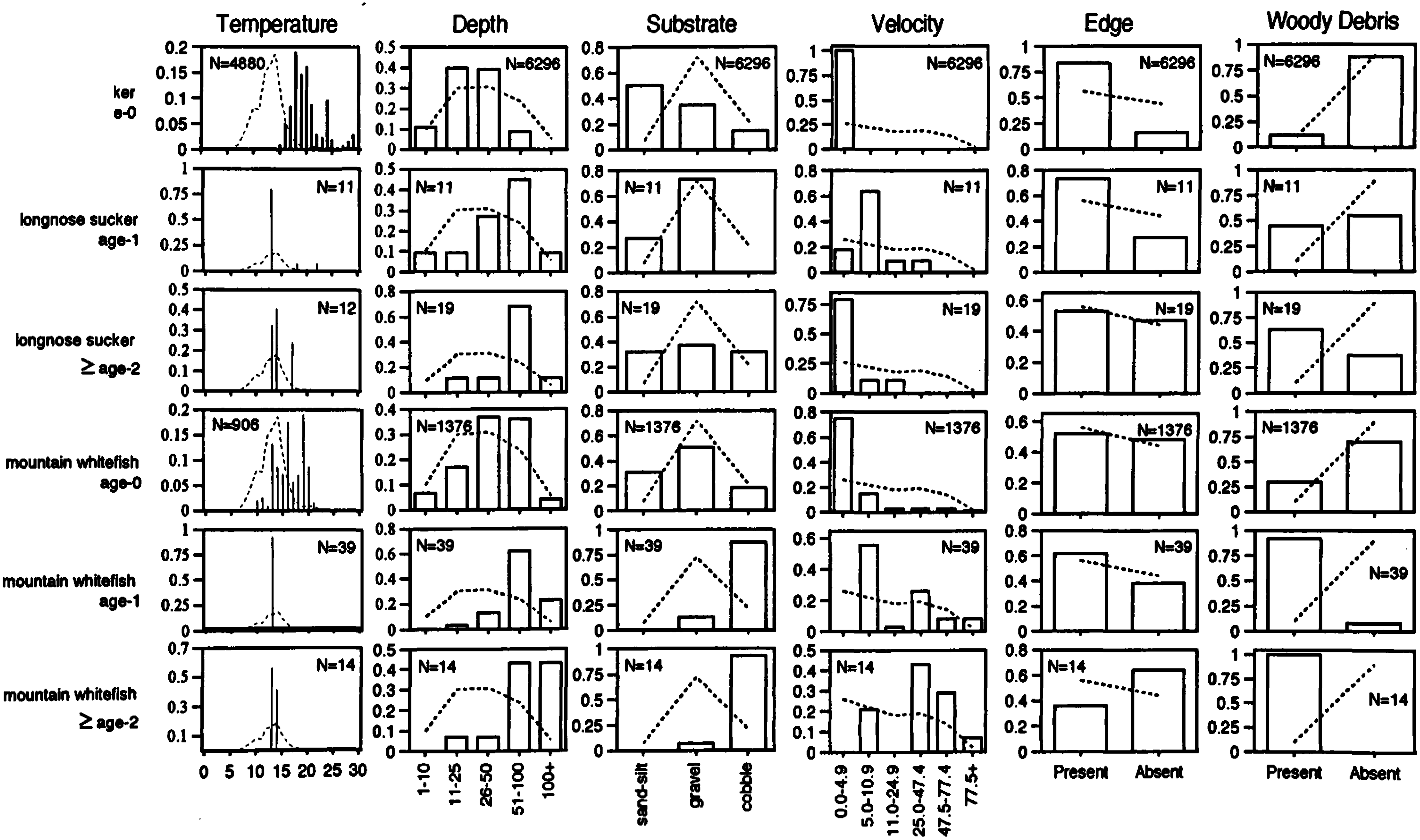

Figure 9: Summer and fall microhabitat distributions for sucker and whitefish species-age classes across all reach types. Vertical bars represent percent availability, dotted lines represent percent availability.

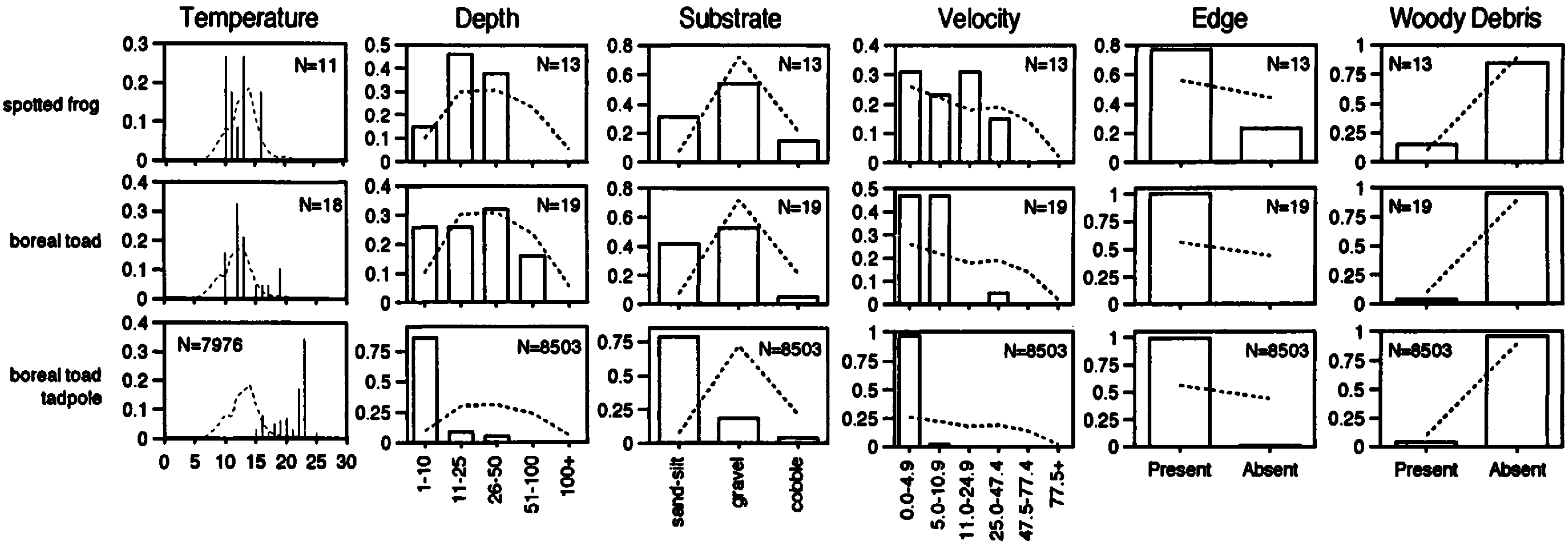

Figure 10: Summer and fall microhabitat distributions for selected amphibians across all reach types. Vertical bars represent percent utilization, dotted lines represent percent availability.

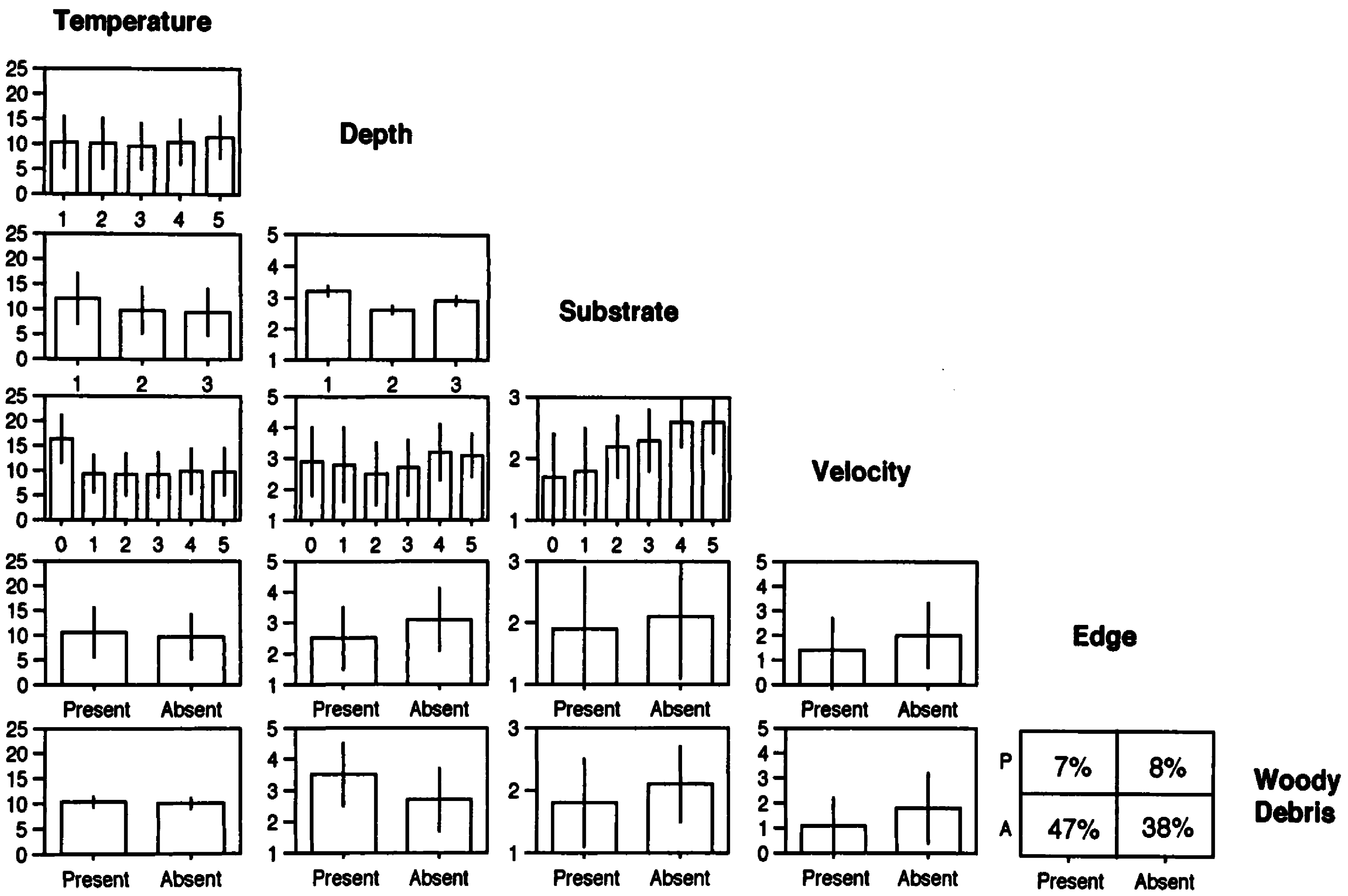

Figure 11: Two-way matrix showing patterns of covariation between pairs of habitat variables for all reach types. Bars are means with SD. Temperature data are from summer spatial thermal surveys. See Table 1 for definitions of habitat variable codes (i.e. for substrate 1 = sand-silt, 3 = cobble).

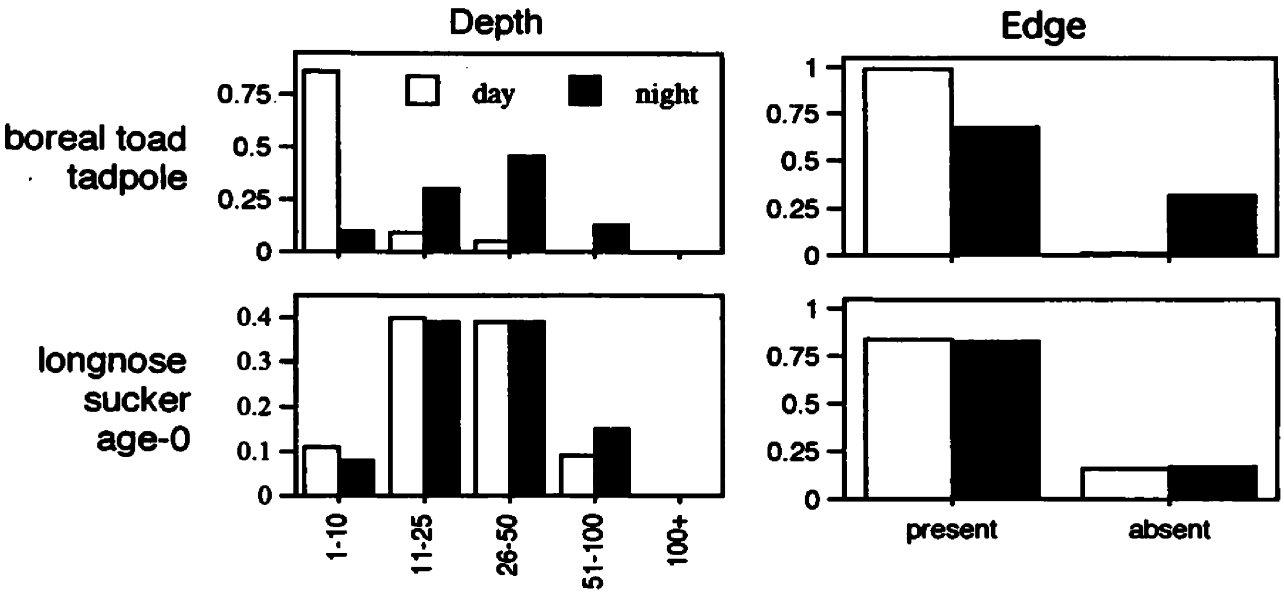

Figure 12: Summertime day and night depth and edge microhabitat distributions for boreal toad tadpoles and age-0 longnose suckers.

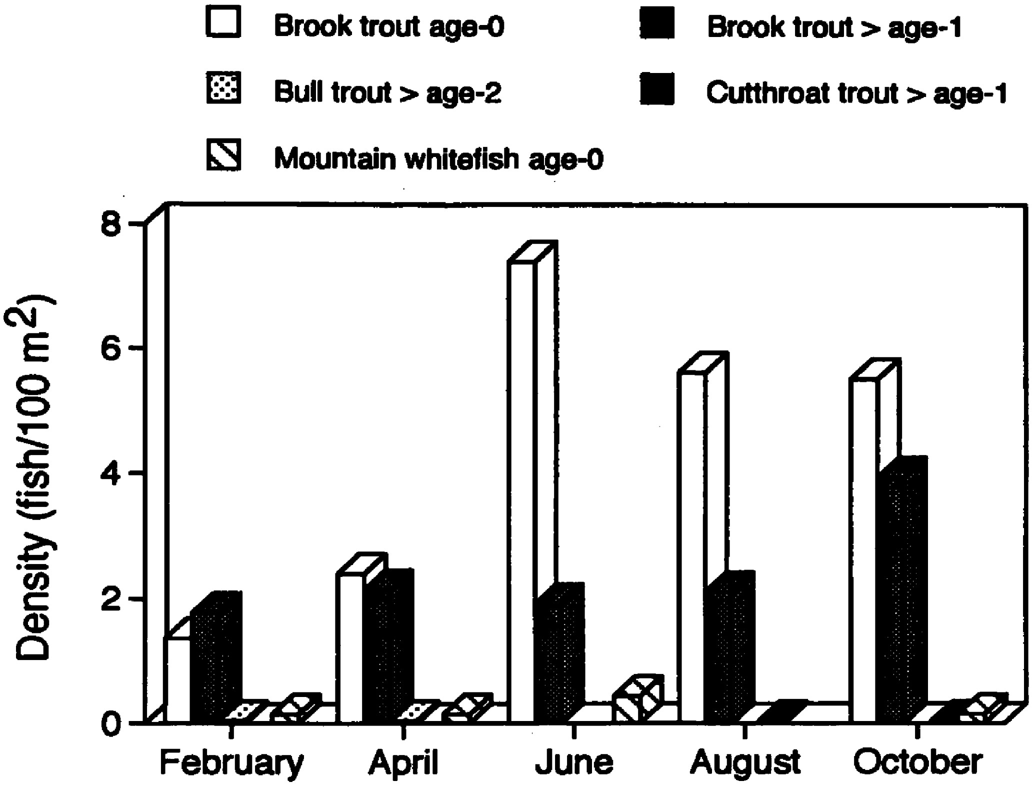

Figure 13: Seasonal densities of salmonid species-age classes for upper Beaver springbrook in 1995.

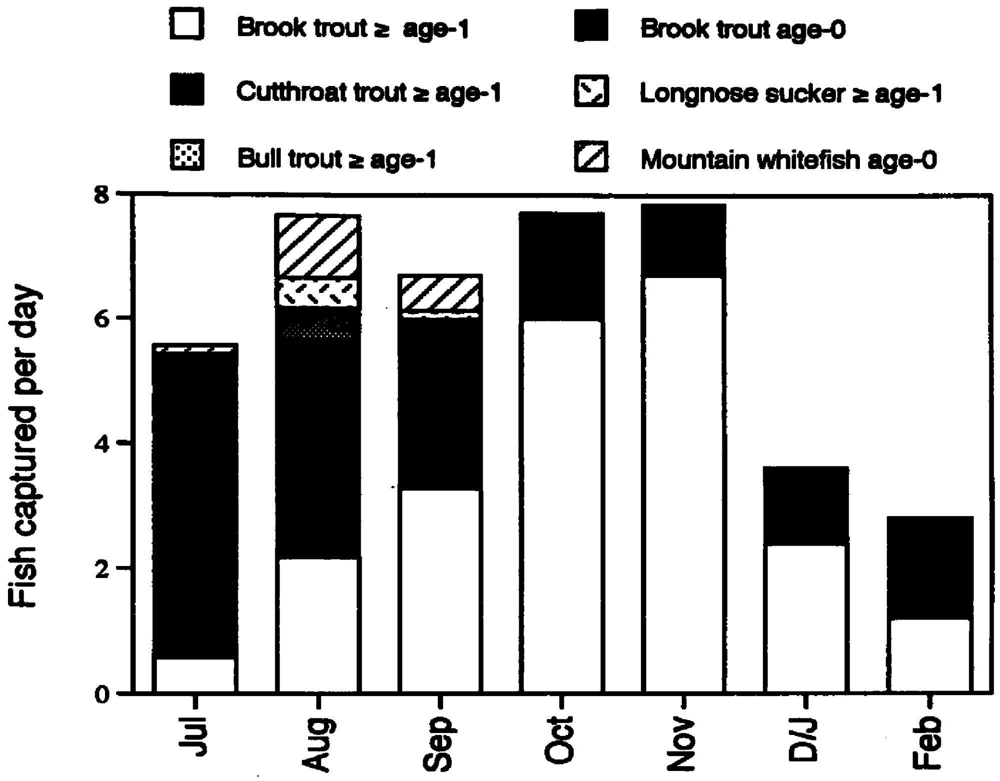

Figure 14: Mean daily upstream captures of brook trout in upper Beaver springbrook weir from 1995 through early 1996.

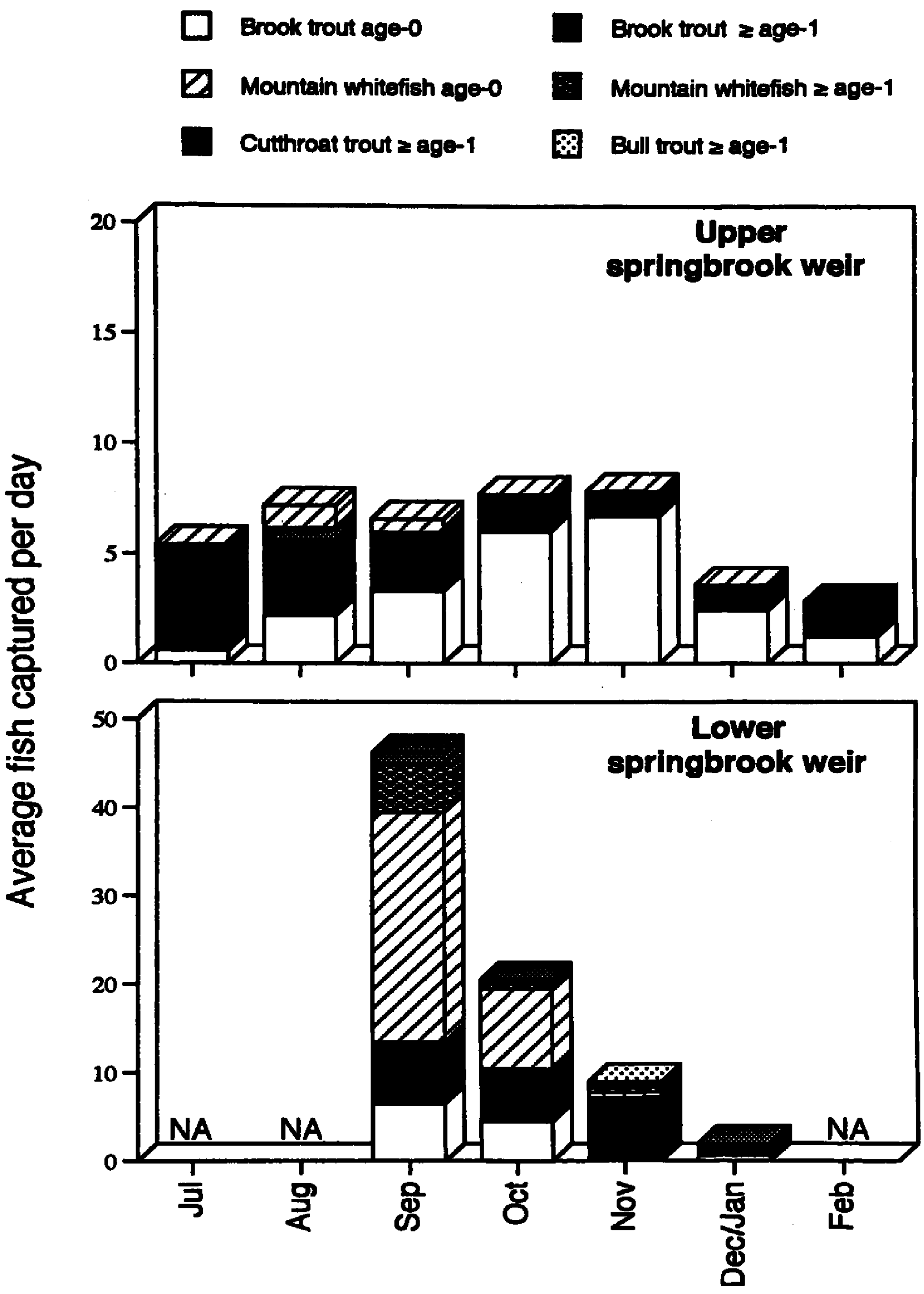

Figure 15: Stacked mean daily captures (upstream + downstream) in upper and lower springbrook weirs, 1995 through early 1996.

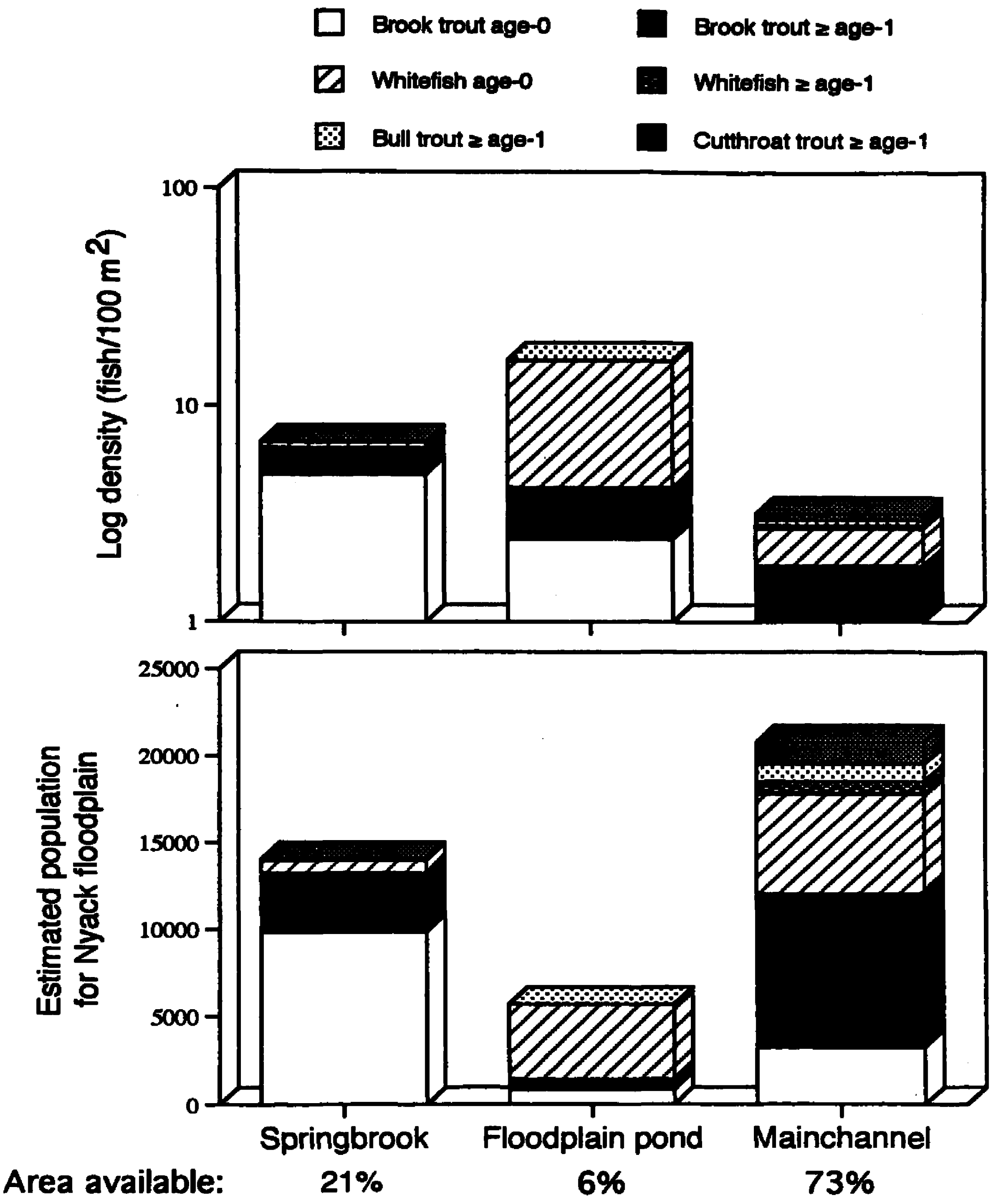

Figure 16: Stacked average summer/fall densities of salmonids in floodplain reach types (uper graph). Total estimated population for Nyack floodplain based on availability of habitat and densities (lower graph). Note log scale in upper graph.

CHAPTER 3

DO FISH SLEEP AT NIGHT OR JUST BIOLOGISTS? NOCTURNALISM IN COLDWATER RIVERINE FISH ASSEMBLAGES AND ITS METHODOLOGICAL AND ECOLOGICAL IMPLICATIONS

Introduction

Everyone, especially fishermen, seems to know that fish don't sleep at night, but curiously, this fact is routinely overlooked in ecological studies of temperate stream fishes. While community-level accounts of fish nocturnal activity are available for marine systems (reviewed by Helfman 1978, 1993), and temperate lakes (Emery 1973), few accounts of similar patterns exist among temperate streams. The implicit assumption supporting reliance on daytime observations and sampling appears to be either that nocturnal activity is not important relative to daytime activity, or that daytime studies are in fact representative of what goes on at night. However, as evidence for greater nocturnal activity and different nocturnal behavioral modes subtly accumulate, these assumptions, and the validity of a daytime sampling bias, appear increasingly dubious.

Currently a review of nocturnal activity patterns and behaviors among temperate stream fishes is not available, but in my literature review I found much evidence, often embedded within papers focusing on different subjects, demonstrating distinct and ecologically significant nocturnal behaviors among stream fishes. The purpose of this paper is to present evidence from my study of a Montana floodplain river system, and to review evidence available from the literature in attempting to document patterns of nocturnal activity among temperate stream fishes. I also speculate on possible causes, implications and significance of nocturnalism as they relate to sampling methods and our understanding of the ecology of riverine fishes. Because most of the relevant behavioral and ecological literature on diel activity patterns concern salmonids, and since they were the dominant taxa in my study area, they will serve as the focus of discussion.

Most fishes specialize as either diurnal, nocturnal or twilight foragers (Helfman 1981) and salmonids are generally recognized, at least potentially, as both diurnally and nocturnally active. However, studies on fishes which are primarily visual foragers (including salmonids) often assume that visual foragers are also obligate daytime feeders (Allan 1978; Cunjak and Power 1987; O'Brien 1987; Thorpe et al. 1988; Beers and Culp 1990; Walsh 1988), and are largely inactive at night (Hoar 1942; Edmunson et al. 1968; Blaxter 1977). Studies have attempted to illustrate the primacy of daytime activity and feeding through analysis of stomach contents (Tusa 1969; Bisson 1978; Tippets and Moyle 1978; Johnson and Johnson 1981; Walsh et al. 1988; Angradi and Griffith 1990; Forrester et al. 1994), and laboratory feeding experiments (Hoar 1942; Ali 1964; Tanaka 1970). Typically these studies have found minimal nocturnal foraging relative to daytime food intake. However, experiments have demonstrated that salmonids have the capacity for successful foraging at low light levels (< 0.1 lux, see Table 1). Jenkins (1969) found that brown and rainbow trout were capable of feeding on drifting terrestrial insects in moonlight and starlight conditions. Elliot (1973) and Jenkins et al. (1970) showed a relationship between nocturnal peaks in insect drift and feeding activities of trout (but see Angradi & Griffith 1990). Among arctic char, studies have also revealed that during parts of the year the majority of food is consumed during darkness (Jorgensen & Jobling 1989). Similarly, Fraser et al. (1993) found in a laboratory study that juvenile Atlantic salmon were active and fed nocturnally at water temperatures below 10 °C. Lastly, while Hoar (1942) and Tanaka (1970) found that day time feeding rates were highest, they also demonstrated that trout were capable of feeding at below 0.030 lux and even in total darkness.

Behavior and diel activity patterns among salmonids are known to change seasonally. During summer months, some field studies show higher nocturnal actvity relative to daytime activity (e.g. Matthews et al. 1994; Bonneau et al. 1995), although few investigations have taken this possiblity into consideration. Winter surveys however, increasingly demonstrate dramatic shifts in habitat use and diel activity patterns. During daytime in winter, salmonids are often observed aggregated under cover (Bustard and Narver 1975; Tschaplinski and Hartman 1983; McMahon and Hartman 1989), in low water velocities (Edmunson et al. 1968; Campbell and Neuner 1985; Cunjak and Power 1986; Heggenes et al. 1993), or concealed under substrate (Hartman 1963; Hartman 1965; Chapman and Bjornn 1969; Rimmer et al. 1983; Campbell and Neuner 1985; Cunjak 1988; Fraser 1993 ; Heggenes et al. 1993; Gurnell et al. 1995). These findings have led to the common assumption that salmonids, while continuing to feed to some degree (Cunjak and Power 1987), remain relatively inactive in winter. Presently, few published records of paired day and night winter fish surveys of the same habitats exist. The available literature shows that in many cases juvenile salmonids become nocturnal in winter, hiding during the day, but emerging at night (Chapman and Bjornn 1969; Rimmer et al. 1983; Campbell and Neuner 1985; Cunjak 1988; Fraser 1993; Riehle and Griffith 1993). In the only such studies available for adult salmonids in winter, Heggenes et al. (1993) and Campbell and Neuner (1985) reported that brown trout and rainbow trout, respectively, also remained hidden during the day, but emerged from concealment at night.

My observations of day and night activity patterns of fishes across several habitat types in a floodplain river in Montana also suggest that nocturnalism can be a more common, and year-round phenomena than is generally recognized. The objective of this study was to evaluate the effectiveness of day and night visual surveys in detecting the presence or relative abundance of species-age classes of fishes and amphibians across floodplain habitats (springbrooks, ponds, and mainchannel anabranches) characterized by dinstinct physical conditions and environmental gradients.

Study site

The study was conducted on the Nyack floodplain of the Middle Fork Flathead River, at the southern boundary of Glacier National Park, Montana. This alluvial intermountain river segment, bounded upstream and downstream by narrow canyons, is about 7 km long and 1-2 km wide. The Middle Fork is a 5th-order river with a catchment approximatly 3200 km^2 in area. It drains heavily glaciated, high-relief terrain underlain by uplifted sedimentary and metasedimentary rocks of the Belt series. Thick deposits of glacial and periglacial origin mantle the valley floors and many side slopes. The main river channel annually traverses or inundates a swath of the valley floor between 300 and 700 m wide; within this band lies a dynamic mosaic of low flow channels, recently abandoned channels, and coarse gravel bars with early successional herbaceous and shrub vegetation. Channel patterns range from meandering to braided. This annually active zone is nested within a broader zone comprising an anastmosed network of relict channel traces and floodplain surfaces. Most of the lower surfaces in this zone are inundated or reoccupied by the river during high flow events on what appears to be a decadal time frame. During high flow stages, some surfaces are typically occupied by overflow from river sources, others are inundated by groundwater that emerges at the surface when the water table is raised during high river stages.

The upstream portion of the Nyack segment is known to be strongly downwelling, with net loss of about 20 percent of the river's flow in the first 2 kilometers (Stanford et al. unpublished). This flow deficit is reportedly regained through upwelling of groundwater into surface waters before the river exits into a canyon downstream. Off-channel habitats such as springbrooks and floodplain ponds, many maintaining strong perennial flow, erupt in some abandoned channels and are a common and distinct component of aquatic habitats in the floodplain (Stanford and Ward 1993). Springbrooks emerge on the floodplain surface and are disconnected from surface water at the upstream end, except during extreme flood events, and flow downvalley for distances of hundreds of meters to several kilometers before converging with the main river channel. Floodplain ponds are variably influenced by groundwater seepage, and are typically connected to surface waters annually or at higher frequencies.

Methods

Reach selection

I designated nine reaches which attempted to capture three general categories of aquatic biotopes present on the floodplain surface. Originally, three study reaches were relegated to each aquatic habitat type: springbrook, floodplain pond and main channel anabranches. However, one of the springbrook reaches (lower) was later reclassified as a main channel reach when it became clear it received a significant portion of its flow from surface waters, and exhibited other main channel-like thermal and physical characteristics. Springbrook and main channel reaches were arrayed on three transverse transects running roughly east-west down valley (Figure 1). By necessity, floodplain pond sites were clustered across from the confluence of a major tributary, Nyack Creek. This portion of the floodplain is highly unstable and avulsive, and thus frequently the site of pond formation. Springbrook and main channel reaches consisted of at least three consecutive pool-riffle sequences and included such lateral habitats as backwaters and side channels, if present. A floodplain pond reach consisted of a single pond isolated from other surface waters. Table 2 further summarizes the physical characteristics of each of these reach types.

Sampling design

In the summer of 1994 detailed physical surveys were initially conducted on each of the study reaches. Utilizing measuring tape, Sonin® electronic distance meter and compass, I constructed two-dimensional maps for all study reaches. Maps included location of woody debris, overhanging vegetation, wetted area, and boundaries of within-reach habitat units such as riffles, pools, and backwaters. Depth, substrate, velocity categories were defined to reflect the range of physical attributes observed within the study area. These habitat variables were recorded on reach maps dispersed every 2-5m^2 of wetted area, the scale depending on the size and physical complexity of the study reach.. Finer resolutions (2m^2) were utilized in smaller study reaches (e.g. 300m^2 floodplain pond) and areas with more complex microhabitat structure, while coarsest resolution was applied in largest and most physically homogeneous study units (e.g.

9000m^2 main channel branch reach). Physical habitat surveys and maps were repeated when reach habitat conditions changed. All mainchannel and pond reaches were resurveyed in summer 1995 as a result of channel changes which occurred in the spring run-off of 1995. Springbrook reaches were stable throughout the study period and did not require repeated surveys. In reaches that were surveyed twice, habitat variables were largely consistent between survey dates.

Temperatures were monitored by a network of Onset StowAway® and Hobo® thermistor devices throughout the study period. Initially, at least two temperature recorders were placed in each study reach to continuously monitor ambient temperatures. The harsh physical conditions during winter and spring in main channel reaches resulted in the loss of several data loggers and fewer devices were operating in these reaches by the 1995 field season.

Beginning in the summer of 1994 and continuing through winter 1996 in some cases, study reaches were surveyed for aquatic vertebrates every 2 to 4 months except during winter and spring when ice and poor visibility precluded sampling of some main channel reaches and floodplain ponds. Water clarity was typically excellent in all study reaches (visibility ≥ 5 m), and all surveys were conducted by visual observations of divers and bank observers. Depending on reach width, one or two snorkelers swam slowly, zigzagging upstream through the reach. Divers searched intensively by regularly overturning and replacing rocks and exploring under banks and woody debris with dive lights. Bank observers (one or two, also equipped with lights) followed close behind to check for fish in shallow edges and lateral habitats, and to record observations. Only daytime surveys were conducted during the summer and fall of 1994, but thereafter most surveys were conducted during day and night. Day surveys took place between 13:00 and 2 hours before darkness. Night surveys utilizing dive lights began 1 hour after sunset and were completed before 01:00. The time required to complete each surveyed varied from 1.5 to 3 hours depending on the number of fish observed, and the size or the reach. All fish and amphibian species were identified and their total length estimated to the nearest centimeter. Individuals were occasionally captured by hand net to verify length estimates and species identification. The position of each individual observed was recorded on the corresponding reach map, or in the case of night surveys, was marked with a colored washer, and the position was mapped the following day.

Data analysis

Fish observations were summarized in terms of density (#/100 m^2 of total reach surface area) and total counts for survey dates, times and reaches (Appendix). Length estimates were used to divide species into approximate year class categories based on my own length-frequency data and other published sources (especially Brown 1971). Species-age classes provided a convenient way to account for the ontogenetic changes in distribution, abundance and behavior which are commonly observed within age classes of a species (Polis 1984). Sculpins *Cottus* spp. were abundant and were observed in virtually all habitats, survey dates and times of day, but were not included in my analysis because of low confidence in the effectiveness of visual sampling for this benthic family. I computed the availability and usage of microhabitats and within reach habitat units by breaking down reach maps into grid cells ranging in size from 2 to 5 m^2. Once delineated, the cell grid was held constant between day and night surveys and acros sample dates within a reach. All physical and biological data were recorded into the corresponding cell based on the reach map position onto which data were recorded in the field. These data were entered into a relational database (FoxPro™ software) that facillitated analysis of habitat associations or other distributional patterns at nested spatial scales and with various levels of sampling effort.

In this paper, reach surveys served as one basic sampling unit in the analysis of my data. I compared reach level densities of species-age classes during day and night surveys in two ways. The first grouped observations from all seasons, so that gross patterns of nocturnal and diurnal activity could be compared. The second split surveys into summer/fall and winter/spring categories. These seasons were grouped to address warm (summer/fall) and cold seasons (winter/spring) separately since temperatue is though to be an important variable mediating changes in diel activity patterns among fishes (see Discussion). Mean densities were compared with nonparameteric Wilcoxon rank sum tests. Although small sample sizes prevented a meaningful application of statistical tests in seasonal comparisons, means and standard were used to allow discretionary comparisons.

Species-area curves are often used by ecologists examining patterns of diversity among different scales of habitat size, structure and heterogeneity (Begon et al. 1990). I developed species-area curves (or collection curves) to evaluate patterns of nocturnalism and to identify potential shortcomings of exclusively diurnal or nocturnal sampling regimes that assume. Collection curves were generated by a custom program (FoxPro™ software) which applied "bootsrap" techniques (Potvin and Roff 1993) in resampling cells, with replacement, from my biological survey database. Species-area curves are generally based on simple presence /absence data and are generated by tabulating the total number of species encountered for a given area of habitat sampled. In my case, cells sampled (area) served as the most appropriate index of sampling effort. However, cell size differed among reaches (see above), and it was necessary to standardize cell size to 1 m^2, and my approach to this was to base the number of species-age classes encountered on fractional units. For each cell drawn, the program sampled and tabulated fractions of species-age classes observed. Upon reaching a cumulative fraction equalling a density of 1.0 individuals/m^2 the program would stop counting that species-age class. However, the program sampled species-age classes independently such that cells containing species-age classes that already met the cumulative density of 1/m^2 were not ignored, but remained subject to random resampling so that other species-age classes co-occurring in the cell, and not yet at the cut-off density, could continue to be cumulated. The program could be parameterized to sample from any total area desired, with any number of replicates, and from surveys conducted during either day or night. I present two collection curves (Figure 3), one for daytime and one for nighttime surveys, which include all speices-age classes listed in Table 3 (total 18), and is drawn from surveys conducted in all reach types and all seasons. I ran 200 iterations for each sample area of 5, 10, 25, 50, 100, 250, 500, 1000, 2500, 5000, 10000, and 20000 m^2.

Results

Observed densities differed among night and day surveys, and among species-age classes and among three habitat types. Brook trout of all age classes exhibited a strong tendency toward nocturnalism, with significantly higher densities observed at night in both mainchannel and springbrook reaches (Table 4). Among age-2 and older bull trout, all observations were made during night surveys, regardless of reach type (Table 4). Suckers one year and older were also strongly nocturnal with significantly higher densities observed during night (Table 4). More westslope cutthroat trout were also observed at night, although differences were not as large as those observed among chars (bull and brook trout) and suckers. Mountain whitefish showed weak evidence for increased nocturnal activity in springbrooks and main channel reaches, but appeared more diurnally active in floodplain ponds.

Among many species and age classes, nocturnalism was prevalent across all seasons, especially in springbrook reaches. Fishes in main channel reaches were less nocturnal in summer/fall but became strongly so during spring/winter (Table 5). No fish were observed in main channels during daytime surveys in winter/spring, and densities observed at night were low for most species, suggesting that many individuals may have moved out of my main channel study reaches and into less hostile overwintering areas (e.g. deep, large pools). Across all habitats, age ≥1 brook trout, bull trout and suckers generally exhibited strong nocturnalism in the both winter/spring and summer/fall (Table 5). The principle exception was in floodplain ponds where age-1 and older brook trout appeared less nocturnal in summer/winter. Water temperatures differed seanally and between reach types but we observed no threshold or relationship with water temperature and the number of salmonids observed in paired day and night surveys (Figure 4). Young-of-the-year suckers and whitefish were abundant and more active in daytime surveys of floodplain ponds in both cold and warm seasons.

Overall, nocturnalism was especially prevalent among springbrook reaches where virtually all fish, other than some young-of-the-year were in concealment and not visible to searching divers during daytime surveys. Brook trout were by far the most abundant species occurring in these springbrook reaches, and for individuals greater than age-0 they exhibited near absolute nocturnalism year-round (Figure 2). During day surveys, divers infrequently observed fish concealed under debris jams or undercut banks, but they never occurred in positions suitable for classic visual feeding behavior. In the fall of 1995 and 1996 small aggregations of brook trout, including spawning adults, were visible during daylight hours on several occasions. However, this diurnal activity was fleeting, and after a brief window of activity all of these fishes apparently returned to diurnal concealment.

In any study, interpretations of abudance and activity patterns are easily biased by unequal sampling effort across seasons or habitat types. Random resampling of databases, as with the collection curve, is one way to address this problem. In my collection curve species-age class detection efficency differed dramtically between day and night surveys (Figure 3). At all levels of sampling effort, night sampling detected significantly more species age classes (Figure 3). For example, detecting half of the speices-age classes observed in my study would require twice as much daytime sampling effort (area) as nighttime effort (Figure 3). Furthermore, since three species-age classes were exclusively observed at night, and only one was esclusively observed during daytime (Table 3), day and night collection curves would not converge at any sampling effort.

Discussion

Daytime concealment and nocturnal activity was common year-round among many species-age classes across all three of the floodplain reach types surveyed. The fact that salmonids and other fishes are sometimes nocturnal is not a novel discovery. In my literature review however, I found no studies which had documented such pervasive and year-round nocturnalism among riverine salmonid communities. If daytime concealment and nocturnal activity is not uncommon in other streams and rivers it poses many interesting implications both for fish sampling methodologies and our understanding of stream ecology.

Effectiveness of sampling methods is an obvious area of concern with regard to nocturnal activity. Visual observation is increasingly utilized by biologists attempting to enumerate fish populations or document habitat use while minimizing intrusion into the study system. Clearly species detection and abundance estimates can be severely biased by timing of visual surveys if aquatic vertebrates are not equally observable at all times of day. In our study, observed assemblage composition and densities of fishes within reach types differed dramatically different between day and night surveys. During summer for example, night surveys are necessary to truthfully estimate abundances for brook trout, bull trout, ≥ age-1 longnose suckers, and boreal toad adults; particularly in springbrook and mainchannel reach types (Figure 5). Day surveys on the other hand, are adequit or better for detecting mountain whitefish, age-0 longnose suckers, boreal toad tadpoles and spotted frog adults (Figure 5). These findings suggest that visual surveys conducted during day and night hours are necessary (at least until behavioral assumptions are verified) to ensure accurate estimates of abundance and habitat use, as well as a complete characterization of aquatic vertebrate coummunity structure.

Daytime concealment also has implications for non-observational sampling techniques. The extent to which electrofishing can successfully bring fish out of hiding under substrates, woody debris, or undercut banks is poorly documented. However, even if abundance could be estimated accurately by electrofishing under such conditions, interpretation of findings in the absence of knowledge about diel activity might lead to erroneous conclusions about habitat associations and behavior. Seine, gill net or hook and line sampling would be subject to similar limitations.

Visual stream surveys have been used to estimate populations, determine habitat use and study interspecific interactions, but comparisons of day and night surveys (which are few) have focused on sampling efficiency, and scientists have seemed strangely reluctant to make logical inferences regarding observed diel behavior and activity patterns. Bonneau et al. (1995) for example, explicitly tested the relative sampling efficiencies of night and day visual surveys, and found that daytime surveys regularly underestimated juvenile bull trout populations, but were more effective for juvenile cutthroat trout. Higher abundances of juvenile bull trout and cutthroat trout during night surveys were also reported by Spangler (1997). Conversely, Thurow and Schill (1996) found that densities of bull trout estimated during day and night visual surveys were similar.

Concerns regarding potential artifacts of visual sampling methodologies may explain some of the hesitancy to step beyond methodological interpretations of observed differences between day and night surveys. It might be argued for example, that wary fish avoid divers during the day, or that fishes are simply more visible at night (their scales brightly reflecting dive lights). Thorough and cautious surveys are however, unlikely to be affected by such sampling artifacts. Furthermore, visual surveys seem to provide the most practical and effective method for documenting patterns of diel activity that pose important ecological implications not just for fish, but for their predators and prey.

My observations led me to recognize that present understanding of salmonid ecology is to an inordinate degree based on the assumption of salmonids as obligate visual, diurnally active predators. Salmonid foraging models are, for example, largely based on the classic scenario of drift feeding trout distributed in a behavioral hierarchy in which the largest individuals maximize energy intake by maintaining the most bioenegentically favorable feeding position (Fausch 1984; Hughes and Dill 1990; Hughes 1992b; Hughes 1992a). Similarly, attempts to quantify habitat requirements for trout, such as instream flow incremental methodology (Bovee 1986), are typically based on observed habitat use of respective year classes during daytime in summer (Orth and Maughan 1982; Campbell and Neuner 1985). Although I do not dispute that diurnal activity is generally the more common pattern, my data suggest that some species (e.g. brook trout in springbrooks) can thrive entirely in the absence of such classical diurnal behavior modes, and others may spend substantial portions of their life history in predominately nocturnal activity patterns; yet we know virtually nothing about foraging and behavior of these fishes at night.

Several studies have documented the occurrence of night feeding through anecdotal observation (e.g. Campbell and Neuner 1985), or through experiments (Hoar 1942; Jenkins 1969; Jenkins et al. 1970; Tanaka 1970; Elliot 1973; Jorgensen and Jobling 1989; Fraser 1993). Often the night feeding was viewed by its observers only as supplemental to diurnal foraging, and thus authors did not further consider questions of causes, mechanisms, and potential for success of fish feeding primarily at night. Similarly, the studies which report daytime concealment with nocturnal activity include few observations on the feeding behavior of night active fishes, perhaps because most observations were made in winter when feeding rates are presumably low. The activity of fish biologists in the field is also typically low during winter (especially at night). In a laboratory study however, Fraser et el. (1993) reported that juvenile Atlantic salmon, after emerging from day time concealment, fed predominantly and successfully at night when temperatures were below 10 °C. During my night surveys I often observed trout eating large aquatic insect larvae, but these observations where made in the presence of artifical lights which likely allow visual foraging mechanisms to operate. It appears from my study and others that salmonids are capable of foraging successfully in darkness at or below 0.1 lux, the general threshold suggested for visual teleosts by Blaxter (1977). But how are they feeding?

Salmonids in streams are widely described as drift feeders, darting from holding positions to intercept prey items passing in the current. Studies reporting nocturnal foraging rarely speculate on likely feeding tactics, but seem to assume that feeding in darkness occurs very much the same way it does during the day. Jenkins (1969), Jenkins et al. (1970), Elliot (1973) and Riehle and Griffith (1993) all report evidence of salmonids feeding on drifting insects at night, but offer no alternatives to traditional visual drift feeding tactics in their explanations. For example, Jenkins et al. (1970) note that their observations of rainbow trout provide, "...no indication that trout significantly alter their feeding behavior at night." However, profitable positions for drift feeding are to a large part determined by the quality, abundance and detectability of prey that are passing nearby (Fausch 1984; Hughes and Dill 1990), and reaction distances are known to dramatically decrease with decreasing light intensities (Confer et al. 1978; Henderson and Northcote 1985). This being the case, there is little reason to expect drift feeding fishes to select the same holding positions at night as during the day. In fact, several published papers that contrast day and night microhabitat selection suggests that in many cases fishes select strikingly different holding positions in darkness. At night stream dwelling salmonids often select low velocity, in-shore areas, away from expected daytime feeding lanes, and stay at or near the bottom (Edmunson et al. 1968; Campbell and Neuner 1985; Walsh et al. 1988; Heggenes et al. 1993; Riehle and Griffith 1993). Matthews et al. (1994) found that brown trout and rainbow trout were more active at night, and also tended to select downstream, shallow portions of pools, away from higher velocity, inflow areas where fishes were more often located during the day. In my study, springbrook reaches, where nocturnalism was most prevelent, had more low velocity habitats than other lotic floodplain habitats (Table 2), and I often observed nocturnal fishes selecting low velocity habitats, tending to be oriented inshore rather than into currents. On average, age-1 and older trout selected slower velocies at night (mean velocity class=1.5) than during the day (mean velocity class=1.8), but differences where not signficant (t-test, p=0.057). Curiously, such microhabitat observations have sometimes been offered as evidence for the absence of nocturnal feeding and activity (Edmunson et al. 1968; Walsh et al. 1988). However, I suggest that relatively quiet and shallow microhabitats might prove more desirable than high-velocity daytime feeding stations when fish are foraging in low light conditions with reduced reaction distances to prey items. Significantly, the selection of weak current areas for feeding is also reportedly common among nocturnal planktivores on coral reefs (Helfman 1993).

Salmonids are often described as quiescent or inactive during night observations. This seemingly lethargic behavior of holding on or near the bottom is also observed among nocturnal fishes in temperate lakes (Emery 1973), and marine reef environments (Hobson et al. 1981). The foraging strategy of these nocturnally active fishes appears to be to hover motionless until prey items betray themselves with turbulent producing movements which may be detected by fish tactilely through the lateral line system. Alternatively, fish may detect moving prey using visual systems that maximize sensitivity to motion rather than high resolution (McFarland 1991). Non-visual prey detection has apparently never been explicitly tested among salmonids, but it is well known among many fishes, including mottled sculpins (Hoekstra and Janssen 1985), and longnose dace (Beers and Culp 1990). Limited light and reduced visual reaction distances at night might also increase reliance on non-visual prey detection mechanisms among nocturnal salmonids.

The physical limitations of feeding at night along with evidence for nocturnal selection of low velocity, in-shore microhabitats suggest that traditional drift feeding is not the likely method of nocturnal foraging. I hypothesize that nocturnal salmonids may, under the appropriate conditions, adopt a strategy more closely resembling very low velocity drift feeding, or even epi-benthic foraging. Under these conditions fish could feed on slowly drifting prey items detected visually, and on moving prey items in the water column or near the benthos detected through the lateral line, chemoreception, or direct tactile response. While the number of foraging attempts and total prey consumed when feeding in this manner are likely to be much less than with diurnal drift feeding, the necessary selection of active prey might result in a higher ingestion rate and less energy spent moving and pursuing non-ingested items (e.g. Biro et al. 1996). The nocturnal foraging strategy I propose might also explain the often weak relationships observed between stomach contents and night time drift composition peaks (Bisson 1978; Angradi and Griffith 1990). Evidence for increased reliance on benthic feeding at night (e.g. Bisson 1978; Jorgensen and Jobling 1990; Jorgensen and Jobling 1992; Forrester et al. 1994) also suggests that classic drift feeding may not be an effective foraging strategy in darkness. Although some authors (e.g. Jenkins 1970) have been critical of benthic foraging and found little evidence supporting it, these conclusions are largely based on the tenuous interpretation of prey capture location as inferred from stomach content analysis. Benthic foraging may be easy to detect in cases where algae, detritus or non-drifting organisms such as snails are consumed, but it is difficult to imagine how an aquatic insect gleaned off a rock or consumed while swimming briefly, as with fish avoidance response (Culp et al. 1991), might be distinguished from true drifting prey through post-hoc examination of stomach contents. The weakness of traditional diet analyses in this regard is further highlighted by the fact that insect taxa most likely to enter the drift (and thus captured in drift samples) are also more likley to exhibit greater activity on the benthos (Elliot 1968), and therefore would be most susceptible to capture by benthic or epibenthic foraging fishes.

A few previous studies have speculated on the adaptive significance of daytime concealment and nocturnal activity among salmonids. The most common explanation relates to cold winter water temperatures, which are known to reduce swimming performance in salmonids (Brett et al. 1958; Webb 1978). Daytime concealment in cold waters thus might be expected to reduce predation risk from endothermic, visual aerial or terrestrial predators that can be quite active when water is cold (Campbell and Neuner 1985; Fraser 1993; Heggenes et al. 1993). Heggenes et al. (1993) hypthosizes that brown trout emerge nocturnally from daytime refuge primarily as a response to dangers posed by night time ice formation. However, predator avoidance and energetic explanations together seem to provide the most cogent explanation. As Fraser et al. (1993) explained, "it may be adaptive for salmon to forage by night at low temperatures because maximum food intake rates are low due to slower metabolic and digestion rates, so making a reduction in feeding efficiency less costly, and predation risk may be reduced." I agree with this interpretation, but offer several other prospective conditions, not necessarily restricted to winter, under which nocturnal foraging might be a highly adaptive strategy. (1) Cold water. Metabolic demands for fish increase with water temperature so relatively cold water temperatures (e.g. in springbrook habitats) are likely to make nocturnal activity energetically viable, despite potential losses in food intake relative to diurnal foraging. Several studies provide evidence for a temperatue dependent switch (typically from 7-10 °C) between diurnal and nocturnal activity (e.g. Fraser et al. 1993; Riehle and Griffith 1993), but temperature may not be the sole factor directing shifts in diel activity. In my study, warm season nocturnalism was indeed stongest in cold springbrook reaches, but I observed no pattern between increasing water temperatue and decreasing nocturnal activity as might be expected (Figure 4). (2) Abundant food. In very productive streams (again, as in springbrooks) with abundant, available and often large-bodied prey items it may be feasible for fish to feed only at night and still meet their energetic requirements. (3) High predation risk. Streams with limited cover in the form of surface turbulence, overhanging vegetation, woody debris, macrophytes, coarse substrates or deep pools may present inordinate predation risks, particularly to aerial or terrestrial predators, making diurnal activity highly unselective. (4) High water clarity and slow water velocities. Day time predation risk is likely greater with high water clarity and laminar, non-turbulent flow, but these conditions are also likely to facilitate nocturnal foraging by increasing reaction distance for visual (Gregory and Northcote 1993; O'Brien and Showalter 1993), and non-visual foraging in low light conditions.

Innate physiological characteristics of species are also likely to influence diel activity patterns. Species with acute low light visual capabilities, or effective non-visual sensory systems would be more successful and inclined to adopt nocturnal foraging strategies. Furthermore, studies suggest that interspecific differences in feeding efficiency under various light levels can serve as potential mechanisms of niche partitioning. Robinson and Tash (1979) for example, found that brown trout (*Salmo trutta*) fed more successfully at low light levels than apache trout (*Oncorhynchus apache*). Differences in visual capabilities have also been shown to influence foraging success, and hence spatial and prey segregation among dolly varden char (*Salvelinus malma*) and cutthroat trout (*Oncorhynchus clarki*) (Henderson and Northcote 1985; Northcote 1995). My study found that brook trout and bull trout exhibited the strongest tendency towards nocturnalism, which is consistent with other evidence suggesting char may be well suited to activity and feeding in darkness. Bull trout counts are typically higher during night than day surveys (Goetz 1989; Bonneau et al. 1995; Spangler 1997), suggesting a preference for nocturnal activity. The explanation for potentially greater nocturnal activity among chars is unclear, but some evidence suggests that they may have heightened low light feeding abilities. Dolly varden char, for example, were found to be better than cutthroat trout at detecting both planktonic (Henderson and Northcote 1985) and benthic prey items (Schutz and Northcote 1972) under low light conditions. The underlying mechanisms for these findings apparently relate to species specific retinal structure, and the composition and quantity of visual pigments (Allen et al. 1973; Allen et al. 1982; Henderson and Northcote 1988). In situations where nocturnal activity is favored and presumably enhances fitness, the inherent effectiveness of visual and non-visual sensory systems could largely determine the success of foraging, predator avoidance and competition among species and individuals. Superior low-light visual systems among brook trout may in part explain their highly successful invasion of floodplain springbrooks in Montana, where nocturnalism is the dominant behavioral strategy among native westslope cutthroat trout and non-native brook trout (Chapter 4).

Coral-reefs, temperate lakes, and temperate marine reefs fish assemblages all express similar shifts in species composition and behavior between day, night, and twilight (Helfman 1993). Shifts between diurnal and nocturnal fish assemblages in temperate streams are likely not as dramatic as those observed in coral-reefs, but my study demonstrates that winter and summer daytime observations are not necessarily representative of nighttime fish assemblage and behavior. The nocturnal emergence and increased activity of fishes such as bull trout, brook trout and longnose suckers may also have significant ecological ramifications for riverine communities in general. Adult fishes, for example, would be less available to avian and terrestrial predators if nocturnal, but at the same time might represent an unanticipated predation risk to small fishes hiding in shallows, and to nocturnally active and drifting aquatic invertebrates. As I speculated earlier, the rules regulating successful nocturnal foraging and predator avoidance in streams are likely very different between night and day. This new set of rules may allow some species to forage effectively at night where they could not during the day. For example, during night surveys we often observed large, predacious diving beetles (*Dytiscidae*) apparently hunting young-of-the-year salmonids in shallow margins of springbrook reaches.

Clearly, stream studies based solely on daytime sampling and observations may result in biased perceptions of aquatic vertebrate assemblage composition and ecological function. More surprising than this conclusion is the lack of studies documenting community-level activity patterns among temperate streams and rivers. Certainly insufficient information is available regarding the patterns, causes and significance of nocturnalism among fish assemblages in temperate streams and rivers. Discussions with fisheries colleagues, however, suggest that much unpublished information in the form of reports, theses, personal observations and unanalyzed data supports the generality of nocturnal emergence and increased activity among some species. More evidence will likely accumulate as study design and sampling methods begin to take into account the potential for nocturnal behavior, as they already have in many cases (e.g. Matthews 1996). My speculation on the adaptivenss, causes and strategies of nocturnal activity and foraging are offered as concepts to be tested through appropriate experiments and observation. Among the potential topics for research, study of nocturnal behavior and feeding strategies among salmonids in natural streams is in much need of attention. While stomach analysis and introduction of marked food items are effective techniques for detecting the occurrence of nocturnal feeding, they provide few reliable insights as to the behaviors and mechanisms of prey capture. Careful field and laboratory studies using living, mobile and large prey items (>2mm) and infrared-sensitive cameras (as in Culp 1989, Beers and Culp 1990) seem to hold substantial promise.

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Light Categories	Lux
starlight	0.0005-0.001
	0.005-0.01
moonlight	0.05-0.1
	0.5-1.0
dusk	5-10
	50-100
cloudy day	500-1000
	5 000-10 000
bright sunlight	50 000-100 000

Table 1. Illumination in lux relative to general categories of natural ambient light conditions (modified from Contor and Griffith 1995).

		Reach type		
		Springbrook	Floodplain Pond	Main Channel
Temperature	Mar-Jun	4.1±2.5	5.1±6.7	5.3±7.1
average ± range	Jul-Sep	7.3±3.5	14.2±10.0	13.2±8.6
	Oct-Nov	9.5±2.3	5.8±7.2	4.0±6.9
	Dec-Feb	6.6±2.9	1.4±3.3	0.8±3.7
Average reach width (m)		8	10	15
Average reach area (m2)		2714	2180	5713
Depth classes	1-10	13.0 (3.0)	10.3 (4.5)	10.0 (4.2)
(cm)	11-25	35.7 (5.9)	29.3 (6.6)	32.0 (7.7)
	26-50	33.3 (4.0)	22.0 (9.8)	28.3 (4.1)
	51-100	16.3 (5.1)	31.0 (6.0)	24.2 (7.8)
	100+	1.3 (2.3)	7.2 (3.3)	5.3 (2.6)
Velocity classes	0.0-0.9	2.7 (4.6)	99.3 (1.0)	4.2 (2.6)
(cm/s)	1.0-10.9	40.3 (16.5)	0.7 (0.0)	30.3 (10.3)
	11.0-24.9	39.0 (16.5)	0	21.3 (10.3)
	25.0-47.4	17.0 (11.5)	0	24.0 (9.4)
	47.5-77.4	1.0 (1.0)	0	17.8 (16.8)
	77.5+	0	0	2.2 (2.6)
Groundwater influence		High	Medium-Low	Low
Surface water influence		Infrequent	Seasonal	Continuous

Table 2. Summary of thermal and other physical habitat characteristics of floodplain reach types. Data for depth and velocity are repoted as average percent reach area, SD in paranthesis.

Species	Age class	Day	Night
Brook trout[a]	0	405	1129
Salvelinus fontinalis	1	27	592
	≥2	104	261
Westslope cutthroat trout	0	1	2
Oncorhynchus clarki lewisi	1	1	6
	≥2	10	6
Bull trout	≥2	0	18
Salvelinus confluentus			
Mountain whitefish	0	861	758
Prosipium williamsoni	1	50	36
	≥2	19	31
Longnose/Largescale sucker[b]	0	6341	1333
Catostomus catostomus	1	0	16
Catostomus macrocheilus		0	25
Boreal toad	tadpole	8503	8268
Bufo boreas	toadlet	17	0
	adult	5	18
Spotted frog	adult	11	3
Rana pretiosa			
Tailed frog	tadpole	1	0
Ascaphus truei			

[a] nonnative species

[b] only longnose suckers were positively identified, age-0 largescale suckers my have been present, but are difficult to distinguish

Table 3. Common and scientific names for all aquatic vertebrate species-age classes observed in study area. Day and night columns represent total number of individuals observed during day and night surveys across all seasons and habitat types.

		Reach type					
		Mainchannel		Floodplain pond		Springbrook	
Species	Age class	Day N=14	Night N=8	Day N=8	Night N=3	Day N=9	Night N=11
Brook trout	0	0	0.12 ***	1.87	0.05	0.96	2.35 **
	1	0.01	0.22 ***	0.26	0.45	0.04	1.26 ***
	≥2	0.03	0.14 **	0.64	0.48	0	0.44 ***
Cutthroat trout	0	<0.01	<0.01	0	0	0	0
	1	<0.01	0.03 *	0	0	0	<0.01
	≥2	0.02	0.03	0	0	0	<0.01
Bull trout	≥2	0	0.04 **	0	0.08 **	0	0.01 *
Whitefish	0	0.17	0.35	9.98	2.69	0.05	0.16
	1	0.03	0.03	0.22	0.02	0	<0.01
	≥2	0.01	0	0	0	0	0
Suckers	0	0.15	0.02	119.80	65.92	0	<0.01
	1	0	0.03 **	0	0.04 **	0	0
	≥2	0	0.04 *	0	0.10 **	0	0

Table 4. Mean densities for common species-age classes observed in our study area. Means are calculated from survey densities within reach types across all seasons. Asterisks represent statistically significant differences between day and night pairs (***p>0.01, **p>0.05, *p>0.10; Wilcoxon rank sum tests).

Summer/Fall		Reach type					
		Mainchannel		Floodplain pond		Springbrook	
Species	Age class	Day N=10	Night N=4	Day N=6	Night N=2	Day N=6	Night N=5
Brook trout	0	0	0.49 (0.35)	2.41 (1.53)	0	1.13 (0.51)	4.03 (0.81)
	1	0.05 (0.05)	0.74 (0.35)	0.44 (0.16)	0.70 (0.31)	0.06 (0.04)	1.73 (0.39)
	≥2	0.09 (0.05)	0.80 (0.34)	1.37 (0.44)	0.98 (0.69)	0.01 (0.01)	0.95 (0.24)
Cutthroat trout	0	> 0.01 (0.01)	0	0	0	0	0
	1	> 0.01 (0.01)	0.10 (0.09)	0	0	0	> 0.01 (0.01)
	≥2	0.06 (0.05)	0.09 (0.09)	0	0	0	0.02 (0.01)
Bull trout	≥2	0	0.15 (0.07)	0	0.01 (0.01)	0	> 0.01 (0.01)
Whitefish	0	0.35 (0.11)	0.87 (0.35)	11.9 (4.26)	4.14 (3.47)	0.13 (0.11)	0.30 (0.25)
	1	0.08 (0.05)	0.02 (0.01)	0	0	0	0.01 (0.01)
	≥2	0.03 (0.01)	0.03 (0.03)	0	0	0	0
Suckers	0	0.31 (0.23)	0.07 (0.07)	160 (92.9)	99.4 (87.9)	0	> 0.01 (0.01)
	1	0	0.06 (0.04)	0	0.03 (0.03)	0	0
	>2	0	0.12 (0.08)	0	0.12 (0.12)	0	0
Winter/Spring							
Species	Age class	Day N=4	Night N=4	Day N=2	Night N=1	Day N=3	Night N=6
Brook trout	0	0	0.02 (0.01)	0.26 (0.26)	0.17 (----)	1.87 (0.33)	3.01 (0.95)
	1	0	0.20 (0.11)	0	0.05 (----)	0	1.41 (0.39)
	≥2	0	0.06 (0.03)	0.03 (0.03)	0.26 (----)	0	0.22 (0.08)
Cutthroat trout	0	0	0.02 (0.02)	0	0	0	0
	1	0	> 0.01 (0.01)	0	0	0	0
	≥2	0	0.01 (0.01)	0	0	0	0
Bull trout	≥2	0	0	0	0.03 (----)	0	0.01 (0.01)
Whitefish	0	0	0.23 (0.09)	7.25 (6.08)	0.42 (----)	0.01 (0.01)	0.17 (0.07)
	1	0	0.07 (0.07)	0.86 (0.81)	0.09 (----)	0	0
	≥2	0	0.07 (0.07)	0	0	0	0
Suckers	0	0	0	1.3 (0.70)	0.26 (----)	0	0
	1	0	0	0	0.06 (----)	0	0
	≥2	0	0	0	0.06 (----)	0	0

Table 5. Mean densities with SE in paranthesis for common species-age classes observed in our study area for summer/fall (top) and winter/spring (bottom). Bold values designate higher density between day and night pairs.

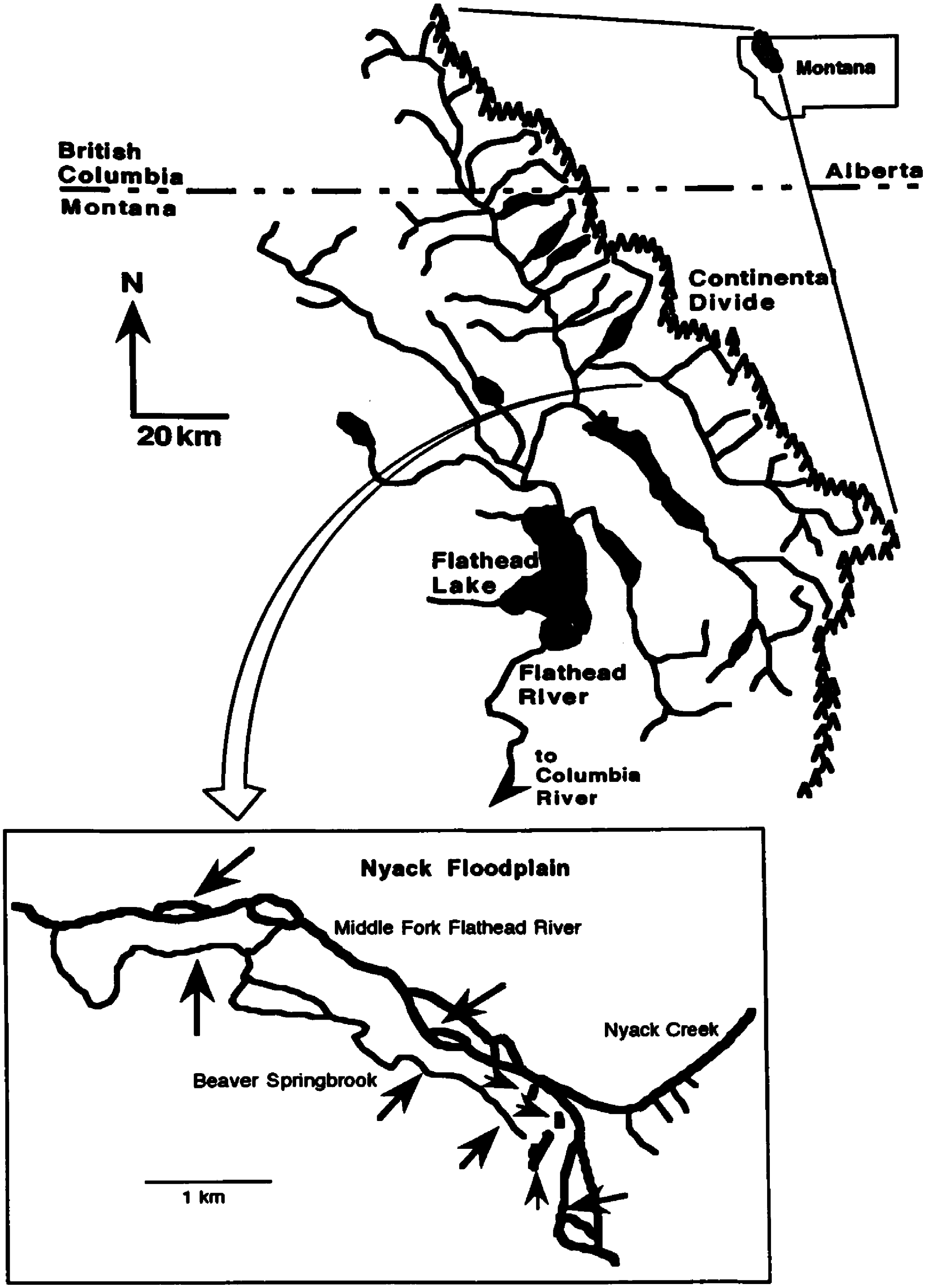

Figure 1: Map of study area on the Middle Fork Flathead River, Montana. Study sites are depicted with arrows on the Nyack floodplain inset. Large arrows designate main channel and springbrook reaches, small arrows identify floodplain ponds.

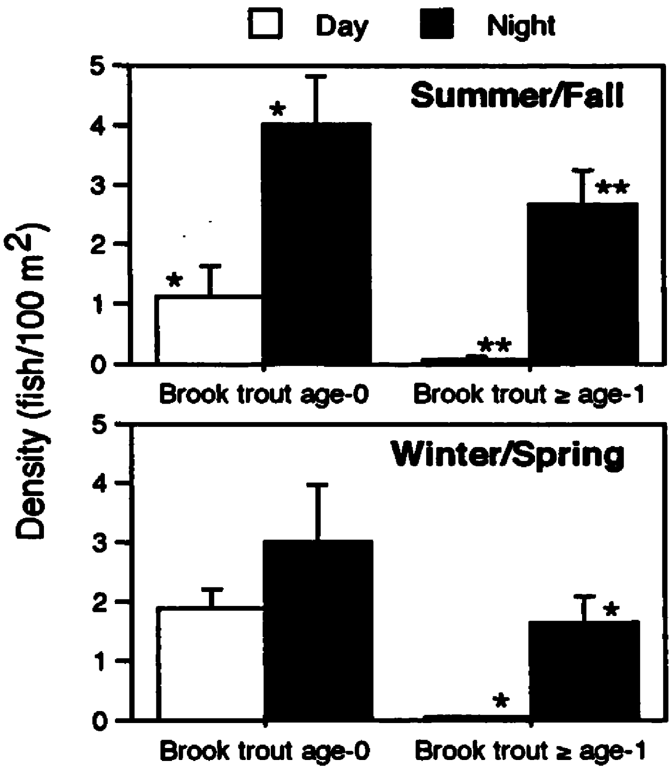

Figure 2: Mean densities with SE bars for day and night surveys of sprinbrook reaches in Summer/Fall and Winter/Spring. Asterisks represent statistically significant differences between day and night pairs (** $p<0.01$, * $p<0.05$; Wilcoxon rank sum tests)

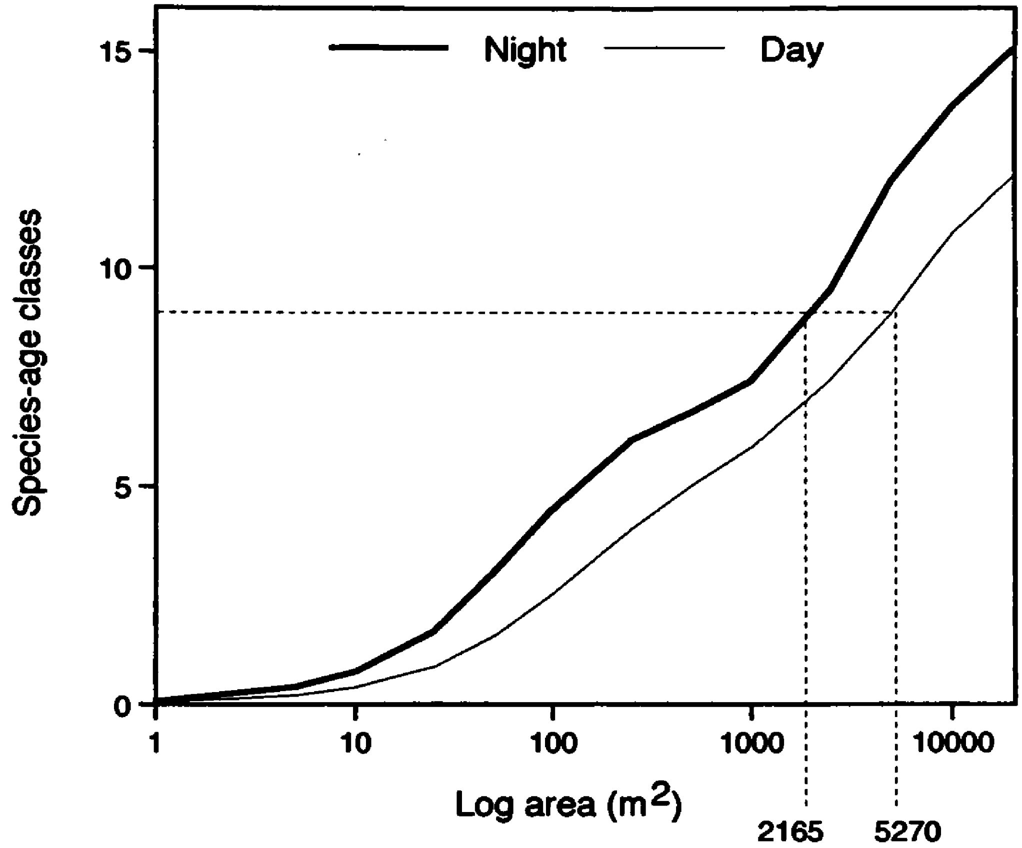

Figure 3: Collection curve generated by "bootstrap" resampling of biological database. Day and night curves based on data from all reach types and across all seasons. Curves based on mean (200 iterations) fractal species-age classes detected at sampling areas of 5, 10, 25, 50, 100, 250, 500, 1 000, 2 500, 10 000, 20 000 m^2. 95% confidence intervals too small to appear on graph. Lines falling to x-axis indicate sample area required to detect half (9) of all observed speices-age classes.

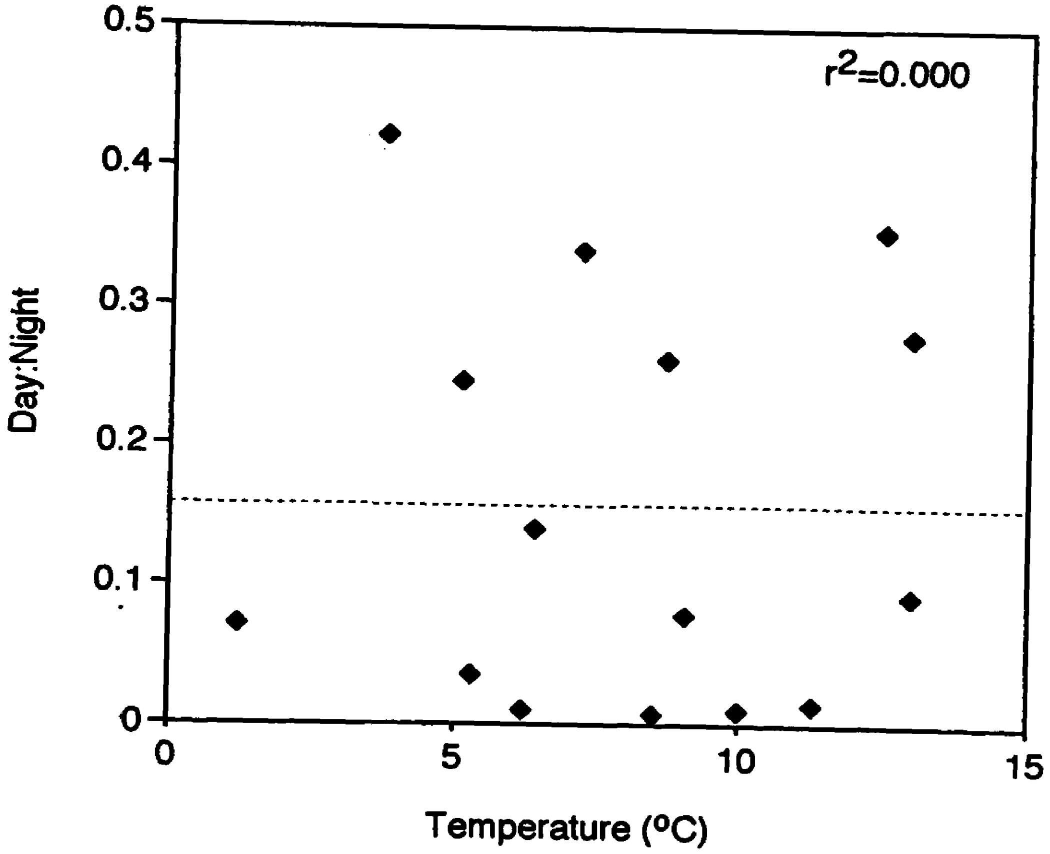

Figure 4: Ratio of day to night counts of salmonids for paired surveys (all seasons, mainchannel and springbrook reaches) plotted against average temperature during daytime survey.

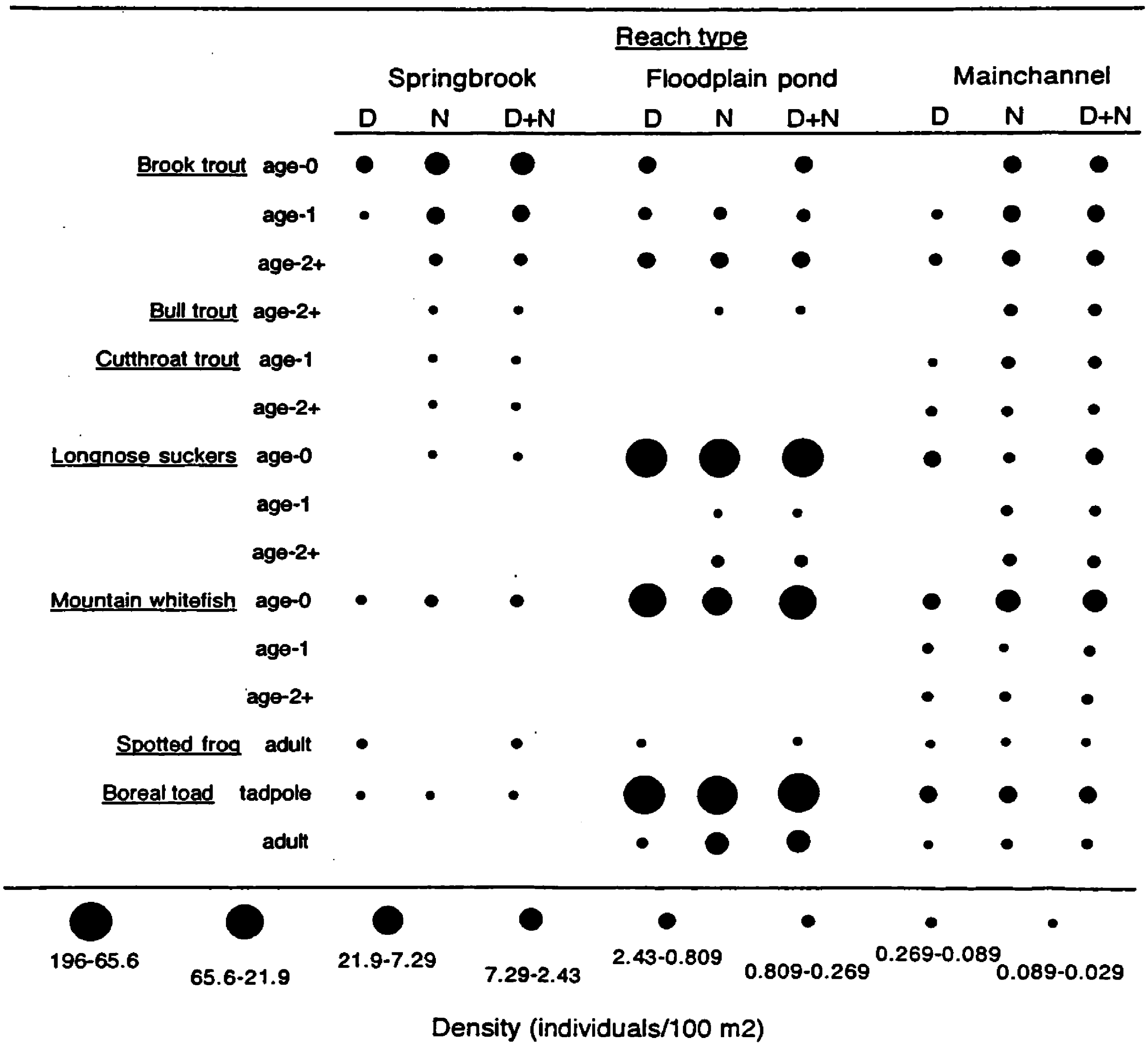

Figure 5: Summertime assemblage composition perceived by day, night and day+night visual surveys across three reach types. Filled circle size based on logarithmic scale of observed mean densities for each category. Day+night densities represent best estimate from day and night surveys.

CHAPTER 4

COLD, LOW-GRADIENT FLOODPLAIN SPRINGBROOKS: REFUGE FOR NATIVE CUTTHROAT TROUT OR INVADING BROOK TROUT?

Introduction

In North America, interbasin transplants and introductions of salmonids have often led to declines among native salmonids (Moyle 1976; Larson and Moore 1985; Gresswell 1988). Where native and nonnative salmonids coexist in a drainage, distinct and consistent longitudinal and altitudinal distribution patterns often emerge among species. Brown trout *Salmo trutta* and/or rainbow trout *Oncorhynchus mykiss* in the western, northern and eastern United States, for example, are typically found in downstream reaches, while brook trout *Salvelinus fontinalis* dominate upstream reaches (reviewed in Fausch 1989). Several potential mechanisms can be offered to explain observed patterns of species replacement along altitudinal gradients, but none provide an entirely consistent or cogent explanation. Upstream reaches may serve as refugia for species if downstream competitors are unable to colonize, or if environmental conditions prevailing within upstream reaches somehow favor native species such that they can prevail in biotic interactions with potential invaders.

Water temperature is among the most significant factors influencing salmonid distribution and behavior. Thermal optima, preferences and critical maxima are known to differ among salmonid species (Dickson and Kramer 1971; McCormick et al. 1972; Dwyer and Kramer 1975; De Staso and Rahel 1994), and these physiological characteristics presumably influence distribution and competitive ability. Brook trout distribution in streams for example, is strongly governed by availability of summer thermal habitats below 24° C (Meisner 1990b; Meisner 1990a), and in Japan, Fausch et al. (1994) found that the distribution of two congeneric chars at whole island and regional scales was strongly influenced by water temperature. However, Fausch (1989) found altitudinal and latitudinal distribution boundaries of brown trout and rainbow trout were poorly predicted by water temperature. Temperature can also potentially influence distribution through mediation of competitive or predatory interactions among fishes (Magnuson et al. 1979; Baltz et al. 1982; Reeves et al. 1987; Hill and Magnuson 1990; Vigg and Burley 1991), and in some cases, individuals are known to actively seek thermal patches serving as refugia from predation (Fraser and Cerri 1982) or competition (Gehlbach et al. 1978; Magnuson et al. 1979). Laboratory studies conducted on salmonids demonstrate that water temperature can influence the outcome of competitive interactions among species. Brook trout, for example, have a lower thermal optima than rainbow trout, and in tests of behavioral interactions brook trout dominated rainbow trout in colder water temperatures (Cunjak and Green 1986). Similarly, De Staso and Rahel (1994) showed that in laboratory tests brook trout and cutthroat trout *Oncorhynchus clarki* were equal competitors at 10 °C, but at 20 °C brook trout showed clear competitive dominance over cutthroat trout.

In the Rocky Mountain region of the western US, nonnative brook trout are widely distributed and are the species most commonly associated with the displacement and decline of native salmonids, particularly cutthroat trout subspecies (Griffith 1988; Fausch 1989; Behnke 1992). Where they occur sympatrically with brook trout in a drainage, cutthroat trout are often restricted to upstream, headwater reaches while brook trout dominate downstream reaches (MacPhee 1966; Griffith 1988; Fausch 1989; Behnke 1992). Water temperature and stream gradient are thought to regulate these distribution patterns, but neither factor provides an entirely consistent explanation. De Staso and Rahel (1994) found support for the primacy of temperature in mediating interspecific interactions and distribution. On the other hand, Fausch (1989) hypothesized that the downstream dominance of invading brook trout and the upstream displacement of native cutthroat trout subspecies was most likely a gradient effect, whereby brook trout were not able to colonize and reproduce in stream gradients above about 7%. These observed patterns, and the ambiguities of their putative explanations led Fausch (1989) to call for studies investigating the interacting effects of temperature and gradient on distribution and interactions between native and introduced salmonids.

Interpretation of physical variables or mechanisms directing distribution patterns among fishes are inherently problematic in typical upstream-downstream study designs because temperature, gradient and hydrologic factors are all unavoidably confounded. However, floodplain springbrooks, being cold (groundwater-fed) and low gradient, overcome many of these complications and provide a unique, but underutilized, field setting in which to test hypotheses regarding the relative importance of temperature in mediating interactions between fish species in low gradient streams.

The role of disturbance (e.g. floods, human habitat alterations) in determining the invasion success of nonnative fishes is another topic of interest to stream ecologists. River regulation resulting in discharge stabilization and elimination of peak flows (reduced natural disturbance), is thought render native communities more susceptible to invasion by introduced fishes which may be better adapted to the altered hydrologic regime (Meffe 1984; Li et al. 1987; Baltz and Moyle 1993; Moyle 1996)]. Unfortunately dam-induced alterations in hydrologic regime are almost always associated with other human disturbances, complicating interpretations of mechanisms causing decline of native fishes. However, springbrooks are hydrologic stable (e.g. Manga 1996), and thus provide also provide an excellent setting in which to evaluate invasibility in streams naturally free of hydrologic disturbance and anthropogenic habitat alterations, a contingency conspicuously absent from current literature on nonnative fish invasions.

The purpose of this paper is to demonstrate the utility of springbrooks as a natural experimental setting which overcomes many complications associated with upstream-downstream distributional studies (numerous confounded variables) and laboratory investigations (artificial, oversimplified conditions). I present data from two springbrook reaches of the Middle Fork Flathead River basin, Montana. One springbrook occurring in a floodplain segment where brook trout are known to be present (Beaver springbrook) and another springbrook where brook trout have not yet colonized (McDonald springbrook) Specifically, my study addressed the following questions: Do floodplain springbrooks serve as coldwater refugia for native westslope cutthroat trout as might be expected, based on available experimental and distributional evidence? What are the differences or similarities in habitat use and behavior among native westslope cutthroat trout and introduced brook trout living in springbrooks? I addressed these questions by conducting surveys in both springbrooks to compare salmonid abundance, habitat use and behavior.

Study Area

The study was conducted on two floodplain segments of the Middle Fork Flathead River drainage in northwest Montana (Figure 1). The middle fork is a 5th order river with a catchment approximating 3200 km^2 in area. It drains heavily glaciated, high-relief terrain underlain by uplifted sedimentary and metasedimentary rocks of the Belt series. Thick deposits of glacial and periglacial origin mantle valley floors and many side slopes. Floodplains in this region are characterized by an expansive alluvium and high volumes of hyporheic flow through porous substrates of glacial outwash (Stanford and Ward 1993). These hyporheic aquifers are tightly linked hyrdologically and ecologically to overlying river channels. Typically, river water downwells into the aquifer as it enters the floodplains and then emerges back to the surface some distance downstream, either directly into the main channel or into relict channel habitats on the floodplain surface.

Sampling was primarily conducted on the Nyack floodplain of the Middle Fork Flathead River at the confluence of Nyack Creek, a third order tributary. The second floodplain site was in the McDonald Creek drainage, a 4th order tributary to the middle fork located within the boundaries of Glacier National Park. These alluvial valley river segments were selected because of similarities in channel pattern, vegetation and hydrogeologic properties. Due to the aggraded nature of these floodplain segments, channel patterns ranged from meandering and anabranching channels to braided river segments. In response to bedload dynamics and coarse woody debris accumulation, rivers channels appear to experience frequent avulsion events. River channels abandoned during avulsions often maintain hydrologic connections to the underlying hyporheic aquifer, and as such, serve as an outlet for alluvial groundwaters entrained as the river entered the floodplain. These springbrooks are common on the floodplain surface, but vary in their permanence, isolation from surface waters, as well as in the quantity and consistency of their flows. My study focused on McDonald springbrook and Beaver springbrook, both large volume, perennial springbrooks (Figure 1). These springbrooks have no upstream connection to surface waters, and receive surface water input only during severe runoff events. Springbrook thermal and hydrologic regimes are very stable and the seasonal variations which occur generally track main river channel patterns, but are heavily dampened and, in the case of temperature, exhibit 2-3 month response lags (Figure 2). Temperatures in these springbrooks typically vary between 4 and 10° C, and are thus colder in summer, but warmer in winter relative to most tributaries and main channel reaches. Floodplain springbrooks are relatively undescribed in the literature, but appear very similar to wall-based channels described by Peterson and Reid (1984).

Methods

Reach selection and sampling design

In order to facilitate comparisons of fish abundance and habitat use, I selected two study reaches with similar physical characteristics in each floodplain springbrook (Figure

3). In the Nyack floodplain I focused on the upper Beaver springbrook reach (see Chapters 2, 3). Middle and lower Beaver springbrook reaches were not included because, although biologically similar, their physical characteristics were not as comparable with the McDonald springbrook reach. Study reaches consisted of at least three consecutive pool-riffle sequences and included such lateral habitats as backwaters and side channels. (Table 1). Rather than pseudoreplicating within springbrooks, problematic due to the small size of springbrooks and scarcity of comparable study reaches, I opted for seasonally repeated sampling on relatively large singles reaches.

Detailed physical surveys were conducted on both study reaches. Utilizing measuring tape, Sonin® electronic distance meter and compass, I constructed two-dimensional maps for study reaches. Maps included location of woody debris, overhanging vegetation, wetted area, and boundaries of within-reach habitat units such as riffles, pools, and backwaters. Depth, substrate, velocity categories were designated to reflect the relevant physical attributes observed within the study area. Habitat variables were recorded on these maps every 3 m^2 wetted area in the Beaver Springbrook reach and every 2 m^2 in McDonald springbrook. Water temperature was monitored by a network of Onset StowAway® and Hobo® thermistor devices throughout the study period.

In Beaver springbrook, reaches were surveyed for aquatic vertebrates every 2 to 4 months beginning in the summer of 1994 and continuing through winter 1996. Multiple, seasonal surveys were conducted because I expected and wanted to account for possible seasonal movements and transient fish invasions. McDonald springbrook was surveyed in late summer of 1996. Water clarity was excellent (visibility ≥ 5 m) at all times, and all surveys were conducted by visual observations of divers and bank observers. Surveys were conducted by one diver who swam slowly, zigzagging upstream through the reach. Divers searched intensively by regularly overturning rocks and exploring under banks and woody debris with dive lights. Bank observers (1 or 2) followed close behind to check shallow edges and lateral habitats, and to record notes on fish observations. Surveys were conducted during day and night. Day surveys took place between 13:00 and 2 hours before darkness. Night surveys utilizing dive lights began 1 hour after sunset and were completed before 01:00. The time required to complete each surveyed varied somewhat depending on the behavior of the fish observed. All fish species were identified and their total length estimated to the nearest centimeter. Individuals were occasionally captured by hand net to verify length estimates and species identification. The position of each individual observed was recorded on the corresponding reach map, or in the case of night surveys, was marked with a colored washer, and the position recorded the following day.

Data analysis

Reach surveys served as the basic sampling unit in the analysis of data. Fish observations were summarized in terms of density (#/100 m^2 of total reach surface area) and total abundance for survey dates, times and reaches. Length estimates for fish species were used to break down species into year class categories based on my own length frequency data and other published sources (especially Brown 1971). Sculpins *Cottus* spp. were generally abundant in surveys, but were not included in analysis because of low confidence in sampling effectiveness for this benthic family. Computation of availability and usage of microhabitats and within reach habitat units was accomplished by breaking reach maps into 2 and 3 m^2 grid cells. All physical and biological data were recorded into these cells based on the reach map position onto which data were recorded in the field. When appropriate, mean densities were compared with nonparameteric Wilcoxon rank sum tests.

Results

Brook trout dominated fish communities in Beaver springbrook (Figure 4). Brook trout abundance changed seasonally as adults moved into Beaver springbrook for spawning, and as young-of-the-year emerged in the spring. Age-0 mountain whitefish *Prosopium williamsoni* were consistently present in low numbers, while westslope cutthroat trout and bull trout were rare (Figure 4). Brook trout in Beaver springbrook were strongly nocturnal at all times of year, particularly among fishes ≥ age-1 (Figure 5). Fish observed at night appeared to remain in concealment during the day, emerging at night to feed. In McDonald springbrook, westslope cutthroat trout were the only salmonid species observed. Age-0 and age-1 cutthroat trout were also primarily night active and occurred at densities comparable to those observed in Beaver creek at the same time of year (Figure 6). Length-frequency distributions were also similar between brook trout in Beaver springbrook and cutthroat trout in McDonald springbrook; although curiously, age-0 cutthroat trout were 1-2 cm larger than brook trout (Figure 7).

I also observed many parallels in habitat utilization among brook trout in Beaver springbrook and cutthroat trout in McDonald springbrook. Both age-0 brook and cutthroat trout demonstrated preferential selection of shallow to moderate depths, slow water velocities, and edge habitats (Figure 8). Age-1 and greater brook and cutthroat trout both selected deeper habitats and slower water velocities, but differed in that brook trout showed a preference for microhabitats near woody debris while cutthroat trout did not.

Discussion

Some authors have speculated about the potential significance of riverine thermal complexity, especially coldwater habitats, in mediating biotic interactions between native and introduced fishes (Li et al. 1987; Moyle and Leidy 1992). Cold water temperatures are vital to the success and survival of native cutthroat trout and bull trout, and cold, headwater or spring fed streams appear to function as refugia for these species in many cases (Howell and Buchanan 1992; De Staso and Rahel 1994; Young 1995). Based on these observations, floodplain springbrooks might be expected to serve as strongholds for native salmoninds. However, my surveys on the Middle Fork Flathead River found that these habitats are instead almost completely dominated by nonnative brook trout (see Chapter 2). The infrequent occurrence of bull trout and westslope cutthroat trout in Beaver springbrook suggests that native species may have been excluded through predation or competition with brook trout.

My findings in the McDonald Creek drainage, where brook trout are not present, support the hypothesis that cutthroat trout have been functionally excluded from the

Middle Fork Flathead River springbrook. In McDonald springbrook I observed age distributions, densities and habitat utilization of westslope cutthroat trout strikingly similar to that observed among brook trout in Beaver springbrook. Bull trout are not known to occur in the upper McDonald Creek basin, but it seems likely that both bull trout and cutthroat trout utilized springbrooks to a greater extent on the Middle Fork Flathead River prior to the invasion of brook trout. These findings conflict strongly with experimental evidence and altitudinal, elevational distribution patterns which suggest cold water temperatures favor cutthroat trout (Fausch 1989; De Staso and Rahel 1994; Young 1995) and bull trout (Howell and Buchanan 1992) in interactions with nonnative brook trout.

Springbrooks provide an exceptional opportunity to evaluate the influence of cold temperatures on distribution and abundance of salmonids in low gradient, natural streams. My study indicates that cold water temperature alone does not prevent invasion of brook trout and the subsequent displacement of westslope cutthroat trout. However, in springbrooks, as in controlled laboratory settings, factors besides temperature may influence the outcome of interactions between native and introduced salmonids. Brook trout are, for example, known to strongly select groundwater fed sites for spawning (Curry and Noakes 1995), and this fact alone may predispose springbrooks to invasion. However, brook trout are not just reproducing, but are completing their entire life history in Beaver springbrook, residing their in a range of size classes and at high densities. Bull trout and westslope cutthroat trout certainly had access to these habitats, being that they were occasionally observed in surveys (Figure 3) and captured in weirs (Chapter 3), but native salmonid assemblages apparently did not exhibit biotic resistance to brook trout invasion, and appear unable to persist or reproduce in springbrook reaches colonized by brook trout.

Regulated rivers lacking natural flood pulses are known to exhibit high susceptibility to invasion by introduced fishes (Meffe 1984; Baltz and Moyle 1993; Moyle 1996). Hydrologic and thermal stability may also render springbrooks very susceptible to invasion to nonnatives not otherwise adapted to prevailing regional climatic and hydrologic regimes. Supporting this hypothesis is the fact that brook trout ,while dominating springbrook reaches, were less abundant in main channel sites (Chapter 2) which experience a full range of environmental extremes.

All fishes living in McDonald and Beaver springbrooks exhibited a strong tendency towards daytime concealment and nocturnal activity. These diel activity patterns are another factor that may influence the outcome of interactions and result in the observed distribution and abundance of species. The fact that brook trout and westslope cutthroat trout have independently adopted nocturnalism in two disparate springbrooks suggests it is a highly adaptive strategy (Chapter 3). Success under these conditions would be profoundly influenced by effectiveness of low light visual, or non-visual sensory systems, such that species with innately superior low light sensory systems would gain a distinct advantage in foraging, predator avoidance, and competition. Nocturnal activity and daytime concealment has been observed among some chars (Adams et al. 1988; Goetz 1989; Bonneau et al. 1995; Spangler 1997) and their sensory physiology may be well suited to activity and feeding in darkness. Dolly varden char, for example, were found to be better than cutthroat trout at detecting both planktonic (Henderson and Northcote 1985) and benthic prey items (Schutz and Northcote 1972) under low light conditions. The underlying mechanisms for these findings apparently relate interspecific differences in retinal structure, and the composition and quantity of visual pigments (Allen et al. 1973; Allen et al. 1982; Henderson and Northcote 1988).

The fact that brook trout and cutthroat trout, as well as other species-age classes are capable of adopting predominately nocturnal behavioral modes has some profound implications for our ecological understanding of these species, and for coldwater riverine fish assemblages in general (Chapter 3). In the most basic sense, night (and daytime) surveys are necessary to insure that species assemblage and abundances are accurately estimated. More importantly however, studies need to take into account that crucial behaviors and biotic interactions may potentially take place strictly at night. Nocturnal mechanisms and outcomes of competition and predation, as well as feeding tactics are likely very different, yet we know virtually nothing about nighttime behavior of salmonids or other coldwater, riverine fishes. As an example, differences in low light visual, or non-visual sensory systems among brook trout and cutthroat trout may critically influence the outcome of competition, yet no experimental studies have addressed this potential mechanism (e.g. Griffith 1970; De Staso and Rahel 1994; Thomas et al. 1996).

My findings do not support water temperature alone as an important variable influencing biotic resistance of native salmonids to invasion by brook trout. Cold water temperature may become significant however, when interacting with other variables such high stream gradient, food availability, or water velocity. Weak or absent hydrologic disturbance regimes on the other hand, which are commonly associated with groundwater-fed habitats, may facilitate successful brook trout invasion, and subsequent exclusion of natives. Although I am not aware of any studies explicitly documenting the pattern, brook trout in the western United States typically proliferate in low gradient spring-fed habitats such as beaver ponds and spring creeks. This pattern, along with my own findings, are consistent with literature demonstrating that benign hydrologic regimes can be a significant factor regulating the success of nonnative fish invasions in streams (Meffe 1984; Baltz and Moyle 1993; Moyle 1996).

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Springbrook	Mean August Temperature (SD)	Reach area (m^2)	Reach length (m)	Average width (m)	Average depth (cm)	Gradient
Beaver	7.7 (0.7)	2754	204	11	37	<1%
McDonald	6.6 (1.3)	1084	120	9.5	30	<1%

Table 1. Summary of reach characteristics of springbrook study reaches on McDonald springbrook and Beaver springbrook.

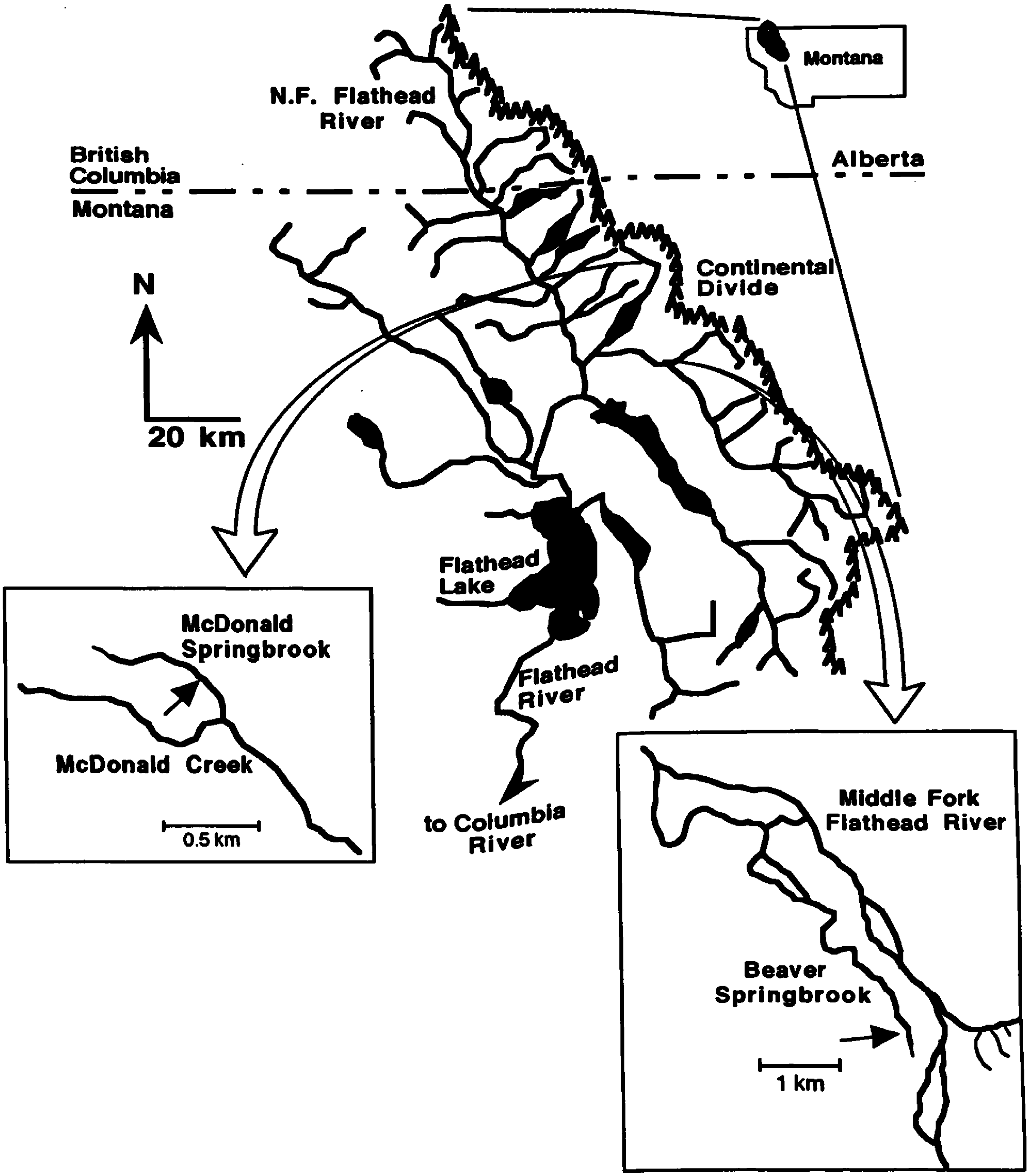


Figure 1: Map of study reaches in the MF Flathead River drainage. Arrows on inset maps of springbrooks desigate study reaches.

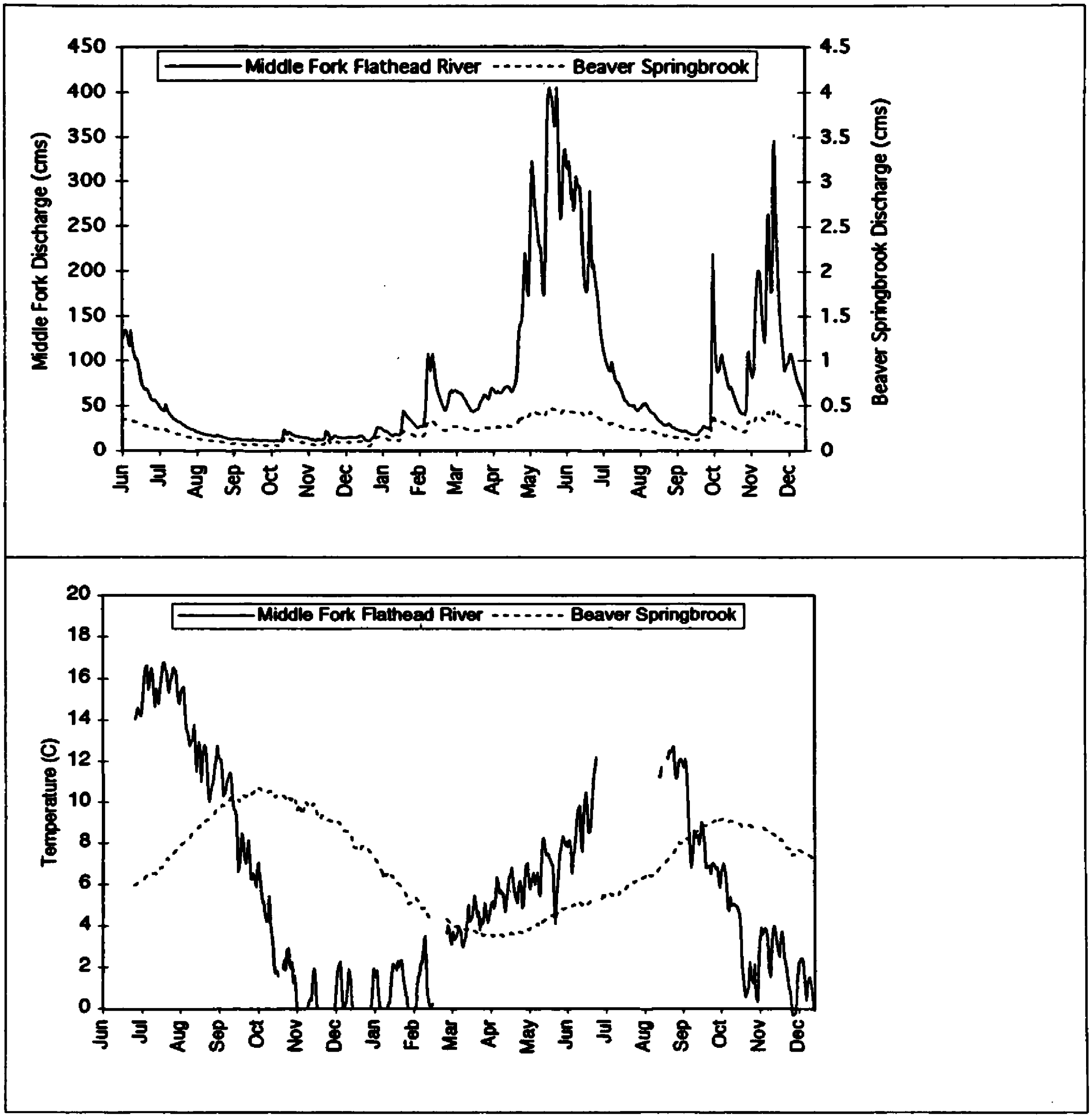
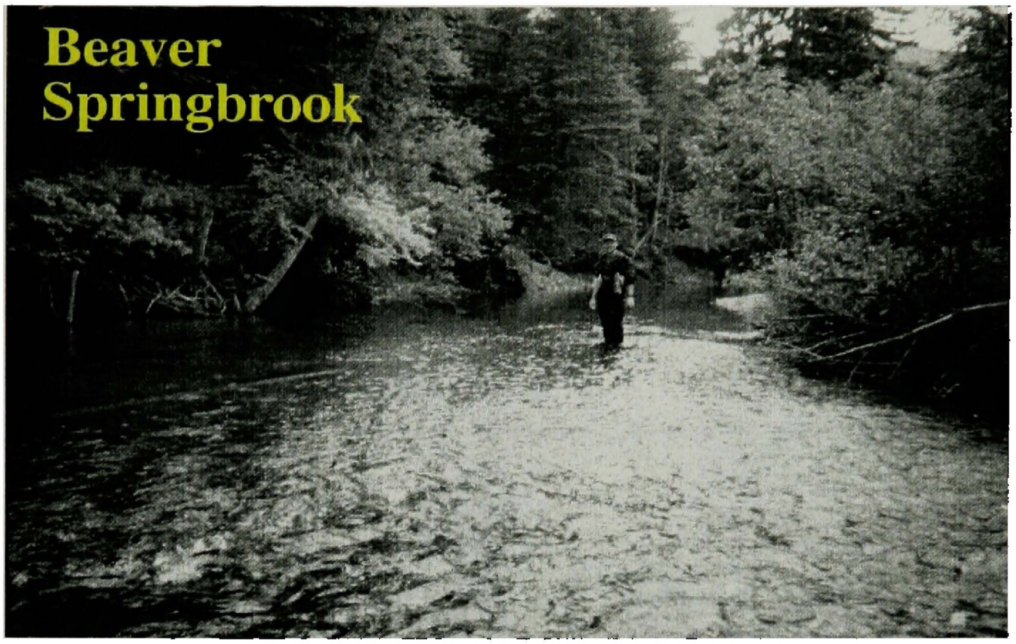


Figure 2: Hydrologic and thermal regimes from 1994-1995 in Beaver springbrook and the MF Flathead River. Mean daily discharge is plotted in top graph on two y-axis. Note that scales for y-axis are different, but with proportional ranges. Bottom graph is mean daily temperatures from a representative site in Beaver springbrook and river mainstem.



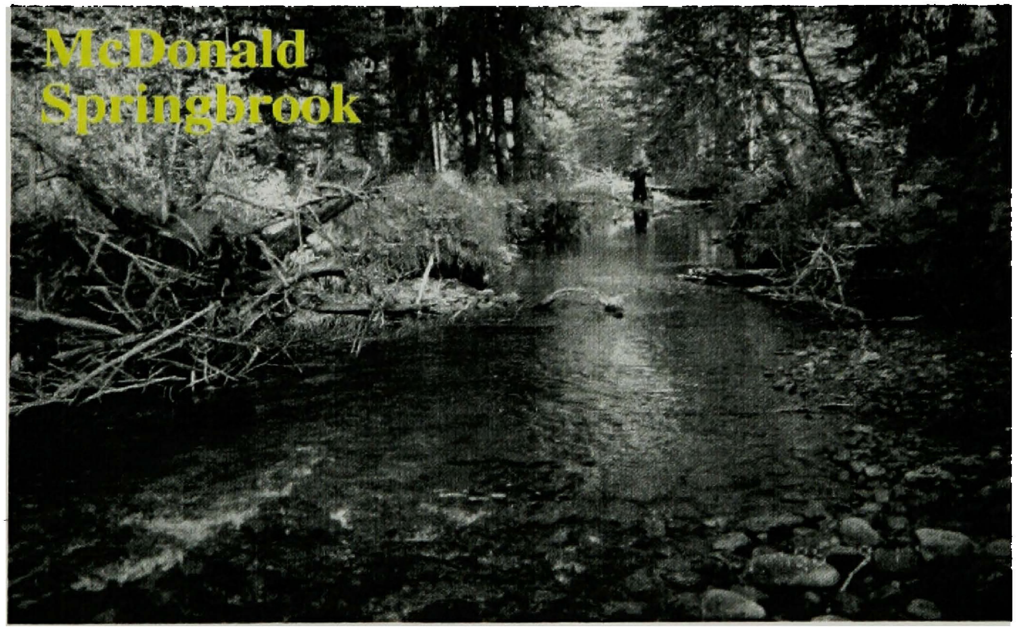


Figure 3: Photographs illustrating similarity of study reaches in Beaver springbrook (top) and McDonald springbrook (bottom).

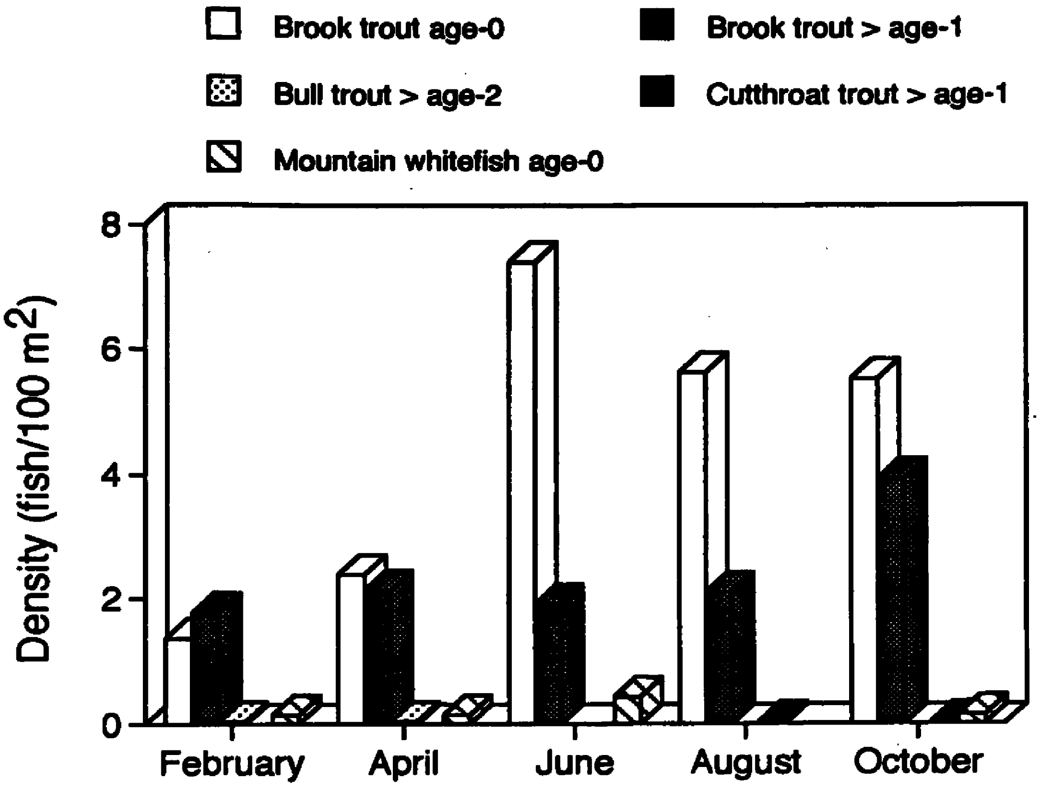


Figure 4: Seasonal densities of salmonid species-age classes for upper Beaver springbrook in 1995.

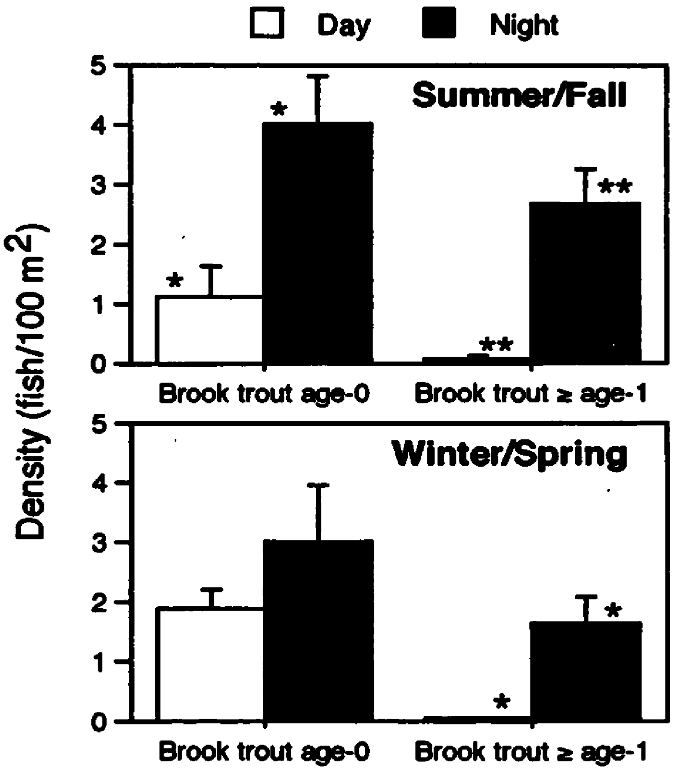


Figure 5: Mean densities with SE bars for day and night surveys of sprinbrook reaches in Summer/Fall and Winter/Spring. Asterisks represent statistically significant differences between day and night pairs (** $p<0.01$, * $p<0.05$; Wilcoxon rank sum tests)

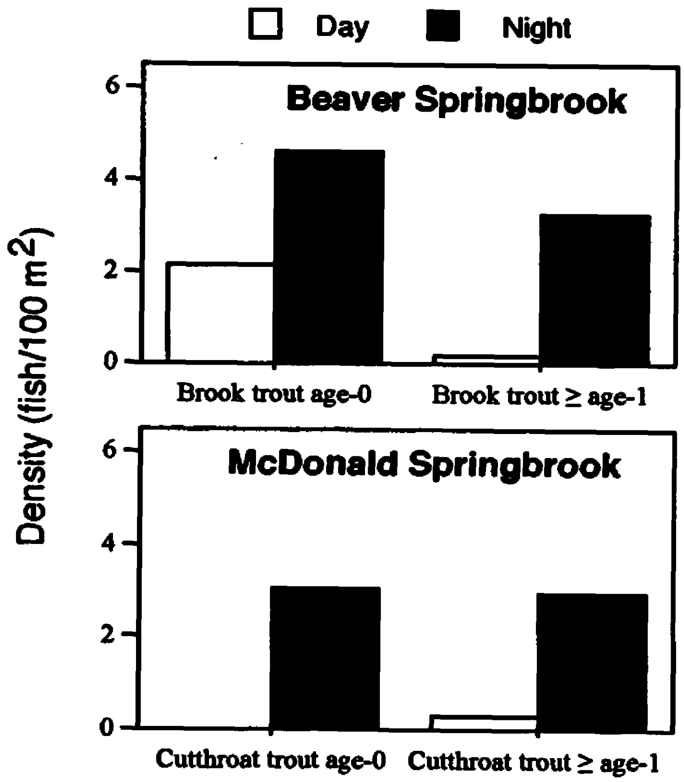


Figure 6: Densities of brook trout and cutthroat trout observed in Beaver and McDonald springbrooks, respectively. Based on day and night surveys conducted in late August 1996.

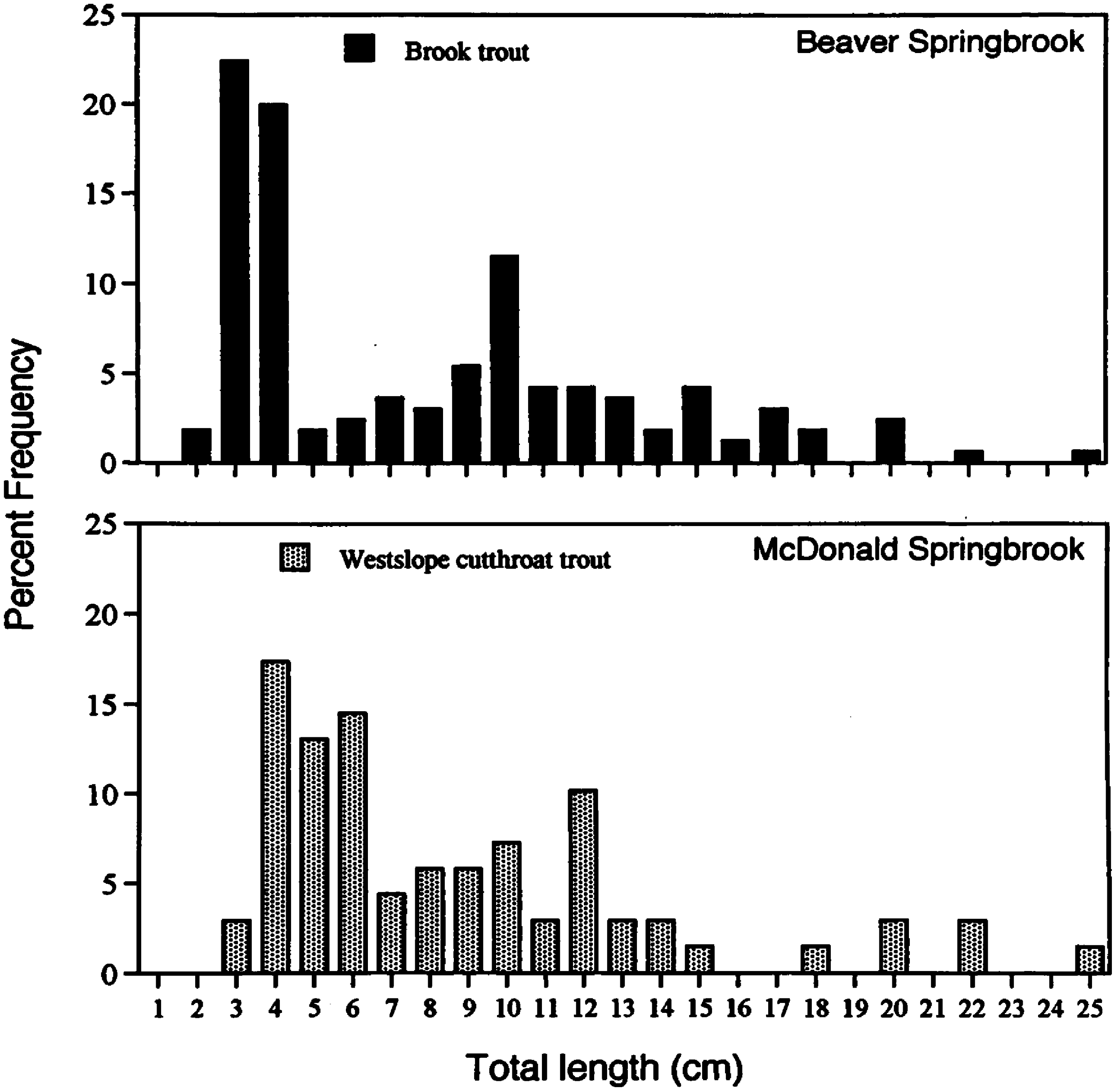


Figure 7: Length-frequency distribution for brook trout and cutthroat trout surveyed in Beaver springbrook and McDonald springbrook, respectively. Data is based on surveys conducted in late August 1996.

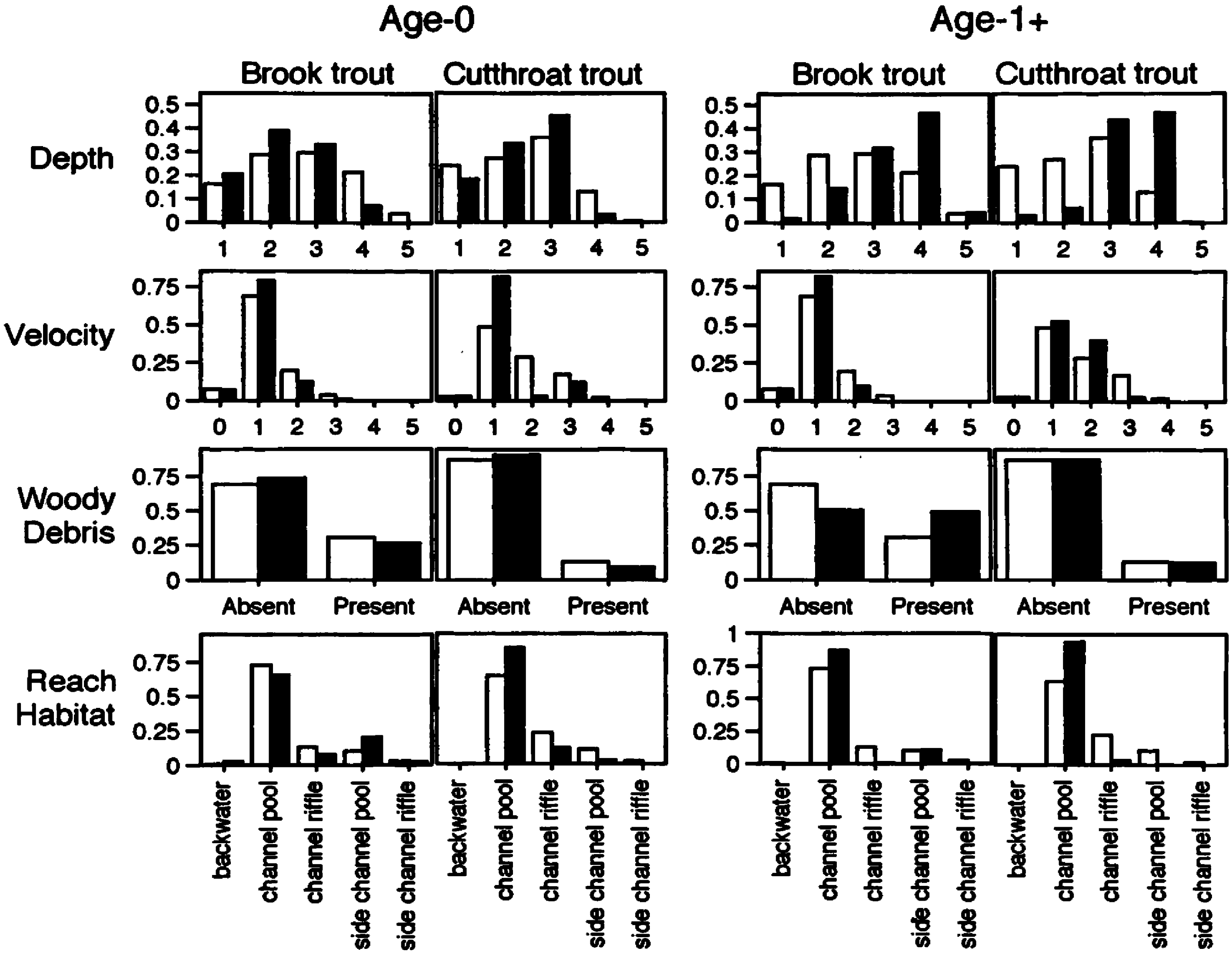


Figure 8: Habitat utilization for age-0 and ≥ age-1 brook trout and cutthroat trout in Beaver springbrook and McDonald springbrook. White bars represent availability, black bars utilization. Depth classes range from 1 (1-10 cm) to 5 (100+cm) and velocity classes range from 0 (0.0-0.9 cm/s) to 5 (77.5+ cm/s). All value are reported as percentage of total for each variable.

Appendix: Total count over density (fish/100m2) for all surveys. Floodplain pond reach codes are numbered sequentially, upstream (fp1) to downstream (fp3), for mainchannel reaches the first letter of two letter code designates reach location (i.e. 'l'=lower, downstream most reach).

			Survey	Brook trout			Bull trout	Cutthroat trout			Mountain whitefish		
Reach type	Reach	Date	time	0	1	2+	2+	0	1	2+	0	1	2+
Floodplain ponds	fp1	8/19/94	Day	0	3	26	0	0	0	0	227	0	0
				0.00	0.05	0.43	0.00	0.00	0.00	0.00	3.78	0.00	0.00
		3/31/95	Day	33	0	3	0	0	0	0	76	3	0
				0.51	0.00	0.05	0.00	0.00	0.00	0.00	1.17	0.05	0.00
		4/10/95	Night	11	3	17	2	0	0	0	27	6	0
				0.17	0.05	0.26	0.03	0.00	0.00	0.00	0.42	0.09	0.00
		9/7/95	Night	0	25	19	1	0	0	0	493	0	0
				0.00	0.39	0.29	0.02	0.00	0.00	0.00	7.61	0.00	0.00
		9/13/95	Day	0	3	36	0	0	0	0	142	0	0
				0.00	0.05	0.56	0.00	0.00	0.00	0.00	2.19	0.00	0.00
	fp2	8/19/94	Day	12	2	5	0	0	0	0	29	0	0
				6.67	1.11	2.78	0.00	0.00	0.00	0.00	16.11	0.00	0.00
		9/13/95	Day	19	1	6	0	0	0	0	75	0	0
				7.79	0.41	2.46	0.00	0.00	0.00	0.00	30.74	0.00	0.00
	fp3	8/20/94	Day	0	1	1	0	0	0	0	30	0	0
				0.00	0.33	0.33	0.00	0.00	0.00	0.00	10.00	0.00	0.00
		4/1/95	Day	0	0	0	0	0	0	0	40	5	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.33	1.67	0.00
		9/12/95	Night	0	3	5	0	0	0	0	2	0	0
				0.00	1.00	1.67	0.00	0.00	0.00	0.00	0.67	0.00	0.00
		9/13/95	Day	0	2	5	0	0	0	0	27	0	0
				0.00	0.67	1.67	0.00	0.00	0.00	0.00	9.00	0.00	0.00
Main channel reaches	lm	9/6/94	Day	0	0	1	0	1	1	0	51	5	6
				0.00	0.00	0.01	0.00	0.01	0.01	0.00	0.52	0.05	0.06
		2/18/95	Day	0	0	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		3/31/95	Night	0	1	1	0	0	1	0	41	25	25
				0.00	0.01	0.01	0.00	0.00	0.01	0.00	0.42	0.26	0.26
		9/7/95	Day	0	0	0	0	0	0	1	12	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.17	0.00	0.00
	mm	8/23/94	Day	0	0	2	0	0	0	0	6	0	0
				0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.18	0.00	0.00
		1/27/95	Day	0	0	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		2/18/95	Night	0	0	0	0	2	0	0	12	0	0
				0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.36	0.00	0.00
		9/8/95	Day	0	0	0	0	0	0	0	9	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00
		9/12/95	Night	3	18	8	3	0	1	0	63	1	0
				0.09	0.54	0.24	0.09	0.00	0.03	0.00	1.89	0.03	0.00
	um	9/7/94	Day	0	0	2	0	0	0	0	38	0	0
				0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.64	0.00	0.00
		3/31/95	Day	0	0	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/23/95	Day	0	0	2	0	0	0	5	30	30	8
				0.00	0.00	0.03	0.00	0.00	0.00	0.08	0.47	0.47	0.13
		9/10/96	Day	0	0	0	0	0	0	1	0	6	5
				0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.12	0.10
			Night	0	4	5	7	0	0	0	20	1	6
				0.00	0.08	0.10	0.14	0.00	0.00	0.00	0.39	0.02	0.12
		9/10/96	Day	0	3	3	0	0	0	3	1	1	0
				0.00	0.53	0.53	0.00	0.00	0.00	0.53	0.18	0.18	0.00
			Night	2	10	9	2	0	2	2	4	0	0
				0.35	1.75	1.58	0.35	0.00	0.35	0.35	0.70	0.00	0.00
	lb	4/9/95	Day	0	0	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	1	19	5	0	0	0	2	1	0	0
				0.02	0.44	0.12	0.00	0.00	0.00	0.05	0.02	0.00	0.00
		8/17/95	Day	0	0	2	0	0	0	0	0	0	0
				0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/24/95	Night	65	25	21	0	0	0	0	22	1	0
				1.52	0.59	0.49	0.00	0.00	0.00	0.00	0.51	0.02	0.00
		2/23/96	Night	2	15	4	0	0	0	0	5	0	0
				0.05	0.35	0.09	0.00	0.00	0.00	0.00	0.12	0.00	0.00
		8/23/09	Day	0	0	8	0	0	0	0	46	0	0
				0.00	0.00	0.19	0.00	0.00	0.00	0.00	1.08	0.00	0.00

Appendix: Total count over density (fish/100m2) for all surveys. Floodplain pond reach codes are numbered sequentially, upstream (fp1) to downstream (fp3), for mainchannel reaches the first letter of two letter code designates reach location (i.e. 'l'=lower, downstream most reach).

Reach type	Reach	Date	Survey time	Suckers			Spotted frog	Boreal toad			Tailed frog
				0	1	2+	adult	adult	toadlet	tadpole	tadpole
Floodplain ponds	fp1	8/19/94	Day	3625	0	0	0	1	0	57	0
				60.42	0.00	0.00	0.00	0.02	0.00	0.95	0.00
		3/31/95	Day	39	0	0	0	0	0	0	0
				0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		4/10/95	Night	17	4	4	0	0	0	0	0
				0.26	0.06	0.06	0.00	0.00	0.00	0.00	0.00
		9/7/95	Night	744	3	15	0	5	0	7379	0
				11.49	0.05	0.23	0.00	0.08	0.00	113.96	0.00
		9/13/95	Day	532	0	0	2	1	17	7288	0
				8.22	0.00	0.00	0.03	0.02	0.26	112.56	0.00
	fp2	8/19/94	Day	1092	0	0	0	0	0	0	0
				606.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		9/13/95	Day	8	0	0	0	0	0	424	0
				3.28	0.00	0.00	0.00	0.00	0.00	173.77	0.00
	fp3	8/20/94	Day	508	0	0	0	1	0	0	0
				169.33	0.00	0.00	0.00	0.33	0.00	0.00	0.00
		4/1/95	Day	6	0	0	0	0	0	0	0
				2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		9/12/95	Night	562	0	0	0	1	0	801	0
				187.33	0.00	0.00	0.00	3.30	0.00	267.00	0.00
		9/13/95	Day	338	0	0	0	0	0	309	0
				112.67	0.00	0.00	0.00	0.00	0.00	103.00	0.00
Main channel reaches	lm	9/6/94	Day	22	0	0	1	1	0	0	0
				0.23	0.00	0.00	0.01	0.01	0.00	0.00	0.00
		2/18/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		3/31/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		9/7/95	Day	6	0	0	0	0	0	0	0
				0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	mm	8/23/94	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		1/27/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		2/18/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		9/8/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		9/12/95	Night	9	6	4	0	4	0	0	0
				0.27	0.18	0.12	0.00	0.12	0.00	0.00	0.00
	um	9/7/94	Day	140	0	0	0	0	0	425	0
				2.36	0.00	0.00	0.00	0.00	0.00	7.16	0.00
		3/31/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/23/95	Day	25	0	0	0	0	0	0	1
				0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.02
		9/10/96	Day	0	0	0	1	0	0	0	0
				0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
			Night	0	1	0	0	4	0	0	0
				0.00	0.02	0.00	0.00	0.08	0.00	0.00	0.00
		9/10/96	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	0	0	2	0	0	0	0	0
				0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.00
	lb	4/9/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/17/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/24/95	Night	0	2	0	3	1	0	88	0
				0.00	0.05	0.00	0.07	0.02	0.00	2.06	0.00
		2/23/96	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/23/09	Day	0	0	0	1	0	0	0	0
				0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00

Appendix: Total count over density (fish/100m2) for all surveys. Two-letter code designates reach location ('l'=lower, 'm'=middle, 'u'=upper, downstream to upstream).

				Brook trout			Bull trout	Cutthroat trout			Mountain whitefish		
Reach type	Reach	Date	Survey time	0	1	2+	2+	0	1	2+	0	1	2+
Springbrook reaches	mb	6/22/95	Day	34	0	0	0	0	0	0	0	0	0
				1.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		6/23/95	Night	91	7	2	0	0	0	0	0	0	0
				3.40	0.26	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/18/95	Day	0	0	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/19/95	Night	79	11	8	0	0	0	0	0	0	0
				2.96	0.41	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		10/26/95	Day	0	1	0	0	0	0	0	0	0	0
				0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		10/27/95	Night	38	67	24	0	0	0	0	1	0	0
				1.42	2.51	0.90	0.00	0.00	0.00	0.00	0.04	0.00	0.00
		3/13/96	Night	23	11	0	0	0	0	0	0	0	0
				0.86	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	ub	8/18/94	Day	85	0	0	0	0	0	0	18	0	0
				3.09	0.00	0.00	0.00	0.00	0.00	0.00	0.65	0.00	0.00
		2/3/95	Night	38	43	6	1	0	0	0	4	0	0
				1.38	1.56	0.22	0.04	0.00	0.00	0.00	0.15	0.00	0.00
		4/1/95	Day	54	0	0	0	0	0	0	1	0	0
				1.96	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
			Night	66	56	3	1	0	0	0	4	0	0
				2.40	2.03	0.11	0.04	0.00	0.00	0.00	0.15	0.00	0.00
		6/22/95	Day	66	0	0	0	0	0	0	0	0	0
				2.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	204	40	13	0	0	0	0	12	0	0
				7.41	1.45	0.47	0.00	0.00	0.00	0.00	0.44	0.00	0.00
		8/18/95	Day	30	0	0	0	0	0	0	0	0	0
				1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	155	35	23	0	0	0	1	0	0	0
				5.63	1.27	0.84	0.00	0.00	0.00	0.04	0.00	0.00	0.00
		10/26/95	Night	152	58	50	0	0	0	1	4	2	0
				5.52	2.11	1.82	0.00	0.00	0.00	0.04	0.15	0.07	0.00
		10/27/95	Day	13	6	2	0	0	0	0	0	0	0
				0.47	0.22	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		3/15/96	Night	72	76	13	0	0	0	0	7	0	0
				2.61	2.76	0.47	0.00	0.00	0.00	0.00	0.25	0.00	0.00
		8/27/96	Day	59	5	0	0	0	0	0	3	0	0
				2.14	0.18	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00
			Night	127	65	25	1	0	2	0	36	0	0
				4.61	2.36	0.91	0.04	0.00	0.07	0.00	1.31	0.00	0.00

Appendix: Total count over density (fish/100m2) for all surveys. Two-letter code designates reach location ('l'=lower, 'm'=middle, 'u'=upper, downstream to upstream).

			Survey	Suckers			Spotted frog	Boreal toad			Tailed frog
Reach type	Reach	Date	time	0	1	2+	adult	adult	toadlet	tadpole	tadpole
Springbrook reaches	mb	6/22/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		6/23/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/18/95	Day	0	0	0	3	0	0	0	0
				0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
		8/19/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		10/26/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		10/27/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		3/13/96	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	ub	8/18/94	Day	0	0	0	0	1	0	0	0
				0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
		2/3/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		4/1/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		6/22/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/18/95	Day	0	0	0	1	0	0	0	0
				0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
			Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		10/26/95	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		10/27/95	Day	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		3/15/96	Night	0	0	0	0	0	0	0	0
				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		8/27/96	Day	0	0	0	2	0	0	0	0
				0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
			Night	1	0	0	0	3	0	0	0
				0.04	0.00	0.00	0.00	0.11	0.00	0.00	0.00