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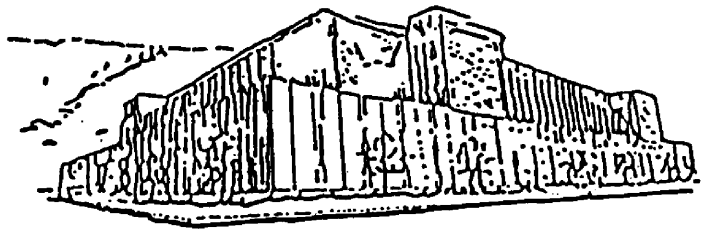
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GEOMORPHOLOGY, LAND-USE, AND GROUNDWATER-SURFACE WATER INTERACTION: A MULTI-SCALE, HIERARCHICAL ANALYSIS OF THE DISTRIBUTION AND ABUNDANCE OF BULL TROUT (*SALVELINUS CONFLUENTUS*) SPAWNING

by

Colden V. Baxter

B.A., University of Oregon 1993

Presented in partial fulfillment of the requirements

for the degree of

Master of Science

The University of Montana

1997

Approved by

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Baxter, Colden V., M.S., Summer 1997   Biological Sciences

Geomorphology, land-use, and groundwater-surface water interaction: a multi-scale, hierarchical analysis of the distribution and abundance of bull trout (*Salvelinus confluentus*) spawning.

Director: F. Richard Hauer

ABSTRACT

The Swan basin in northwest Montana is considered a stronghold of regional significance for the bull trout, a native char whose populations are fragmented and declining throughout their range. We characterized the variation of vertical hydraulic exchange and patterns of bull trout spawning habitat selection across four hierarchically-nested spatial scales in tributary streams of the Swan River. Use of mini-piezometers revealed that interactions of ground and surface waters were closely linked to specific geomorphic characteristics at each scale. The selection of spawning habitat by bull trout was apparently influenced by variation in vertical hydraulic exchange. The relationship between vertical hydraulic exchange and spawning differed across spatial scales. Bull trout redds were preferentially distributed in alluvial valley segments bounded longitudinally by geomorphic knickpoints. These bounded alluvial segments possessed significant variation in vertical hydraulic exchange and strong groundwater discharge zones. Bull trout spawned in reaches that were strongly influenced by upwelling ground water. However, within reaches redds were constructed in transitional bedform units that displayed localized downwelling and high intragravel flow rates.

In addition, examination of spatial and temporal variation of bull trout redd counts (1982-1995) among the nine principal spawning tributaries showed that the numbers of redds and changes in tributary redd densities over time were positively correlated with the extent of bounded alluvial valley segments in a catchment. In contrast, redd numbers and rates of change varied inversely with the extent of logging roads in catchments. The extent of logging roads in tributaries did not correlate with any measures of their geomorphic variation.

These results suggest the importance of groundwater-influence to bull trout spawning habitat, and are consistent with the hypothesis that prior land-use has adversely affected local population abundance. The changing relationship between vertical hydraulic exchange and spawning habitat selection across spatial scales emphasizes the importance of considering gradients and species response across multiple spatial scales within a hierarchical geomorphic context. Identifying, conserving and monitoring spawning habitat for bull trout will require consideration of the role of groundwater-surface water interactions in the structure and selection of this habitat.

ACKNOWLEDGMENTS

TEXT ORGANIZATION

Chapter one is a brief introductory section that outlines the rationale for this study. Chapters two and three were written as manuscripts to be submitted for journal publication. Though it decided to split the results of this work into two papers, some overlap in content between the two was essential. Chapters two and three include methods, results, and discussion sections, as well as separate bibliographies. Much of the raw data collected in this study was included in the appendices

CONTENTS

CONTENTS
(continued)

CONTENTS
(continued)

LIST OF TABLES
(Chapter II)

LIST OF TABLES
(Chapter III)

LIST OF FIGURES

(Chapter II)

LIST OF FIGURES

(Chapter II continued)

LIST OF FIGURES

(Chapter II continued)

LIST OF FIGURES

(Chapter III)

LIST OF FIGURES
(Chapter III continued)

CHAPTER I

Introduction: Geomorphology, land-use, and groundwater-surface water interaction: a multi-scale, hierarchical analysis of the distribution and abundance of bull trout spawning

Stream ecologists have long recognized the interactive relationship between a stream and its valley (Hynes 1975). Patterns and processes of stream ecosystems are closely tied to interactions with the surrounding terrestrial environment (e.g. Fisher and Likens 1973, Gregory et al. 1991), longitudinal gradients (Vannote et al. 1980, Hauer and Stanford 1982, Hawkins 1984), and interactions between ground and surface waters (Stanford and Ward 1993, Gibert et al. 1994, Valett et al. 1994). Because of this connectivity, it is essential that stream ecosystems be examined holistically within the context of their landscapes (Swanson et al. 1988, Minshall 1988).

The fluxes of water and alluvium in stream systems create geomorphic units at multiple, spatially nested scales. Change in geomorphometry and the interactive response of the lotic environment result in alternating cut and fill alluviation. This process is tightly coupled to spatio-temporal heterogeneity of physical habitat gradients important to stream organisms. Hence stream habitat is structured and can be classified hierarchically (Frissell et al. 1986).

The habitat use patterns of any organism in an ecosystem are related to many environmental gradients (Hall et al. 1992). However, for any organism, the variation of a particular habitat gradient may be perceived as information at one scale, while it may be noise at another (Dutilleul and Legendre 1993). Consequently, studying the distribution and abundance of any species relative

to habitat gradients requires applying a multi-scalar approach, in order to provide insight into their relative importance under the observed circumstances (Maurer 1985, Morris 1987, Wiens et al. 1987, Powell 1989, Kotliar and Wiens 1990).

Relationships between fish populations and their habitat have primarily been examined at fine spatial scales (Bayley and Li 1992). In recent studies, however, the efficacy of a multi-scalar approach has been clearly demonstrated (Morris 1987, Poizat and Pont 1996). There is a particular need to include landscape scale analyses in studies of fish-habitat relationships, and functional interactions at terrestrial-aquatic ecotones may be a particularly critical landscape attribute to examine (Schlosser 1995).

The hyporheic zone is a portion of the surface water - groundwater interface that is becoming increasingly recognized as an important component of stream ecosystems (e.g., Stanford and Simons 1992, Valett et al. 1990, Dahm and Valett 1996). The hyporheic zone is ecotonal in nature, as the boundaries between surface waters and ground waters are spatially and temporally dynamic (Vervier et al. 1992). General observations of geomorphic structure at the landscape scale, recent study of groundwater - surface water exchange in large, coarse-substratum alluvial floodplains (Stanford and Ward 1988), and patterns of spawning habitat-use by bull trout *Salvelinus confluentus*. (e.g. Weaver and White 1985) led us to the hypothesis that these biophysical variables may be dynamically linked across multiple spatial scales.

Our objective in this study was to examine the relationship between geomorphology, ground and surface water exchange patterns, and the structure and selection of bull trout spawning habitat. This was done within the context of

a geomorphic-unit hierarchy that included catchment, valley segment, reach, and pool/riffle scales.

Bull trout, whose populations are fragmented and declining throughout their range, have become a focal point of concern, research, debate, and litigation in the Pacific Northwest over the past several years. In the Columbia and Klamath basins they will soon be proposed for listing under the Endangered Species Act (Larry Lockhart, USFWS, Kalispell, MT personal communication). Since conservation of the bull trout as well as other species requires considering these organisms within the context of their connections in a dynamic landscape that includes human activities, we expanded our study to incorporate an analysis of anthropogenic factors. Bull trout monitoring and conservation efforts of the future depend, in part, on the interpretation and application of fourteen years of redd count data from the Swan basin of northwest Montana.

In contrast to their range-wide decline, bull trout redd counts have been reported to have significantly increased ($p < .05$) in the Swan basin (Montana Bull Trout Scientific Committee 1996, Weaver in press). Various causes for the apparent increase have been theorized. Sub-adult bull trout in Swan Lake may be experiencing improved growth and survival as a result of feeding on the introduced opossum shrimp *Mysis relicta* (Montana Bull Trout Scientific Committee 1996). Recent angling restrictions to protect bull trout could also contribute to such an increase in spawner density. The increasing trend, based on data from four annually-monitored streams, is being popularly cited as evidence that large-scale, intensive land use is not associated with population trends of this species, since the majority of land in the Swan basin is managed for timber harvest. However, among the nine principal spawning tributaries the

number of observed bull trout redds varies considerably (Montana Bull Trout Scientific Committee 1996), suggesting the presence of some environmental factor(s) that influence between-tributary spawning distribution and abundance.

In a recent analysis that included four annually-monitored spawning streams of the Swan basin, Rieman and McIntyre (1996) found that temporal population trends from spatially proximal tributaries were not well correlated with each other. The weakness of these correlations suggest the presence of variation among tributaries that could not be explained by common events in the lake environment. Rather, they proposed that heterogeneity in stream habitat availability or condition might account for this lack of synchrony among tributary populations.

Accurate interpretation and effective application of existing population data requires examination within a landscape context. Critical evaluation of the nature and effectiveness of past and present monitoring and management efforts may also be demanded. Therefore, we also investigated spatial and temporal variation in bull trout redd numbers among the nine principal spawning tributaries of the Swan River in relation to land-use activity and landscape geomorphology. In light of the results of these analyses, we examined the efficacy of the current monitoring design for assessing the status of bull trout in the basin.

LITERATURE CITED

Bayley, P.B. and H.W. Li. 1992. Riverine fishes. p. 251-281 *In* P. Calow and G.E. Petts [ed.] The rivers handbook: Hydrological and ecological principles. Blackwell, Oxford.

Dahm, C.N. and H.M. Valett. 1996. Hyporheic zones. p. 107-119 *In* F.R. Hauer and G.A. Lamberti [eds.] Methods in Stream Ecology. Academic Press.

Dutilleul, P. and P. Legendre. 1993. Spatial heterogeneity against heteroscedasticity: An ecological paradigm versus a statistical concept. Oikos 66(1):152-171.

Fisher, S.G. and G.E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421-439.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Gibert, J., D.L. Danielopol and J.A. Stanford [Ed]. 1994. Groundwater Ecology. Academic Press, San Diego, California, USA. 571 pp.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540-551.

Hall, C.A.S., J.A. Stanford, and F. R. Hauer. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos 65(3):377-390.

Hawkins, C.P. 1984. Substrate associations and longitudinal distributions in species of Ephemerellidae (Ephemeroptera: Insecta) from western Oregon. Freshwater Invertebrate Biology 3:181-188.

Hauer, F.R. and J.A. Stanford. 1982. Ecology and life histories of three net-spinning caddisfly species (Hydroppsychidae: *Hydropsyche*) in the Flathead River, Montana. Freshwater Invertebrate Biology 1:18-29.

Hynes, H.B.N. 1975. The stream and its valley. Verh. Int. Ver. Theor. Ang. Limnol. 19:1-15.

● Kotliar, N.B. and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure-A hierarchical framework for the study of heterogeneity. Oikos 59:253-260.

Maurer, B.A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. Ecological Monographs 55:295-312.

Minshall, G.W. 1988. Stream ecosystem theory: A global perspective. Journal of the North American Benthological Society 7:263-288.

Montana Bull Trout Scientific Group. 1995. Swan river drainage bull trout status report. United States Government Memorandum. 35 p.

● Morris, D.W. 1987. Ecological scale and habitat use. Ecology 68:362-369.

Orians, G.H. and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:529-549.

Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. Freshwater Biology 36(3):611-622..

Powell, T.M. 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. *In* J. Roughgarden, R.M. May, and S.A. Levin [ed.] Perspectives in ecological theory. pp 140-156. Princeton University Press, Princeton, New Jersey.

Rieman, B.E. and J.D. McIntyre. 1996. Spatial and temporal variability in bull trout redd counts. North American Journal of Fisheries Management 16: 132-141.

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

Stanford, J.A. and J.J. Simons (Eds.). 1992. Proceedings of the First International Conference on Ground Water Ecology. American Water Resources Association, Bethesda, MD.

Stanford, J. A. and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature 335:64-66.

Stanford, J. A. and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12: 48-62.

• Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience 38(2): 92-98.

Valett, H.M., S.G. Fisher, N.B. Grimm, and P. Camill. 1994. Vertical hydraulic exchange and ecological stability of a desert stream ecosystem. Ecology 75:548-560.

Valett, H.M., S.G. Fisher, E.H. Stanley. 1990. Physical and chemical characteristics of the hyporheic zone of a desert stream ecosystem. Journal of the North American Benthological Society 9:201-215.

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

Vervier, P., J. Gibert, P. Marmonier, and M.J. Dole-Olivier. 1992. A perspective on the permeability of the surface freshwater - groundwater ecotone. Journal of the North American Benthological Society 11: 93-102.

Weaver, T.M. in press. Status of adfluvial bull trout populations in Montana's Flathead drainage: The good, the bad, and the unknown. Proceedings, Friends of the Bull Trout Conference, Calgary, Alberta, TU Canada.

Weaver, T.M. and R.G. White. 1985. Coal Creek Fisheries Monitoring Study number III. USFS Flathead National Forest contract no. 53-0385-3-2685. 94 pp.

Wiens, J.A., J.T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132-147.

CHAPTER II

Geomorphology, interaction of ground and surface waters, and the selection of spawning habitat by bull trout (*Salvelinus confluentus*): A multi-scale, hierarchical approach

ABSTRACT

We characterized the variation of vertical hydraulic exchange and patterns of bull trout spawning habitat selection across four hierarchically-nested spatial scales in streams of the Swan basin of northwest Montana. Use of mini-piezometers revealed that variation of vertical hydraulic exchange was closely linked to specific geomorphic characteristics. At the catchment scale, the extent of groundwater discharge was related to the size and frequency of alluvial valley segments bounded longitudinally by geomorphic knickpoints. These bounded alluvial valley segments possessed significant variation in vertical hydraulic exchange and strong groundwater discharge zones. Furthermore, the greater the area of a bounded alluvial valley segment, the stronger the groundwater input to that segment. Within bounded alluvial segments, the longitudinal positioning of reaches relative to geomorphic knickpoints was linked to their vertical hydraulic gradient and groundwater input. Within reaches, areas possessing convex and transitional bed slopes displayed localized downwelling, while areas of concave bed topography were typically upwelling.

The selection of spawning habitat by bull trout was apparently influenced by variation in vertical hydraulic exchange. The relationship between vertical hydraulic exchange and spawning differed across spatial scales. Among spawning tributary streams, the abundance of bull trout redds increased with the extent of bounded alluvial valley segments and the strength of groundwater input. Among valley segment types bull trout redds were preferentially distributed in bounded alluvial valley segments, and the greater the groundwater discharge in a segment, the greater the redd density. Within bounded alluvial segments, bull trout selected stream reaches strongly influenced by groundwater discharge. However, within reaches bull trout redds were primarily located in transitional bedform units that possessed strong localized downwelling and high intragravel flow rates.

The changing relationship between vertical hydraulic exchange and spawning habitat selection across spatial scales emphasizes the importance of considering gradients and species response across multiple spatial scales within a hierarchical geomorphic context.

INTRODUCTION

Stream ecologists have long recognized the interactive relationship between a stream and its valley (Hynes 1975). Patterns and processes of stream ecosystems are closely tied to interactions with the surrounding terrestrial environment (e.g. Fisher and Likens 1973, Gregory et al. 1991), longitudinal gradients (Vannote et al. 1980, Hauer and Stanford 1982, Hawkins 1984), and interactions between ground and surface waters (Stanford and Ward 1993, Gibert et al. 1994, Vallett et al. 1994). Because of this connectivity, it is essential that stream ecosystems be examined holistically within the context of their landscapes (Swanson et al. 1988, Minshall 1988).

The fluxes of water and alluvium in stream systems create geomorphic units at multiple, spatially nested scales. Change in geomorphometry and the interactive response of the lotic environment result in alternating cut and fill alluviation. This process is tightly coupled to spatio-temporal heterogeneity of physical habitat gradients important to stream organisms. Hence stream habitat is structured and can be classified hierarchically (Frissell et al. 1986).

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Wiens 1990).

Relationships between fish populations and their habitat have primarily been examined at fine spatial scales (Bayley and Li 1992). In recent studies, however, the efficacy of a multi-scalar approach has been clearly demonstrated (Morris 1987, Poizat and Pont 1996). There is a particular need to include landscape scale analyses in studies of fish-habitat relationships and functional interactions at terrestrial-aquatic ecotones may be a particularly critical landscape attribute to examine (Schlosser 1995).

The hyporheic zone is a portion of the surface water - groundwater interface that is becoming increasingly recognized as an important component of stream ecosystems (e.g., Stanford and Simons 1992, Valett et al. 1990, Dahm and Valett 1996). The hyporheic zone is ecotonal in nature as the boundaries between surface waters and groundwaters are spatially and temporally dynamic (Vervier et al. 1992). General observations of geomorphic structure at the landscape scale, recent study of groundwater - surface water exchange in large, coarse-substratum alluvial floodplains (Stanford and Ward 1988), and patterns of spawning habitat use by bull trout *Salvelinus confluentus*. (e.g. Weaver and White 1985) led us to the hypothesis that these biophysical variables may be dynamically linked across multiple spatial scales.

Our objective in this study was to examine the relationship between geomorphology, ground and surface water exchange patterns, and the structure and selection of bull trout spawning habitat. This was done within the context of a geomorphic-unit hierarchy that included catchment, valley segment, reach, and pool/riffle scales.

Bull Trout Life History and Spawning Habitat

Bull trout are a native char that have recently become the focus of concern, research, debate and litigation in the Pacific Northwest. In the Columbia and Klamath basins they will soon be proposed for listing under the Endangered Species Act (L. Lockhart, USFWS, Kalispell, MT personal communication). Local populations have been restricted or eliminated range-wide due to over-harvest, displacement by exotic species (e.g., Donald and Alger 1993, Leary et al. 1993) and habitat degradation, including seasonal or permanent obstructions, detrimental changes in water quality, increased temperatures, and alteration of natural stream flow patterns (Fraley and Shepard 1989, Howell and Buchanan 1992, Rieman and McIntyre 1993). Even in the Flathead river/lake ecosystem of northwest Montana, an area long considered a stronghold for the species, redd counts over the last decade have declined dramatically (Weaver in press). In apparent contrast to these regional trends, an increase in bull trout spawning has been reported in the Swan basin (Weaver in press), a drainage that has been isolated by a dam from the rest of the Flathead watershed since the turn of the century (Fig 1). However, this trend is based on data from only four annually-monitored spawning tributaries, and the tenability of extrapolating the trend to the entire Swan basin metapopulation remains debatable (Chapter 3 this thesis).

Bull trout display adfluvial and fluvial migratory life history forms associated with large lake and river systems. They also express a non-migratory, resident form that is much smaller sized and typically remains in headwater streams. Migratory bull trout in the Swan basin spawn in second and third order streams from August through October. Juveniles remain in the natal streams for 1-3

years prior to migrating to Swan Lake where they spend 2-4 more years growing before sexual maturity (Fraley and Shepard 1989). In the Swan basin, adult bull trout may spend considerable periods of time in the main river (Frissell personal communication); however, it is unknown if the Swan basin possesses distinct resident, fluvial, and adfluvial forms. Though they are known to be iteroparous (Fraley and Shepard 1989), little is understood of bull trout longevity, spawning frequency, or post-spawning mortality.

Bull trout have very specific habitat needs. Channel stability, streambed composition, cover, migratory corridors, and water temperature have all been identified as important to bull trout growth, survival, and reproduction (see Rieman and McIntyre 1993 for a recent review). However, quality spawning and rearing habitat may be the primary limiting factors affecting population size in any specific area (Fraley and Shepard 1989, Rieman and McIntyre 1993). Graham et al. (1981) observed that spawning bull trout in tributary streams of the North and Middle Forks of the Flathead River used less than 28% of accessible stream lengths. Leathe and Enk (1985) and Rumsey (1991) reported that over 75% of the spawning in the Swan basin takes place in less than 10% of the available stream length.

Typical stream reaches utilized for spawning are characterized by low gradient. In higher gradient streams bull trout appear to use microhabitats of suitable substrata (Pratt 1992). Channel instability and frequent winter floods have been associated with high variation or significantly suppressed redd counts in Idaho (Cross 1992, Rieman and McIntyre 1993), and Leathe and Enk (1985) found that spawning occurred in tributaries with late summer flows exceeding 10 c.f.s. Thus, relatively stable channels and stream flows are

probably important factors.

Substrata of spawning sites are characterized by loosely compacted gravel and cobble (McPhail and Murray 1979, Shepard et al. 1984). Because embryos and alevins over-winter within the gravel for more than 200 days, bull trout development and fry emergence are particularly vulnerable to increased fine sediment and associated water quality degradation (Fraley and Shepard 1989, Weaver and Fraley 1991).

Concealment cover is a critical aspect of habitat selection for all life history stages of bull trout (Fraley and Shepard 1989, Pratt 1984;1985;1992, Platts et al. 1993, Rieman and McIntyre 1993), and is often associated with spawning sites (McPhail and Murray 1979, Shepard et al. 1984).

Coarse woody debris (CWD), in addition to providing cover, can play a role in creating and maintaining other spawning habitat characters (Hauer et al. unpublished), though the relationship is not well defined and probably varies with local hydrologic and geomorphic characteristics. CWD influences substrata characteristics by retaining organic matter and controlling the distribution and movement of sediment (Bilby and Likens 1980, Webster et al. 1990, Swanson et al. 1976, Harmon et al. 1986) and may create concavity and convexity of stream bed topography and water surface slope, which is thought to enhance shallow surface-subsurface hydraulic flux (Vaux 1962, Leopold et al. 1964, Harvey and Bencala 1993).

Water temperature also plays an important role in the distribution of the stenothermic bull trout (Pratt 1984, Shepard et al. 1984, Fraley and Shepard 1989, Adams 1994, and others). Multiple studies have indicated that the onset of spawning is triggered by temperatures dropping below 9° Celsius (Needham

and Vaughn 1952, Leggett 1969, McPhail and Murray 1979, Shepard et al. 1984, Weaver and White 1985, and others). Eggs generally hatch between 350 and 440 degree days (°C). Although embryo development appears to require fewer degree days with decreasing temperature (Weaver and White 1985), optimal incubation temperatures occur between 2-4 °C (McPhail and Murray 1979).

Despite gathering considerable information on these habitat factors, researchers have long recognized that many stream segments of visually acceptable habitat (i.e. substrata, gradient, cover, etc.) were never used by spawning bull trout (T. Weaver personal communication). Numerous authors have noted that stream habitats selected for spawning are often influenced by ground water (Heimer 1965, Graham et al. 1981, Shepard et al. 1984, Weaver and White 1985). However, a quantitative, multi-scale assessment of this habitat factor and its importance to bull trout has not been carried out.

Vertical Hydraulic Exchange

Vertical hydraulic exchange is the exchange of waters between the surface and subsurface, and varies across a hierarchy of spatial scales (Fig 2). Most montane alluvial river systems are characterized by a series of unconfined alluvial valley segments bounded longitudinally by bedrock knickpoints and interspersed with confined valley segments. Because the alluvial valley segments are bounded longitudinally by knickpoints and laterally by montane valley walls, throughout this paper we refer to these landscape geomorphic features as bounded alluvial valley segments (BAVS). Confined valley segments act primarily as conduits for surface water, but within these BAVS

considerable groundwater-surface water interaction takes place (Stanford and Ward 1993). This exchange includes interaction with deep-storage ground waters, as well as with the shallow unconfined aquifer immediately below, and lateral to the active channel. This alluvial aquifer includes the area known as the hyporheic zone (Gibert et al. 1994), the region that is influenced by groundwater that was once water in the channel of the stream. Based on the importance of BAVS to hyporheic flow patterns, we hypothesized that the spatial extent of BAVS would be associated with a tributary catchment's capacity for this type of surface-subsurface hydraulic exchange.

In studies in northwest Montana, Stanford and Ward (1993) observed that water typically downwelled at the upstream end of one of a large alluvial floodplain and flowed through the unconfined aquifer. This hyporheic water was observed to upwell to the surface down-slope by valley constriction at a bedrock knickpoint. In general, some reaches within these bounded alluvial valley segments are predominantly gaining water from the subsurface, while others are neutral or losing in exchange character. Based on these observations and the likelihood that similar patterns of hyporheic exchange would occur in smaller but geomorphically similar systems of bull trout spawning tributaries, we hypothesized that the longitudinal position of reaches within BAVS would be linked to the exchange character of a reach.

At the pool/riffle scale within stream reaches, groundwater-surface water interaction also includes local, shallower exchange. This shallow component of hyporheic flow has been shown to vary with discharge, gradient, bedform and water surface slope (Vaux 1962, 1968, Cooper 1965, Kennedy et al. 1984, Thibodeaux and Boyle 1987, Harvey and Bencala 1993). Bedform units also

demonstrate considerable variation in permeability (and hence, intragravel flow rates) associated with heterogeneity in the composition of the streambed material (Vaux 1968). Thus, we hypothesized that similar small-scale variation of subsurface flow would exist in bull trout spawning habitat, and that it would be associated with the bedform of the stream channel.

STUDY AREA

The Swan drainage in northwestern Montana is a densely forested, north-south trending, glaciated basin between the Swan and Mission fault block mountain ranges with an approximate area of 2070 km^2. From peak elevations in excess of 1500 m above the valley floor, waters drain through tributary canyons carved in Precambrian metasedimentary rock and morainal deposits in the broad Swan Valley before reaching their confluence with the sinuous, locally anabranched Swan River, which flows north into Swan Lake and then into Flathead Lake. The current geomorphic template for the dynamic fluvial processes of the Swan River alluvial plain and its tributaries was established by the processes of two major glacial advances. These occurred in the Mid (70,00-35,000 y.b.p.) and Late (16,000-12,000 y.b.p.) Pinedale, with the first being followed by a period of fluvial transport and mass wasting, and the second followed by thickening of the alluvium by in-filling from glacial outwash (Anderson 1992). The bounded alluvial valley segments (BAVS) of the Swan tributary drainages are apparently associated with faulting and local accumulations of valley fill from alluvial and glacial sources.

MATERIALS AND METHODS

Though observational scales should be chosen based on ecological criteria, rather than human perspectives or constraints (Orians and Wittenberger 1991 and others), without previous studies these ecologically meaningful scales may not be known. Considering that habitats and biological communities may scale in the same way (Frissell et al. 1986, Powell 1989, Wiens 1989), primary scales of habitat heterogeneity may constitute appropriate observational scales for studying organisms' relationships with their environment (Poizat and Pont 1996). We employed a hierarchical, stratified sampling design in order to quantify the main scales of variation in vertical hydraulic exchange and identify primary geomorphic constraints. This allowed us to analyze the effects of this habitat variable on bull trout spawning site selection at its corresponding scales of variation. The hierarchy included the catchment, valley segment, reach, and pool/riffle scales.

At the catchment scale, standard U.S.G.S. topographic (1:24,000 scale) and structural geological (1:250,000 scale) maps were used to measure 28 quantitative geomorphic variables for all of the nine principle spawning streams of the Swan drainage (Table 1 and Appendix 1). In addition to traditional drainage geomorphic metrics (Strahler 1964, Leopold et al. 1964), measures were taken to delineate the presence of landforms we hypothesized would enhance a catchment's capacity for large scale surface-subsurface hydraulic exchange. These included measures of valley bottom widths (as a surrogate for floodplain widths) and the number of constrictions and major gradient steps (i.e. knickpoints). Subsequently, we were able to estimate the number, lengths and areas of alluvial valley segments bounded by knickpoints (BAVS) (Fig 3). For

the purposes of this study, BAVS were defined as any unconfined alluvial valley segment at least 500m in length and bounded longitudinally by reaches with valley widths < 50m and/or gradient steps in excess of 10%. Delineating the area of a few BAVS which were located partially or entirely on the Swan valley floor required air photo examination and field reconnaissance. The remaining spawner-accessible stream length outside of bounded alluvial valley segments was broken into two other valley segment categories; 1) confined valley segments, and 2) unbounded alluvial valley segments that lack downstream knickpoints. The latter were always the most downstream segment of a tributary where it emerged onto the Swan valley floor and flowed into the Swan River without encountering another knickpoint. Of the total spawner-accessible stream length, 5% was classified as occurring in confined valley segments, 38% in BAVS, and 56% was in unbounded alluvial valley segments.

We quantified vertical hydraulic exchange through direct measurement of vertical hydraulic gradient (VHG) using mini-piezometers (Fig 4). VHG is calculated with the equation:

$$VHG = \frac{dh}{dL};$$

where dh is the difference in head between the water surface in the piezometer and the level of the stream's surface water, and dl is the depth to which the piezometer was driven. Hence, VHG is positive when upwelling is taking place and negative under downwelling conditions. An installation technique for mini-piezometers, based on the concept of the hollow-auger drilling rig, was developed and used to install more than 500 mini-piezometers. The development of this technique was essential, as it allowed hydraulic exchange data to be gathered at relatively remote sites where it was necessary to carry

equipment while hiking. The procedure was as follows: 1) the driver mechanism (3/4" galvanized pipe with a pointed steel shaft fitted snugly inside) was driven into the streambed with a hammer cap and sledge, 2) the steel driver shaft was removed, while its casing remained imbedded in the substratum, 3) the mini-piezometer (5/8" PVC pipe, inner diameter = 7/16", 1.5 m in length, bottom 15 cm perforated, corked at the end) was slipped into the casing, 4) while the mini-piezometer was held in place, the casing was removed, leaving only the piezometer inserted in the streambed, and 5) the piezometer was bailed and tested for good communication with subsurface flow before being left to equilibrate. Following equilibration, a chalked wire and stilling well were used to obtain the differential head measurement. Piezometers were consistently installed to depths ranging between 25 to 35 cm, though nested series were periodically sampled to check for vertical variation in VHG. VHG has been shown elsewhere to vary temporally (e.g. see Valett 1993). In an attempt to account for the presence of any major seasonal variation in VHG, we monitored a number of piezometers over the entire sampling period (June through October 1995). We did not observe any marked changes in VHG magnitude, and no shifts of VHG direction were detected over the period of observation. Where we wanted to utilize measures of VHG as indicators of flow magnitude, rather than just direction, we had to assume relatively homogenous permeability between sample sites. We felt this was appropriate at coarse scales, though we examined variation in permeability as a potentially important factor at the pool/riffle scale.

In order to quantify hydraulic exchange characters across scales, we sampled four representative spawning streams; Elk and Lion Creeks and Cold

and Lost Creeks (see Fig 1). All spawner-accessible alluvial valley segments in these catchments were sampled for VHG (Appendix 2). However, confined valley segments were not sampled, as it was generally impossible to install piezometers in the extremely coarse bed material of these areas. Based on the relatively little accessible stream length found in confined segments, we assumed that sampling of VHG in only the alluvial segments would allow us to generate VHG data representative of the hydraulic exchange characters of each catchment as a whole.

At least two reaches in each of the spawner-accessible alluvial valley segments were sampled for VHG. Within BAVS, three reaches were positioned at upper, middle, and lower positions, to test our hypothesis that the longitudinal position of reaches within BAVS was associated with exchange character (Fig 5). Within unbounded alluvial valley segments, however, reaches were randomly positioned. At least six reaches of approximately 200m length were sampled in each tributary catchment. At least 15 mini-piezometers were installed in each reach. Following a preliminary test of spatial variation in VHG, we used a spacing of roughly 10-15 m between piezometers as representing VHG patterns at this scale. Large-scale geomorphic features of each reach (e.g. valley bottom width, gradient) were obtained from maps. We also examined temperature and winter ice conditions, factors we believed might be strongly influenced by patterns in vertical hydraulic exchange. Within these four catchments we used Onset^{TM} data loggers to monitor water temperature at sites along the longitudinal gradient of the spawner-accessible stream length. Additionally, we performed several winter surveys, estimating percent ice cover and documenting the occurrence of anchor ice in these streams.

For the smallest scales of the study, two spawning reaches, one on Cold and one on Lion creek, were selected for more detailed geomorphic and pieziometric work. Following installation of a network of roughly 50 piezometers per reach, detailed planimetric maps of floodplain and channel morphometry, as well as bull trout redds and piezometer locations, were constructed of each of these reaches. SURFER^{TM} mapping software was used to construct the topographic contour maps, as well as to interpolate isopleths of VHG and Q (flow) and plot the positions of redds. The channel morphometry maps were utilized to break the streambed into patches of homogenous bedslope character according to three categories; 1) concave, 2) convex, and 3) areas of transition between concave and convex. Concave patches typically were associated with riffles and pools, convex areas with pool tail-outs, and transitional patches were located at the downstream edge of pool tail-outs.

Also at the pool/riffle scale, falling head tests were performed (sensu Lee and Cherry 1978) to estimate the coefficient of permeability and subsurface flow rates at each piezometer site. At most sites, however, equilibration took place so quickly that it was impossible to use the conventional technique to acquire an accurate estimate of permeability. For the few sites where it was possible, we generated an equilibration curve (Figure 6), from which we estimated the basic time lag. The basic time lag was then utilized to estimate permeability using the Hvorslev (1951) equation:

$$k = \frac{(\pi)\ (D)}{(11)\ (T_0)}\ ;$$

where k is the coefficient of permeability, D is the inside diameter of the piezometer, and T_0 is the basic time lag (also see Cedergren 1989 for

summary of calculation). In order to obtain estimates of permeability for all of the piezometer sites, we derived an alternative equation:

$$k = \frac{(.2501)\ (D)}{(dt)}\ (\ln h_o/h);$$

where D is the inside diameter of the piezometer, and dt is the time it takes for the head level to drop from h_o to h. Use of this simplified equation required making a few assumptions. The diameter of the piezometer was the same as the diameter of the perforated interval, whose length was 10 cm. We assumed that the slug of water traveled through the sediment a distance of 10 cm, and that the head prior to filling the tube in the perforated interval was about equal to the stream water level. In the situations where we were able to estimate permeability using the Hvorslev method as well as our own simplified equation, we detected no appreciable difference between these estimates. For the sake of simplicity, then, we used only the values obtained by the latter approach. Following estimation of k, we were able to calculate the vertical component of flow at each of these sites, using the basic principle of groundwater flow expressed in Darcy's equation:

$$Q = (k)\ (A)\ (dh/dl);$$

where Q is the flow, k is the permeability, A is the surface area of the mini-piezometer, and dh/dl is the VHG.

Bull trout redd surveys, conducted by Montana Department of Fish Wildlife and Parks (MFWP) personnel, were used as an index of spawner density. Duplicate redd surveys were performed by the principle author on Elk, Lion, Cold and Lost Creeks. Based on multiple surveys done to identify times that

would result in the most complete estimate of the spawning population (Weaver 1991), redd surveys were conducted in September and October.

ANALYSIS

Initially, we constructed a correlation matrix of geomorphic features and bull trout redd numbers in the nine principal spawning catchments. We did not use multivariate statistical procedures because we wanted to avoid obscuring possible significant and interesting associations, and because of concerns about co-linearity among variables. Rather, we applied step-wise regressions in instances where we felt the variables of interest were generally continuous in nature and not easily broken into meaningful categories.

Where we felt categorization was appropriate, we applied non-parametric Chi^2 analysis to determine differences between observed patterns of bull trout redd distribution across scales and the distribution that would be expected if spawning was distributed randomly throughout the available habitat. For example, at the valley segment scale we estimated the expected random distribution based on the proportion of available stream length found in each valley segment type. At the pool/riffle scale, random sub-sampling of the detailed reach maps allowed us to estimate the proportion of habitat associated with each bedform type as well as the percent of habitat that possessed positive or negative VHG. We used these proportions to calculate distribution of redds that would be expected assuming that redds were distributed at random among these categories. At this scale, we also applied nearest-neighbor analysis (coupled with the non-parametric Mann-Whitney U test) to determine the presence of spatial association between bull trout redds and VHG.

When the Chi^2 tests resulted in significant differences between used and available habitat, Jacobs' D, a modification of Ivlev's electivity index, was used as a non-statistical indication of where differences between use and availability occurred (Jacobs 1974). The equation for calculating D is:

$$D = \frac{(u - a)}{(u - a - 2ua)};$$

where u is the proportion of redds distributed in a given habitat, and a is the proportion of that habitat available to spawning bull trout. A value of D between 0 and -1 indicates negative selection, while a value between 0 and +1 indicates positive selection for a particular habitat.

Preliminary analyses of the non-transformed VHG data from the three larger scales resulted in few consistent associations. In an effort to examine each piezometer site for its relative potential for groundwater discharge, we transformed the VHG data by changing all negative VHG values to zero, while all positive values remained the same. We refer to this value, for the sake of simplicity, as groundwater input, though we recognize that it is a surrogate for the actual volume of groundwater discharge.

RESULTS

Catchment Scale

Among the four tributaries sampled for VHG, the mean of non-transformed VHG values per stream was significantly associated with only one geomorphic factor, the number of spawner-accessible BAVS (p < .043). However, the mean of transformed positive VHG readings (groundwater input) per stream was positively correlated with the area of spawner-accessible BAVS (p < .05) (Fig 7),

as was the maximum positive VHG measurement from each stream (p < .01). We recognize that combining BAVS-associated measures for a whole tributary (e.g. area of accessible BAVS per catchment) may not result in a true catchment-scale variable in a physical sense. However, from a biological perspective, this variable may be an important factor that influences habitat use at the catchment level.

Among all nine principle spawning streams, counts of bull trout redds per tributary drainage were not associated with any of the traditional geomorphic metrics examined (see Appendix 1). Rather, these counts were positively correlated (p < .002) with the area of spawner-accessible bounded alluvial segments (BAVS) (Fig 8). The total area of BAVS, regardless of accessibility, was also correlated with among-tributary redd distribution, though the association was weaker (p < .015). The accessible stream length within BAVS per tributary was also positively correlated with the number of redds in BAVS (p < .020). Furthermore, the proportion of the accessible stream length found in BAVS was strongly correlated with the density of redds (counts per accessible stream length) (Fig 9). The area of accessible BAVS per tributary was positively correlated with the number of redds located in BAVS (p < .004) as well as the number of redds found in unbounded alluvial valley segments (p < .019), but not with the number in confined valley segments.

Finally, among the four streams sampled for VHG, we found that the groundwater input per stream was positively associated with redd counts (p < .02) (Fig 10), as was the maximum positive VHG measurement from each stream (p < .006).

Valley Segment Scale

Within the four streams sampled for VHG, bounded and unbounded alluvial valley segment types differed significantly in their vertical hydraulic exchange character (Mann-Whitney U, p < .008). All BAVS displayed significant groundwater discharge and variation in vertical hydraulic exchange, while three of the four unbounded alluvial valley segments were losing to neutral in exchange character. Examining BAVS alone revealed that the area of a bounded alluvial valley segment was associated with its groundwater input (p < .010) (Fig 11). Among the four unbounded alluvial segments, the one on Cold Creek was unique in that it possessed significant regions of groundwater discharge that appeared to be associated with the presence of a large beaver dam complex. Water was observed to downwell in the reach above the complex, while relatively weak upwelling occurred for several hundred meters downstream of it. This situation represented large-scale hydraulic exchange that was not predicted by the longitudinal position of a reach relative to a knickpoint.

Among all valley segments in the nine principal spawning streams, bull trout redds were preferentially distributed in BAVS (Chi-Square = 917, p < .0001). Of the total redds observed, 88.5% were located in BAVS habitat, while 8 % were found in unconfined, unbounded valley segments, and only 3.5% were observed in confined valley segments . The availability of BAVS relative to their usage was suggestive of positive selection (Jacobs' D = 0.450) (Fig 12). Additionally, among the BAVS of the four VHG-sampled tributaries, the extent of groundwater input in a BAVS was associated (p < .010) with the number of redds observed there (Fig 13). Finally, the number of redds in a bounded

alluvial valley segment was weakly associated with its area (p < .164).

Reach Scale

Within alluvial valley segments, the longitudinal, geomorphic context of a reach was often indicative of its overall exchange character, but this was not consistently predictable. Reaches that were located at the downstream end of a bounded alluvial valley segment, just upstream of a knickpoint or valley constriction, were always gaining water from the subsurface and always contained bull trout redds (Fig 14). The mean VHG per reach was negatively associated with the mean valley bottom width at each reach (p < .002). Reaches in the middle of BAVS had very wide valley bottom widths and were typically neutral or downwelling. In addition, several strongly downwelling reaches with wide valley-bottom widths were located in the unbounded alluvial valley segments of the four streams.

As was the case within the unbounded alluvial segment of Cold Creek, not all of the reaches possessing groundwater discharge were located at the downstream end of a bounded alluvial segment. Another notable exception was the high density spawning reach located at the upstream end of the middle bounded alluvial segment on Elk Creek. The hydrogeology of this valley segment appears to be very complex. The uppermost reach, just below a large confined canyon segment, receives upwelling groundwater from an alluvial fan-wetland complex, as evidenced by a positive (0.035) groundwater input. However, it also appeared to receive considerable lateral groundwater input, as there are many seeps located along the banks of this reach. The middle reach of this valley segment appears to be fairly neutral in exchange character

(groundwater input = 0.008) and contained no redds, while the lowest reach above another canyon segment was weakly gaining water from the subsurface (groundwater input = 0.012) and contained only one redd.

Reaches that were gaining water (mean VHG = .0169) had the highest number of observed bull trout redds (94). There were no significant differences in redd distribution associated with reach gradient, valley bottom width, or other geomorphic variables among the reaches sampled. Rather, the number of bull trout redds per reach was positively correlated ($p < .001$) with the groundwater input per reach (Fig 15). Furthermore, since the scatter of points on this graph was suggestive of a groundwater input threshold of about 0.03, we tested the observed versus random distribution of redds among reaches possessing inputs > 0.03 versus those < 0.03, and found the difference to be highly significant (Chi-Square = 215, $p < .0001$). Hence, reaches with high groundwater input values were preferentially selected for spawning relative to their availability (Jacobs' D = 0.795) (Fig 16).

Additionally, the thermal regimes of gaining reaches were significantly moderated by the groundwater effect (e.g. Fig 17). These reaches possessed the least ice cover, and anchor ice was never observed to occur.

Though three reaches that were predominantly downwelling did have bull trout redds in them, all three of these reaches were positioned immediately downstream of inaccessible upwelling groundwater sources (both hyporheic and non-hyporheic). Temperature data from several such reaches displayed the moderating effect of groundwater influence, particularly when the reaches were exposed to extreme air temperatures. Winter ice condition data from these reaches show that percent cover was low and there was no incidence of anchor

ice. These moderating effects were observed to dissipate with downstream distance from the upwelling zone.

There were no redds located in losing or neutral reaches (mean VHG = -0.3921) that were not positioned to receive strong volume and thermal effects from an upwelling zone. These reaches displayed greater temperature range and variation, while they were also subject to anchor ice formation. One such reach, located in the middle of a bounded alluvial valley segment on Lion Creek, was frozen solid to the substratum for an extended period of time each winter. These conditions allowed easy identification of the longitudinal boundary of the next upwelling reach downstream. This boundary was noted in the winter of 1994-95, confirmed with piezometer readings during the summer of 1995, and observed again the following winter.

Pool/Riffle Scale

Within the two mapped reaches on Lion and Cold creeks, we also observed a scale-specific association between morphology and vertical hydraulic exchange, as well as between vertical hydraulic exchange and redd distribution. Both of these reaches possessed significant sources of groundwater discharge. Within them, however, VHG varied significantly with bedform character. Convex and transitional streambed patches were significantly different in VHG from concave areas (Mann-Whitney U = 64, p < .0001). In addition, convex and transitional slope classes varied significantly in VHG character, and concave areas were different from convex patches (Mann-Whitney U = 87, p < .0001) (Fig 18). Areas of the streambed that were in transitional or convex slope categories possessed negative VHG with means of

-0.099 and -0.042, respectively, while concave patches displayed upwelling VHG's (mean = 0.038). Estimated permeability ranged approximately five orders of magnitude, from 2.32 x 10^{-6} cm/sec to a maximum of 0.337 cm/sec (Appendices 3A and 3B). Finally, the falling head test data indicated that transitional bedform units possessed significantly higher intragravel flow rates than either of the other categories (Mann Whitney U, p < .0001).

Bull trout redds were preferentially distributed in the transitional slope class rather than in either the convex or concave class (Chi-square = 54, p < .0001). Of the 15 redds found in the two reaches, only one of these was located in a concave bedform unit. There were two transitional units where no redds were constructed, however the availability of transitional areas relative to their usage was suggestive of positive selection (Jacobs' D = 0.895) (Fig 19). Looking at redds individually, we found that spawning sites were strongly associated spatially with downwelling piezometers to the second nearest neighbor (Mann-Whitney U = 32, p < .0008) (Figs 20 and 21) . The median distance from redds to the nearest downwelling piezometer was only 2.1 m, while the median distance to the nearest upwelling piezometer was 14.6 m. Furthermore, after accounting for the relative availability of downwelling versus upwelling habitat within these reaches, we found a significant difference between the expected (assuming randomness) and the observed distributions of redds (Chi-square = 8.99, p < .002), suggesting positive selection of downwelling areas (Jacobs' D = 0.751) (Figs 22 and 23).

The distribution of redds was also associated with the magnitude of intragravel flow. Redds were located in areas with the highest flow rates (up to .058 cm^3/second), while those with the weakest flow (< .001 cm^3/sec) were

never used (Fig 24). We broke all of the estimates of Q from the two mapped reaches into three categories of low (< .001 cm^3/sec), medium (> .001 but <.01 cm^3/sec) and high (>.01 cm^3/sec) flow rates. After accounting for the relative availability of habitat in each intragravel flow category, we found a significant difference between the expected (assuming randomness) and the observed distributions of redds (Chi-square = 17.98, p < .0001), suggesting positive selection of areas with high intragravel flow rates (Jacobs' D = 0.727) (Figure 25).

Though quantified measures of substratum character were not made, qualitative observations indicated that the bedform units selected by bull trout possessed the expected gravel-cobble size (McPhail and Murray 1979, Shepard et al. 1984), as well as transitional bedslope, negative VHG, and high intragravel flow rates. At this scale, the presence of boulders or coarse woody debris (CWD) did not appear to explain a significant portion of the variance in redd position among bedform units. Of interest, however, were several situations in which the presence of CWD appeared to be the mechanism creating variation in bed topography. As a consequence, we observed heterogeneity in the magnitude and direction of vertical hydraulic gradient associated with the CWD. In these cases, we observed shallow downwelling above the spill log, and upwelling in the pool below the log. Under extreme air temperatures, we were also able to detect slight (.1 - .2 ^{o}C) variation in temperature associated with this CWD-induced hydraulic exchange.

DISCUSSION

The results of this study revealed the presence of several major scales of

variation in the interactions of surface and subsurface waters in bull trout spawning streams. The results also pointed to the scale-specific role of geomorphology in patterning this variation. In addition, bull trout redd site selection was observed to be strongly associated with vertical hydraulic exchange across the nested spatial hierarchy. This study does not identify the actual mechanisms of spawning habitat selection, and bull trout may not respond directly to vertical hydraulic exchange in itself. Nonetheless, we suggest that at a minimum vertical hydraulic exchange plays a critical role in structuring other habitat factors (i.e. temperature, low-flow volumes, ice conditions) that may be directly important to the integrated process of spawning habitat selection.

Among catchments, the amount of groundwater discharge in a tributary appears to vary closely with the extent of bounded alluvial valley segments. The importance of BAVS in constraining hyporheic flow has been observed in the floodplains of large montane rivers (Stanford and Ward 1993), and our results are consistent with the hypothesis that this landform plays a significant role in patterning hyporheic exchange in much smaller systems as well.

Bull trout redds were preferentially distributed in catchments with the greatest spatial extent of accessible bounded alluvial valley segments (BAVS), and, hence, the most groundwater-influenced habitat. Previous landscape-scale spatial analyses of bull trout redd variation have suggested there are significant correlations between redd frequencies and drainage area and/or stream order (Graham et al. 1981, Mullan et al. 1992, and others). Although these conventional catchment metrics may be important discriminators for presence/absence of bull trout spawning at broad landscape scales (as was

suggested by Rieman and McIntyre 1995), our results suggest that they are not useful predictors of variation in abundance or distribution among the principle spawning streams of the Swan basin.

Although the potential for surface water-hyporheic zone connectivity is expressed in the spatial extent of BAVS, upwelling of non-hyporheic ground waters is not so predictable. Because some major non-hyporheic springs in the Swan drainage spawning streams (such as those proximal to spawning habitat on Jim Creek) do not correspond to the largest BAVS, redd numbers in these streams could be higher than predicted by the spatial extent of BAVS alone. In addition, since length and area of accessible BAVS are closely correlated, it is difficult to determine at present if it is simply the length of stream available within BAVS that is more important, or if the lateral extent of the unconfined valley segment contributes to the quality of the spawning habitat. We suspect that there is probably a range of fairly large areas over which the length of stream habitat available is most important, but that there may be some point at which smaller BAVS do not possess the depth of alluvial fill and lateral complexity required to establish major hyporheic flow paths.

There are several reasons groundwater-influence may be important to bull trout spawning-site selection at the catchment scale. Because vertical hydraulic exchange (or the lack thereof) may structure the cumulative thermal and flow regime of a tributary, it could indirectly determine the permeability of a catchment to migrating bull trout. In particular, the downstream extent of a BAVS effect (i.e. the strength of the groundwater plume), or the exchange character of reaches nearest to the confluence with the main river might be critical. For example, the lowermost reach of Lost Creek is far downstream from

the nearest groundwater discharge area, and waters there downwell into an alluvial fan so strongly that surface flow is lost there during the dry months in the fall. The temporal extent of this particular flow barrier appears to vary from year to year. Additionally, when a low flow is present, high temperatures occur in this reach. At least some bull trout appear to enter the tributary prior to the reach drying up, as redds have been observed in Lost Creek every year it has been surveyed (Montana Bull Trout Scientific Group 1996). However, in the late fall of 1995, we observed a dead adult bull trout in a dried-out pool of this lower reach, presumably stranded during its post-spawning out-migration. The frequency of this occurring is not known, but it could have a significant impact on repeat spawning among fish using Lost Creek spawning habitat.

Baxter et al. (Chapter 3 this thesis) suggest groundwater discharge may also play an important role in bull trout population dynamics. They demonstrated positive correlations between the rate of change in redd numbers over the last 14 years among all nine of the principle spawning catchments and the spatial extent of BAVS per catchment. In addition, they postulated that vertical hydraulic exchange may actually be contributing to the resiliency of a tributary's spawning population in the face of roading and associated land-use impacts.

Though this study does not address it, the nature of groundwater-surface water interactions also varies across geological regions (Freeze and Cherry 1979). In a study of brook trout (Salvelinus fontinalis) spawning site selection in waters of three different geologic regions, Curry and Noakes (1995) discuss some of this regional hydrogeological variation. They suggest that the importance of groundwater discharge to brook trout spawning site selection

varies, depending on the limiting habitat factors of each region. The relationship between bull trout and vertical hydraulic exchange may differ similarly. For instance, there are significant geological differences between the Swan and North Fork of the Flathead basins that could result in variation in the extent of groundwater-influenced habitat . Consequently, bull trout spawning habitat selection patterns could vary between these two basins.

Within tributary catchments of the Swan basin, we found that BAVS possessed the most significant groundwater discharge and variation in vertical hydraulic exchange. Furthermore, the area of a bounded alluvial valley segment was associated with its groundwater input, further evidence for the geomorphic constraints on this process. Among the valley segment types, bull trout spawning occurred predominantly in BAVS. Of the total redds observed, 88.5% were located in BAVS habitat, with 8% found in unbounded alluvial valley segments, and only 3.5% observed in confined segments. Though the number of redds in a bounded alluvial valley segment varied weakly with its area, a particular BAVS' groundwater input was consistently predictive of the number of redds in it. As we suggested for catchment scale selection, the importance of hydraulic exchange to spawning bull trout at the valley segment scale may be the influence of groundwater discharge on thermal and flow gradients. Numerous researchers have identified alluvial valley segments as critical spawning habitat for many fish species. For example, Frissell (1992) observed that spawning of salmon and steelhead in coastal river systems of southern Oregon occurred almost exclusively in alluvial segments. Besides possessing significant habitat influenced by groundwater discharge, these segments contain large, stable expanses of well-sorted gravel and cobble. The

presence of floodplain surfaces in these segments allows overbank flow, which, in concert with hyporheic storage, can partially buffer the channel from scouring and depositional effects of flooding. In contrast, within confined valley segments suitable spawning gravel is patchy, and flooding is not attenuated by a floodplain as in unconfined segments.

Although bull trout do utilize habitat outside of BAVS for spawning, redds are found only in pockets of suitable habitat in confined stream segments. Some are also found in unbounded alluvial segments that lack downstream knickpoints and occur where the tributaries emerge onto the Swan valley floor. Because of a spill-over effect on temperature and flow factors, it is possible that the downstream-effect of BAVS (i.e. the strength of the groundwater plume) may influence the use of such habitat outside BAVS.

Within alluvial valley segments, the longitudinal, geomorphic context of a reach was associated with its overall exchange character, though there were a few significant exceptions. Reaches positioned in unbounded alluvial valley segments were typically neutral or downwelling. However, an area of significant groundwater discharge did occur in the unbounded segment of Cold Creek where hyporheic flow appears to have been enhanced by the presence of a very large beaver dam complex. Though there have been few quantitative studies of altered flow paths associated with beaver dams, our results are consistent with the findings of White (1990) and Lowry (1993) who also demonstrated downwelling at and above the dam, followed by upwelling immediately downstream.

With this exception, gaining reaches were primarily located within BAVS, just upstream of bedrock knickpoints. A few instances were observed in which

relatively impermeable clay layers may have contributed to localized upwelling measurements. Valley widths of gaining reaches were less than those of neutral and losing reaches, partly because the valley walls of BAVS typically begin to pinch together as the downstream knickpoint (and, thus, the gaining reach) is reached. Though reaches located at the downstream ends of BAVS were predictably gaining water from the subsurface, the location of a reach within a bounded alluvial valley segment was not necessarily a consistent predictor of the groundwater input to that reach, a result we attribute to the fact that non-hyporheic inputs did not always appear to be responding to the same geomorphic influences as hyporheic flow. In addition, we observed one reach, positioned just upstream from a confined valley segment on Elk Creek, which was gaining water only weakly. Study of the geologic map of the area suggests that the material creating this constriction is more permeable, perhaps thick morainal materials or an old fluvial terrace. In such a case, considerable hyporheic flow may be occurring throughout what might otherwise be considered a confined stream segment.

Bull trout selected stream reaches within bounded alluvial valley segments that contained strong groundwater upwelling zones or were influenced by groundwater inputs from a source immediately upstream. Reach-scale observations of temperature and ice condition further support the idea that the influences of groundwater discharge spill over into downstream habitat, with the longitudinal extent of the plume dependent on the strength of the groundwater discharge. A few losing reaches had redds in them, however these were receiving inputs from proximal, but inaccessible discharge sources upstream. The fact that redds were found at the heads of such downwelling reaches

further suggests that, though a strong positive association with groundwater discharge exists, it is most likely the flow and thermal effects of upwelling that underlay the integrative mechanism of spawning reach selection.

The lack of correlation between mean VHG and redd distribution at the catchment, valley segment, and reach scales may be a result of two factors. First, the majority of downwelling VHG values were characteristically greater in magnitude than upwelling VHG values. Consequently, the presence of a few downwelling values in a reach could drastically reduce the mean. Without estimates of permeability, we were unable to determine actual flow volumes. However, since upwelling water must balance the water that is downwelling , these results suggest that downwelling and upwelling may not take place in the same fashion. Perhaps upwelling of hyporheic waters is a more diffuse process overall, when compared to downwelling. Secondly, at these scales, the directly important factor to spawning bull trout may not be VHG, but rather the input of groundwater to the catchment, segment or reach. This appears to be the case, as we found the strongest associations at these scales between redd distribution and the mean of positive VHG readings, or what we called the groundwater input (really a surrogate for the actual volume of groundwater discharge).

Areas influenced by groundwater discharge possess relatively stable thermal and flow regimes important to bull trout egg incubation, emergence success, and the survival of juvenile bull trout. Groundwater discharge sources provide coldwater refugia for salmonids in summer (Latta 1964, Gibson 1966, Kaya et al. 1977, Bilby 1984, Nielson 1993, and others) and warmwater refugia in winter (Craig and Poulin 1975, Cunjak and Power 1986, and others).

Benson (1953) observed that reaches of the Pigeon River in Michigan appeared to be selected as spawning reaches by another char, the brook trout. Latta (1964) also found that years of high survival of brook trout fry in the Pigeon River corresponded to years of high groundwater levels. In addition, warm groundwater temperatures in winter inhibit the formation of anchor ice (Maciolek and Needham 1952, Needham and Jones 1959), which can cause high mortality in post-emergent salmonids (Benson 1955). In fact, we observed that reaches within the spawning streams that were influenced by upwelling ground water possessed less winter ice cover and experienced no formation of anchor ice. This was in contrast to frequent anchor ice events in neutral and especially losing reaches that were not positioned to receive flow and thermal effects spilling from an upstream groundwater discharge zone.

Within the two mapped reaches on Lion and Cold creeks, we also observed a scale-specific association between morphology and vertical hydraulic exchange, as well as between this exchange and the distribution of bull trout redds. We observed that VHG varied significantly with bedform character, as has been shown by numerous authors (Vaux 1962; 1968, Cooper 1965, Kennedy et al. 1984, Thibodeaux and Boyle 1987, Harvey and Bencala 1993). Convex and transitional bedforms displayed localized, shallow downwelling while concave areas possessed upwelling VHGs.

Our experience performing falling head tests provides further testament to the extremely high permeability of spawning-bed gravels. More accurate sampling of permeability requires the use of an elaborate standpipe construction and techniques such as those developed by Terhune (1958). Our data do indicate that considerable heterogeneity of permeability and intragravel

flow rate occurs within bull trout spawning reaches. Qualitative observations of piezometer screens in these situations suggested the presence of clay or fine sediment lenses at varying depths probably contributed to this variation. Interestingly, transitional patches possessed faster flow rates than convex units. This observation concurs with the lab flume experiments of Cooper (1965) and Vaux (1968) who both identified the fastest intragravel flow velocities took place at the crest of the wave-form.

Though bull trout spawned in reaches possessing significant groundwater discharge (such as the two mapped sections of Lion and Cold Creeks), within these reaches they appeared to select actual redd sites that corresponded to areas of localized downwelling. More bull trout redds were located in the transitional slope class than in either the convex or the concave class, and redds were spatially associated with the corresponding localized downwelling. Numerous salmonid species prefer to spawn in the transitional zone between pools and riffles (Bjornn and Reiser 1991). In addition to possessing downwelling intragravel flow, the substratum of such transitional patches may be more stable than the concave riffle/pool areas, and velocities there high enough to keep the gravel clean of silt and debris that could clog the interstices of the redd environment.

The importance of intragravel flow to the growth, development and survival of salmonid eggs and fry has long been recognized by fisheries biologists. Percolation through the redd is thought to provide a constant supply of oxygen to the eggs and effectively remove metabolic waste materials (Bjornn and Reiser 1991). Whether the direction of intragravel flow is important remains uncertain. Conceivably, either local upwelling or downwelling could provide

sufficient flow through the redd for removal of wastes, though in some situations upwelling groundwater might possess a lower dissolved oxygen content while downwelling waters would generally be saturated. Hansen (1975) found that brown trout *Salmo trutta* appeared to avoid spawning over oxygen-poor upwelling groundwater, but selected sites nearby where a certain amount of mixing with surface water had taken place. In contrast, numerous authors have observed bull trout, as well as the related brook trout, spawning directly over groundwater springs (e.g. Heimer 1965, Webster and Eiriksdottir 1976, Curry and Noakes 1995). Since the movements of non-hyporheic ground waters are not controlled by streambed slope, non-hyporheic upwelling may be more likely to coincide with the appropriate substratum conditions than hyporheic upwelling zones. We cannot dismiss the possibility that the observed association between redd distribution and VHG direction may be due, in part, to the fact that neither of the mapped reaches of this study contained discernible non-hyporheic groundwater springs. Additionally, the construction of the redds themselves may have altered very localized patterns of VHG direction. For example, Cooper (1965) demonstrated that waveforms were produced by spawning salmon that could establish a shallow pattern of exchange through the redd environment.

At the pool/riffle scale, we found redd distribution was associated with both the direction and the magnitude of vertical hydraulic exchange. At this scale, redds were preferentially distributed in areas of strong, downwelling intragravel flow. Therefore, it is possible that either the rate of intragravel flow, or the direction, or both, may be critical to spawning habitat selection. Two previous studies of bull trout spawning habitat yielded somewhat equivicol observations

with respect to permeability. A study of an artificial spawning channel revealed no significant correlations between redd site selection and either dissolved oxygen concentration or permeability (Heimer 1965). In a spawning tributary of the North Fork of the Flathead River, Weaver and White (1985) detected significantly greater permeabilities in a spawning area than in a non-spawning area, though no significant difference was observed between selected versus utilized sites within the spawning area. Studies of rainbow trout *Salmo gairdneri* have shown greater growth and survival to emergence in redds with higher rates of subsurface flow (in these cases upwelling groundwater) (Coble 1961, Sowden and Power 1985), but no such studies have been done for bull trout.

It is important to consider that bull trout redd construction probably positively influences the permeability of the disturbed site. Ringler and Hall (1975) observed that intragravel dissolved oxygen levels were significantly higher within salmon redds than in permanent standpipes nearby, suggesting that either 1) the spawning activities themselves had increased the intragravel flow rates, or 2) the salmon were able to select the sites with the highest subsurface flow rates. The idea that redd construction itself may be interactive with habitat conditions raises the possibility that, as has been postulated for salmon (Everest et al. 1987 and others), the annual spawning activity of these fish over many years may have critical positive feedback impacts on the quality (e.g. permeability) of their spawning habitat. The effect of redd construction on permeability is unclear, however, and may vary with other factors. For example, Curry et al. (1995) documented warmer winter substratum temperature and higher dissolved oxygen levels within brook trout redds compared to sites

nearby, while they found no differences in intragravel flow. Their results also typify the relatively ambiguous relationship between observed permeability and dissolved oxygen levels.

Because we did not want to disturb bull trout eggs, piezometers were not installed directly into redds. However, our results do suggest that bull trout may be able to sense and select habitat in direct response to variation in intragravel flow rates. Whether it is the direction or the magnitude of vertical hydraulic exchange, or both, that is actually involved in habitat selection, these data are insufficient to surmise. Finer spatial resolution in measures of VHG and intragravel flow rate, along with quantification of substrate characters and intragravel dissolved oxygen levels, would further delineate the relative importance of vertical hydraulic exchange to spawning site selection at the pool/riffle and microhabitat scales. Coupling this work with experiments on growth and survival to emergence in habitats possessing variable hydraulic exchange characters could shed more light on the underlying biological mechanisms of these habitat-use patterns. In addition, obtaining direct measures of intragravel flow inside the redd environment (perhaps through the limited use of Mark IV standpipes) (Terhune 1958) could provide important information.

The results of this study exemplify the way in which organisms' relationships with their physical environment are scale-dependent in nature. Bull trout may be responding to variation in vertical hydraulic exchange differently at different scales. Without a hierarchically-nested spatial approach to the interaction between vertical hydraulic exchange and bull trout spawning, we would have obtained an erroneous picture of spawning habitat selection. For example, if

we had only examined vertical hydraulic exchange in the immediate vicinity of redds, we might have concluded that spawning habitat selection had nothing to do with upwelling groundwater. Alternatively, had we ignored the smaller scale, the unique associations we observed there would have been missed. Variation of some habitat factors may not be detectable or important to bull trout at all scales (an example could be cover, which plays a role at fine scales, but may have little meaning when examined across landscape scales). Vertical hydraulic exchange, however, appears to be important to the spawning habitat selection process across the scales examined. In much of the fish habitat-use research to date, habitat variables have been considered as describing local conditions, regardless of their primary scales of heterogeneity. As we and other authors (e.g. Poizat and Pont 1996) have observed, this approach may mix organism's responses to habitat factors varying differently at different scales, and lead to obscuring meaningful patterns.

Our results also raise two debated and critical ecological questions. First, at what spatial scale is habitat selection occurring? Fine-scale habitat selection may be constrained by larger scale selection, as suggested by Johnson (1980) and Orians and Wittenberger (1991). Alternatively, fine-scale requirements may define large-scale distribution of a species (Ricklefs 1987, Wiens 1989, Bayley and Li 1992). Bull trout spawning site selection may fit either of these scenarios, depending on the circumstances. For example, the strength and longitudinal extent of a catchment's groundwater discharge plume may influence the accessibility of the catchment to spawning bull trout, regardless of the quality of reach or habitat unit-scale spawning grounds within it. Alternatively, from the small to large-scale perspective, the bull trout's

stenothermic thermal requirements probably limit the southern extent of its range.

Secondly, it may be important to question what component of redd site selection is taking place at the individual vs. the population level. How much of this habitat 'selection' is active behavior by individuals that are sensing their way to a redd site possessing certain characters, and how much is the result of fidelity to certain sites that yielded survival to reproductive age? These cannot be answered without more intensive study of bull trout physiology (including sensory capabilities), social interactions, learned behavior, survival to emergence under varied conditions, and spawning site fidelity. At present, it can only be said that observations of bull trout do not appear to support a uni-directional spawning habitat selection scenario.

Finally, our work suggests that conservation of the bull trout and the maintenance and restoration of their spawning habitat will require consideration, within a geomorphic context and over a spatial hierarchy, the importance of vertical hydraulic exchange to this species. First, it will be important to gather and apply information regarding groundwater influence as a part of the process of identifying and doing inventory of potential bull trout spawning habitat. Currently, researchers spend time in bull trout spawning habitat predominantly while doing redd surveys in the fall. This coincides with a time of thermal transition, when stream temperature measurements may not reflect the presence of upwelling groundwater. Though typically fish habitat assessment is not done in winter, we encourage winter surveys of temperature and ice conditions as a method to gather useful information regarding the low-flow and thermal effects of groundwater influence. Alternatively, the

longitudinally integrated effects of upwelling can also be observed under extreme summer temperatures.

Secondly, in assessing and monitoring spawning habitat, we recommend stratification with respect to the occurrence of BAVS. This process could aid in addressing the functional diversity inherent in these systems. However, such a stratified approach should also address the downstream effects of BAVS (e.g. water temperature or low-flow volume). Furthermore, it is likely that a more detailed approach to valley segment typing in the Swan basin would result in identifying additional segment types. For example, areas currently identified as BAVS may include two or three functionally distinct classes. A more rigorous classification of valley segment habitat within the streams of the Swan basin would further enhance the contextual perspective on bull trout spawning, as well as many other integral ecosystem processes. In addition, we recommend that redd surveyors utilize direct measures of distance rather than observer paces during routine surveys. This would significantly increase the spatial resolution of data on spawning distribution patterns and expedite the analyses of these patterns in space and time.

Thirdly, we feel it is important to stress the relative ease by which direct measures of VHG and permeability can be obtained, and to encourage further use of mini-piezometers in studying the ecology of fishes and other aspects of stream ecosystems. From the backpack-portable technique utilized in our study, to methods developed for use in the Columbia River (Geist et al. 1996), it is obvious that the basic piezometer design can be modified to obtain information in many settings. In retrospect, we also recommend utilizing synoptic stream flow measures (or "seepage runs") (see Riggs 1985 for

methodology details) to aid in quantifying hydraulic exchange patterns. Incorporating this approach would help circumvent the difficulty of using piezometers in confined valley segments.

This study has contributed a quantified perspective on vertical hydraulic exchange and the geomorphology that patterns it across multiple scales. We also characterized the association between this habitat factor and bull trout spawning habitat selection across scales. It is apparent that vertical hydraulic exchange plays a unique role in the structure of the collage of physical gradients presented to this organism. As other influent habitat variables are examined in this fashion, better information can be brought to bear on the task of describing a complete picture of the habitat use of this species. Furthermore, we recognize the importance of groundwater-surface water interaction to many other biota of the stream ecosystem, as well its integral role in structuring critical processes at the water-land interface, and we are hopeful that the methods and approach of our study will contribute to research in these areas as well.

LITERATURE CITED

Adams, S.B. 1994. Bull trout distribution and habitat use in the Weiser River drainage, Idaho. M.S. thesis, University of Idaho, Moscow, Idaho.

Anderson, R.C. 1992. Hydrogeology of the Swan River Oxbow Preserve area, Lake County, Montana. Master's thesis. University of Montana, Missoula, Montana.

Bayley, P.B. and H.W. Li. 1992. Riverine fishes. p. 251-281 *In* P. Calow and G.E. Petts [ed.] The rivers handbook: Hydrological and ecological principles. Blackwell, Oxford.

Benson, N.G. 1953. The importance of groundwater to trout population in the Pigeon River, Michigan. pages 269-281 in Proceedings of the Eighteenth North American Wildlife Conference.

Benson, N.G. 1955. Observations on anchor ice in a Michigan trout stream. Ecology 36:3:529-530.

Bilby, R.E. 1984. Characteristics and frequency of cool-water areas in a western Washington stream. J. Freshwater Ecol. 2: 593-602.

Bilby, R.E. and G.E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61: 1107-1113.

Bjornn, T.C. and D.W. Reiser. 1991. Habitat requiremenst of salmonids in streams. p. 83-138 *In* Meehan, W.R. [ed.] Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Cedregren, H.R. 1989. Seepage, drainage, and flow nets. John Wiley and Sons, New York, NY.

Coble, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society 90:469-474.

Cooper, A.C. 1965. The effect of transported stream sediments on the survival of sockeye and pink salmon eggs and alevins. International Pacific Salmon Fishery Commission Bulletin 18.

Craig, P.C. and V.A. Poulin. 1975. Movements and growth of arctic grayling (*Thymallus arcticus*) and juvenile arctic char (*Salvelinus alpinus*) in a small arctic stream, Alaska. J. Fish. Res. Board Can. 32: 689-697.

Cross, D. 1992. Status of bull trout on the Idaho Panhandle National Forests. U.S. Forest Service. Coeur d'Alene, Idaho.

Cunjak, R.A. and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. 43: 1970-1981.

Curry, R.A. and D.L.G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus confluentus*). Can. J. Fish. Aquat. Sci. 52: 1733-1740.

Curry, R.A., D.L.G. Noakes, and G. E. Morgan. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus confluentus*). Can. J. Fish. Aquat. Sci. 52: 1741-1749.

Dahm, C.N. and H.M. Valett. 1996. Hyporheic zones. p. 107-119 *In* F.R. Hauer and G.A. Lamberti [eds.] Methods in Stream Ecology. Academic Press.

Donald, D. B. and D. J. Alger. 1993. Geographic distribution, species displacement and niche overlap for lake trout and bull trout in mountain lakes. Can. J. Zool. 71:238-247.

Dutilleul, P. and P. Legendre. 1993. Spatial heterogeneity against heteroscedasticity: An ecological paradigm versus a statistical concept. Oikos 66(1):152-171.

Everest, F.H., R.L. Beschta, J.C. Scrivener, K.V. Koski, J.R. Sedell, and C.J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. IN Salo, E.O. and T.W. Cundy (eds.) Streamside management: forestry and fishery interactions. University of Washington Institute of Forest Resources Contribution No. 57.

Fisher, S.G. and G.E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421-439.

Fraley, J., and B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake vand River system, Montana. Northwest Science 63(4): 133-143.

Freeze, R.A. and J.A. Cherry. 1979. Groundwater. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Frissell, C.A. 1992. Cumulative effects of land use on salmon habitat in southwest Oregon coastal streams. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Geist. D. R., M.C. Joy, and D.R. Lee. 1996. A method for installing piezometers within the hyporheic zone of a large cobble river. Bulletin of the North American Benthological Society, Annual Program Issue Abstract 373.

Gibert, J., D.L. Danielopol and J.A. Stanford [Ed]. 1994. Groundwater Ecology. Academic Press, San Diego, California, USA. 571 pp.

Gibson, R.J. 1966. Some factors influencing the distribution of brook trout and young Atlantic salmon. J. Fish. Res. Board. Can. 23: 1977-1979.

Graham, P.J., B.B. Shepard, and J.J. Fraley. 1981. Use of stream habitat classifications to identify bull trout spawning areas in streams. p. 186-191 *In* Acquisition and utilization of aquatic habitat inventory information. The Western Division of the American Fisheries Society, Portland, Oregon, USA.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540-551.

Hall, C.A.S., J.A. Stanford, and F. R. Hauer. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos 65(3):377-390.

Hansen, E.A. 1975. Some effects of groundwater on brown trout redds. Trans. Amer. Fish. Soc. 104:100-110.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J. D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Leinkaemper, K. Cromack, Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in ecological research 15:133-302.

Harvey, J.W. and K.E. Bencala. 1993. The effect of streambed topography on surface-subsurface water exchange in mountain catchments. Water Resources Research 29(1): 89-98.

Hawkins, C.P. 1984. Substrate associations and longitudinal distributions in species of Ephemerellidae (Ephemeroptera: Insecta) from western Oregon. Freshwater Invertebrate Biology 3:181-188.

Hauer, F.R. and J.A. Stanford. 1982. Ecology and life histories of three net-spinning caddisfly species (Hydroppsychidae: *Hydropsyche*) in the Flathead River, Montana. Freshwater Invertebrate Biology 1:18-29.

Heimer, J.T. 1965. A supplemental Dolly Varden spawning area. M.S. thesis, University of Idaho, Moscow, Idaho.

Howell, P.J. and D.V. Buchanan [ed]. 1992. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon, USA.

Hvorslev, M.J. 1951. Time lag and soil permeability in ground-water observations. Bulletin No. 36, Waterways Experiment Station, Corps of Engineers, Vicksburg, MS.

Hynes, H.B.N. 1975. The stream and its valley. Verh. Int. Ver. Theor. Ang. Limnol. 19:1-15.

Jacobs, J. 1974. Quantitative measurement of food selection; a modification of the forage ratio and Ivlev's electivity index. Oecologia 14: 413-417.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Kaya, C.M., L.R. Kaeding, and D.E. Burkhalter. 1977. Use of coldwater refuge by rainbow and brook trout in a geothermal heated stream. Prog. Fish Cult. 39: 37-39.

Kennedy, V.C., A.P. Jackman, S.M. Zand, G.W. Zellweger, and R.J. Avanzino. 1984. Transport and concentration controls for chloride, strontium, potassium and lead in Uvas Creek, a small cobble-bed stream in Santa Clara County, California, U.S.A. 1. Conceptual model. Journal of Hydrology 75:67-110.

Kotliar, N.B. and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure-A hierarchical framework for the study of heterogeneity. Oikos 59:253-260.

Latta, W.C. 1964. Relationship of young-of-the-year trout to mature trout and groundwater. Trans. Amer. Fish. Soc. 94:32-39.

Leary, R.F., F.W. Allendorf and S.H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath river drainages. Conservation Biology 7: 856-865

Leathe, S.A. and M.D. Enk. 1985. Cumulative effects of micro-hydro development on the fisheries of the Swan River drainage, Montana. Volume I: Summary Report. project no. 82-19. MDFWP, Kalispell, Montana. 114 p.

Lee, D.R. and J.A. Cherry. 1978. A field exercise on groundwater flow using seepage meters and mini-peizometers. J. Geological Education 27:6-10.

Leggett, J.W. 1969. The reproductive biology of the Dolly Varden char *Salvelinus malma*. M.S. thesis, University of Victoria, Victoria, British Columbia, Canada.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial Processes in Geomorphology, W.H. Freeman, New York.

Lowry, M. M. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. M.S. thesis, Oregon State University, Corvallis, Oregon.

Maciolek, J.A. and P.R. Needham. 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Trans. Am. Fish. Soc. 81: 202-361.

Maurer, B.A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. Ecological Monographs 55:295-312.

McPhail, J.D. and C.B. Murray. 1979. The early life history and ecology of Dolly Varden(*Salvelinus malma* in the upper Arrow Lakes. Report to the British Columbia Hydro and Power Authority and Kootenay Dept. of Fish and Wild.

Minshall, G.W. 1988. Stream ecosystem theory: A global perspective. Journal of the North American Benthological Society 7:263-288.

Montana Bull Trout Scientific Group. 1996. Swan river drainage bull trout status report. United States Government Memorandum. 35 p.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology 68:362-369.

Mullan, J.W., K. Williams, G. Rhodus, T. Hillman, and J. McIntyre. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. U.S. Fish and Wildlife Service Monograph 1.

Needham, P.R. and T.M. Vaughan. 1952. Spawning of the Dolly Varden, *Salvelinus malma*, in Twin Creek, Idaho. Copeia. 3: 197-199.

Needham, P.R. and R.C. Jones. 1959. Flow temperature, solar radiation, and ice in relation to activities of fishes in Sagehen Creek. Ecology 40: 465-474.

Nielsen, J.L. 1993. The role of cold-pool refugia in the freshwater fish assemblage in northern California rivers. p. 79-95 *In* Proceedings of the Symposium on Biodiversity of Northwestern California, October 28-30, 1991, Santa Rosa, California.

Orians, G.H. and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:529-549.

Platts, W. S., M. Hill, T. W. Hillman and M. D. Miller. 1993. Preliminary Status Report on Bull Trout in California, Idaho, Montana, Nevada, Oregon and Washington. Intermountain Forest Industry Association.

Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. Freshwater Biology 36(3):611-622..

Powell, T.M. 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. *In* J. Roughgarden, R.M. May, and S.A. Levin [ed.] Perspectives in ecological theory. pp 140-156. Princeton University Press, Princeton, New Jersey.

Pratt, K.L. 1984. Habitat use and species interactions of juvenile cutthroat(*Salmo clarki lewisii*) and bull trout(*Salvelinus confluentus*) in the upper Flathead River Basin. M.S. thesis, University of Idaho, Moscow, Idaho.

Pratt, K.L. 1985. Pend O'Reille trout and char life history study. Idaho Dept. Fish and Game.

Pratt, K.L. 1992. A review of bull trout life history. p. 5-9 *In* P.J. Howell and D.V. Buchanan [ed.] Proceedings of the Gearhart Mountain Bull Trout Workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

Rieman, B. E. and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. US Forest Service, Intermountain Research Station. General Technical Report INT-308, 38 p.

Rieman, B.E. and J.D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124: 285-296.

Ricklefs, R.E. 1987. Structure in ecology. Science 236:206-207.

Riggs, H.C. 1985. Streamflow characteristics. p. 172-174 *IN* Developments in Water Science, Volume 22. Elsevier.

Ringler, N.H. and J.D. Hall. 1975. Effects of logging on water temperature and dissolved oxygen content in spawning beds. Trans. Am. Fish. Soc. 104: 111-121.

Rumsey, S. 1991. Interoffice memorandum to Swan drainage files. Montana Department of Fish, Wildlife, and Parks, Kalispell, Montana.

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

Shepard, B.B., K. Pratt, P. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River basin, Montana. Montana Department of Fish, Wildlife, and Parks, Kalispell, Montana. 85p.

Sowden, T.K. and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Trans. Am. Fish. Soc. 114:804-812.

Strahler, A.N. 1964. Quantitative geomorphology of drainage basins and channel networks. In Ven te Chow [ed.] Handbook of Applied Hydrology. McGraw-Hill, New York.

Stanford, J.A. and J.J. Simons (Eds.). 1992. Proceedings of the First International Conference on Ground Water Ecology. American Water Resources Association, Bethesda, MD.

Stanford, J. A. and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature 335:64-66.

Stanford, J. A. and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12: 48-62.

Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience 38(2): 92-98.

Swanson, F.J., G.W. Lienkaemper, and J.R. Sedell. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. USDA FS Gen. Tech. Rept. PNW-56.

Terhune, L.D.B. 1958. The Mark VI standpipe for measuring seepage through salmon spawning gravel. J. Fish Res. Bd. Canada 15(5): 1027-1063.

Thibodeaux, L.J. and J.D. Boyle. 1987. Bedform-generated convective transport in bottom sediment. Nature 325:341-343.

Valett, H.M. 1993. Surface-hyporheic interactions in a Sonoran Desert stream: hydrologic exchange and diel periodicity. Hydrobiologia 0:1-12.

Valett, H.M., S.G. Fisher, N.B. Grimm, and P. Camill. 1994. Vertical hydraulic exchange and ecological stability of a desert stream ecosystem. Ecology 75:548-560.

Valett, H.M., S.G. Fisher, E.H. Stanley. 1990. Physical and chemical characteristics of the hyporheic zone of a desert stream ecosystem. Journal of the North American Benthological Society 9:201-215.

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

Vaux, W.G. 1962. Interchange of stream and intragravel water in a salmon spawning riffle. U.S. Fish and Wildlife Service Special Sciences Report Fisheries 405.

Vaux, W.G. 1968. Intragravel flow and interchange of water in a streambed. U.S. Fish and Wildlife Service Fishery Bulletin 66:479-489.

Vervier, P., J. Gibert, P. Marmonier, and M.J. Dole-Olivier. 1992. A perspective on the permeability of the surface freshwater - groundwater ecotone. Journal of the North American Benthological Society 11: 93-102.

Weaver, T.M. 1991. Coal Creek Fisheries Monitoring Study number IX and forest-wide fisheries monitoring-1990. Montana Department of Fish, Wildlife, and Parks Special Projects, Kalispell, Montana.

Weaver, T.M. in press. Status of adfluvial bull trout populations in Montana's Flathead drainage: The good, the bad, and the unknown. Proceedings, Friends of the Bull Trout Conference, Calgary, Alberta, TU Canada.

Weaver, T.M. and R.G. White. 1985. Coal Creek Fisheries Monitoring Study number III. USFS Flathead National Forest contract no. 53-0385-3-2685. 94 pp.

Weaver, T.M. and J. Fraley. 1991. Fisheries habitat and fish populations. Flathead basin forest practices, water quality and fisheries cooperative program. Flathead Basin Commission, Kalispell, Montana. 47pp.

Webster, D.A. and G. Eiriksdottir. 1976. Upwelling as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 105:416-421.

Webster, J.R., S.W. Golladay, E.T. Benfield, D.J. D'Angelo, and G.T. Peters. 1990. Effects of forest disturbance on particulate organic matter budgets of small streams. Journal of the North American Benthological Society 9(2): 120-140.

White, D.S. 1990. Biological relationships to convective flow patterns within stream beds. Hydrobiologia 196: 149-158.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wiens, J.A., J.T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132-147.

Table 1. Geomorphic variables that were examined as a part of this study. Accessibility refers to whether migratory bull trout can navigate the stream.

Geomorphic Variables Examined		
Morphometric Measures	Slope Classes	BAVS - Related
Drainage area	% drainage < 1 % slope	Maximum valley bottom width
Stream order	% drainage 1-2 % slope	Mean valley bottom width
Total stream length	% drainage 2-7 % slope	Variation in valley bottom width
Accessible stream length	% drainage 7-20 % slope	Number of gradient steps > 10%
Drainage density	% drainage 20-40 % slope	Number of BAVS
Drainage length	% drainage 40-55 % slope	Total area of BAVS
Average stream gradient	% drainage >55 % slope	Length of accessible BAVS
Gradient of accessible stream length	% drainage >55 % slope	Area of accessible BAVS
Relief ratio		
Form ratio		
Elongation ratio		
Mean bedrock dip angle		

Figure 1. Map of the Swan River basin. The nine primary bull trout spawning tributary streams are identified by name. Inset indicates the location of the Swan River basin in western Montana.
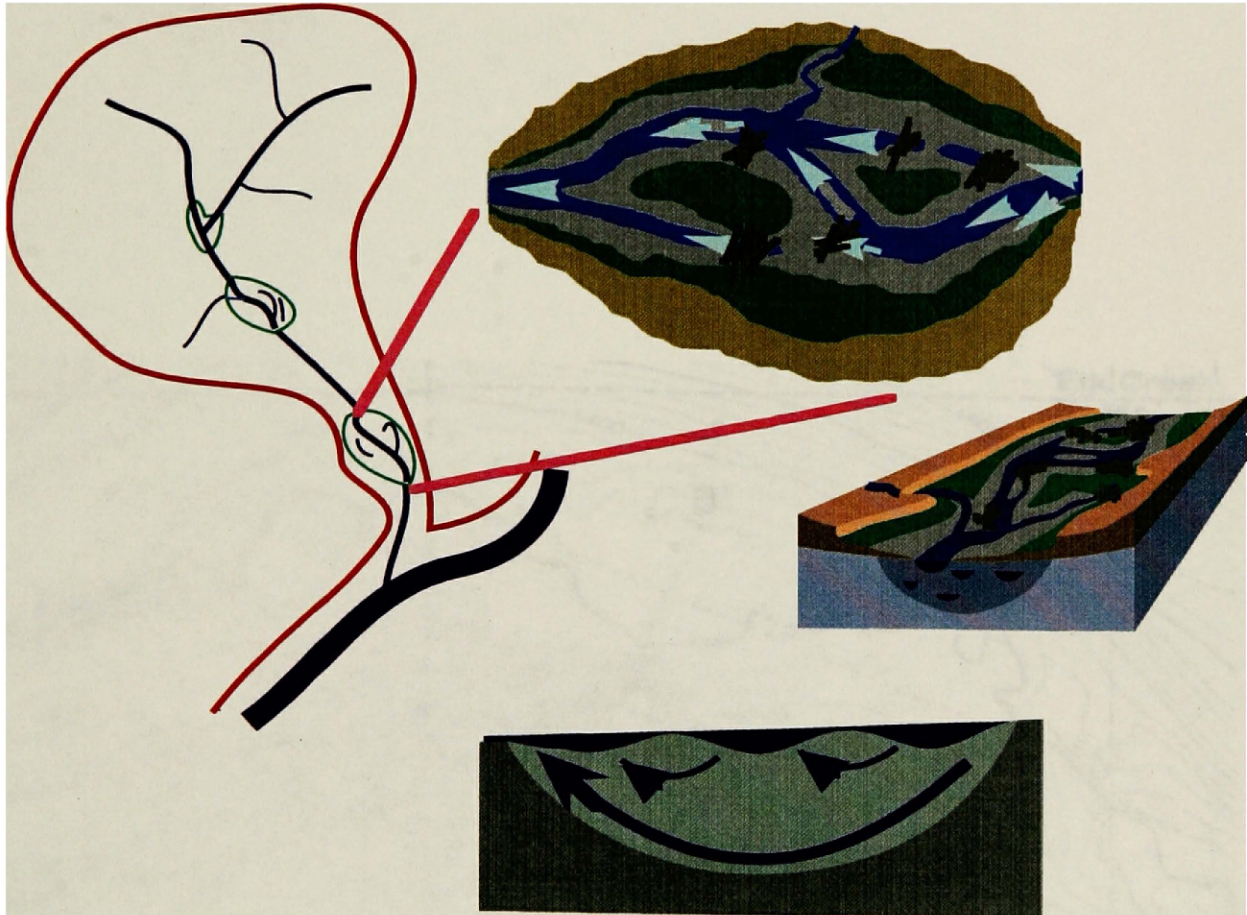
Figure 2. Schematic diagram of vertical hydraulic exchange across a hierarchy of nested spatial scales
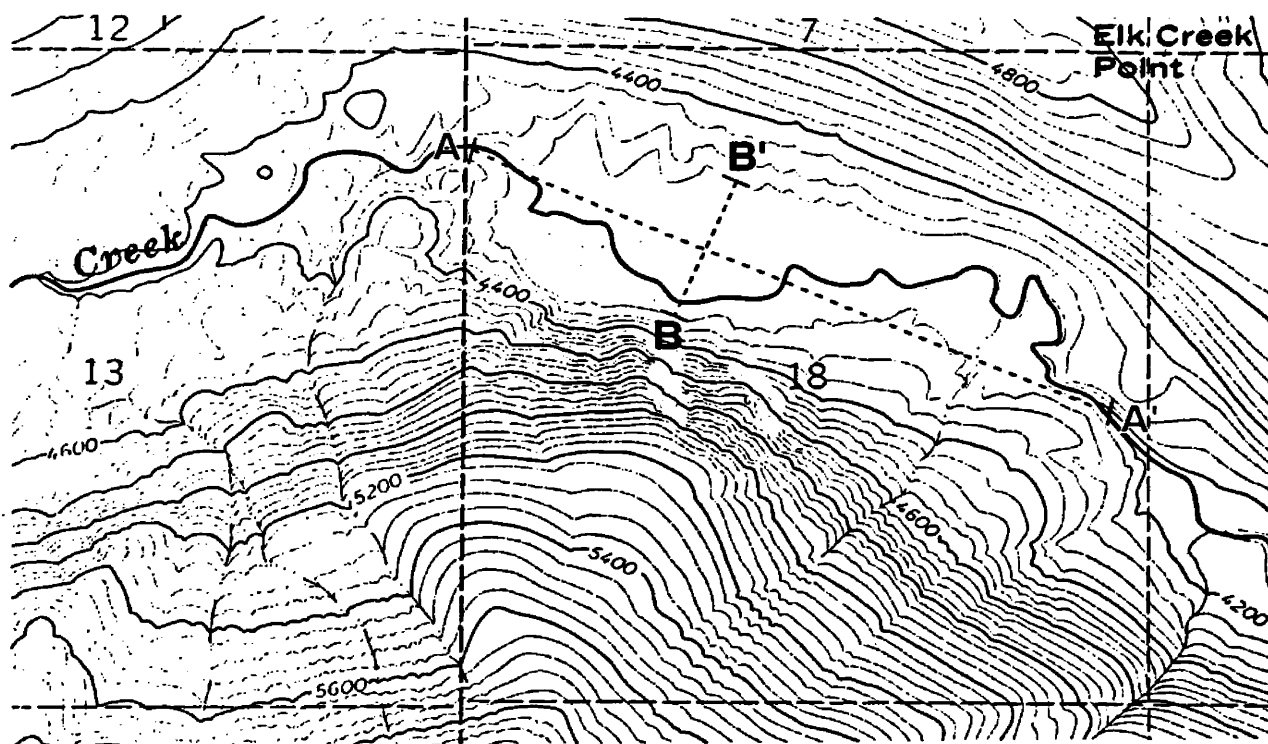
Figure 3. One of the bounded alluvial valley segments (BAVS) in the Elk Creek catchment. The dimensions of BAVS were measured directly from topographic quad maps (A - A' = length, B - B' = maximum valley bottom width.
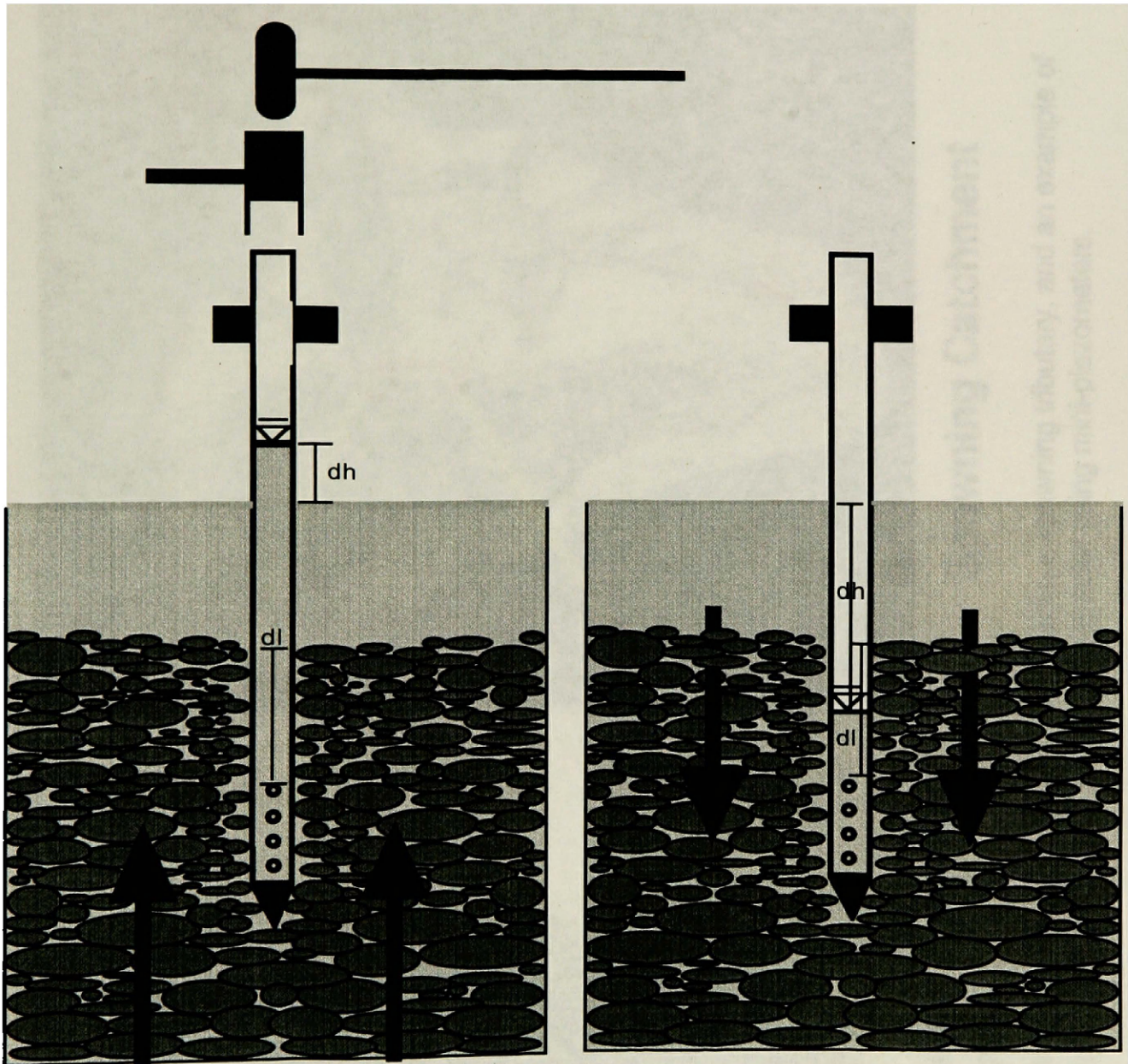
Figure 4. Generalized features of mini-piezometers, their installation, and principles behind their use

Bounded Alluvial Valley Segment and Reaches
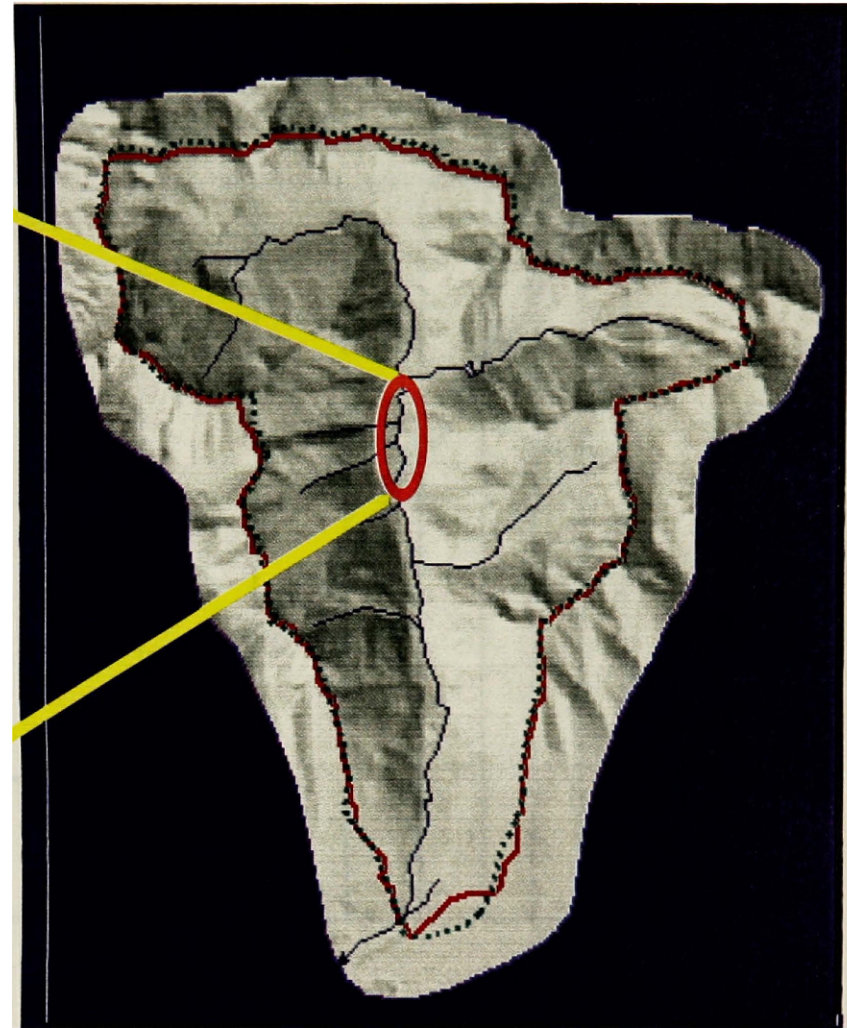
Spawning Catchment

Figure 5. Context of a bounded alluvial valley segment within a spawning tributary, and an example of three reaches sampled for vertical hydraulic exchange character using mini-piezometers.
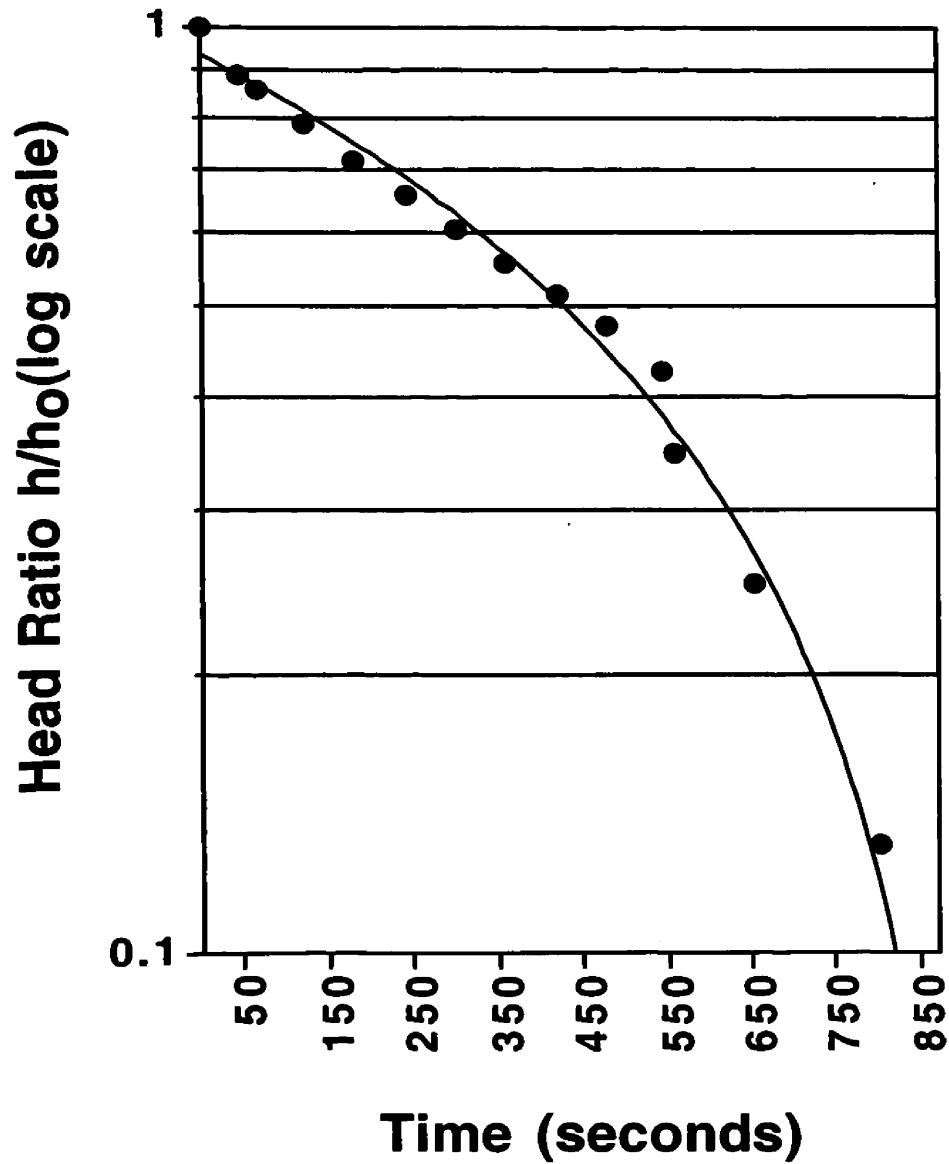
Figure 6. An example equilibration curve generated from falling head test data. The basic time lag (To) is used to estimate permeability.
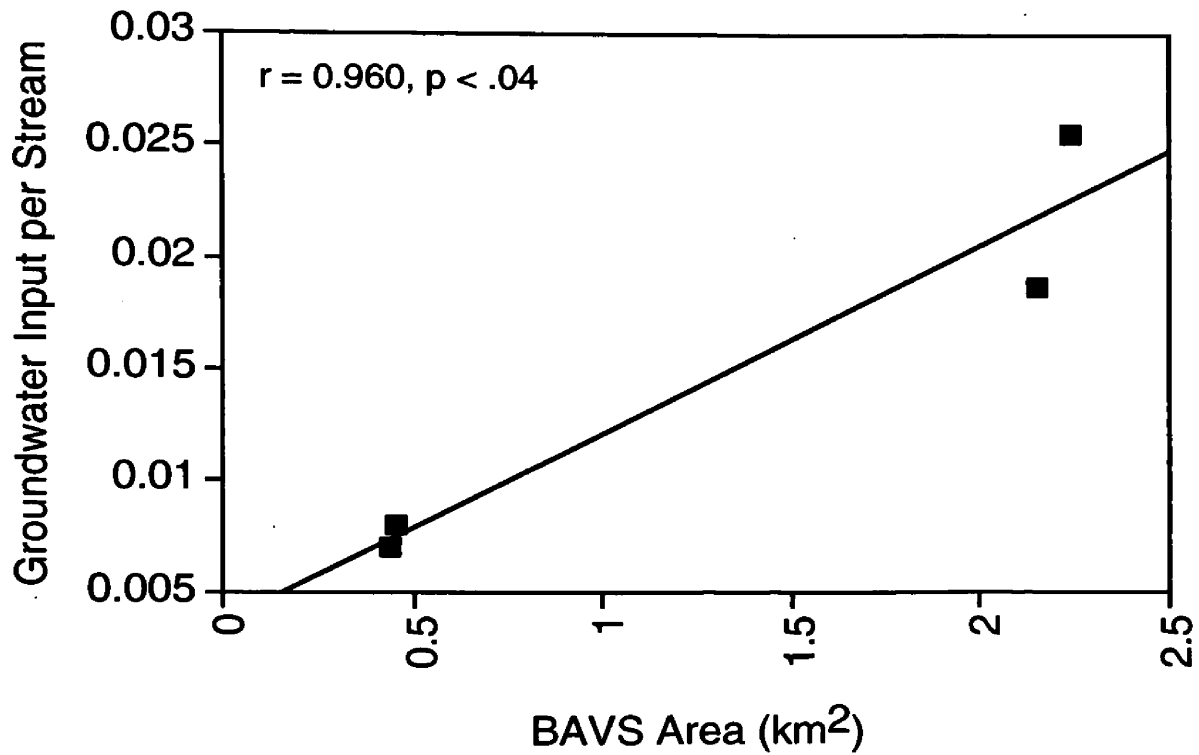
Figure 7. The mean of positive VHG readings (referred to as groundwater input) per catchment versus the area (km²) of bounded alluvial valley segments (BAVS) accessible to spawning bull trout
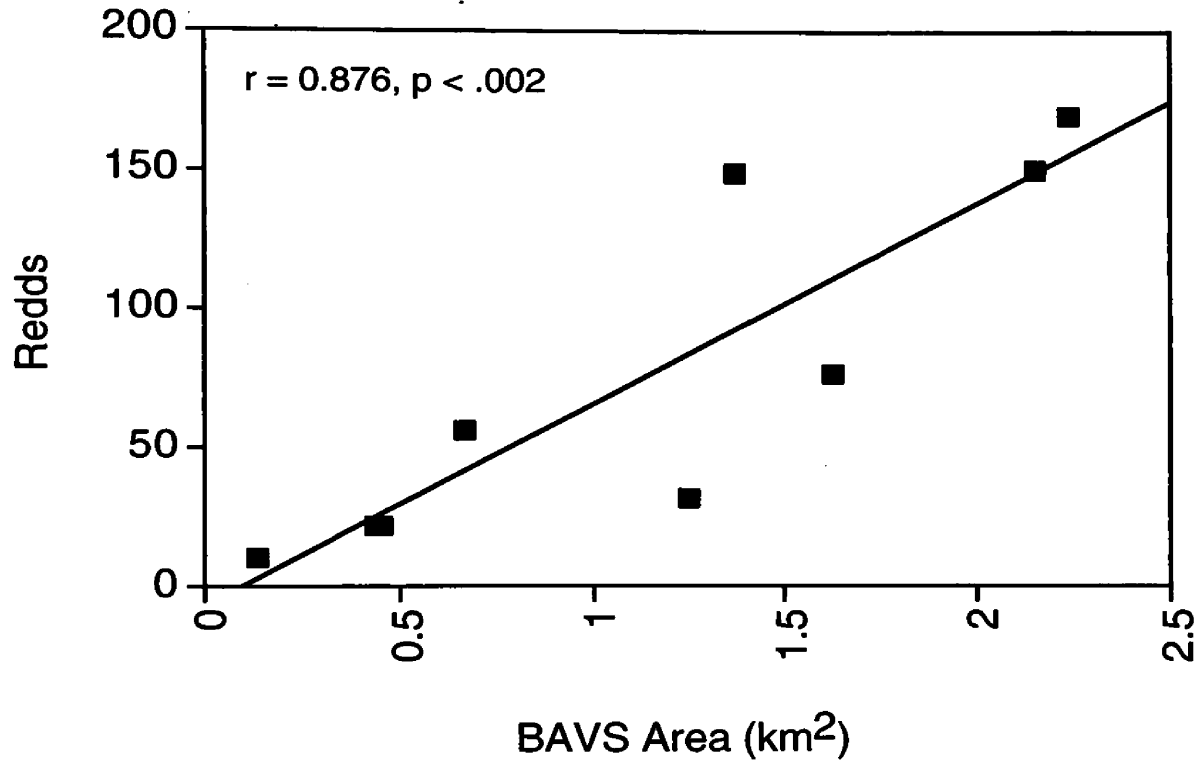
Figure 8. Total number of bull trout redds counted in 1995 surveys versus the area (km²) of bounded alluvial valley segments (BAVS) accessible to spawning bull trout for the nine tributary spawning streams in the Swan River basin.
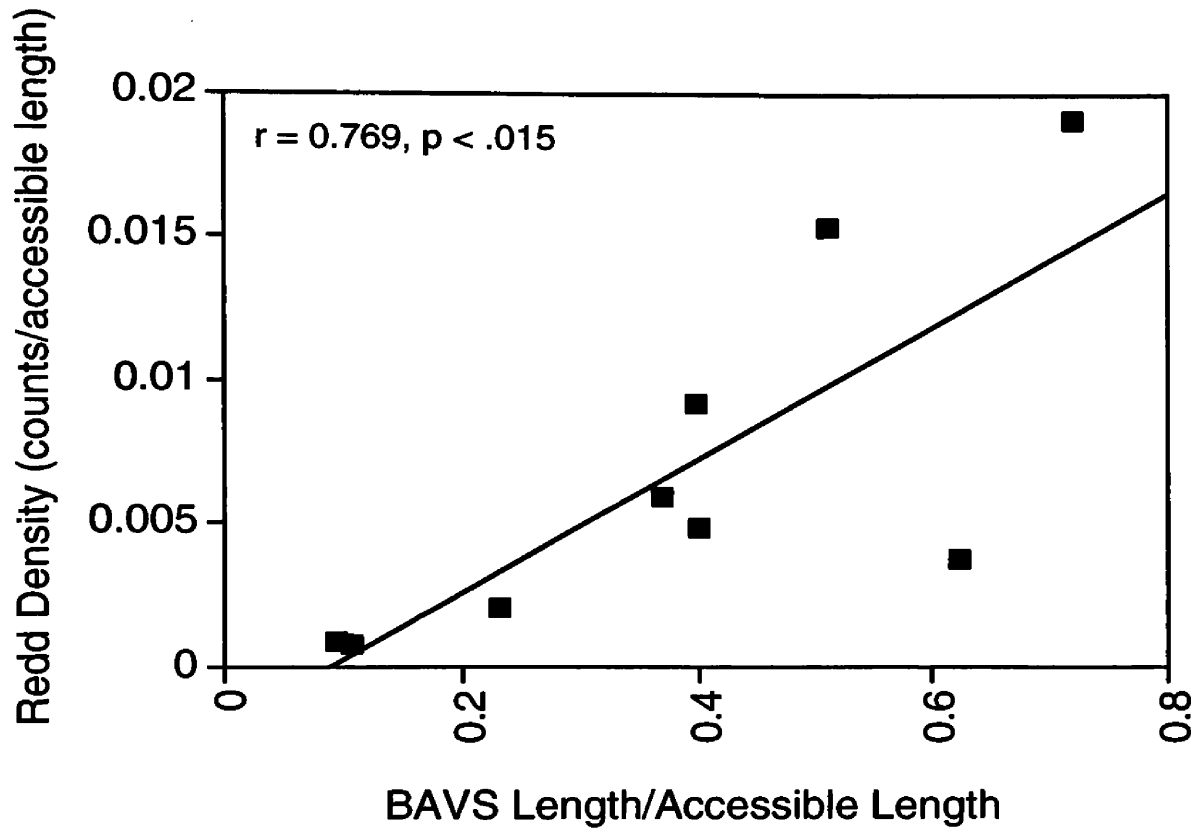
Figure 9. The density of bull trout redds per available streamlength in 1995 versus the proportion of a catchment's available habitat that is found in bounded alluvial valley segments (BAVS length/accessible length).
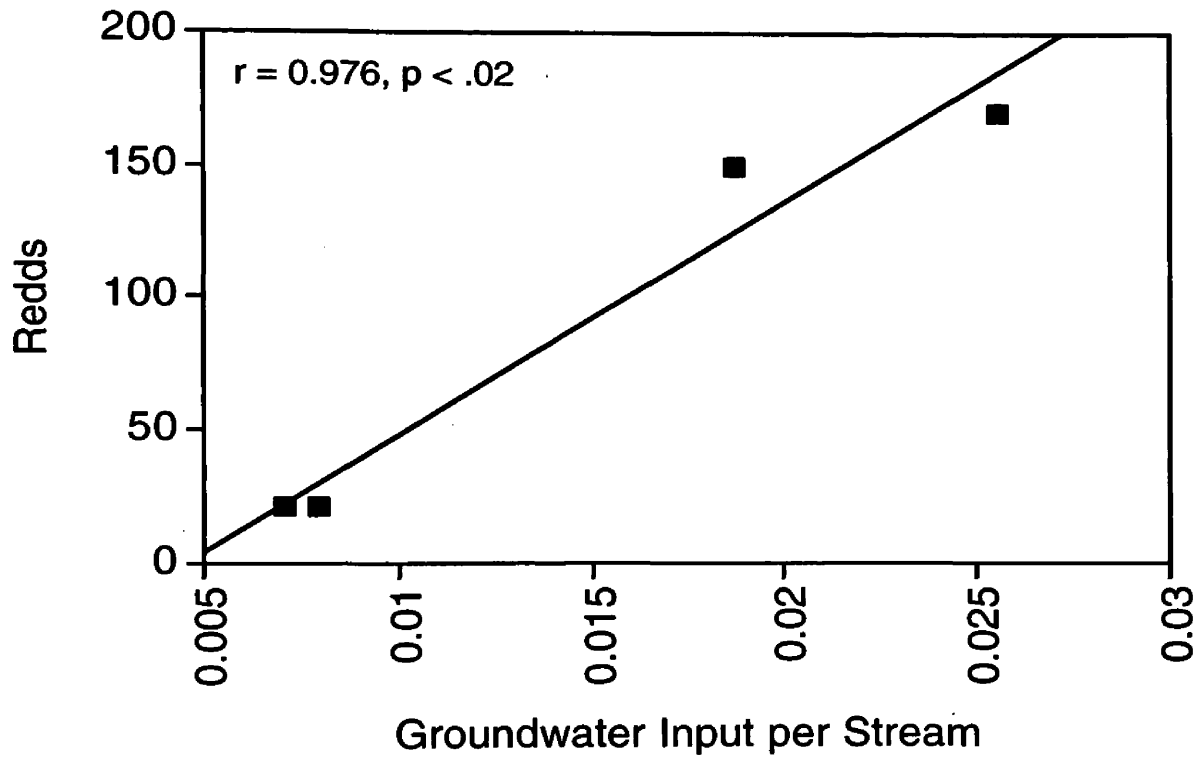
Figure 10. The groundwater input per catchment versus the total number of redds per spawning tributary.
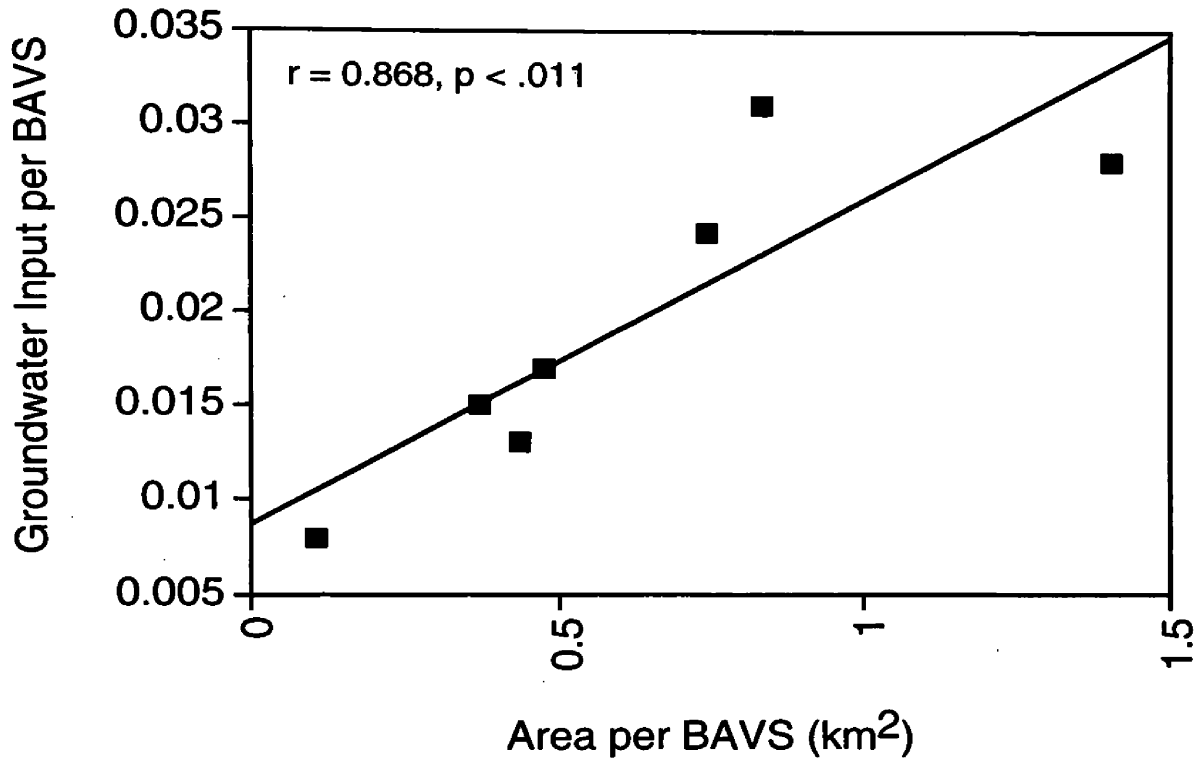
Figure 11. The mean of transformed VHG readings (referred to as groundwater input) per bounded alluvial valley segment (BAVS) versus the area (km2) per BAVS for each of the BAVS in the four catchments sampled for VHG.
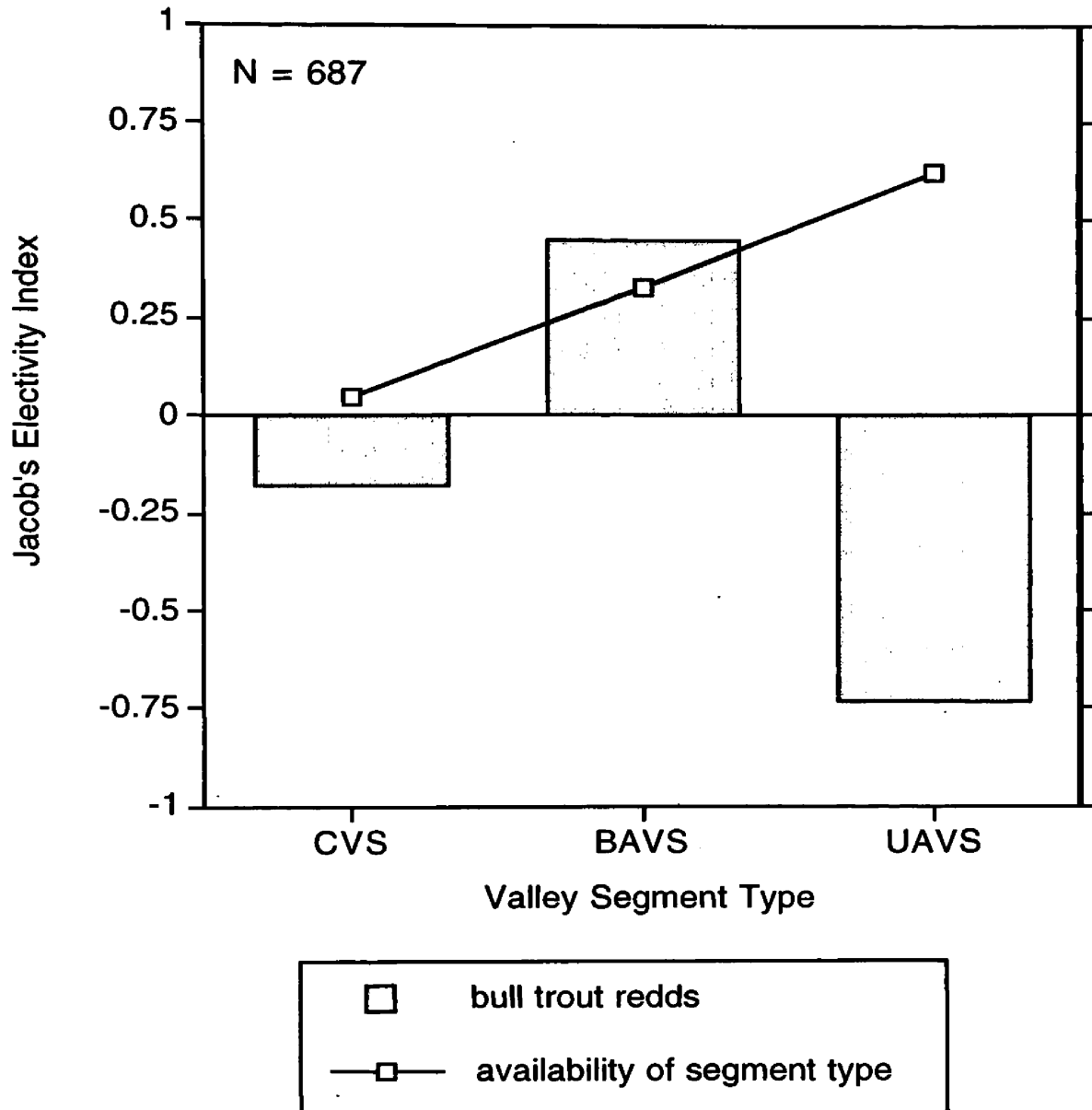
Figure 12. Valley segment types used by and available to spawning bull trout of the Swan basin. BAVS = bounded alluvial, CVS = confined, and UAVS = unbounded alluvial.
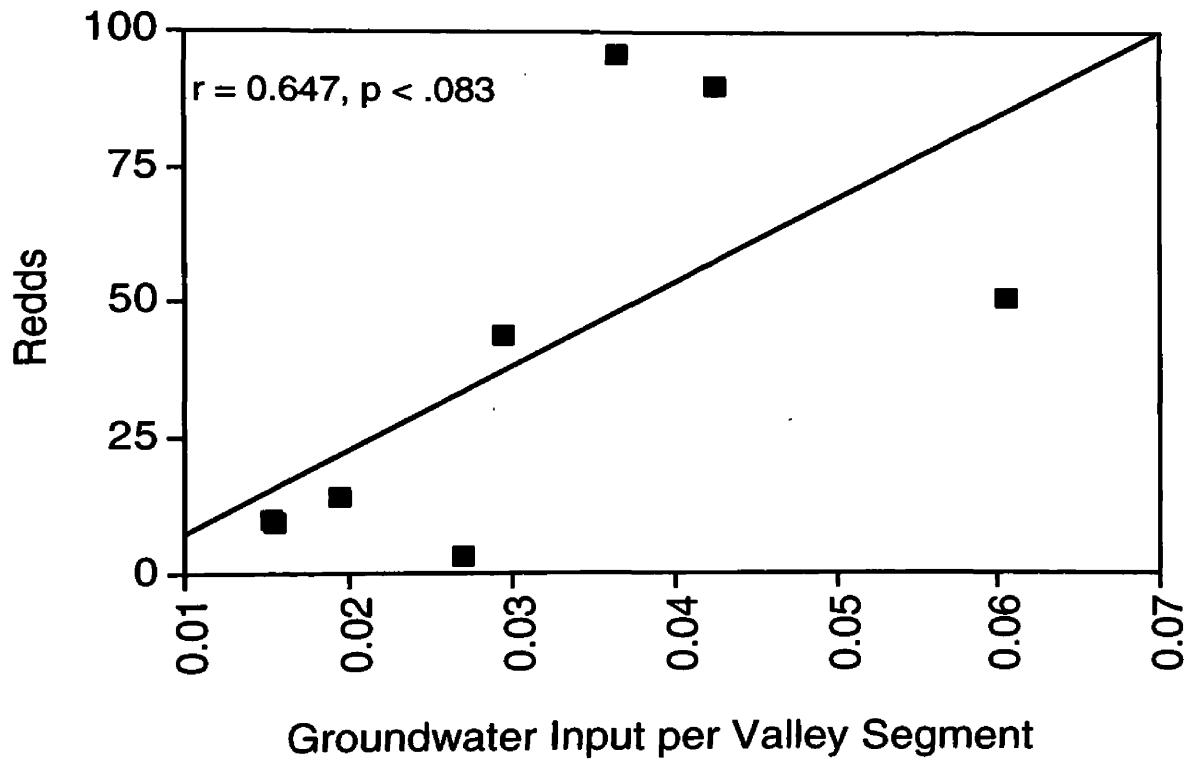
Figure 13. The groundwater input of BAVS versus the number of redds in each.
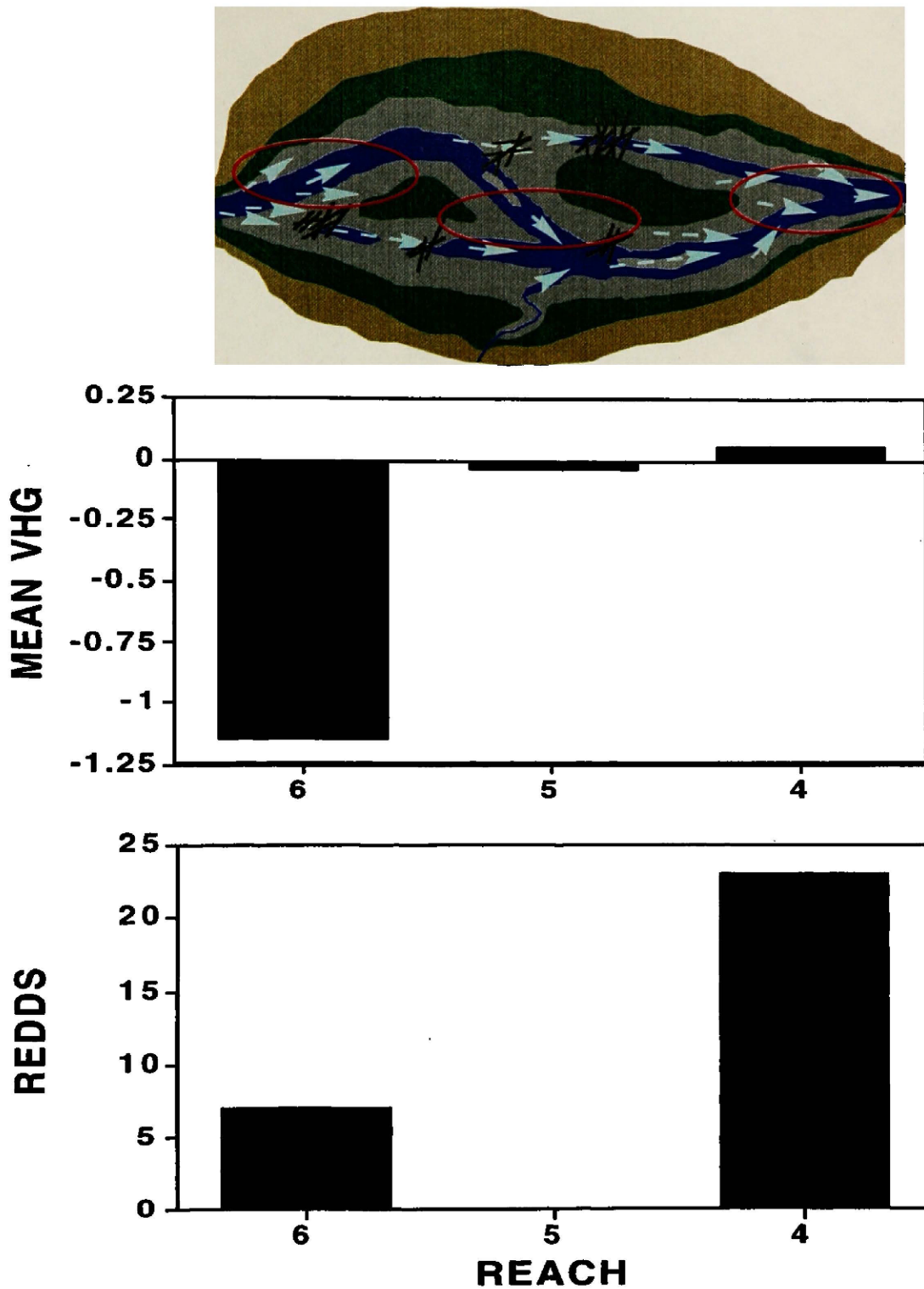
Figure 14. The geomorphic context of reaches within a bounded alluvial valley segment of Lion Creek, their mean VHG, and the number of redds observed in each
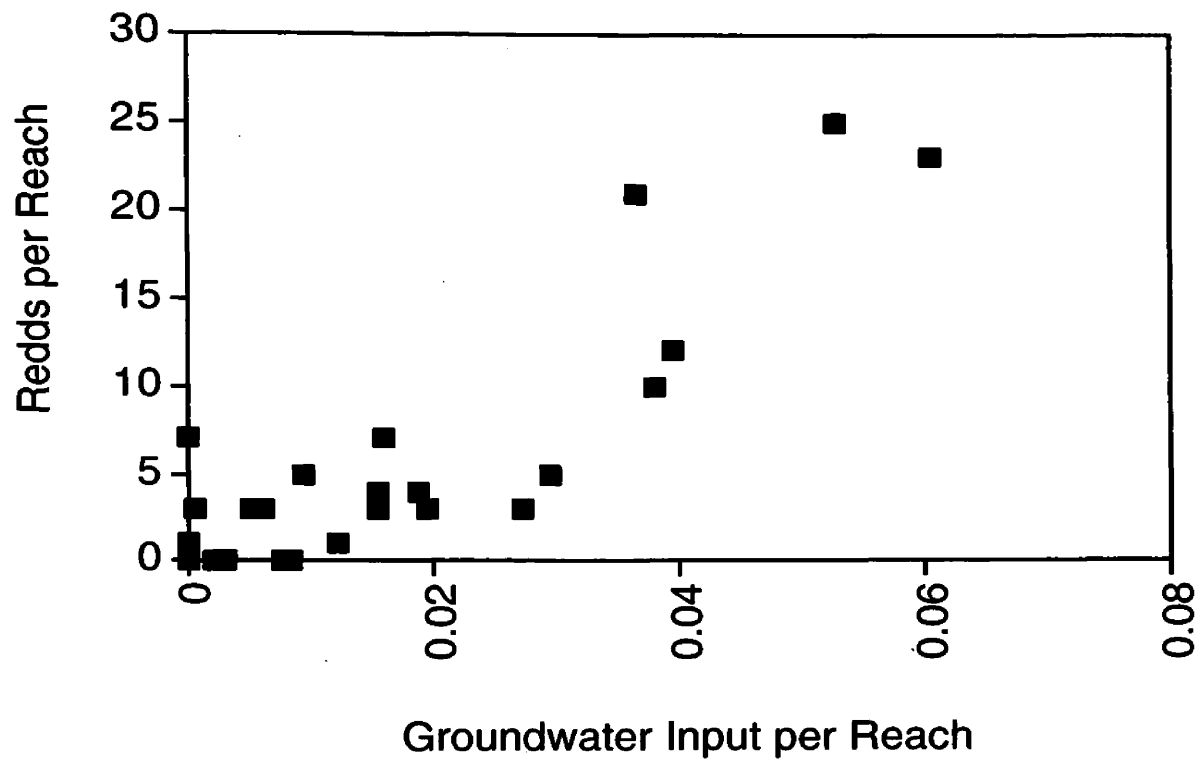
Figure 15. The number of bull trout redds observed in each of the reaches of

the four VHG-sampled tributaries versus the mean of transformed VHG readings

(referred to as groundwater input) for each reach.
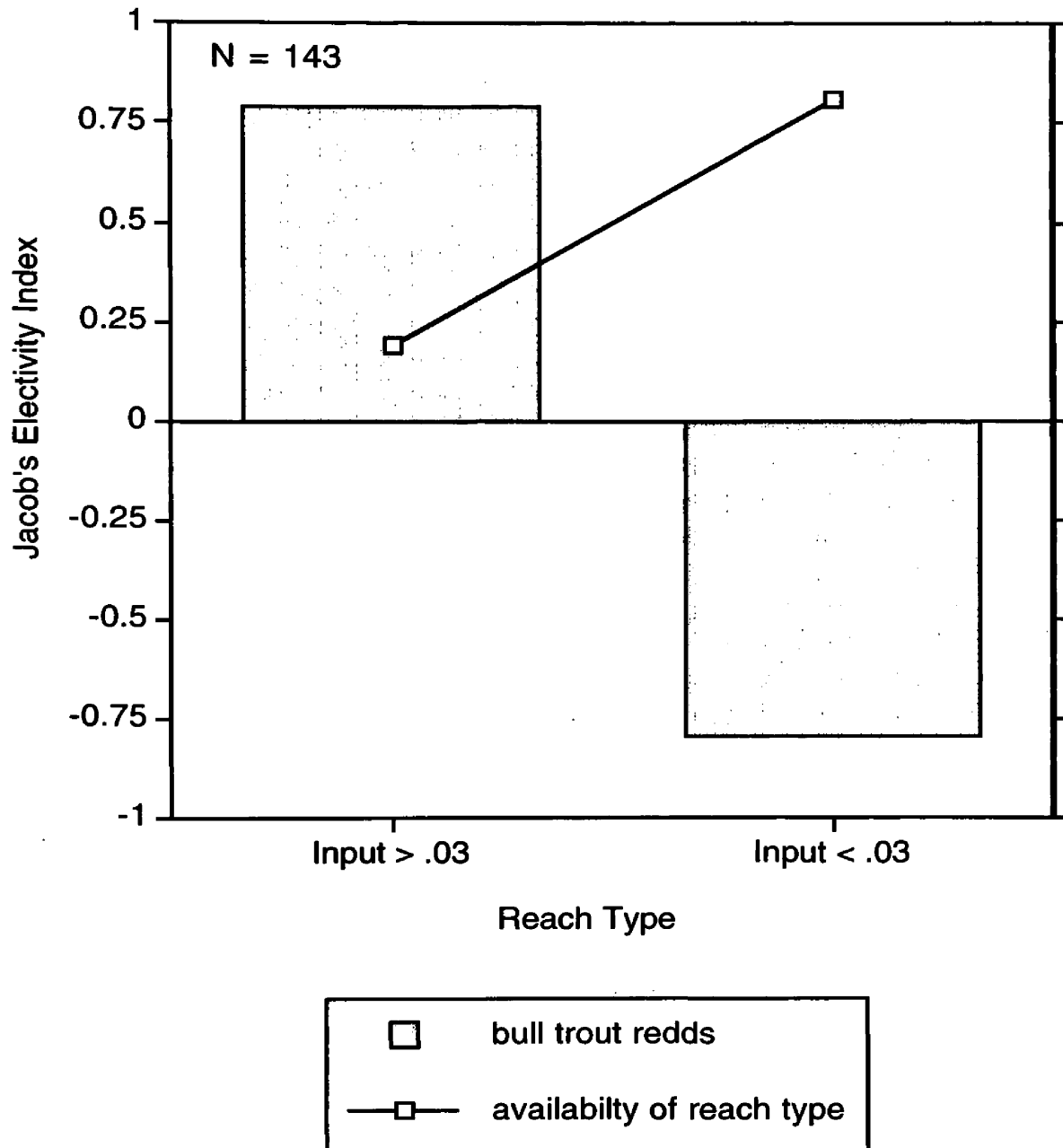
Figure 16. The spawning usage of reaches with mean transformed VHG (referred to as groundwater input) greater than .03 versus those with mean inputs less than .03, relative to the availability of these reach types.
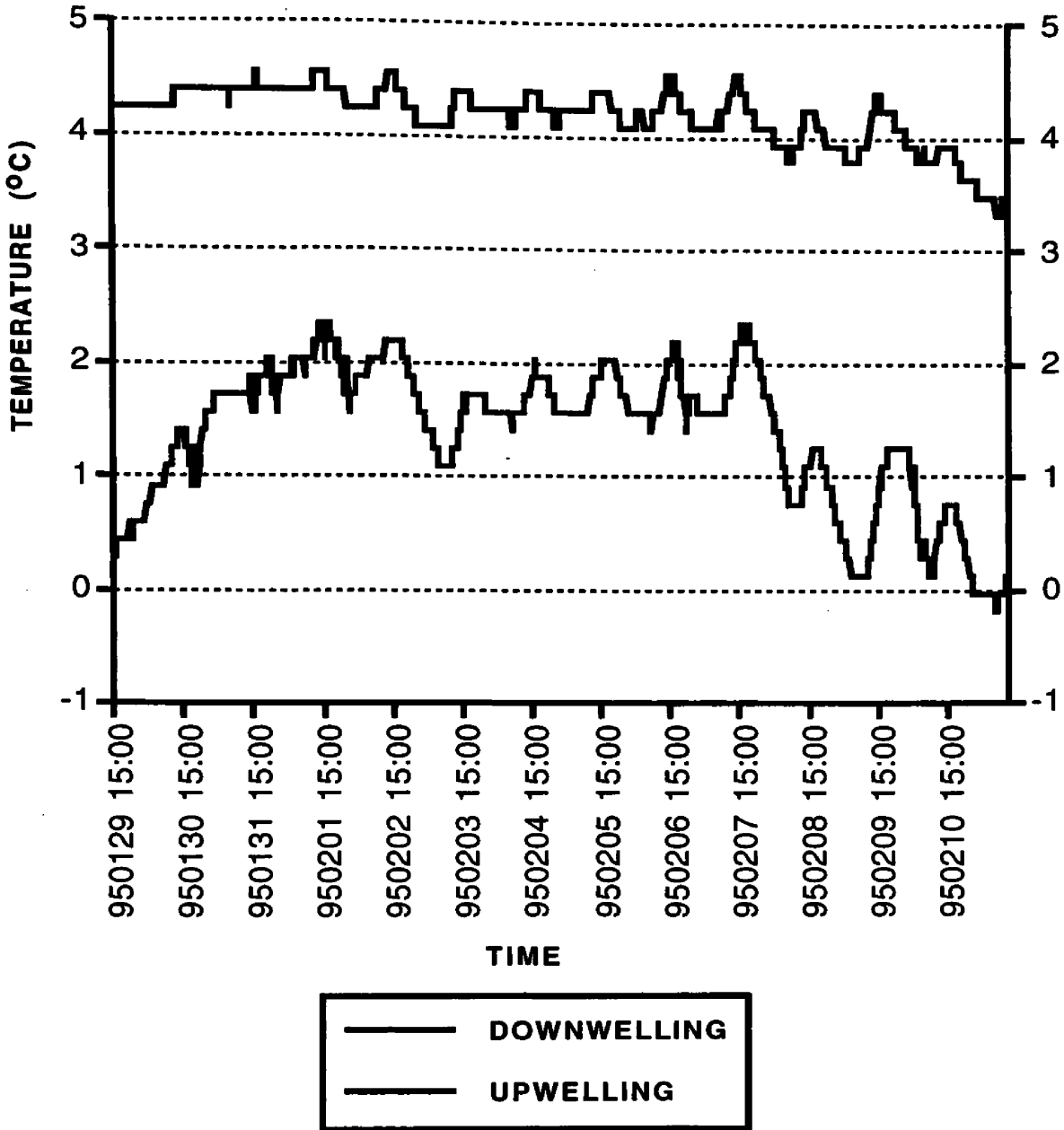
Figure 17. Two-week winter temperature profiles from gaining and losing reaches of Lion Creek clearly show the moderating effect of groundwater. 23 bull trout redds were counted in the gaining reach, while none were found in the losing reach.
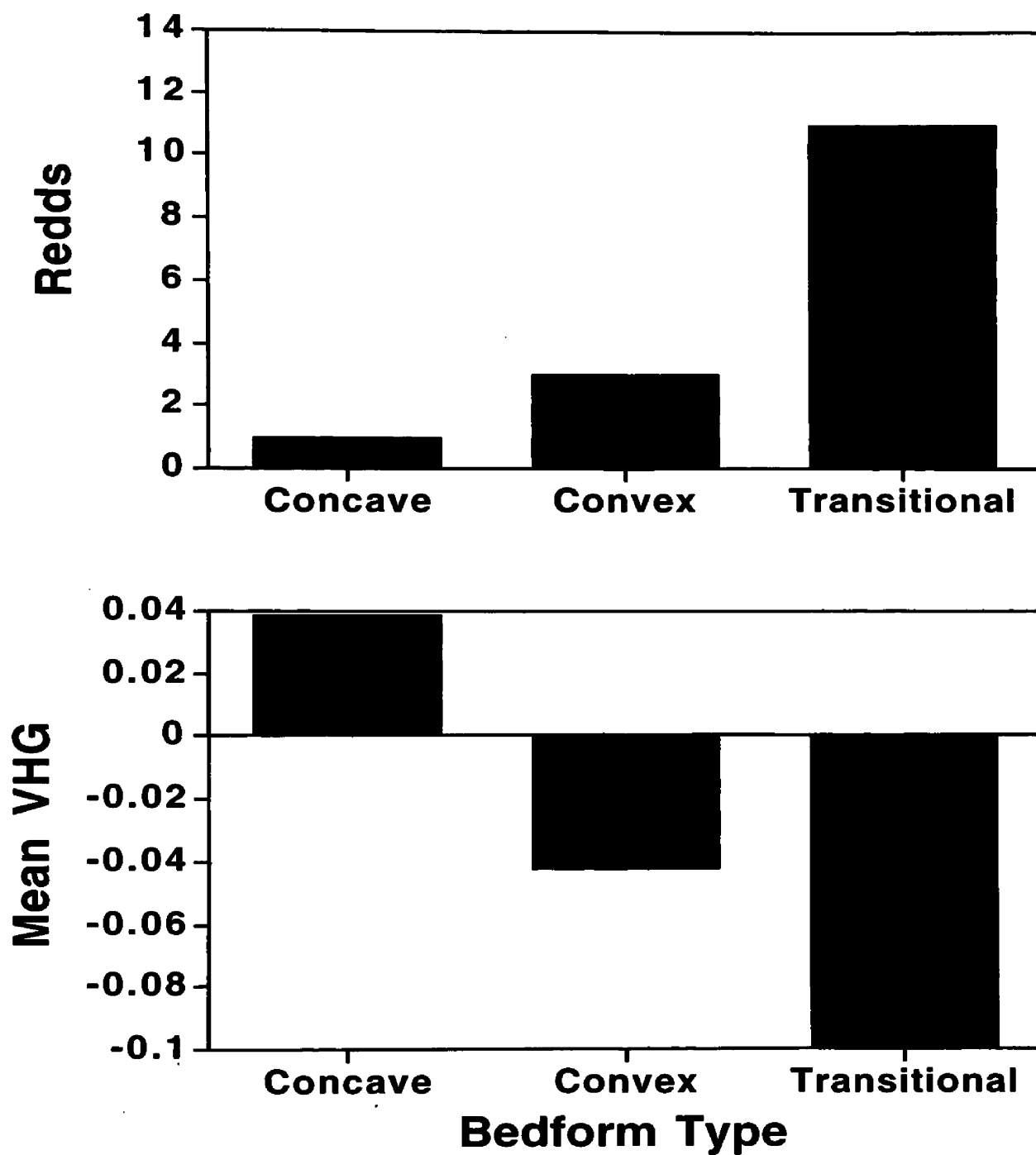
Figure 18. Differences in mean VHG and redd distribution among bedform categories.
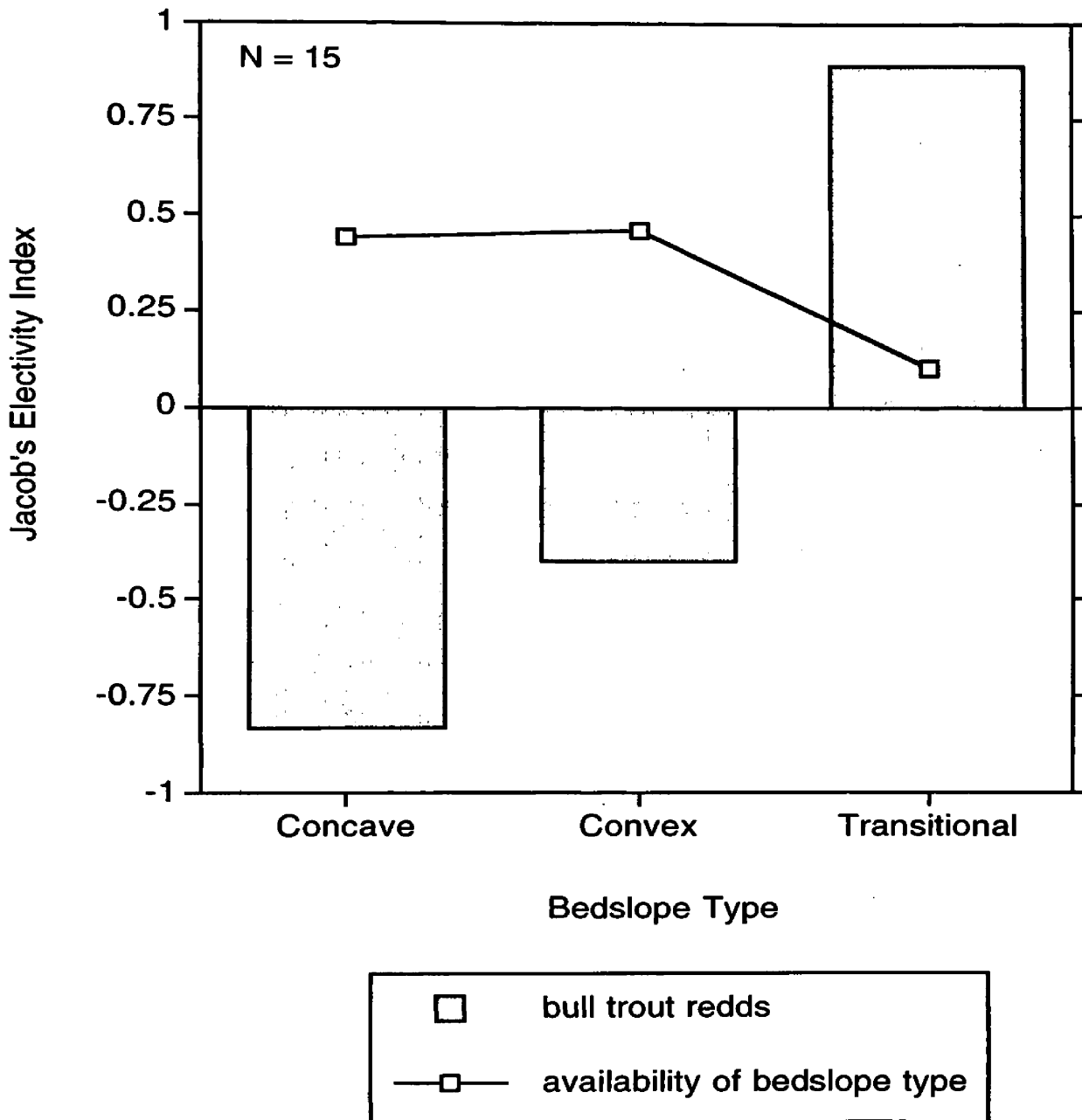
Figure 19. Bedslope types used by and available to spawning bull trout in selected spawning reaches of Lion and Cold Creeks.

LION CREEK SPAWNING REACH

0M 50M 100M
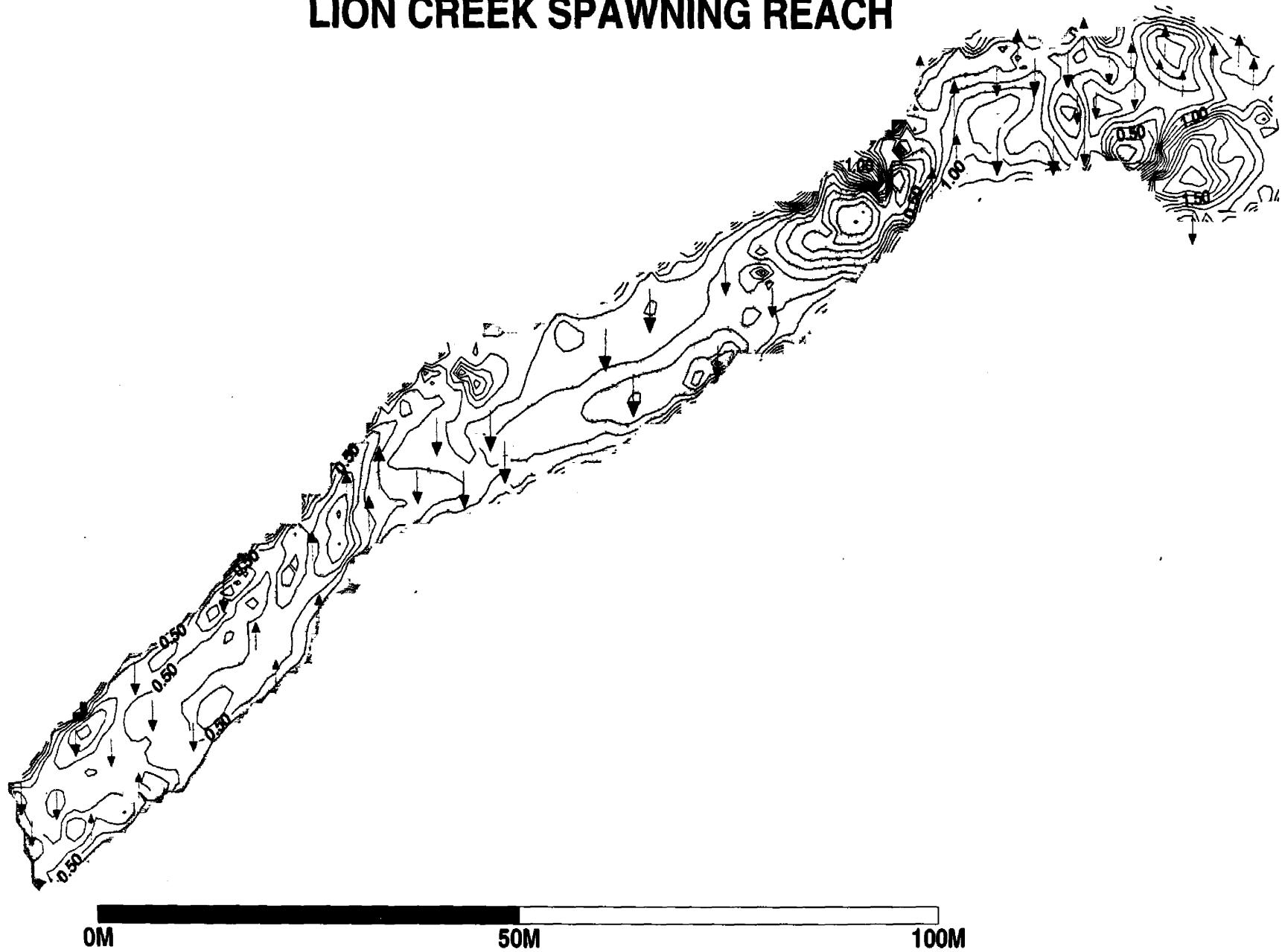
Figure 20. Channel topography, upwelling (blue arrows) and downwelling (red arrows) piezometers, and the locations of bull trout redds (yellow dots) in the mapped spawning reach of Lion Creek.

COLD CREEK SPAWNING REACH
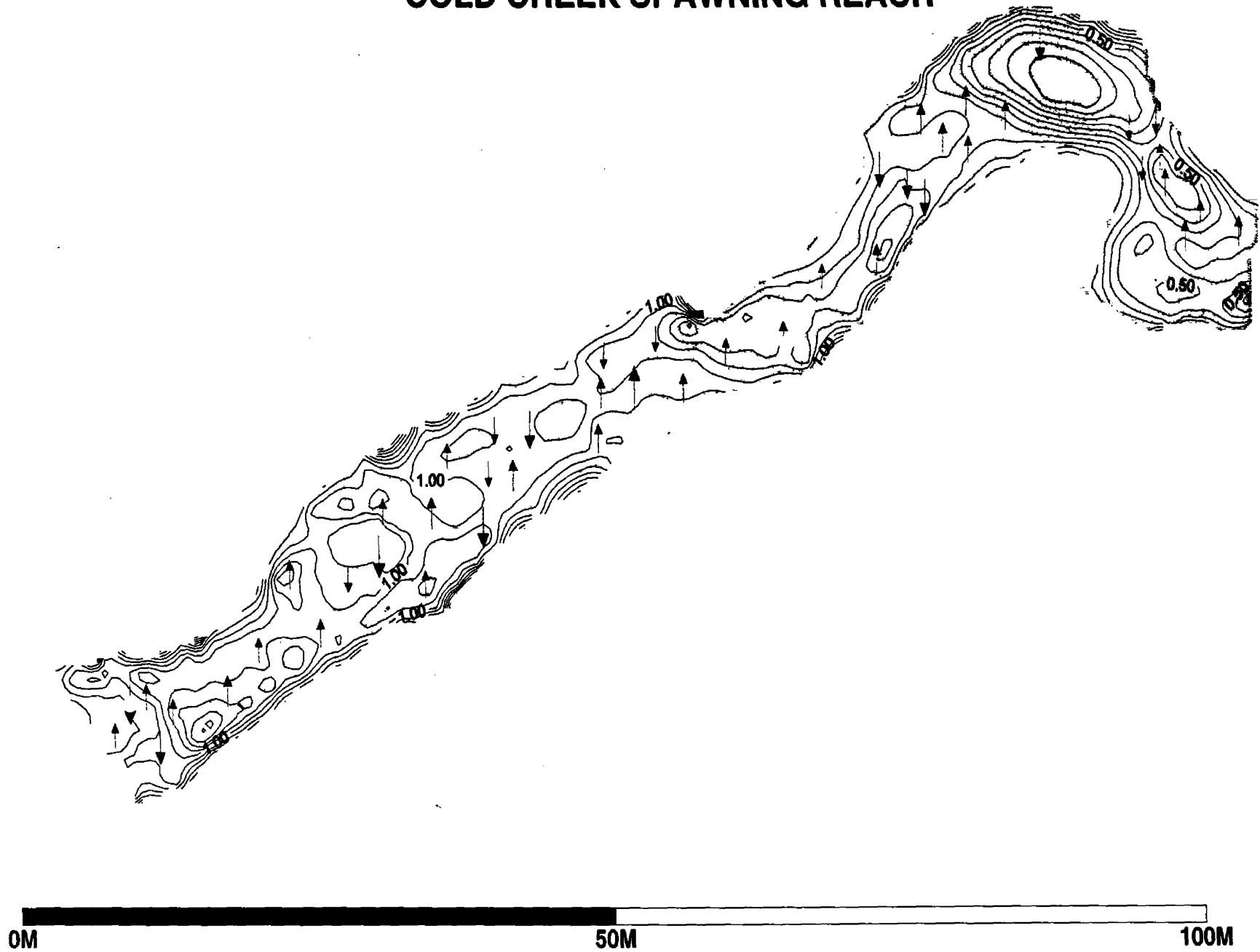
Figure 21. Channel topography, upwelling (blue arrows) and downwelling (red arrows) piezometers, and the locations of bull trout redds (yellow dots) in the mapped spawning reach of Cold Creek.

VHG ISOPLETHS AND REDD DISTRIBUTION
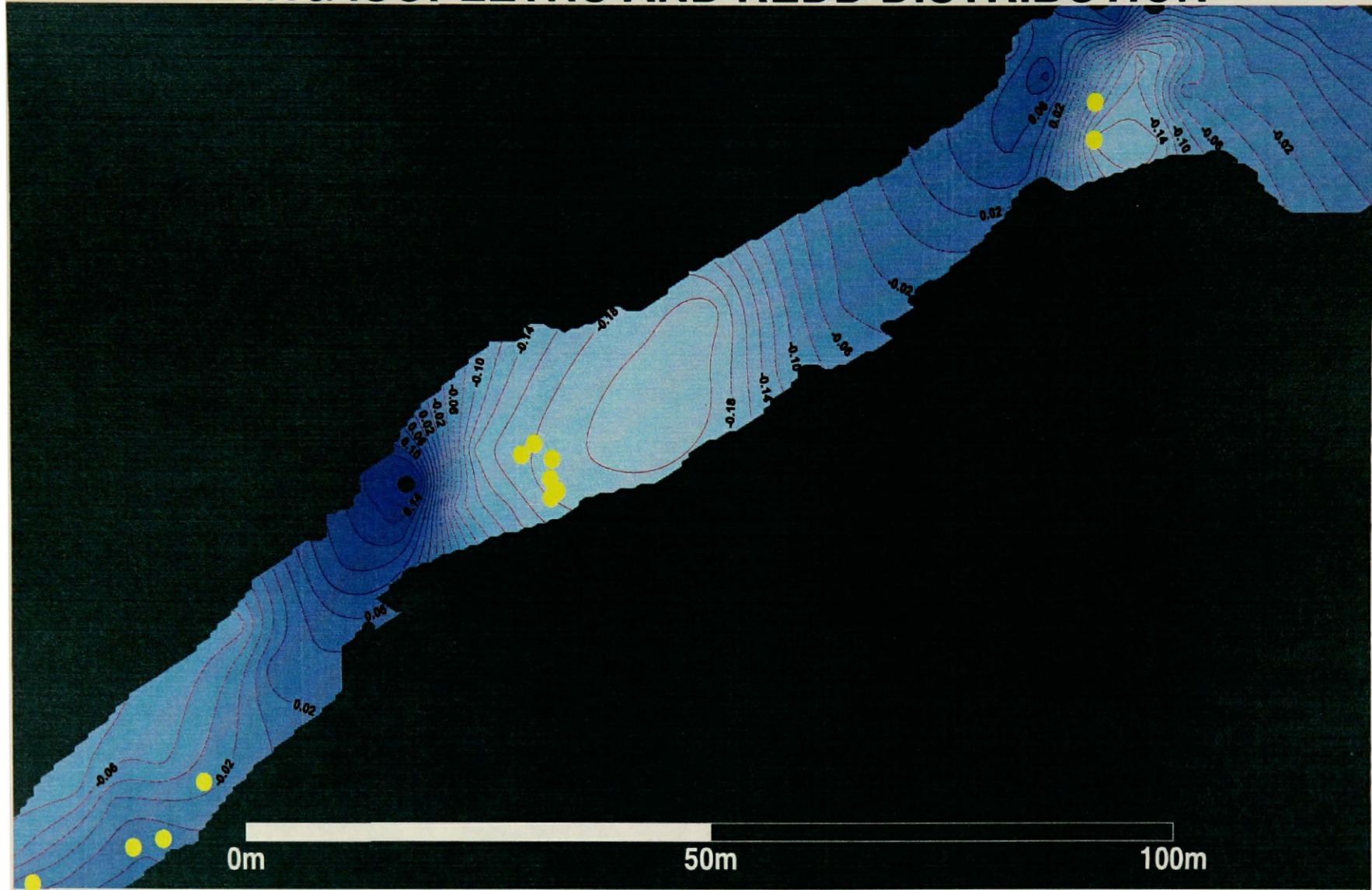
Figure 22. Isopleths of VHG and the distribution of bull trout redds (yellow dots) within the mapped reach on Lion Creek. VHG grades from dark purple (positive VHG) to light blue (negative VHG).
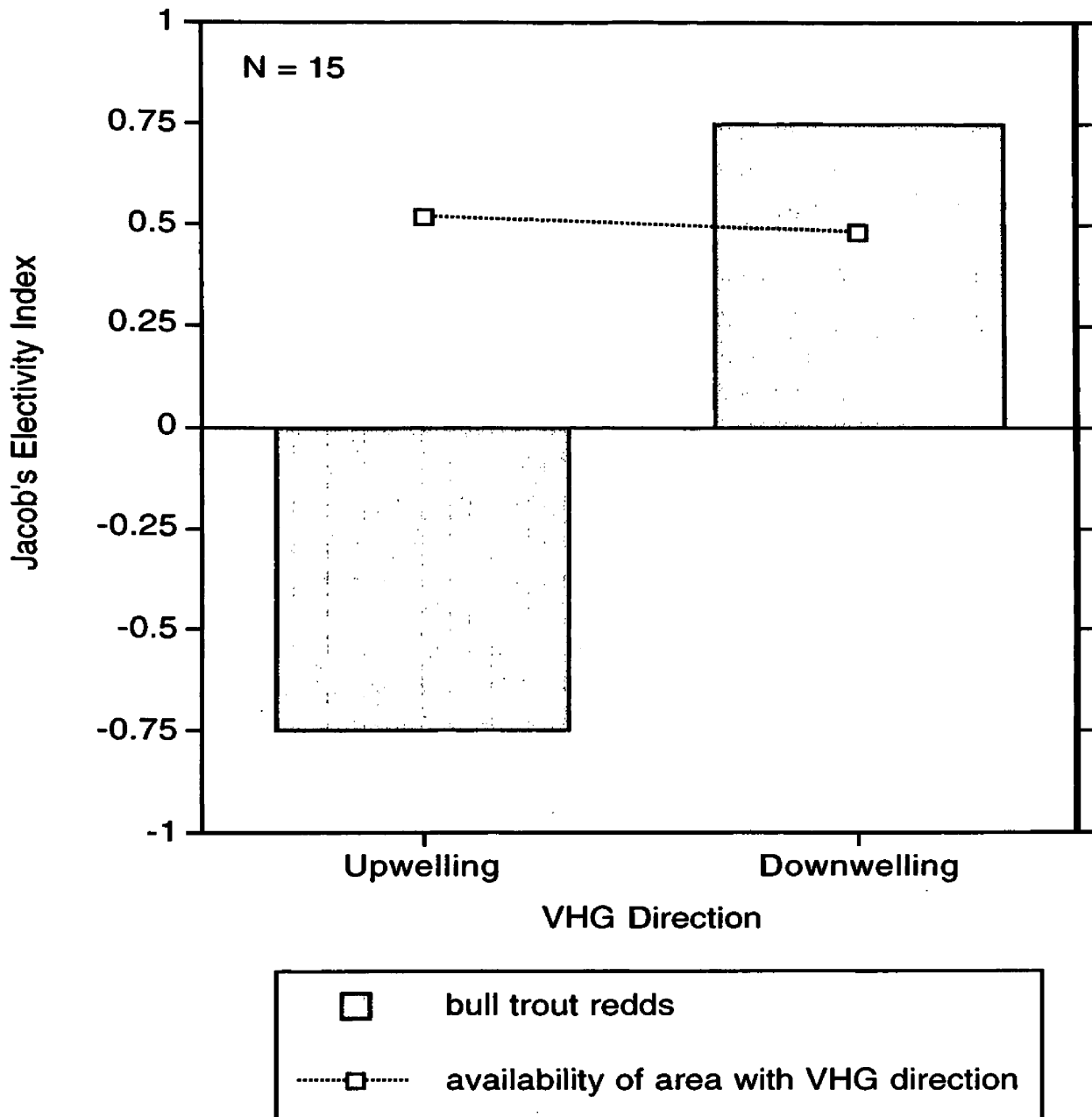
Figure 23. The distribution of redds with respect to local patterns of VHG direction within two selected spawning reaches of Lion and Cold Creek, relative to the availability of habitat possessing positive and negative VHG values.

INTRAGRAVEL FLOW ISOPLETHS AND REDD DISTRIBUTION
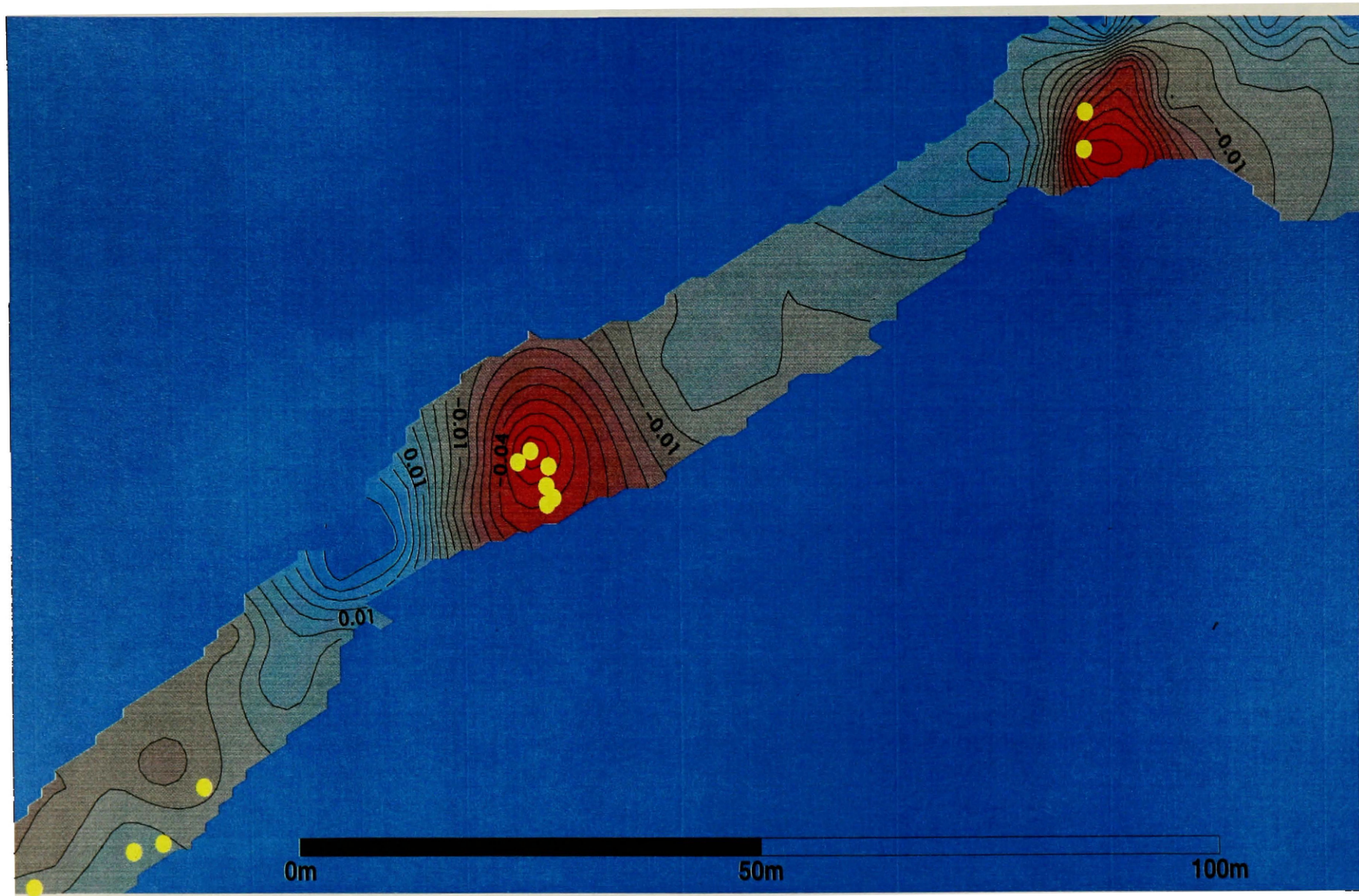
Figure 24. Isopleths of intragravel flow grading from strong downwelling flow (red) to strong upwelling flow (blue). Bull trout redd locations are indicated by the yellow dots.
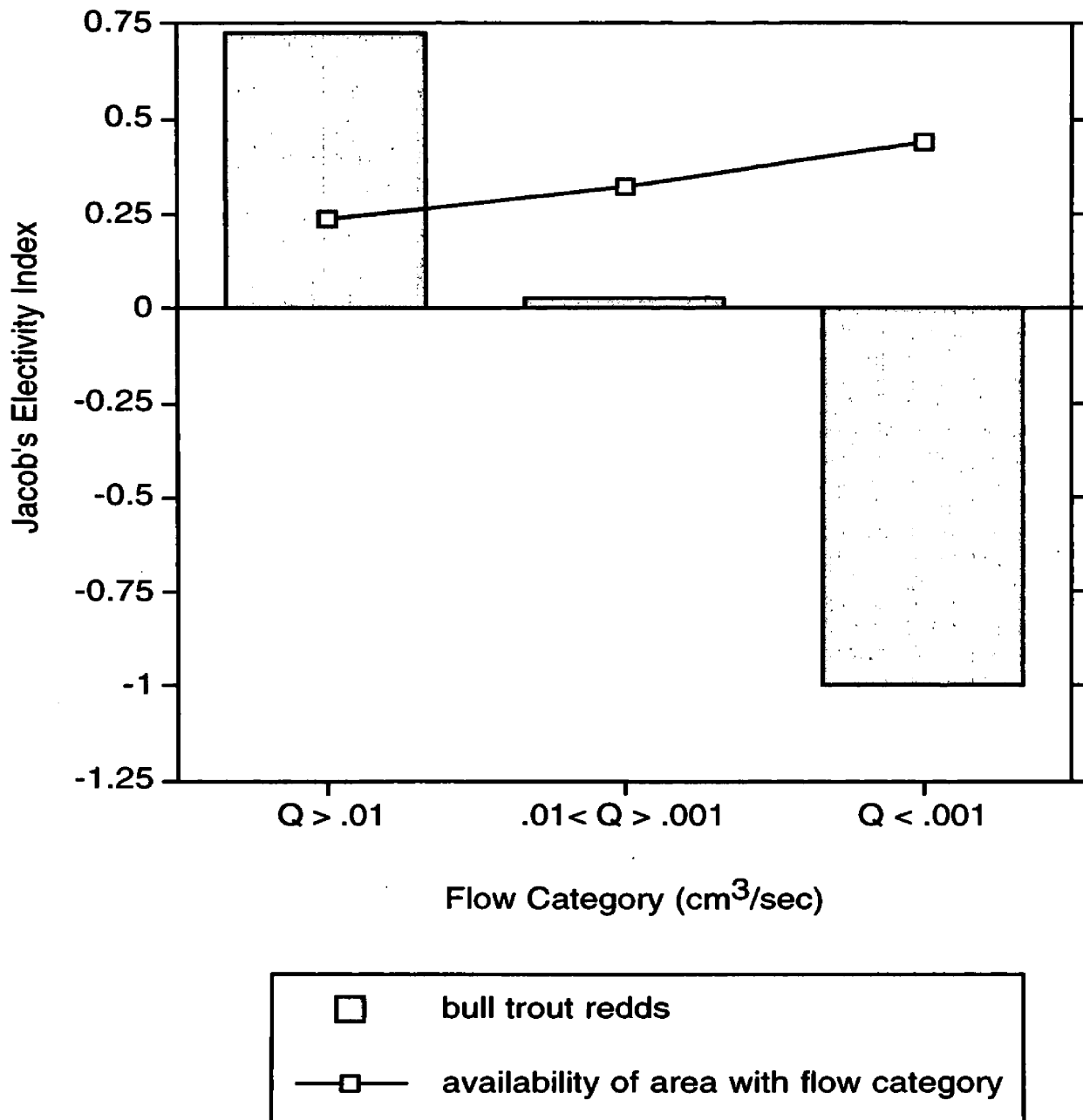
Figure 25. The distribution of redds with respect to local patterns of intragravel flow rates within the two selected spawning reaches of Lion and Cold Creeks, relative to the availability of habitat possessing high (Q >.01 cm3/sec), medium (.01< Q >.001 cm3/sec), and low (Q <.001 cm3/sec) flow rates.

CHAPTER III

Geomorphology, logging roads and the distribution of bull trout (*Salvelinus confluentus*) spawning in a forested river basin: implications for management and conservation

ABSTRACT

The Swan basin, at the headwaters of the Columbia basin in Montana, is considered a stronghold of regional significance for the bull trout, a native char whose populations are fragmented and declining throughout their range. Spatial and temporal variation of bull trout redd counts (1982-1995) among nine principal spawning tributaries of the Swan River were examined with respect to potential geomorphic and land-use factors. Bull trout redd counts were positively correlated with alluvial valley segments bounded by knickpoints, landscape features associated with groundwater-surface water exchange. Redd numbers also varied inversely with the extent of logging roads in their catchments. The extent of logging roads in tributary catchments did not correlate with any measures of their geomorphic variation.

Temporal trends were also variable among the principle spawning streams. Four of the nine principal spawning populations displayed significant increases in spawning, while others displayed no significant change. Meanwhile, the between-tributary variance of redd counts has doubled from 1983 to 1995. Changes in tributary redd densities over time were negatively correlated with road densities, while these rates of change were positively associated the spatial extent of alluvial valley segments bounded by knickpoints.

The results of these analyses suggest the importance of groundwater-influence to bull trout spawning habitat, and are consistent with the hypothesis that prior land use has adversely affected local population abundance. In addition, the four index streams selected by the state to monitor population trends over time provide a somewhat biased sample of catchment conditions and probably an overly optimistic assessment of bull trout status in the Swan basin.

Protection of the few remaining productive tributary catchments from additional road building and associated land use disturbance will likely be essential to the maintenance of viable bull trout populations in the Swan basin.

INTRODUCTION

Scientists and managers dedicated to the conservation of species and the integrity of ecosystems must interpret and apply existing population data. Accurate interpretation and effective application of these data may require examination within a landscape context. Critical evaluation of the nature and effectiveness of past and present monitoring and management efforts may also be demanded. In the case of the bull trout (*Salvelinus confluentus*), a char whose populations are fragmented and declining throughout their range, monitoring and conservation efforts of the future depend, in part, on the interpretation and application of fourteen years of redd count data from the Swan basin of northwest Montana.

In contrast to their range-wide decline, bull trout redd counts have been reported to have significantly increased ($p < .05$) in the Swan basin (Montana Bull Trout Scientific Group 1996, Weaver in press). Various causes for the apparent increase have been theorized. Sub-adult bull trout in Swan Lake may be experiencing improved growth and survival as a result of feeding on the introduced opossum shrimp *Mysis relicta* (Montana Bull Trout Scientific Group 1996). Recent angling restrictions to protect bull trout could also contribute to such an increase in spawner density. The increasing trend, based on data from four annually-monitored streams, is being popularly cited as evidence that large-scale, intensive land use is not associated with population trends of this species, since the majority of land in the Swan basin is managed for timber harvest. However, among the nine principal spawning tributaries the number of observed bull trout redds varies considerably (Montana Bull Trout Scientific Group 1996), suggesting the presence of some environmental factor(s) that

influence between-tributary spawning distribution and abundance.

In a recent analysis that included four annually-monitored spawning streams of the Swan basin, Rieman and McIntyre (1996) found that temporal population trends from spatially proximal tributaries were not well correlated with each other. The weakness of these correlations suggest the presence of variation among tributaries that could not be explained by common events in the lake environment.. Rather, they proposed that heterogeneity in stream habitat availability or condition might account for this lack of synchrony among tributary populations. In this study we investigated spatial and temporal variation in bull trout redd numbers among the nine principal spawning tributaries of the Swan River in relation to two potential environmental factors 1) landscape geomorphology and 2) land-use activity. In light of the results of these analyses, we also examined the efficacy of the current monitoring design for assessing the status of bull trout in the basin.

Bull Trout Status, Life History, and Spawning Habitat

Bull trout have become a focal point of concern, research, debate, and litigation in the Pacific Northwest over the past several years. In the Columbia and Klamath basins they will be proposed for listing under the Endangered Species Act (L. Lockhart, USFWS, Kalispell, MT personal communication). Local populations have been restricted or eliminated throughout their range from overharvest, displacement by exotic species (e.g., Donald and Alger 1993, Leary et al. 1993) and habitat degradation, such as seasonal or permanent obstructions, water quality degradation, and alteration of natural temperatures and streamflow patterns (Fraley and Shepard 1989, Howell and Buchanan

1992, Rieman and McIntyre 1993).

Bull trout display adfluvial and fluvial migratory life history forms associated with large lake and river systems. They also express a non-migratory, resident form that is much smaller sized and typically remains in headwater streams. Migratory bull trout in the Swan basin spawn in second and third order streams from August through October. Juveniles remain in the natal streams for 1-3 years prior to migrating to Swan Lake where they spend 2-4 more years growing before sexual maturity (Fraley and Shepard 1989). In the Swan basin, adult bull trout may spend considerable periods of time in the main river (Frissell unpublished data); however, it is unknown if distinct resident, fluvial, and adfluvial forms exist there. Though they are known to be iteroparous (Fraley and Shepard 1989), little is understood of bull trout spawning frequency, longevity, or post-spawning mortality.

Bull trout have very specific habitat needs. Channel stability, streambed composition, cover, migratory corridors, and water temperature have all been identified as important to bull trout growth, survival, and reproduction (Rieman and McIntyre 1993). However, quality spawning and rearing habitat may be the primary limiting factors affecting population size in any specific area (Fraley and Shepard 1989, Rieman and McIntyre 1995). Graham et al. (1981) observed that spawning bull trout in tributary streams of the North and Middle Forks of the Flathead River used less than 28% of accessible stream lengths. Leathe and Enk (1985) and Rumsey (1991) reported that over 75% of the spawning in the Swan basin takes place in less than 10% of the available stream length.

Typical stream reaches utilized for spawning are characterized by low

gradient. Substrata of spawning sites are loosely compacted gravel and cobble (McPhail and Murray 1979, Shepard et al. 1984). Because embryos and alevins over-winter within the gravel for more than 200 days, bull trout development and fry emergence are particularly vulnerable to increased fine sediment and associated water quality degradation (Fraley and Shepard 1989, Weaver and Fraley 1991). Monitoring of substrate quality indicates that major spawning tributaries of the Swan basin possess inherently high background levels of fine sediment. Consequently, slight sediment increases in this basin may adversely impact bull trout fry survival to emergence and juvenile survival (Weaver and Fraley 1991). Relatively stable channels and stream flows are also potentially important spawning habitat factors (Leathe and Enk 1985, Cross 1992, Rieman and McIntyre 1993). Concealment cover has been shown to be a critical aspect of habitat selection for all life history stages (Fraley and Shepard 1989, Pratt 1984;1985;1992, Platts et al. 1993, Rieman and McIntyre 1993), and is often associated with spawning sites (McPhail and Murray 1979, Shepard et al. 1984).

Coarse woody debris (CWD), in addition to providing cover, may play a critical role in creating and maintaining other spawning habitat characters (Hauer et al. unpublished), though the relationship is not well defined and probably varies with local hydrologic and geomorphic characteristics. CWD influences substrata characteristics by retaining organic matter and controlling the distribution and movement of sediment (Bilby and Likens 1980, Webster et al. 1990, Swanson et al. 1976). CWD contacting the stream sediment surface may enhance surface-subsurface hydraulic flux (Chapter 2 this thesis) by creating alternately concave and convex streambed topography and changes in

water surface slope (Vaux 1962, Leopold et al. 1964, Harvey and Bencala 1993).

Water temperature also plays an important role in the distribution of the stenothermic bull trout (Pratt 1984, Shepard et al. 1984, Fraley and Shepard 1989, Adams 1994, and others). Multiple studies have indicated that the onset of spawning is triggered by temperatures dropping below 9° Celsius (Needham and Vaughn 1952, Leggett 1969, McPhail and Murray 1979, Shepard et al. 1984, Weaver and White 1985, and others). Eggs appear to require between 350 and 440 degree days (°C) to hatch. Embryos require fewer degree days with decreasing temperature (Weaver and White 1985) and optimal incubation temperatures occur between 2-4 °C (McPhail and Murray 1979).

Numerous authors have noted that stream habitats selected for spawning are often influenced by ground water (Heimer 1965, Allan 1980, Graham et al. 1981, Shepard et al. 1984 and others). Groundwater-surface water exchange varies across a hierarchy of spatial scales and is constrained by geomorphic patterns at these scales (Chapter 2 this thesis). Most montane alluvial river systems are characterized by a series of unconfined alluvial valley segments bounded longitudinally by bedrock knickpoints and interspersed with confined valley segments. Because the alluvial valley segments are bounded longitudinally by knickpoints and laterally by montane valley walls, throughout this paper we refer to these landscape geomorphic features as bounded alluvial valley segments (BAVS).

Confined valley segments typically act only as conduits for surface water, but within these BAVS considerable groundwater-surface water interaction occurs (Stanford and Ward 1993, Chapter 2 this thesis). This exchange includes

interaction with deep-storage ground waters, as well as with the shallow unconfined aquifer immediately below, and lateral to the active channel. This alluvial aquifer includes the area known as the hyporheic zone (see Gibert et al. 1994 for a recent review), the region that is influenced by groundwater that was previously channel water. Since BAVS structure hyporheic flow patterns and possess significant areas of groundwater discharge, the spatial extent of BAVS in a tributary catchment is associated with a its capacity for groundwater-surface water exchange (Chapter 2 this thesis). Consequently, we hypothesized that the spatial extent of BAVS per spawning tributary would be associated with the variation in observed redd numbers among the nine principal spawning tributaries of the Swan basin.

STUDY AREA

Geomorphology

The Swan basin in northwestern Montana is a densely forested, north-south trending, glaciated basin between the Swan and Mission fault block mountain ranges with an approximate area of 2070 km^2. From peak elevations in excess of 1500 m above the valley floor, waters drain through tributary canyons carved in Precambrian metasedimentary rock and morainal deposits in the broad Swan Valley before reaching their confluence with the sinuous, locally anabranched Swan River, which flows north into Swan Lake, and then into Flathead Lake. The current geomorphic template for the dynamic fluvial processes of the Swan River alluvial plain and its tributaries was established by the processes of two major glacial advances. These occurred in the Mid (70,00-35,000 y.b.p.) and Late (16,000-12,000 y.b.p.) Pinedale, with the first being

followed by a period of fluvial transport and mass wasting, and the second followed by thickening of the alluvium by in-filling from glacial outwash (Anderson 1992). The BAVS of the Swan tributary drainages are apparently associated with faulting and local accumulations of valley fill from alluvial and glacial sources.

Land Use History

The earliest disturbance associated with European humans in the Swan basin was the construction of a hydroelectric dam one mile above the mouth of the Swan River near Flathead Lake in 1902. Located 22 km downstream of Swan Lake, this dam severed any upstream migration of Flathead Lake bull trout to Swan basin spawning and rearing habitat, and isolated the Swan basin populations from the rest of the Flathead bull trout assemblage (Leathe and Graham 1983). Small, low-elevation homesteads began to be cleared by 1910, and roading and logging operations expanded the following decade. Sluice dams and associated logging activity affected the lower main river and a few tributaries during the 1920's, resulting in increased sedimentation rates in Swan Lake (Spencer 1991). Logging and homesteading remained at a slow pace until construction of State Highway 83 through the basin in 1946-1947. Road construction on federal Forest Service lands and clearcutting of corporate and public lands accelerated from the 1960's to the 1980's. More than half of the drainage has been disturbed by these intensive activities, with the lower elevations most heavily impacted (Frissell et al. 1995). Flow records for the Swan River suggest a trend of earlier snowmelt runoff during the 1970's and 1980's than occurred prior to 1950, possibly a result of decreased canopy

cover due to logging in the basin (Hauer 1991). The drainage has a "checkerboard" of ownership, with approximately 45 percent of the drainage managed by the Flathead National Forest, 20 percent by Plum Creek Timber Company, 10 percent by Montana Department of Natural Resources and Conservation, and another 25 percent in other private ownership. The majority of the drainage is currently managed for timber production.

Bull Trout

The original bull trout assemblage of the Flathead basin was highly interconnected, and is thought to have been of major importance to the range-wide metapopulation (Montana Bull Trout Scientific Group 1996). Adult adfluvial bull trout historically occupied the large lakes of the Flathead watershed, with spawning and rearing taking place in tributaries of the three forks of the Flathead, as well as the Stillwater, Whitefish and Swan river basins. Some straying among spawning tributaries probably occurred, but preliminary genetic analysis has indicated strong fidelity to specific river basins (Kanda et al. 1995).

Quantitative historic information about bull trout distribution and abundance in the Swan basin is sparse. However, anecdotal accounts suggest a high density of large fish (Evermann 1892, Montana Bul Trout Scientific Group 1996). In 1982, Montana Fish Wildlife and Parks (MFWP) field crews began monitoring redd numbers in tributaries used by migratory bull trout. These redd counts reflect only adfluvial or fluvial fish, since counting redds is not possible for smaller resident bull trout (whose presence in the Swan basin is uncertain). Currently, migratory bull trout are known to spawn in thirteen tributary streams of

the Swan River. Of these, spawning has been consistently observed in nine. Since 1982, MFWP has annually surveyed four high density spawning streams, with the others being surveyed periodically. Basin-wide surveys of all the principal spawning streams were done in 1983, 1991 and 1995.

MATERIALS AND METHODS

Redd Surveys, Geomorphology, and Land-Use

Nine tributary drainages supporting substantial bull trout spawning runs were examined for landscape-scale geomorphic characteristics and land use histories that might affect variation in redd density and distribution. Redd count data from three basin-wide surveys (1983, 1991 and 1995), as well as a mean for all years sampled for each stream, were used as an index of spawner density. Redd surveys were conducted by Montana Fish, Wildlife and Parks (MFWP). Surveys were conducted in September and October, though multiple surveys have been done in some years to identify the dates that would result in the most complete estimate of the spawning population (Weaver 1991). Several streams were surveyed along their entire spawner-accessible length (Weaver 1992). We analyzed total redd counts per stream and redd numbers as density per stream length (counts/km surveyed). Eight of the nine drainages (all except Woodward Creek) had more than four years of redd survey data. We plotted total redd count per stream and redd densities against survey year. The slopes of the simple linear regression lines were included in our analyses as the annual rate of change in bull trout redds per stream and the annual rate of change in bull trout redd density (Table 1).

Standard USGS topographic (1:24,000 scale) and structural geologic

(1:250,000 scale) maps were used to measure 28 quantitative geomorphic variables (Table 2). We also used air photographs and field reconnaissance to aid in discrimination of features. In addition to traditional drainage geomorphic features (Strahler 1964, Leopold et al. 1964), metrics were taken to delineate the presence of landscape features that are known to correlate with a catchment's capacity for large scale groundwater-surface water exchange (Chapter 2 this thesis). We included measures of valley bottom width (i.e. an estimate of floodplain width) and the number of lateral constrictions and major gradient steps (i.e. knickpoints). Subsequently, we were able to estimate the number, length, and area of bounded alluvial valley segments (BAVS). We defined BAVS as any unconfined stream reach at least 500m in length bounded laterally by valley widths >50m and longitudinally by narrowing of the valley walls and gradient steps in excess of 10% (Figure 2).

Road density and road crossings of the stream were used as indicators of land use activity in a drainage. We selected road density as a surrogate of total forest management activity because road density has been found to be highly correlated ($r^2=0.98$) with estimates of equivalent clear-cut areas in the Swan basin (Hauer and Blum 1991), and because a good data time series was available across all ownerships in the basin. As timber harvest is the primary land use activity in the Swan drainage, road density was considered representative of land use activity. We made no apriori assumptions regarding the causal mechanisms that could underlie any association we might detect between roads and local spawning populations. Therefore, we utilized total catchment road density without spatial segregation, and all roads accrued over time with no temporal weighting assigned. Regardless, very few roads were

located below the downstream extent of bull trout spawning in these tributaries.
Furthermore, nothing is known of the longitudinal distribution of spawning prior
to 1982 when monitoring began.

We did anticipate that the number of road crossings (road-stream
intersections) might reflect some aspects of direct road effects on tributary
populations more accurately than catchment-scale road density, which does not
account for spatial distribution of the road network. National Forest, BLM and
USGS maps were used to delineate a chronological sequence of road
densities (1954, 1966, 1976, 1983, 1991) and the number of road crossings
(1982, 1991) for each drainage. We developed a time series of road densities
and road crossings in order to examine possible changes in correlations over
time that might be indicative of time lags between upland disturbance and the
biological response of spawning populations. Since we found the data for road
crossings were highly correlated with road density, road crossing data were
examined for 1982 and 1991 only.

Analysis

Two streams (Woodward Creek and Lost Creek) divide into major forks near
their confluence with the Swan River, and we were uncertain whether these
forks should be treated as aggregated or separate populations. Therefore, two
between-tributary correlation matrices of geomorphic features, land use history,
and bull trout redd variables were constructed. In the first matrix, the north and
south forks of Lost Creek and the north and south forks of Woodward Creek
were treated as separate drainages, resulting in a total of eleven streams. In
the second matrix, these forks were lumped by stream, resulting in a total of

nine cases.

The purpose of these analyses was to screen for potentially important environmental correlates that could explain spatial and temporal variation in redd counts among tributaries. Consequently, we applied a univariate approach rather than multivariate statistical procedures. We used step-wise rather than multiple regressions in an effort to avoid obscuring possible significant and interesting associations, and because of concerns about co-linearity among variables. In these analyses, we made no assumption that factors were independent, therefore we made no adjustment for multiple tests. The objectives of the analyses were: 1) to test each variable for significance in explaining between-tributary variation in redd numbers and densities and 2) to examine the four annual monitoring streams for their utility as an unbiased sample of the aggregated Swan basin bull trout metapopulation. We excluded the outlier datum from Piper Creek in 1983 when less than 2 km were surveyed.

RESULTS

Redd Counts And Geomorphology

Results from the two correlation matrices (one combining, the other separating the north and south forks of Lost and Woodward Creeks) were virtually identical. Therefore we present only the results of the nine-stream approach here (Tables 3 and 4). Counts and densities of bull trout redds did not vary with any of the traditional quantitative geomorphic metrics (e.g. drainage area, network density, stream order, stream gradient). Rather, redd counts for the three basin-wide survey years, as well as mean redd counts, correlated positively with the area (p < .002 to .04) and length (p < .004 to .007)

of BAVS accessible to spawning bull trout (Figure 3). Other geomorphic factors that were significantly correlated to redd counts ($p < .05$), though less consistently, included the mean and variation in valley bottom width, the total number of BAVS, and the total area of BAVS per catchment. All of these variables were correlated ($p < .05$) to the best geomorphic descriptors, area and length of accessible BAVS per catchment. Analyses of time series from the nine principle spawning streams revealed that the rate of change in redd density over time was positively associated ($p < .05$) with the area ($p < .009$) and length ($p < .033$) of accessible BAVS per catchment (Figure 4). In addition, the mean valley bottom width and the variation in valley bottom width ($p < .05$) were also correlated with between-tributary variation in the rate of change of redds over time. Finally, the strength of the correlation between redds and all BAVS-related variables increased from 1983 to 1991 to 1995 (Table 3 and Figure 3).

Redd Counts And Land -Use History

Bull trout redd densities and counts per stream were inversely correlated with the density of logging roads and the number of road crossings in their catchment (Table 4). Although not every pairwise case was statistically significant, all redd counts and densities were negatively correlated to all of the road density and crossing factors, exceeding the extent of negative correlation expected. Furthermore, there was no discernible correlation between any of the geomorphic variables (including BAVS-related variables) and the extent of roading in a drainage.

In order to factor out the only effect of geomorphology on between-tributary redd variation that we detected, we divided redd counts by area of accessible

BAVS, producing a redd density adjusted by BAVS. This BAVS-adjusted redd density also varied inversely with road densities and road crossings (Table 4). In addition, the rate of change in redd counts and BAVS-adjusted redd densities over time was significantly negatively correlated to road densities per catchment (Figure 5).

Finally, if there were no lag in biological response to the effects of roading, we would have expected to observe redd counts and densities most closely correlated to their contemporary road densities. Instead, we observed that redd counts and densities were consistently best correlated with road densities 7-12 years previous, and always least correlated with road densities contemporary to the redd counts (Table 4). However, though the correlation strength between the rate of change of BAVS-adjusted redd density and road densities declined over time, this adjusted density displayed no other recognizable pattern in correlation strengths over the period of record.

Temporal Trends In Bull Trout Redd Counts

Of the eight drainages with more than four years of redd survey data, four streams (Elk, Lion, Squeezer and Jim) displayed a significantly positive ($p <$ .05) increase in redd numbers between 1982 and 1995, while the other four (Goat, Cold, Lost and Piper) did not (Table 1). In an all stream-wise analysis including Woodward Creek for the three basin-wide survey years of 1983, 1991 and 1995, the result was a positive, but non-significant ($p <$ .127) trend in redd numbers as well as redd densities (Table 5). However, the spatial variance among tributaries of redd counts and densities doubled from 1983 to 1995 (Table 5).

Annual Monitoring Streams

As previously reported by Weaver (in press), there was a significant increase (p < .05) in the total number of redds over time when only the four annual monitoring streams were examined. Of these streams, three (Lion, Elk, and Squeezer Creeks) displayed significantly positive linear regression trends (p < .05) in redd numbers between 1982 and 1995. Notably, these three streams also possessed the lowest road densities of any of the nine spawning catchments. Goat Creek, however, displayed no positive trend (r = .10), and has one of the highest road densities among spawning tributaries. The rate of change in redd counts for each of the four annual monitoring streams from 1982 to 1995 varied inversely with road densities from 1991 (p < .019) and 1983 (p < .032). Goat Creek had the lowest rate of increase, followed by Squeezer, Lion and Elk, respectively. Among only these four streams, the rate of change was only weakly positively correlated to area and length of accessible BAVS (p < .18).

DISCUSSION

The results of these analyses identify two environmental correlates that appear to influence among-tributary variation in bull trout redd counts. The spatial extent of BAVS (and hence the extent of groundwater-influenced habitat) appears to be positively linked to local population abundance among the spawning tributaries. On the other hand, land-use, particularly as expressed in catchment road density, appears to have had an additional, negative effect on

bull trout spawning populations.

Previous landscape-scale spatial analyses of bull trout spawning have suggested there are significant correlations between redd frequencies and drainage area and/or stream order (Graham et al. 1981, Mullan et al. 1992, and others). Although these conventional catchment metrics may be important discriminators for presence/absence of bull trout spawning at broad landscape scales (as was suggested by Rieman and McIntyre 1995), our results suggest that they are not useful predictors of variation in distribution or abundance among the principle spawning streams of the Swan basin.

Of the geomorphic variables we examined, only the area and length of accessible bounded alluvial valley segments (BAVS) were consistently correlated with bull trout redd numbers. In a companion study (Chapter 2 this thesis), BAVS were shown to be segments possessing extensive hyporheic exchange and areas of strong groundwater discharge. Those analyses of the 1995 redd counts showed that BAVS were preferentially used by spawning bull trout (88% of the total redds). Furthermore, strong associations between groundwater-surface water exchange and bull trout redd site selection were identified across a hierarchy of spatial scales.

Numerous researchers have identified alluvial valley segments as critical spawning habitat for many fish species. For example, Frissell (1992) observed that spawning of salmon and steelhead in coastal river systems of southern Oregon occurred almost exclusively in alluvial segments. Besides possessing significant habitat influenced by groundwater discharge, these segments contain large, stable expanses of well-sorted gravel and cobble. The presence of floodplain surfaces in these segments allows overbank flow, which, in concert

with hyporheic storage, can partially buffer the channel from scouring and depositional effects of flooding. In contrast, within confined valley segments suitable spawning gravel is patchy and flooding is not attenuated by floodplains.

The results of this analysis demonstrates that the association detected between BAVS and spawning (Chapter 2 this thesis) exists over the period of record for redd data from the Swan basin. As a consequence, this work further suggests the importance of groundwater influence on the structure and selection of bull trout spawning habitat at the scale of the tributary catchment. It is important to acknowledge, however, that bull trout do spawn outside of BAVS. Redds were found in pockets of suitable habitat within confined stream segments. They were also observed in unconfined alluvial reaches that lack downstream knickpoints, which occur where the tributaries emerge onto the Swan valley floor (Chapter 2 this thesis). Through spill-over effects on temperature and flow regimes, it is possible that the longitudinal extent of a BAVS-effect (i.e. the strength of the groundwater plume) may limit the use of habitat outside BAVS.

Although the potential for surface water-hyporheic zone connectivity is expressed in the spatial extent of BAVS, upwelling of non-hyporheic ground waters is not so predictable. Because some major non-hyporheic springs in the Swan drainage spawning streams (such as those proximal to spawning habitat on Jim Creek) do not correspond to the largest BAVS, redd numbers in these streams could be higher than predicted by the spatial extent of BAVS alone. In addition, since length and area of accessible BAVS are closely correlated, at present it is difficult to determine at present if it is simply the length of stream

available within BAVS that is more important, or if the lateral extent of the unconfined valley segment contributes to the quality of the spawning habitat. We suspect that there is probably a range of fairly large areas over which the length of stream habitat available is most important, but that there may be some point at which smaller BAVS do not possess the depth of alluvial fill and lateral complexity required to establish major hyporheic flow paths.

In addition to identifying BAVS as an important environmental correlate, we found that redd counts and densities consistently varied inversely with road density and number of road crossings. Factoring out the variation associated with geomorphology (area of accessible BAVS) resulted in strengthening the negative correlation between road density and redds. These results, combined with no evident association between geomorphology and land use history variables, suggests that prior land use has adversely affected local population abundance in the Swan drainage.

Though patterns in spatial variation of redds among spawning tributaries were distinct, we were less successful in resolving temporal lags between land use activities and spawning population response. We observed a suggestive pattern of a 7-12 year lag between road density and redd density, but this was not as consistent when we examined correlations between BAVS-adjusted redd density and road density. We suspect that a longer record of redd surveys, combined with increased temporal resolution of the land-use history data might reveal a clearer pattern. Demonstrating a lagged response might lend stronger support to the hypothesis of a causal influence of roads and associated human activities on bull trout. It would also influence the interpretation of redd count data, as redd counts would be expected to reflect the influences of the

intermediate and distant past, rather than recent habitat changes.

There are many ways geomorphology, groundwater-surface water exchange, and logging roads might interact to influence the number of adult reproducing bull trout. Timber harvest and associated road construction can cause profound changes in the morphology and dynamics of stream channel features that provide habitat for aquatic biota (see Meehan 1991 for review). For example, these activities can be detrimental to the abundance and quality of spawning substrata (Chamberlain et al. 1991). Aside from physical habitat impacts, roads can provide access for anglers and poachers, as well as increase the potential for introduction of non-native species. In addition, improperly designed road crossings can interfere or prevent upstream migration of both adult and juvenile salmonids (Furniss et al. 1991). Frissell et al. (1995) found a significant correlation between high ratings of aquatic biodiversity elements (including bull trout presence) and low road densities in the Swan basin. This is supported by several regional assessments in the western states (Williams 1991, Henjum et al. 1994, Huntington 1994, McIntosh et al. 1994, Wissmar et al. 1994). Sedell et al. (1990) and Frissell (1993a) also suggest that watersheds with significant roadless areas possess proportionately greater native aquatic biodiversity including populations of fishes that are declining or extinct elsewhere.

The negative correlation between the rate of change in spawning and road density suggests that past timber management and associated roads remain detrimental to the capacity of a tributary's spawning population for maintenance or recovery following a basin-wide event such as food web changes in Swan Lake or tributary-specific restrictions on angling. In contrast, the positive

correlations we detected between the rate of change in redd numbers and geomorphic factors associated with groundwater-surface water interactions (i.e. BAVS) suggest that these factors positively influence this capacity.

Rieman and McIntyre (1996) hypothesized that habitat disruption or increased environmental variation resulting from land-use management could lead to increased synchrony among spawning populations. However, adopting this hypothesis requires assuming that habitat disruption is operating at a spatial scale large enough to encompass the populations, and that different tributaries respond in similar fashion to this disturbance. In situations where such assumptions are not met, it is possible that the asynchrony among spawning tributary populations could be attributable to a heterogeneous pattern of habitat disturbance, as well as inherent differences in tributary potential and resilience. Our results indicate that the asynchrony observed among spawning tributary populations in the Swan basin fits the latter scenario. Additionally, the correlation strength between redds and all BAVS-related variables increased from 1983 to 1991 to 1995. Though complicated by the lack of more complete biological data in drainages with high road densities, these results are consistent with the hypothesis that over this time period the Swan bull trout populations have become increasingly associated with groundwater-influenced habitat refugia. Habitat outside of BAVS might be more sensitive to the effects of land-use than habitat within BAVS. Therefore, populations in streams short in BAVS could lack resilience in the face of catchment disturbance.

Areas influenced by groundwater discharge possess relatively stable thermal and flow regimes important to egg incubation, emergence success, and the survival of juvenile bull trout. Groundwater discharge sources provide

coldwater refugia for salmonids in summer (Latta 1964, Gibson 1966, Kaya et al. 1977, Bilby 1984, Nielson 1993, and others) and warmwater refugia in winter (Craig and Poulin 1975, Cunjak and Power 1986, and others). Stream habitat degradation may result in increased reliance on such refugia in all life history stages, including spawning (Fausch 1989, Sedell et al. 1990, Ebersole 1995, Frissell 1993a, and others).

One mechanism by which groundwater-influence may contribute to habitat resilience is suggested by the results of Weaver and Fraley's (1991) experimental study of the effects of fine sediments (< 6.35 mm) on bull trout survival to emergence. One of their artificial redds containing a high level (40%) of fines was located on a small spring and experienced relatively better survival than would have been predicted by percent fines alone. This survival may have been related to the high intragravel flow rates and/or the dissolved oxygen content, which was the highest of any of their sites.

Though upwelling groundwater may provide some refuge from the effects of habitat degradation, surface-subsurface water interchange rates and temperatures are not immune to the effects of roads and their associated land uses, particularly with respect to hyporheic exchange taking place at the reach and habitat unit scales. The temperature of groundwater can be increased by logging or other vegetation removal (Viereck et al. 1993, Pluhowski and Kantrowitz 1963, Holtby 1988, Hewlett and Fortson 1982). Coarse sediments from roads or logging may cause channel aggradation, widening and simplification (Lyons and Beschta 1983), increasing stream channel exposure to solar radiation. Fine sediments may reduce rates of intragravel flow (Bjerklie and LaPerriere 1985, Shalchli 1992), leading to increased summer

temperatures, decreased winter temperatures, and reduced dissolved oxygen (Ringler and Hall 1975). Stable coarse woody debris, which often controls habitat-scale bed topography and water surface slope, and therefore a stream's capacity for shallow hydraulic exchange, can be lost through reduced recruitment, flood-flow blow out, or direct removal from the stream.

Changes in water routing and drainage densities caused by roads can result in altered timing and magnitude of peak flows (see Wemple et al. 1996 for a recent study). These changes may alter floodplain recharge and subsequent release into stream channels (Shephard et al. 1986). Roads in mountainous regions often cut into the hill slope, intercepting subsurface flow paths and diverting ground water to surface runoff (Croft 1952, Haupt et al. 1963, Burroughs et al. 1971, Megahan 1972). In a central Idaho study, Megahan (1972) showed that 5300 ft^2 of road disturbance diverted 97,500 ft^3 of subsurface water to surface runoff in one year. Many authors have suggested that floodplain alteration and channel simplification associated with channelization, logging and other land use activities can sever critical stream-land interactions including groundwater-streamwater interchange (Sedell and Frogatt 1984, Regier et al. 1989, Stanford and Ward 1992, Ebersole 1995). Despite these examples, the results of our work highlight the need for more studies regarding potential relationships between anthropogenic disturbance and groundwater-surface water interactions.

The associations we detected involving geomorphology, land-use, and variation in bull trout redd numbers, coupled with our examination of the annual monitoring streams, have important implications for the management and conservation of the bull trout. The spatial extent of BAVS (and hence the extent

of groundwater-influenced habitat) appears to be positively linked to local population abundance among the spawning tributaries. On the other hand, land-use, particularly as expressed in catchment road density, appears to have had an additional, negative effect on bull trout spawning populations. Furthermore, our results are consistent with the hypothesis that tributaries with extensive groundwater-influenced habitat are more resilient in the face of land use impacts. One way this hypothesis could be tested would be through experiments on growth and survival to emergence in habitats possessing variable groundwater influence and anthropogenic disturbance.

Our analysis demonstrates very equivocal, statistically non-significant support for the hypothesized basin-wide increase in spawning bull trout (see Weaver in press, USFWS 1994). The between-tributary variation of observed spawning has doubled between 1983 and 1995. The evidence for a basin-wide increase appears to stem largely from four tributaries (Elk, Lion, Squeezer and Jim). In the remaining five of the nine principle spawning drainages for which data were available, there is not strong evidence for any increase in bull trout redds between 1982 and 1995. For other potential spawning tributaries (e.g. Soup Creek) there are few data at all. There may be an overall increase in spawning taking place in the Swan basin, but the results of these analyses suggest that any increase appears to be occurring in proportion to tributary catchment conditions. Specifically, we have identified two environmental correlates that may account for trend differences among the principle spawning catchments 1) the density of roads and 2) the spatial extent of BAVS. Thus it appears that combining the redd counts from individual spawning tributaries to examine trends over time might obscure associations that may be important to

bull trout management and monitoring efforts in this area.

Though the Swan monitoring program has given scientists and managers important information and insight, there are several respects in which the current monitoring protocol is biased, thus diminishing its utility for accurately assessing the status of the Swan basin bull trout populations. The annual survey streams were selected primarily because they possessed the highest redd counts (B. Shepard, MFWP at Montana State University personal communication). The habitat in these four streams represents only about 8.5% of the total spawner-accessible stream length in the basin (Leathe and Enk 1985). All four streams possess relatively extensive BAVS. Finally, three of the four streams have the least extensive land-use history of all the spawning tributaries in the basin.

The past emphasis of the monitoring protocol appears to have been sampling a large component of the population (in 1995, 68% of the Swan basin redds were found in the four index areas). Although there is considerable value in maintaining the annual monitoring of these four streams, we recommend that additional effort be focused on assessing the extent to which the available habitat produces bull trout. There is a distinct need to expand future monitoring efforts to include tributaries that have more intensive land-use histories, in particular to those that also possess extensive BAVS (e.g. Woodward Creek). In addition, because BAVS may respond differently to landscape stresses than habitat outside of BAVS, stratification of habitat with respect to the occurrence of BAVS could aid analytic and monitoring efforts in coping with this functional diversity. Suitable habitat may diminish or expand differently inside and outside of BAVS in response to many factors. Any stratified approach should also

address the possible downstream effects of BAVS (e.g. water temperatures or low flow volumes).

Survey conditions such as turbidity or blowdown can influence the selection of long-term monitoring streams. Feedback loops that can arise as a result of monitoring efforts are not always beneficial. Those drainages that are monitored closely become better understood. Management of those areas may become more informed, and they may become the focus of conservation efforts, while other un-monitored, but potentially important tributaries become neglected in a spiral of degradation.

The lack of historic bull trout abundance or distribution data make it difficult to determine whether streams in the Swan basin ever possessed higher redd numbers than at present. The recent increases of observed redds in a few streams could be evidence for any of a number of scenarios. Increases in a few streams could simply be a compensatory population response to poorer recruitment of bull trout from other spawning tributaries in the basin. Considering the variation that can occur in bull trout spawning frequency (Allan 1980, Leathe and Enk 1985), it is also conceivable that improved growth conditions in Swan Lake, and/or stricter angling restrictions (which can lead to older age-class structure and potentially higher reproductive output) may have induced a shift to more frequent spawning among the bull trout of the basin. Superimposed on any scenario may be a pattern of increased reliance of bull trout spawning on groundwater-influenced areas.

Considering the many unknowns associated with interpreting these data, and the evidence that spawning increases have occurred in some tributaries but not in others, we recommend that managers and scientists use caution

before assuming that the Swan bull trout metapopulation is experiencing a basin-wide increase. We concur with Rieman and McIntyre (1996) that regular monitoring of only a few high density spawning streams may not provide a reliable indicator of general trends in bull trout populations. The most recent surveys completed in late 1996, not available for these analyses, may lend increased support to the notion that a general, basin-wide increase of bull trout may be occurring in the Swan basin (T. Weaver personal communication). However, the geomorphic context and land-use status of spawning tributaries must be fully considered in interpreting any data set, and biases in these respects must be taken into account. Furthermore, data from any continued or improved monitoring will require similar conservative, critical interpretation.

Monitoring redds alone may not necessarily be the most sensitive approach for assessing bull trout population trends in order to make adaptive decisions about their management. Physical and biological lags between upland disturbance, stream habitat change, and a perceived response in redd counts could exceed 10-15 years, complicating monitoring and precluding success of short-term adaptive management schemes. Additionally, time trends in redd counts may not be statistically verifiable until after a decline has become difficult or impossible to reverse (B. Rieman, U.S. Forest Service Intermountain Research Station, personal communication). Montana Fish Wildlife and Parks does some assessment of juvenile abundance every year. In addition, in an effort to monitor incubation habitat quality, they sample spawning area gravel composition (based on McNeil core samples) from which they predict fry emergence (Weaver and Fraley 1991). However, more direct measures of growth and survival to emergence would help in monitoring of this portion of

bull trout life history. Along with the redd counts, these approaches may yield a more continuously sensitive perspective (T. Weaver personal communication).

Conserving the bull trout and other species requires that we consider these organisms within the context of their connections in a dynamic landscape that includes human activities. Accurate assessment of present conditions, as well as the conservation of species and ecosystems, depends on adopting this type of contextual perspective, while coupling it with ongoing critical evaluation of scientific and management efforts.

LITERATURE CITED

Adams, S.B. 1994. Bull trout distribution and habitat use in the Weiser River drainage, Idaho. Master's thesis. University of Idaho, Moscow, Idaho.

Allan, J.H. 1980. Life history notes on the Dolly Varden charr(*Salvelinus malma*) in the Upper Clearwater River, Alberta. Alberta Energy and Natural Resources, Fish and Wildlife Division, Red Deer, Alberta.

Anderson, R.C. 1992. Hydrogeology of the Swan River Oxbow Preserve area, Lake County, Montana. Master's thesis. University of Montana, Missoula, Montana.

Bilby, R.E. 1984. Characteristics and frequency of cool-water areas in a western Washington stream. Journal of Freshwater Ecology 2:593-602.

Bilby, R.E. and G.E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61:1107-1113.

Bjerklie, D.M. and J.D. LaPerriere. 1985. Gold-mining effects on stream hydrology and water quality, Circle quadrangle, Alaska. Water Resources Bulletin 21(2):235-243.

Burroughs, E.R. Jr., M.A. Marsden and H.F. Haupt. 1971. Volume of snowmelt intercepted by logging roads. ASCE Nat. Water Resources Eng. Meeting, Phoenix, Arizona, Jan. 11-15, 1971.

Chamberlain, T.W., R.D. Harr, and F.H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. Pages 181-205 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Craig, P.C. and V.A. Poulin. 1975. Movements and growth of arctic grayling (*Thymallus arcticus*) and juvenile arctic char (*Salvelinus alpinus*) in a small arctic stream, Alaska. Journal of the Fisheries Research Board of Canada 32:689-697.

Croft, A.R. 1952. Anderson Creek flood damage survey. Report on file, U.S. Forest Service, Boise National Forest, Boise, Idaho.

Cross, D. 1992. Status of bull trout on the Idaho Panhandle National Forests. U.S. Forest Service, Coeur d'Alene, Idaho.

Cunjak, R.A. and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 43:1970-1981.

Donald, D. B. and D. J. Alger. 1993. Geographic distribution, species displacement and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.

Ebersole, J.L. 1995. Stream habitat classification and restoration in the Blue Mountains of Northeast Oregon. Master's thesis. Oregon State University, Corvallis, Oregon.

Evermann, B.W. 1892. Report of the Commissioner of Fish and Fisheries reflecting the establishment of fish-cultural stations in the Rocky Mountain Region and Gulf states. 52D Congress, Senate, Miscellaneous Document Number 65, U.S. Government Printing Office.

Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiology and Ecology Japan Spec. 1:303-322.

Fraley, J., and B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63(4):133-143.

Frissell, C.A. 1992. Cumulative effects of land use on salmon habitat in southwest Oregon coastal streams. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Frissell, C.A. 1993a. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (U.S.A.). Conservation Biology 7: 342-354.

Frissell, C.A., J. Doskocil, J.T. Gangemi and J.A. Stanford. 1995. Identifying priority areas for protection and restoration of aquatic biodiversity: a case study in the Swan River basin, Montana, USA. Flathead Lake Biological Station, The University of Montana, Open File Report 136-95, Polson, Montana.

Furniss, M.J., T.D. Roelofs, and C.S. Yee. 1991. Road construction and maintenance. Pages 297-323 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Graham, P.J., B.B. Shepard, and J.J. Fraley. 1981. Use of stream habitat classifications to identify bull trout spawning areas in streams. Pages 186-191 *in* N.B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. The Western Division of the American Fisheries Society, Portland, Oregon, USA.

Gibert, J., D.L. Danielopol and J.A. Stanford, editors. 1994. Groundwater Ecology. Academic Press, San Diego, California.

Gibson, R.J. 1966. Some factors influencing the distribution of brook trout and young Atlantic salmon. Journal of the Fisheries Research Board of Canada 23:1977-1979.

Harvey, J.W. and K.E. Bencala. 1993. The effect of streambed topography on surface-subsurface water exchange in mountain catchments. Water Resources Research 29(1):89-98.

Hauer, F.R. 1991. An analysis of the effect of timber harvest on streamflow quantity and regime: an examination of historical records. Flathead Basin Forest Practices, Water Quality and Fisheries Cooperative Program, Flathead Basin Commission, Kalispell, Montana, USA.

Hauer, F.R. and C.O. Blum. 1991. The effect of timber management on stream water quality. Flathead Basin Forest Practices, Water Quality and Fisheries Cooperative Program, Flathead Basin Commission, Kalispell, Montana, USA.

Hauer, F. R., J. T. Gangemi, and C. V. Baxter. in preparation. The role of coarse woody debris in structuring stream channel morphology in bull trout spawning streams in northwestern Montana. Report to the Montana Department of Fish, Wildlife and Parks.

Haupt, H.F., H.C. Rickard, and L.E. Finn. 1963. Effect of severe rainstorms on insloped and outsloped roads. U.S. Forest Service. Research Note INT-1.

Heimer, J.T. 1965. A supplemental Dolly Varden spawning area. Master's thesis. University of Idaho, Moscow, Idaho.

Henjum, M.G., J.R. Karr, D.L. Bottom, D.A. Perry, J.C. Bednarz, S.G. Wright, S.A. Beckwitt, and E. Beckwitt. 1994. Interim protection for late-successional forests east of the Cascade crest, Oregon and Washington. A report to the Congress and President of the United States. The Wildlife Society,Technical Bulletin 92-2, Washington, D.C., USA.

Hewlett, J.D. and J.C. Fortson. 1982. Stream temperature under and inadequate buffer strip in the Southeast Piedmont. Water Research Bulletin 18(6):983-988.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on coho salmon (*Oncorynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Howell, P.J. and D.V. Buchanan [eds]. 1992. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon, USA.

Huntington, C.W. 1994. Fish habitat and salmonid abundance within managed and unroaded landscapes on the Clearwater National Forest, Idaho. Report prepared for the USDA Forest Service, Eastside Ecosystem Management Project, Walla Walla, Washington, USA.

Kanda, N., R.F. Leary, and F.W. Allendorf. 1995. Population genetic structure of bull trout in the Upper Flathead River Drainage. Report to Montana Department of Fish, Wildlife and Parks.

Kaya, C.M., L.R. Kaeding, and D.E. Burkhalter. 1977. Use of coldwater refuge by rainbow and brook trout in a geothermal heated stream. Progressive Fish Culturalist 39:37-39.

Latta, W.C. 1964. Relationship of young-of-the-year trout to mature trout and groundwater. Transactions of the American Fisheries Society 94:32-39.

Leary, R.F., F.W. Allendorf and S.H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath river drainages. Conservation Biology 7:856-865

Leathe, S. A. and P.J. Graham. 1983. Cumulative effects of micro-hydro development on the fisheries of the Swan River drainage, Montana. Progress Report, project no. 82-19. Bonneville Power Administration, Portland, Oregon.

Leathe, S.A. and M.D. Enk. 1985. Cumulative effects of micro-hydro development on the fisheries of the Swan River drainage, Montana. Volume I: Summary Report. project no. 82-19. Montana Department of Fish, Wildlife and Parks, Kalispell, Montana.

Leggett, J.W. 1969. The reproductive biology of the Dolly Varden char Salvelinus malma. Master's thesis. University of Victoria, Victoria, British Columbia, Canada.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial Processes in Geomorphology. W.H. Freeman, New York.

Lyons, J.K. and R.L. Beschta. 1983. Land use, floods, and channel changes: Upper middle fork Willamette River, Oregon (1936-1980). Water Resources Research 19(2):463-471.

McIntosh, B.A., J.R. Sedell, J.E. Smith, R.C. Wissmar, S.E. Clarke, G.H. Reeves, and L.A. Brown. 1994. Historical changes in fish habitat for select river basins of eastern Oregon and Washington. Northwest Science 68:36-53.

McPhail, J.D. and C.B. Murray. 1979. The early life history and ecology of Dolly Varden(*Salvelinus malma* in the upper Arrow Lakes. Report to the British Columbia Hydro and Power Authority and Kootenay Department of Fish and Wildlife.

Meehan, W.R., editor. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Megahan, W.F. 1972. Subsurface flow interception by a logging road in mountains of central Idaho. Pages 350-356 *in* S.C. Csallany, T.G. McLaughlin, and W.D. Striffler, editors. Proceedings, Watersheds in Transition Symposium. American Water Resources Association, Urbana, Illinois.

Montana Bull Trout Scientific Group, 1996. Swan River drainage bull trout status report (including Swan Lake). Report to the Montana Bull Trout Restoration Team, Helena, Montana.

Mullan, J.W., K. Williams, G. Rhodus, T. Hillman, and J. McIntyre. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. U.S. Fish and Wildlife Service Monograph 1.

Needham, P.R. and T.M. Vaughan. 1952. Spawning of the Dolly Varden, *Salvelinus malma*, in Twin Creek, Idaho. Copeia 3:197-199.

Nielsen, J.L. 1993. The role of cold-pool refugia in the freshwater fish assemblage in northern California rivers. Pages 79-95 *in* Proceedings of the Symposium on Biodiversity of Northwestern California, Santa Rosa, California.

Platts, W. S., M. Hill, T. W. Hillman and M. D. Miller. 1993. Preliminary Status Report on Bull Trout in California, Idaho, Montana, Nevada, Oregon and Washington. Prepared for the Intermountain Forest Industry Association, Coeur d' Alene, Idaho.

Pluhowski, E.J. and I.H. Kantrowitz. 1963. Influence of land-surface conditions on groundwater temperatures in Southwestern Suffolk County, Long Island, New York. U.S. Geological Survey Professional Paper 475b.

Pratt, K.L. 1984. Habitat use and species interactions of juvenile cutthroat(*Salmo clarki lewisii*) and bull trout(*Salvelinus confluentus*) in the upper Flathead River Basin. Master's thesis. University of Idaho, Moscow, Idaho.

Pratt, K.L. 1985. Pend O'Reille trout and char life history study. Idaho Department of Fish and Game, Boise, Idaho.

Pratt, K.L. 1992. A review of bull trout life history. Pages 5-9 *in* P.J. Howell and D.V. Buchanan, editors. Proceedings of the Gearhart Mountain Bull Trout Workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

Regier, H.A., R.L. Welcomme, R.J. Steedman, and H.F. Henderson. 1989. Rehabilitation of degraded river systems. Pages 86-97 *in* D.P. Dodge, editor. Proceedings of the International Large River Symposium. Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences 106.

Rieman, B. E. and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service, Intermountain Research Station. General Technical Report INT-308.

Rieman, B.E. and J.D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285-296.

Rieman, B.E. and J.D. McIntyre. 1996. Spatial and temporal variability in bull trout redd counts. North American Journal of Fisheries Management 16: 132-141.

Ringler, N.H. and J.D. Hall. 1975. Effects of logging on water temperature and dissolved oxygen content in spawning beds. Transactions of the American Fisheries Society 104:111-121.

Rumsey, S. 1991. Interoffice memorandum to Swan drainage files. Montana Department of Fish, Wildlife, and Parks, Kalispell, Montana.

Schälchli, U. 1992. The clogging of coarse gravel river beds by fine sediment. Hydrobiologia 235/236:189-197.

Sedell, J.R. and J.L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal. Verhandlungen der Internationalen für Theoretische und Angewandte Limnologie 22: 1828-1834.

Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford and C.P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14(5):711-724.

Shepard, B.B., K. Pratt, P. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River basin, Montana. Montana Department of Fish, Wildlife, and Parks, Kalispell, Montana.

Shepard, B.G., G.F. Hartman, and W.J. Wilson. 1986. Relationships between stream and intragravel temperatures in coastal drainages, and some implications for fisheries workers. Canadian Journal of Fisheries and Aquatic Sciences 43:1818-1822.

Spencer, C.N. 1991. Evaluation of historical sediment deposition related to land use through analysis of lake sediments. Flathead Basin Forest Practices, Water Quality and Fisheries Cooperative Program, Flathead Basin Commission, Kalispell, Montana, USA.

Stanford, J. A. and J. V. Ward. 1992. Management of aquatic resources in large catchments: recognizing interactions between ecosystem connectivity and environmental disturbance. Pages 91-124 in Naiman, R.J., editor. Watershed management. Springer-Verlag, New York.

Stanford, J. A. and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12:48-62.

Strahler, A.N. 1964. Quantitative geomorphology of drainage basins and channel networks. Pages 39-74 in V.T. Chow, editor. Handbook of Applied Hydrology. McGraw-Hill, New York.

Swanson, F.J., G.W. Lienkaemper, and J.R. Sedell. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. U.S. Forest Service. General Technical Report PNW-56.

Vaux, W.G. 1962. Interchange of stream and intragravel water in a salmon spawning riffle. U.S. Fish and Wildlife Service Special Sciences Report Fisheries 405.

Viereck, L.A., K. Van Cleve, P.C. Adams, and R.E. Schlentner. 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. Canadian Journal of Forest Research 23:899-913.

U.S. Fish and Wildlife Service. 1994. Memorandum. Warranted, but precluded administrative 12-month finding on a petition to list the bull trout under the Endangered Species Act. U.S. Fish and Wildlife Service, Portland, Oregon.

Weaver, T.M. 1991. Coal Creek Fisheries Monitoring Study number IX and forest-wide fisheries monitoring-1990. Montana Department of Fish, Wildlife, and Parks Special Projects, Kalispell, Montana.

Weaver, T.M. 1992. Coal Creek Fisheries Monitoring Study number X and forest-wide fisheries monitoring-1991. Montana Department of Fish, Wildlife, and Parks Special Projects, Kalispell, Montana.

Weaver, T.M. in press. Status of adfluvial bull trout populations in Montana's Flathead drainage: The good, the bad, and the unknown. Proceedings, Friends of the Bull Trout Conference, May 1994. Calgary, Alberta.

Weaver, T.M. and R.G. White. 1985. Coal Creek Fisheries Monitoring Study number III. U.S. Forest Service, Flathead National Forest. Contract 53-0385-3-2685.

Weaver, T.M. and J. Fraley. 1991. Fisheries habitat and fish populations. Flathead basin forest practices, water quality and fisheries cooperative program. Report prepared for the Flathead Basin Commission, Kalispell, Montana.

Webster, J.R., S.W. Golladay, E.T. Benfield, D.J. D'Angelo, and G.T. Peters. 1990. Effects of forest disturbance on particulate organic matter budgets of small streams. Journal of the North American Benthological Society 9(2):120-140.

Wemple, B.C., J.A. Jones, and G.E. Grant. 1996. Channel network extension by logging roads in two basins, western Cascades, Oregon. Water Resources Bulletin 32(6):1195-1207.

Williams, J.E. 1991. Preserves and refuges for native western fishes: history and management. Pages 171-189 in W. L. Minckley and J.E. Deacon, editors. Battle against extinction: native fish management in the American west. University of Arizona Press, Tuscon, Arizona, USA.

Wissmar, R.C., J.E. Smith, B.A. McIntosh, H.W. Li, G.H. Reeves, and J.R. Sedell. 1994. A history of resource use and disturbance in riverine basins of eastern Oregon and Washington (early 1800s-1900s). Northwest Science68:1-35.

Table 1. Raw data and results of time trend analysis for the nine principle spawning drainages, of which eight had sufficient data for the analysis[***].

Stream	Redd Counts															Time Trends		
	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	slope	p-value	r
Lion(1)	63	49	88	26	46	33	65	84	58	94	100	123	141	170	7.85	.001	.788
Elk(2)	56	91	93	19	53	162	201	186	136	140	143	139	195	150	8.77	.011	.656
Squeezer(3)	41	57	83	24	55	64	9	67	42	101	115	106	91	149	6.25	.007	.684
Goat(4)	33	39	31	40	56	31	46	34	27	31	17	64	66	32	.60	ns	.175
Piper(5)	0	0	1	*	*	*	*	25	*	18	*	*	*	10	1.21	ns	.356
Jim(6)	*	7	6	*	*	*	*	39	22	40	45	43	53	56	4.26	.001	.949
Cold(7)	1	9	6	*	*	*	*	*	*	5	.*	*	*	21	.99	ns	.744
Lost(8)	11	7	19	*	*	*	*	*	13	6	*	*	17	21	.45	ns	.410
Woodward(9)	0	3	*	*	*	*	*	*	*	36	*	*	*	77		**	

* = No counts conducted ** = Insufficient data for time trend analysis
*** Redd count data provided by Montana Department of Fish, Wildlife and Parks.

Table 2. Geomorphic variables that were examined as a part of this study. Accessibility refers to whether migratory bull trout can navigate the stream.

| Geomorphic Variables Examined | | |
Morphometric Measures	Slope Classes	BAVS - Related
Drainage area	% drainage < 1 % slope	Maximum valley bottom width
Stream order	% drainage 1-2 % slope	Mean valley bottom width
Total stream length	% drainage 2-7 % slope	Variation in valley bottom width
Accessible stream length	% drainage 7-20 % slope	Number of gradient steps > 10%
Drainage density	% drainage 20-40 % slope	Number of BAVS
Drainage length	% drainage 40-55 % slope	Total area of BAVS
Average stream gradient	% drainage >55 % slope	Length of accessible BAVS
Gradient of accessible stream length	% drainage >55 % slope	Area of accessible BAVS
Relief ratio		
Form ratio		
Elongation ratio		
Mean bedrock dip angle		

Table 3. Results of the nine drainage correlation matrix including geomorphic variables that displayed consistently significant associations with bull trout redd counts from the 1983, 1991, and 1995 basin-wide surveys, as well as an average for all years surveyed and the rate of change in redd numbers from 1983 to 1995.

Variable	Redd Counts				
	1983	1991	1995	Average	Rate of Change
Mean valley bottom width	.717 **	.724 **	.779 ***	.787 ***	.723 **
Variation in valley bottom width	.630 *	.671 **	.738 **	.732 **	.694 **
Total area of BAVS	.535	.612 *	.753 **	.700 **	.652 *
Length of accessible BAVS	.795 **	.850 ***	.818 ***	.863 ***	.747 **
Area of accessible BAVS	.731 **	.820 ***	.876 ***	.867 ***	.843 ***

* = p < .10, ** = p < .05, *** = p < .01

Table 4. Results of the nine drainage correlation matrix including land use history variables vs. bull trout redd densities from the 1983, 1991 and 1995 basin-wide surveys, as well as an average for all years surveyed. Densities were calculated as counts/km surveyed and counts/area of accessible BAVS. The densities adjusted for geomorphology are denoted by an 'A'.

Variable	Redd Density							
	1983	1983A	1991	1991A	1995	1995A	Average	AverageA
Road density 1954	-.738 **	-.409	-.670 **	-.829 ***	-.531 *	-.682 **	-.504	-.923 ***
Road density 1966	-.817 ***	-.590	-.671 **	-.794 **	-.397	-.607 *	-.540 *	-.904 ***
Road density 1976	-.836 ***	-.506	-.834 ***	-.666 **	-.522	-.710 **	-.714 **	-.852 ***
Road density 1983	-.671 *	-.261	-.723 **	-.657 **	-.545 *	-.804 ***	-.623 *	-.779 **
Road density 1991	-.741 **	-.485	-.657 **	-.523	-.330	-.505	-.638 *	-.581 *
Number of road crossings 1982	-.835 ***	-.642 *	-.664 **	-.751 **	-.486	-.410	-.498	-.781 **
Number of road crossings 1991	-.863 ***	-.623 *	-.756 **	-.592	-.456	-.305	-.663 **	-.636 *
Crossings per stream length 1982	-.787 **	-.750 **	-.612 *	-.629 **	-.240	-.389	-.498	-.772 **
Crossings per stream length 1991	-.902 ***	-.855 ***	-.793 ***	-.304	-.445	-.247	-.793 ***	-.593 *

* = p < .10, ** = p < .05, *** = p < .01

Table 5. Results of an all stream-wise analysis for the three basin-wide survey years of 1983, 1991, and 1995. Numbers in parentheses are results of the same analysis using redd densities (counts/km surveyed) instead of redd counts.

| | Redd Counts and Densities | | | | Time Trend | |
	1983	1991	1995	slope	p-value	r
Mean	32.9 (3.56)	52.3 (5.90)	76.2 (7.90)	3.47 (.353)	.127 (.130)	.34 (.33)
S.D	31.6 (3.42)	47.7 (5.22)	63.62(6.53)			
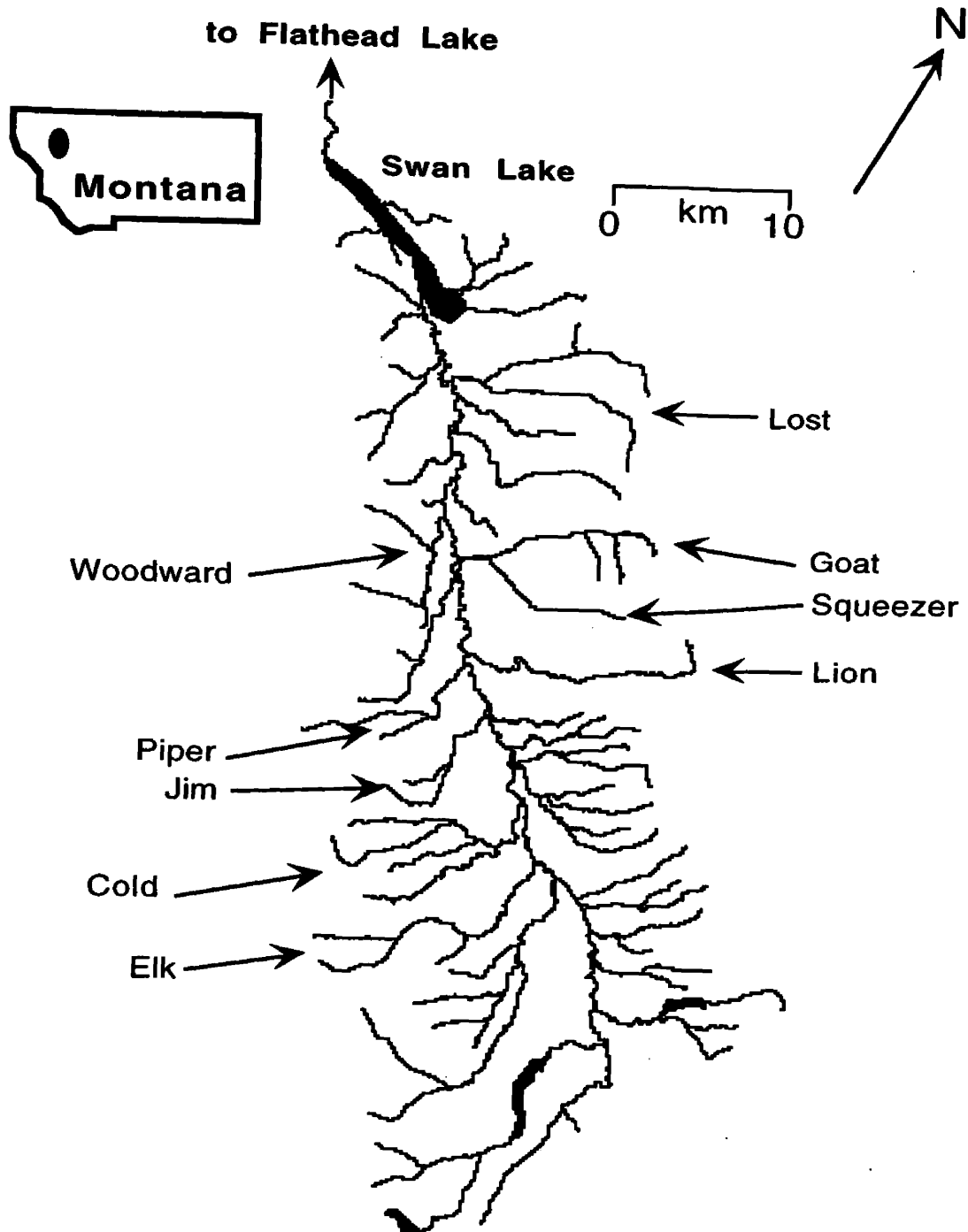
Figure 1. Map of the Swan River basin. The nine primary bull trout spawning tributary streams are identified by name. Inset indicates the location of the Swan River basin in western Montana.
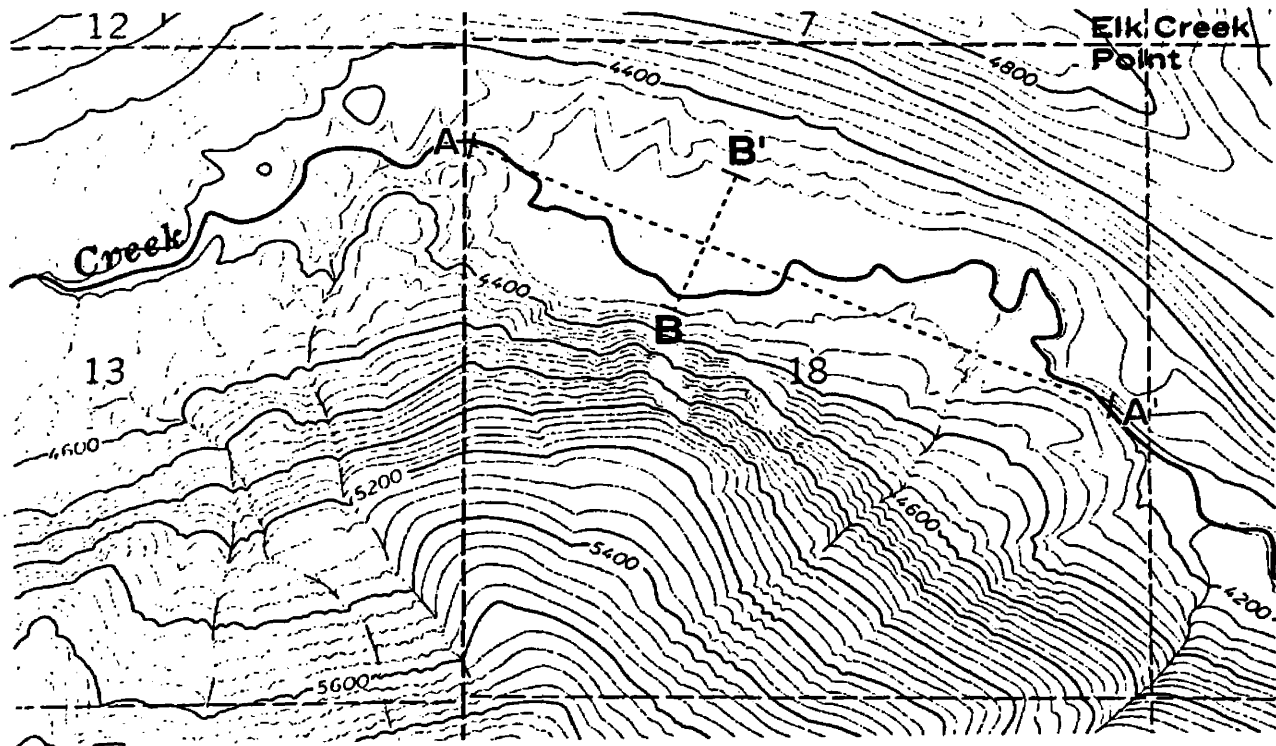
Figure 2. One of the bounded alluvial valley segments (BAVS) in the Elk Creek catchment. The dimensions of BAVS were measured directly from topographic quad maps (A - A' = length, B - B' = maximum valley bottom width.
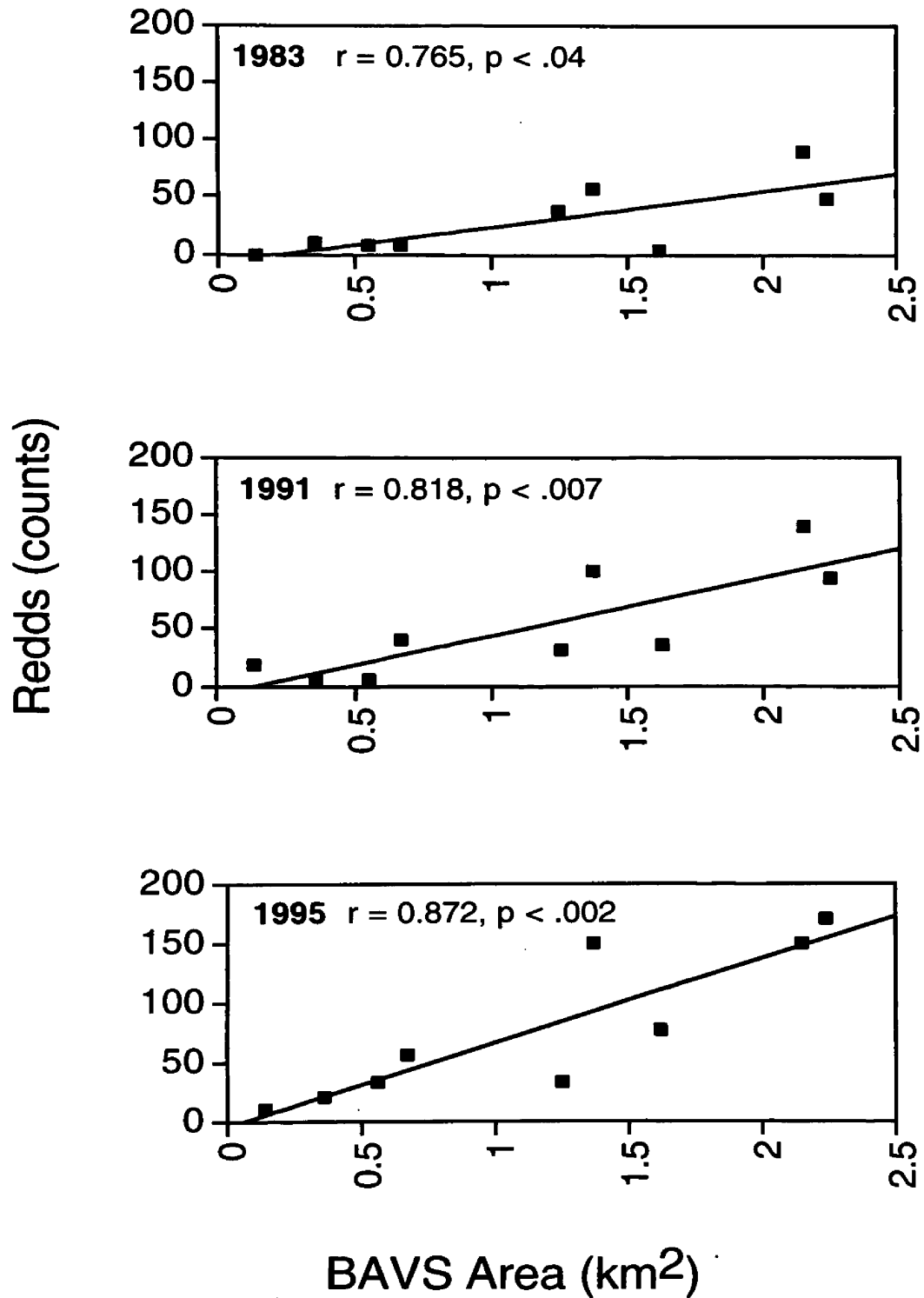
Figure 3. The number of bull trout redds counted in 1983, 1991, and 1995 surveys versus the area (km2) of bounded alluvial valley segments (BAVS) accessible to spawning bull trout for the nine tributary spawning streams (numbered as in Table 1) in the Swan River basin.
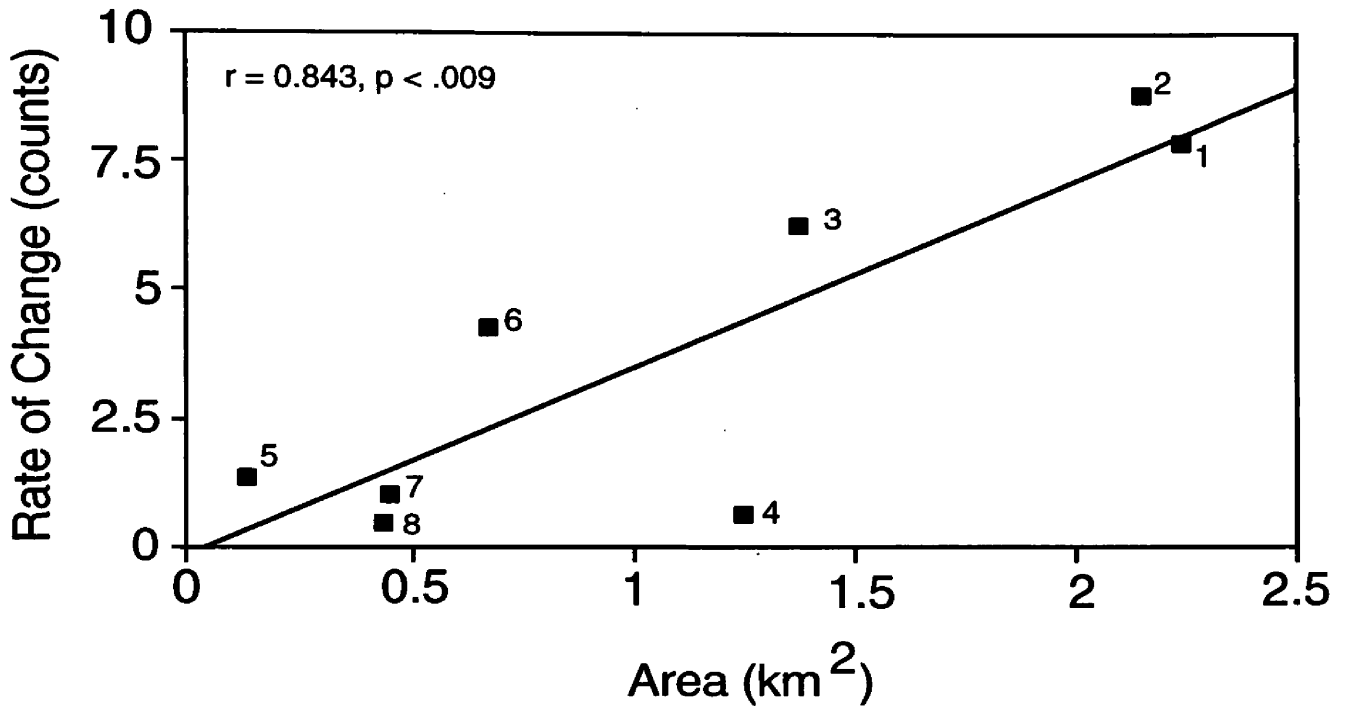
Figure 4. The average annual rate of change (redds/year) in bull trout
spawning between 1983 and 1995 versus the area (km2) of bounded alluvial
valley segments (BAVS) accessible to spawning bull trout for eight tributary
spawning streams (numbered as in Table 1) in the Swan River basin having
long-term data.
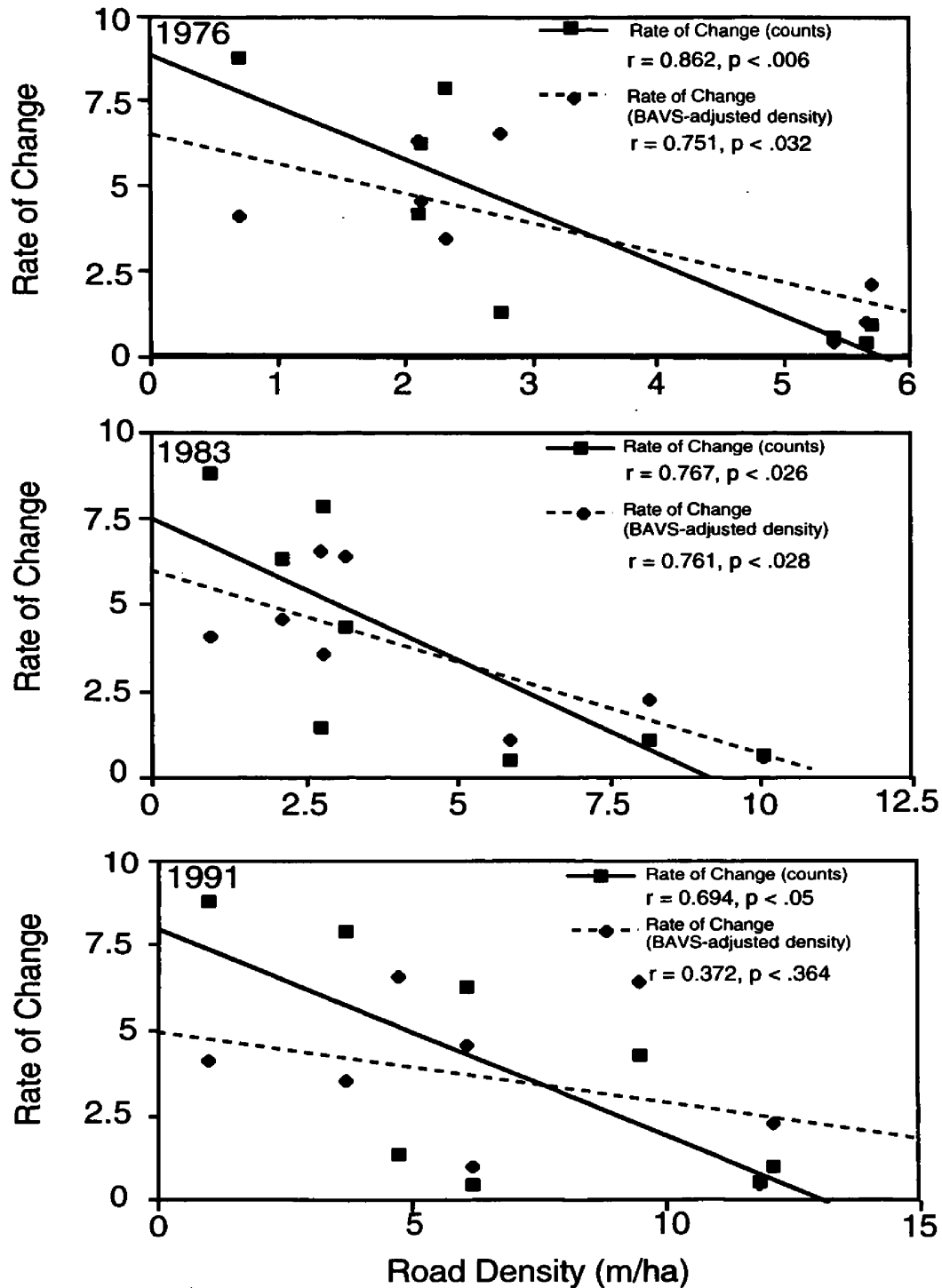
Figure 5. The average annual rate of change in redd density (counts per km surveyed/year) and BAVS-adjusted redd density (counts per area of accessible BAVS/year) between 1983 and 1995 versus 1976, 1983, and 1991 road densities (m/ha) for the eight tributary spawning streams in the Swan River basin having long-term data.

APPENDIX 1

GEOMORPHIC AND LAND-USE CHARACTERS OF THE NINE PRINCIPAL BULL TROUT SPAWNING STREAMS OF THE SWAN DRAINAGE

Variable	Stream			
	Lion	Elk	Cold	Lost
Stream order	3	4	4	4
Drainage area (ha)	8184	6708	8599	7692
Total stream length (m)	56137	55674	90470	41989
Accessible stream length (m)	11100	16300	24000	15500
Drainage density	6.859	8.299642	10.52099	5.458788
Average stream gradient (%)	0.05068	0.04326	0.0546	0.06895
Gradient accessible length (%)	0.0146	0.0174	0.032	0.0268
Drainage length (m)	20121	20241	17470	15904
Form ratio	0.4067	0.331407	0.492215	0.483652
Relief ratio	0.091	0.0753	0.087	0.093
% drainage < 1 % slope	5.5	2.6	5.1	3.9
% drainage 1-2 % slope	2.5	5.7	3.4	0.4
% drainage 2-7 % slope	9.4	8.6	19.5	5.3
% drainage 7-20 % slope	6.7	7.9	20.8	4.4
% drainage 20-40 % slope	20.6	28.2	27.2	19.8
% drainage 40-55 % slope	16.9	13	5.9	18.3
% drainage > 55 % slope	38.4	33.5	18.1	48.1
Mean bedrock dip angle	22.14	14.56	12.78	17.78
Maximum valley bottom width (km)	0.602	0.41	0.241	0.241
Mean valley bottom width (km)	0.6583	0.5509	0.306862	0.249193
Variation in valley bottom width	0.297323	0.227931	0.087001	0.061925
Length of BAVS (m)	5670	6500	2255	3600
Total area of BAVS (km^2)	4.339	2.43	0.357	1.306
Area of accessible BAVS (km^2)	2.237	2.148	0.357	0.556
BAVS length/accessible stream length	0.510810	0.398773	0.093958	0.232258
Road density 1954 (m/ha)	0.41	0.19	0.79	1.26
Road density 1966 (m/ha)	0.79	0.29	3.01	5.27
Road density 1976 (m/ha)	2.3	0.69	5.69	5.65
Road density 1983 (m/ha)	2.83	0.94	8.16	5.84
Road density 1991 (m/ha)	3.66	0.94	12.13	6.13
Road Crossings 1982	23.00	8.00	60.00	54.00
Road Crossings 1991	25	8	90	58
Crossings per stream length 1982	0.000409	0.000143	0.00066	0.001286
Crossings per stream length 1991	0.000445	0.000143	0.00010	0.001381

APPENDIX 1
(continued)

Variable	Stream		
	Woodward	Jim	Goat
Stream order	4	3	3
Drainage area (ha)	6449	4740	5258
Total stream length (m)	44370	41042	41801
Accessible stream length (m)	16000	9500	8500
Drainage density	6.880136	8.658649	7.949980
Average stream gradient (%)	0.07295	0.0491	0.0772
Gradient accessible length (%)	0.0172	0.0373	0.0275
Drainage length (m)	8772	5783	5975
Form ratio	0.418168	0.298038	0.351941
Relief ratio	0.08	0.085	0.102
% drainage < 1 % slope	6.5	5.7	2.9
% drainage 1-2 % slope	2.7	4.4	1.44
% drainage 2-7 % slope	4.8	8.3	7.47
% drainage 7-20 % slope	22.4	26	10.93
% drainage 20-40 % slope	40	39	23.78
% drainage 40-55 % slope	10	6	13.58
% drainage > 55 % slope	13.6	11	39.9
Mean bedrock dip angle	21.43	17.5	33.57
Maximum valley bottom width (km)	0.386	0.289	0.361
Mean valley bottom width (km)	0.331730	0.256578	0.412280
Variation in valley bottom width	0.130689	0.066645	0.149757
Length of BAVS (m)	6430	3500	5300
Total area of BAVS (km^2)	1.623	0.77	1.85
Area of accessible BAVS (km^2)	1.623	0.668	1.252
BAVS length/accessible stream length	0.401875	0.368421	0.623529
Road density 1954 (m/ha)	0.57	0.31	0.83
Road density 1966 (m/ha)	4.34	1.26	2.94
Road density 1976 (m/ha)	5.89	2.11	5.39
Road density 1983 (m/ha)	5.89	3.16	10.04
Road density 1991 (m/ha)	11.4	9.47	11.85
Road Crossings 1982	58.00	19.00	17.00
Road Crossings 1991	63	46	24
Crossings per stream length 1982	0.001307	0.000463	0.000407
Crossings per stream length 1991	0.001420	0.001121	0.000574

APPENDIX 1
(continued)

Variable	Stream	
	Squeezer	Piper
Stream order	3	3
Drainage area (ha)	3652	3289
Total stream length (m)	34779.5	26479.2
Accessible stream length (m)	7800	14000
Drainage density	9.523411	8.050836
Average stream gradient (%)	0.08795	0.0704
Gradient accessible length (%)	0.0355	0.0508
Drainage length (m)	5518	3662
Form ratio	0.256875	0.275760
Relief ratio	0.129	0.118
% drainage < 1 % slope	4.34	1.4
% drainage 1-2 % slope	2	0.43
% drainage 2-7 % slope	11.93	9.5
% drainage 7-20 % slope	9.1	7.7
% drainage 20-40 % slope	18.9	19.9
% drainage 40-55 % slope	14.6	16.8
% drainage > 55 % slope	39.14	44.3
Mean bedrock dip angle	20	18.06
Maximum valley bottom width (km)	0.241	0.145
Mean valley bottom width (km)	0.332758	0.190625
Variation in valley bottom width	0.083557	0.032410
Length of BAVS (m)	5600	1500
Total area of BAVS (km^2)	1.372	0.135
Area of accessible BAVS (km^2)	1.372	0.135
BAVS length/accessible stream length	0.717948	0.107142
Road density 1954 (m/ha)	0	0
Road density 1966 (m/ha)	0.84	0
Road density 1976 (m/ha)	2.12	2.74
Road density 1983 (m/ha)	2.12	2.74
Road density 1991 (m/ha)	6.08	4.75
Road Crossings 1982	12.00	7.00
Road Crossings 1991	18	24
Crossings per stream length 1982	0.000345	0.000264
Crossings per stream length 1991	0.000518	0.000906

APPENDIX 2

VHG AND BULL TROUT REDD DATA
FROM ALLUVIAL REACHES OF LION, ELK, COLD AND LOST CREEK DRAINAGES

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Lion	BAVS	2	C	-2.32353	7
Lion	BAVS	2	C	-0.13636	
Lion	BAVS	2	C	-0.66834	
Lion	BAVS	2	C	-1.66255	
Lion	BAVS	2	C	-2.62069	
Lion	BAVS	2	C	-0.49068	
Lion	BAVS	2	C	-2.17174	
Lion	BAVS	2	C	-1.89697	
Lion	BAVS	2	C	-1.02581	
Lion	BAVS	2	C	-0.29299	
Lion	BAVS	2	C	-1.89091	
Lion	BAVS	2	C	-0.30612	
Lion	BAVS	2	C	-0.26552	
Lion	BAVS	2	C	-0.07586	
Lion	BAVS	2	C	-1.34557	
Lion	BAVS	2	B	-0.10345	1
Lion	BAVS	2	B	-0.11765	
Lion	BAVS	2	B	-0.07813	
Lion	BAVS	2	B	-0.01429	
Lion	BAVS	2	B	-0.00882	
Lion	BAVS	2	B	0	
Lion	BAVS	2	B	0	
Lion	BAVS	2	B	0	
Lion	BAVS	2	B	0	
Lion	BAVS	2	B	-0.01587	
Lion	BAVS	2	B	-0.04464	
Lion	BAVS	2	B	-0.00935	
Lion	BAVS	2	B	-0.05282	
Lion	BAVS	2	B	0	
Lion	BAVS	2	B	0	
Lion	BAVS	2	A	0.0125	23

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Lion	BAVS	2	A	0.019355	
Lion	BAVS	2	A	0.031579	
Lion	BAVS	2	A	-0.00714	
Lion	BAVS	2	A	-0.03056	
Lion	BAVS	2	A	0.041791	
Lion	BAVS	2	A	0.062162	
Lion	BAVS	2	A	0.08	
Lion	BAVS	2	A	-0.02188	
Lion	BAVS	2	A	0.017647	
Lion	BAVS	2	A	0.128125	
Lion	BAVS	2	A	0.04023	
Lion	BAVS	2	A	0.127586	
Lion	BAVS	2	A	-0.01038	
Lion	BAVS	2	A	-0.0507	
Lion	BAVS	2	A	0.057214	
Lion	BAVS	2	A	0.018182	
Lion	BAVS	2	A	0.16129	
Lion	BAVS	2	A	0	
Lion	BAVS	2	A	0.028571	
Lion	BAVS	2	A	0.014706	
Lion	BAVS	2	A	0.096774	
Lion	BAVS	2	A	0.16	
Lion	BAVS	2	A	0.18125	
Lion	BAVS	2	A	0.234286	
Lion	BAVS	1	C	-0.08387	21
Lion	BAVS	1	C	0.020576	
Lion	BAVS	1	C	0.167224	
Lion	BAVS	1	C	-0.02695	
Lion	BAVS	1	C	0.039216	
Lion	BAVS	1	C	0.082759	
Lion	BAVS	1	C	0.025	
Lion	BAVS	1	C	0.062338	
Lion	BAVS	1	C	0.057692	
Lion	BAVS	1	C	-0.01642	
Lion	BAVS	1	C	-0.08182	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Lion	BAVS	1	C	0.027708	
Lion	BAVS	1	C	0	
Lion	BAVS	1	C	0.016667	
Lion	BAVS	1	C	0.047619	
Lion	BAVS	1	B	0.014493	10
Lion	BAVS	1	B	0.040956	
Lion	BAVS	1	B	0.027907	
Lion	BAVS	1	B	-0.04118	
Lion	BAVS	1	B	0.072539	
Lion	BAVS	1	B	0.115152	
Lion	BAVS	1	B	0.053061	
Lion	BAVS	1	B	-0.01563	
Lion	BAVS	1	B	-0.156	
Lion	BAVS	1	B	-0.16959	
Lion	BAVS	1	B	-0.00333	
Lion	BAVS	1	B	-0.0672	
Lion	BAVS	1	B	0.057143	
Lion	BAVS	1	B	-0.04786	
Lion	BAVS	1	B	0.087591	
Lion	BAVS	1	B	-0.04923	
Lion	BAVS	1	A	-0.16757	11
Lion	BAVS	1	A	-0.16615	
Lion	BAVS	1	A	0.023729	
Lion	BAVS	1	A	0.031128	
Lion	BAVS	1	A	0.024476	
Lion	BAVS	1	A	-0.02115	
Lion	BAVS	1	A	-0.00946	
Lion	BAVS	1	A	0.038462	
Lion	BAVS	1	A	0.108844	
Lion	BAVS	1	A	0.032995	
Lion	BAVS	1	A	0.04038	
Lion	BAVS	1	A	0.044776	
Lion	BAVS	1	A	0.010695	
Lion	BAVS	1	A	-0.0438	
Lion	BAVS	1	A	0	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Lion	UAVS	1	B	-0.70357	0
Lion	UAVS	1	B	-0.53878	
Lion	UAVS	1	B	-0.66384	
Lion	UAVS	1	B	-0.60311	
Lion	UAVS	1	B	-0.57042	
Lion	UAVS	1	B	-0.56061	
Lion	UAVS	1	B	-0.71318	
Lion	UAVS	1	B	-0.77049	
Lion	UAVS	1	B	-0.71192	
Lion	UAVS	1	B	-0.77778	
Lion	UAVS	1	B	-0.66897	
Lion	UAVS	1	B	-0.65347	
Lion	UAVS	1	B	-0.70357	
Lion	UAVS	1	B	-0.53878	
Lion	UAVS	1	B	-0.66384	
Lion	UAVS	1	A	0	2
Lion	UAVS	1	A	0.010714	
Lion	UAVS	1	A	-0.24786	
Lion	UAVS	1	A	-0.06122	
Lion	UAVS	1	A	-0.23022	
Lion	UAVS	1	A	0.016779	
Lion	UAVS	1	A	0.019672	
Lion	UAVS	1	A	-0.17705	
Lion	UAVS	1	A	-0.20382	
Lion	UAVS	1	A	-0.12059	
Lion	UAVS	1	A	0.006135	
Lion	UAVS	1	A	0.009524	
Lion	UAVS	1	A	0.013029	
Lion	UAVS	1	A	-0.02756	
Lion	UAVS	1	A	-0.02392	
Elk	BAVS	3	C	-0.07451	3
Elk	BAVS	3	C	-0.07164	
Elk	BAVS	3	C	-0.00889	
Elk	BAVS	3	C	-0.65	
Elk	BAVS	3	C	0	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Elk	BAVS	3	C	-0.38788	
Elk	BAVS	3	C	-0.90227	
Elk	BAVS	3	C	-0.99444	
Elk	BAVS	3	C	-0.29841	
Elk	BAVS	3	C	-0.27143	
Elk	BAVS	3	C	0.008696	
Elk	BAVS	3	C	-0.58636	
Elk	BAVS	3	C	-0.01311	
Elk	BAVS	3	C	-0.0557	
Elk	BAVS	3	C	-0.04	
Elk	BAVS	3	B	-0.05	5
Elk	BAVS	3	B	0.056716	
Elk	BAVS	3	B	0.070621	
Elk	BAVS	3	B	0.032558	
Elk	BAVS	3	B	0.0181	
Elk	BAVS	3	B	0.055556	
Elk	BAVS	3	B	-0.04683	
Elk	BAVS	3	B	-0.0274	
Elk	BAVS	3	B	-0.01538	
Elk	BAVS	3	B	-0.08438	
Elk	BAVS	3	B	-0.017	
Elk	BAVS	3	B	0	
Elk	BAVS	3	B	-0.03315	
Elk	BAVS	3	B	0.077966	
Elk	BAVS	3	B	0.128834	
Elk	BAVS	3	A	0.0375	4
Elk	BAVS	3	A	0.032	
Elk	BAVS	3	A	-0.00375	
Elk	BAVS	3	A	0.027451	
Elk	BAVS	3	A	0.042105	
Elk	BAVS	3	A	0.012618	
Elk	BAVS	3	A	0.037415	
Elk	BAVS	3	A	0.022642	
Elk	BAVS	3	A	0.029412	
Elk	BAVS	3	A	0	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Elk	BAVS	3	A	0.003333	
Elk	BAVS	3	A	0	
Elk	BAVS	3	A	0	
Elk	BAVS	3	A	-0.01188	
Elk	BAVS	3	A	0.006897	
Elk	BAVS	3	A	0.064151	
Elk	BAVS	3	A	0.05	
Elk	BAVS	3	A	0.024	
Elk	BAVS	3	A	0.018182	
Elk	BAVS	3	A	0.021084	
Elk	BAVS	3	A	-0.00667	
Elk	BAVS	3	A	0.027451	
Elk	BAVS	3	A	0.006173	
Elk	BAVS	3	A	0.022409	
Elk	BAVS	3	A	-0.0029	
Elk	BAVS	3	A	-0.03922	
Elk	BAVS	2	C	-0.04242	25
Elk	BAVS	2	C	0.096552	
Elk	BAVS	2	C	0.01	
Elk	BAVS	2	C	0.026059	
Elk	BAVS	2	C	0.013333	
Elk	BAVS	2	C	0.205556	
Elk	BAVS	2	C	0.006667	
Elk	BAVS	2	C	0.060976	
Elk	BAVS	2	C	0.038889	
Elk	BAVS	2	C	0.013605	
Elk	BAVS	2	C	0.028302	
Elk	BAVS	2	C	0.154545	
Elk	BAVS	2	C	0.205714	
Elk	BAVS	2	C	0.018947	
Elk	BAVS	2	C	0.021739	
Elk	BAVS	2	C	0.0225	
Elk	BAVS	2	C	-0.00816	
Elk	BAVS	2	C	-0.02857	
Elk	BAVS	2	C	0.02	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Elk	BAVS	2	B	0.021077	
Elk	BAVS	2	C	0.00823	
Elk	BAVS	2	C	0.049724	
Elk	BAVS	2	C	0.044521	
Elk	BAVS	2	C	0.003257	
Elk	BAVS	2	C	0.040284	
Elk	BAVS	2	C	0	
Elk	BAVS	2	C	0.019169	
Elk	BAVS	2	B	-0.02083	0
Elk	BAVS	2	B	-0.02	
Elk	BAVS	2	B	0.014286	
Elk	BAVS	2	B	-0.17358	
Elk	BAVS	2	B	-0.01983	
Elk	BAVS	2	B	0.019178	
Elk	BAVS	2	B	0.026316	
Elk	BAVS	2	B	0.020202	
Elk	BAVS	2	B	-0.00294	
Elk	BAVS	2	B	-0.0638	
Elk	BAVS	2	B	-0.34414	
Elk	BAVS	2	B	-0.45143	
Elk	BAVS	2	B	0.009042	
Elk	BAVS	2	B	0.020619	
Elk	BAVS	2	B	-0.01923	
Elk	BAVS	2	B	-0.10468	
Elk	BAVS	2	B	-0.02174	
Elk	BAVS	2	B	0.036058	
Elk	BAVS	2	B	-0.09479	
Elk	BAVS	2	A	0.004167	1
Elk	BAVS	2	A	0.017316	
Elk	BAVS	2	A	0.013274	
Elk	BAVS	2	A	0.021053	
Elk	BAVS	2	A	-0.09176	
Elk	BAVS	2	A	0.033333	
Elk	BAVS	2	A	-0.03789	
Elk	BAVS	2	A	0	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Elk	BAVS	2	A	-0.01754	
Elk	BAVS	2	A	0.036496	
Elk	BAVS	2	A	0.002083	
Elk	BAVS	2	A	0.027778	
Elk	BAVS	2	A	0.026882	
Elk	BAVS	2	A	-0.0221	
Elk	BAVS	2	A	-0.00494	
Elk	BAVS	1	C	-0.0597	7
Elk	BAVS	1	C	-0.05415	
Elk	BAVS	1	C	0	
Elk	BAVS	1	C	0	
Elk	BAVS	1	C	-0.0863	
Elk	BAVS	1	C	-0.15	
Elk	BAVS	1	C	-0.06268	
Elk	BAVS	1	C	-0.02222	
Elk	BAVS	1	C	0.051075	
Elk	BAVS	1	C	-0.94444	
Elk	BAVS	1	C	0.067857	
Elk	BAVS	1	C	-0.00896	
Elk	BAVS	1	C	0.015823	
Elk	BAVS	1	C	0.10453	
Elk	BAVS	1	C	-0.07368	
Elk	BAVS	1	B	-0.0507	0
Elk	BAVS	1	B	0	
Elk	BAVS	1	B	0	
Elk	BAVS	1	B	0	
Elk	BAVS	1	B	0.01791	
Elk	BAVS	1	B	0.002198	
Elk	BAVS	1	B	0.011268	
Elk	BAVS	1	B	0	
Elk	BAVS	1	B	0	
Elk	BAVS	1	B	0.013645	
Elk	BAVS	1	B	0.022989	
Elk	BAVS	1	B	-0.09504	
Elk	BAVS	1	B	0.007282	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Elk	BAVS	1	B	0.038961	
Elk	BAVS	1	B	-0.02759	
Elk	BAVS	1	A	-0.30256	3
Elk	BAVS	1	A	-0.34848	
Elk	BAVS	1	A	-0.01667	
Elk	BAVS	1	A	0.050505	
Elk	BAVS	1	A	0.010714	
Elk	BAVS	1	A	-0.01493	
Elk	BAVS	1	A	-0.00952	
Elk	BAVS	1	A	0.145161	
Elk	BAVS	1	A	-0.15194	
Elk	BAVS	1	A	0	
Elk	BAVS	1	A	0.035714	
Elk	BAVS	1	A	0.02449	
Elk	BAVS	1	A	0.019444	
Elk	BAVS	1	A	-0.02903	
Elk	BAVS	1	A	0	
Elk	UAVS	1	B	-1.40714	0
Elk	UAVS	1	B	-0.59444	
Elk	UAVS	1	B	-0.616	
Elk	UAVS	1	B	-0.46364	
Elk	UAVS	1	B	-0.2	
Elk	UAVS	1	B	-1.07778	
Elk	UAVS	1	B	-0.29114	
Elk	UAVS	1	B	-1.00645	
Elk	UAVS	1	B	-0.33571	
Elk	UAVS	1	B	-0.17429	
Elk	UAVS	1	B	-0.10667	
Elk	UAVS	1	B	-1.06024	
Elk	UAVS	1	B	-0.96429	
Elk	UAVS	1	B	-0.66842	
Elk	UAVS	1	B	-0.41	
Elk	UAVS	1	A	-0.17857	0
Elk	UAVS	1	A	-0.41622	
Elk	UAVS	1	A	-0.58065	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Elk	UAVS	1	A	-0.06667	
Elk	UAVS	1	A	-0.04348	
Elk	UAVS	1	A	-0.52203	
Elk	UAVS	1	A	-0.51601	
Elk	UAVS	1	A	-1.12258	
Elk	UAVS	1	A	-0.21181	
Elk	UAVS	1	A	-0.07667	
Elk	UAVS	1	A	0	
Elk	UAVS	1	A	-0.81205	
Elk	UAVS	1	A	-0.58791	
Elk	UAVS	1	A	-0.54474	
Elk	UAVS	1	A	-0.3475	
S.Lost	BAVS	2	C	0.046875	3
S.Lost	BAVS	2	C	0.007407	
S.Lost	BAVS	2	C	-0.00645	
S.Lost	BAVS	2	C	-0.21304	
S.Lost	BAVS	2	C	-0.01579	
S.Lost	BAVS	2	C	0	
S.Lost	BAVS	2	C	0.014706	
S.Lost	BAVS	2	C	0.021212	
S.Lost	BAVS	2	C	-0.11607	
S.Lost	BAVS	2	C	0	
S.Lost	BAVS	2	C	-0.02559	
S.Lost	BAVS	2	C	-0.05556	
S.Lost	BAVS	2	C	-0.048	
S.Lost	BAVS	2	C	-0.02392	
S.Lost	BAVS	2	C	-0.025	
S.Lost	BAVS	2	B	-0.00755	0
S.Lost	BAVS	2	B	-0.24545	
S.Lost	BAVS	2	B	-0.038	
S.Lost	BAVS	2	B	0.013514	
S.Lost	BAVS	2	B	-0.94	
S.Lost	BAVS	2	B	-0.07353	
S.Lost	BAVS	2	B	-0.0075	
S.Lost	BAVS	2	B	-0.29315	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
S.Lost	BAVS	2	B	-0.06234	
S.Lost	BAVS	2	B	0.009677	
S.Lost	BAVS	2	B	0	
S.Lost	BAVS	2	B	0.004878	
S.Lost	BAVS	2	B	0.018421	
S.Lost	BAVS	2	B	-0.02	
S.Lost	BAVS	2	B	-0.06216	
S.Lost	BAVS	2	A	-0.075	3
S.Lost	BAVS	2	A	0.02449	
S.Lost	BAVS	2	A	0.006522	
S.Lost	BAVS	2	A	0.067692	
S.Lost	BAVS	2	A	0.046667	
S.Lost	BAVS	2	A	0.066667	
S.Lost	BAVS	2	A	0.045946	
S.Lost	BAVS	2	A	0	
S.Lost	BAVS	2	A	0.017241	
S.Lost	BAVS	2	A	0.008571	
S.Lost	BAVS	2	A	0.048571	
S.Lost	BAVS	2	A	0	
S.Lost	BAVS	2	A	0.065	
S.Lost	BAVS	2	A	-0.01795	
S.Lost	BAVS	2	A	0	
S.Lost	BAVS	2	A	0.028571	
S.Lost	BAVS	2	A	0.046512	
S.Lost	BAVS	2	A	0.04	
S.Lost	BAVS	2	A	-0.00909	
S.Lost	BAVS	2	A	0.032	
Lost	UAVS	1	C	-0.35122	0
Lost	UAVS	1	C	-0.35979	
Lost	UAVS	1	C	-0.08372	
Lost	UAVS	1	C	-0.10455	
Lost	UAVS	1	C	-0.08095	
Lost	UAVS	1	C	-0.18537	
Lost	UAVS	1	C	-0.27391	
Lost	UAVS	1	C	-0.22979	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Lost	UAVS	1	C	-0.11	
Lost	UAVS	1	C	-0.015	
Lost	UAVS	1	C	0	
Lost	UAVS	1	C	-0.07317	
Lost	UAVS	1	C	-0.12857	
Lost	UAVS	1	C	-0.15714	
Lost	UAVS	1	C	-0.31163	
Lost	UAVS	1	B	-1.73929	0
Lost	UAVS	1	B	-0.4973	
Lost	UAVS	1	B	-0.65323	
Lost	UAVS	1	B	-0.05778	
Lost	UAVS	1	B	-0.06763	
Lost	UAVS	1	B	-0.97268	
Lost	UAVS	1	B	-0.75696	
Lost	UAVS	1	B	-1.39677	
Lost	UAVS	1	B	-0.23958	
Lost	UAVS	1	B	0	
Lost	UAVS	1	B	-1.03086	
Lost	UAVS	1	B	-1.44819	
Lost	UAVS	1	B	-0.93956	
Lost	UAVS	1	B	-0.72105	
Lost	UAVS	1	B	-0.5075	
Lost	UAVS	1	A	-0.18	0
Lost	UAVS	1	A	-0.48428	
Lost	UAVS	1	A	-1.63467	
Lost	UAVS	1	A	-3.07556	
Lost	UAVS	1	A	-1.67027	
Lost	UAVS	1	A	-0.96691	
Lost	UAVS	1	A	-1.66489	
Lost	UAVS	1	A	-1.61751	
Lost	UAVS	1	A	-0.6982	
Lost	UAVS	1	A	-3.2716	
Lost	UAVS	1	A	-2.8903	
Lost	UAVS	1	A	-1.51053	
Lost	UAVS	1	A	-0.95779	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Lost	UAVS	1	A	-1.60616	
Lost	UAVS	1	A	-0.43902	
Cold	UAVS	1	A	-1.44643	0
Cold	UAVS	1	A	-0.55556	
Cold	UAVS	1	A	-0.648	
Cold	UAVS	1	A	-0.24545	
Cold	UAVS	1	A	-0.1122	
Cold	UAVS	1	A	-0.98889	
Cold	UAVS	1	A	-0.26329	
Cold	UAVS	1	A	-1.17742	
Cold	UAVS	1	A	-0.28571	
Cold	UAVS	1	A	-0.14857	
Cold	UAVS	1	A	-1.11333	
Cold	UAVS	1	A	-1.03614	
Cold	UAVS	1	A	-0.88187	
Cold	UAVS	1	A	-0.70526	
Cold	UAVS	1	A	-0.4675	
Cold	UAVS	1	B	0.004651	5
Cold	UAVS	1	B	0.010169	
Cold	UAVS	1	B	0.009368	
Cold	UAVS	1	B	0.010178	
Cold	UAVS	1	B	0.007059	
Cold	UAVS	1	B	0.025559	
Cold	UAVS	1	B	0	
Cold	UAVS	1	B	0.006557	
Cold	UAVS	1	B	0.011268	
Cold	UAVS	1	B	0.002618	
Cold	UAVS	1	B	-0.07184	
Cold	UAVS	1	B	0.022642	
Cold	UAVS	1	B	-0.02424	
Cold	UAVS	1	B	0.027027	
Cold	UAVS	1	B	0.002315	
Cold	UAVS	1	C	0.062323	3
Cold	UAVS	1	C	0.039344	
Cold	UAVS	1	C	0.046296	

Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Cold	UAVS	1	C	0.011628	
Cold	UAVS	1	C	0.024476	
Cold	UAVS	1	C	0.034247	
Cold	UAVS	1	C	0	
Cold	UAVS	1	C	0	
Cold	UAVS	1	C	-0.01408	
Cold	UAVS	1	C	-0.07667	
Cold	UAVS	1	C	-0.06349	
Cold	UAVS	1	C	0	
Cold	UAVS	1	C	-0.01976	
Cold	UAVS	1	C	0	
Cold	UAVS	1	C	0.011696	
Cold	UAVS	1	D	-0.29286	0
Cold	UAVS	1	D	-0.42162	
Cold	UAVS	1	D	-0.62097	
Cold	UAVS	1	D	-0.05333	
Cold	UAVS	1	D	-0.06763	
Cold	UAVS	1	D	-0.57288	
Cold	UAVS	1	D	-0.50534	
Cold	UAVS	1	D	-1.14194	
Cold	UAVS	1	D	-0.17708	
Cold	UAVS	1	D	-0.08667	
Cold	UAVS	1	D	0	
Cold	UAVS	1	D	-0.79277	
Cold	UAVS	1	D	-0.56319	
Cold	UAVS	1	D	-0.67895	
Cold	UAVS	1	D	-0.335	
Cold	BAVS	1	A	0.029851	4
Cold	BAVS	1	A	0.024324	
Cold	BAVS	1	A	0.020833	
Cold	BAVS	1	A	0	
Cold	BAVS	1	A	0	
Cold	BAVS	1	A	0.057018	
Cold	BAVS	1	A	0.087948	
Cold	BAVS	1	A	0	

| Stream	Valley Segment Type	Segment Number	Reach	VHG	Redds per Reach
Cold	BAVS	1	A	-0.02732	
Cold	BAVS	1	A	-0.06303	
Cold	BAVS	1	A	0.008929	
Cold	BAVS	1	A	0.003279	
Cold	BAVS	1	A	-0.07937	
Cold	BAVS	1	A	-0.03684	
Cold	BAVS	1	A	0	
Cold	BAVS	1	C	-0.02778	0
Cold	BAVS	1	C	-0.0902	
Cold	BAVS	1	C	-0.01563	
Cold	BAVS	1	C	-0.00476	
Cold	BAVS	1	C	0	
Cold	BAVS	1	C	0	
Cold	BAVS	1	C	0	
Cold	BAVS	1	C	-0.03111	
Cold	BAVS	1	C	0.013953	
Cold	BAVS	1	C	0.016949	
Cold	BAVS	1	C	-0.05597	
Cold	BAVS	1	C	-0.06061	
Cold	BAVS	1	C	0	
Cold	BAVS	1	C	-0.04015	
Cold	BAVS	1	C	-0.0429	

APPENDIX 3A

VHG, PERMEABILITY, AND FLOW DATA
FROM PEIZOMETERS LOCATED IN THE MAPPED SPAWNING REACH OF LION CREEK

Peizometer Number	Northing	Easting	VHG	K (cm/sec)	Q (cm^3/sec)
1	3.96	-10.634	0.0541667	0.2499096	0.0152965
2	2.587	0.962	0.02	0.1984341	0.0044846
3	6.825	-7.121	0.0272727	0.2370921	0.0073067
4	6.581	-2.001	0.1088235	0.0155487	0.001912
5	11.565	-0.276	-0.03913	0.2372287	-0.01049
6	13.982	3.204	0.1126761	0.2469145	0.0314381
7	15.983	0.178	-0.14	0.2214115	-0.035027
8	11.614	-7.796	-0.165625	0.283777	-0.053111
9	18.2	-7.845	-0.165625	0.2520739	-0.047177
10	21.848	-7.206	-0.08	0.246036	-0.022242
11	19.874	0.82	-0.116667	0.0666654	-0.008789
12	20.985	-3.204	-0.03	0.1075523	-0.003646
13	23.176	-2.64	-0.04	0.2347336	-0.01061
14	21.687	4.591	0.05	0.0217095	0.0012266
15	24.733	0.861	-0.022727	0.2416432	-0.006206
16	27.837	-1.763	0	0.1553368	0
17	27.337	2.22	0.0068966	0.1898495	0.0014795
18	30.73	0.553	0.0107143	0.3017939	0.0036539
19	34.716	-15.471	-0.031818	0.0038461	-0.000138
20	33.473	-0.545	0.01	0.2377326	0.0026864
21	31.347	3.777	0.0607143	0.33272	0.022827
22	37.071	1.854	0.0769231	0.0041742	0.0003628
23	40.019	2.848	0.068	0.2178056	0.0167362
24	41.811	0.454	0.072	0.0667604	0.0054316
25	-14.932	-22.885	-0.036	2.317E-06	-9.42E-08
26	-20.451	-20.419	-0.08	3.497E-06	-3.16E-07
27	-21.368	-29.119	-0.108	3.735E-05	-4.56E-06
28	-29.393	-23.794	-0.212	7.431E-06	-1.78E-06
29	-34.603	-27.861	-0.204	4.935E-06	-1.14E-06
30	-31.337	-32.507	-0.216	3.665E-06	-8.94E-07
31	-46.504	-39.555	-0.191667	0.1967856	-0.04262
32	-48.196	-36.239	-0.179167	0.2843114	-0.057561
33	-51.381	-42.37	-0.133333	0.2363099	-0.035604
34	-54.528	-36.871	-0.145833	0.0968041	-0.015953
35	-56.904	-42.145	-0.083333	0.1018435	-0.00959
36	-61.326	-40.079	0.204	0.1086298	0.0250413
37	-62.619	-44.904	0.128	0.2497805	0.0361282
38	-65.201	-42.342	0.136	0.2442175	0.0375314
39	-69.412	-48.41	0.096	0.3371026	0.0365689
40	-68.757	-54.758	0.044	0.0182324	0.0009065
41	-80.081	-53.569	-0.071875	0.0882108	-0.007164
42	-76.279	-57.657	0.036	0.251036	0.0102121
43	-73.925	-61.487	0.016	0.2260111	0.0040863

APPENDIX 3A
(continued)

Peizometer Number	Northing	Easting	VHG	K (cm/sec)	Q (cm³/sec)
44	-83.94	-68.232	-0.027273	0.2016078	-0.006213
45	-88.726	-66.033	-0.066667	0.2059488	-0.015515
46	-90.694	-62.221	-0.073333	0.0610416	-0.005058
47	-93.722	-69.878	-0.018182	0.0844482	-0.001735
48	-97.939	-68.581	-0.093333	0.0932905	-0.009839
49	-90.44	-73.334	0.016	0.1906885	0.0034476
50	-96.152	-77.608	0.016	0.1401358	0.0025337
51	-100.234	-75.467	-0.027273	0.1842002	-0.005677
52	-104.457	-74.835	-0.067857	0.1323326	-0.010147
53	-103.203	-78.348	0	0.3247999	0

LION CREEK SPAWNING REACH
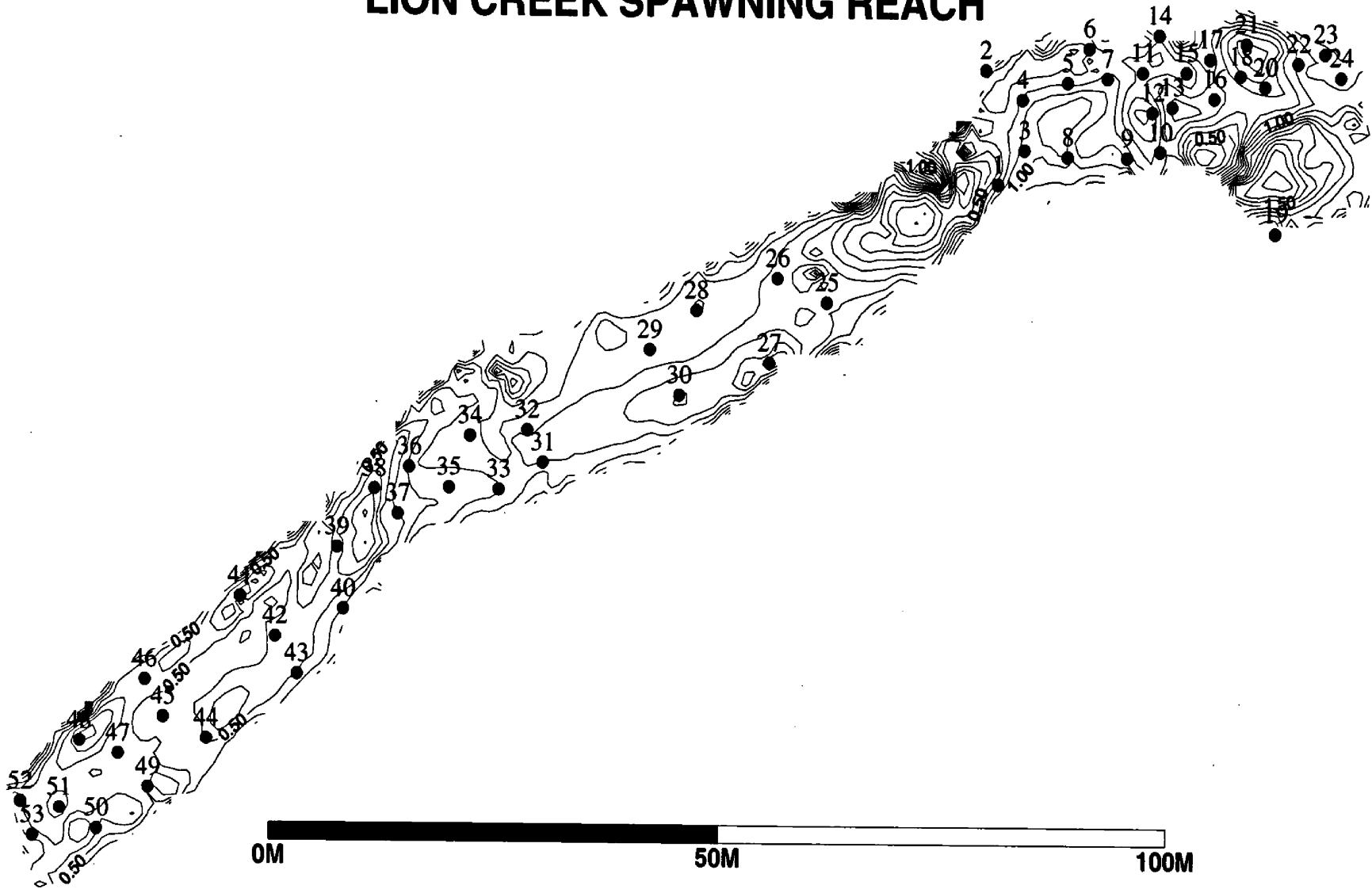
Appendix 3A. The locations and point numbers of peizometer sites in the mapped spawning reach of Lion Creek.
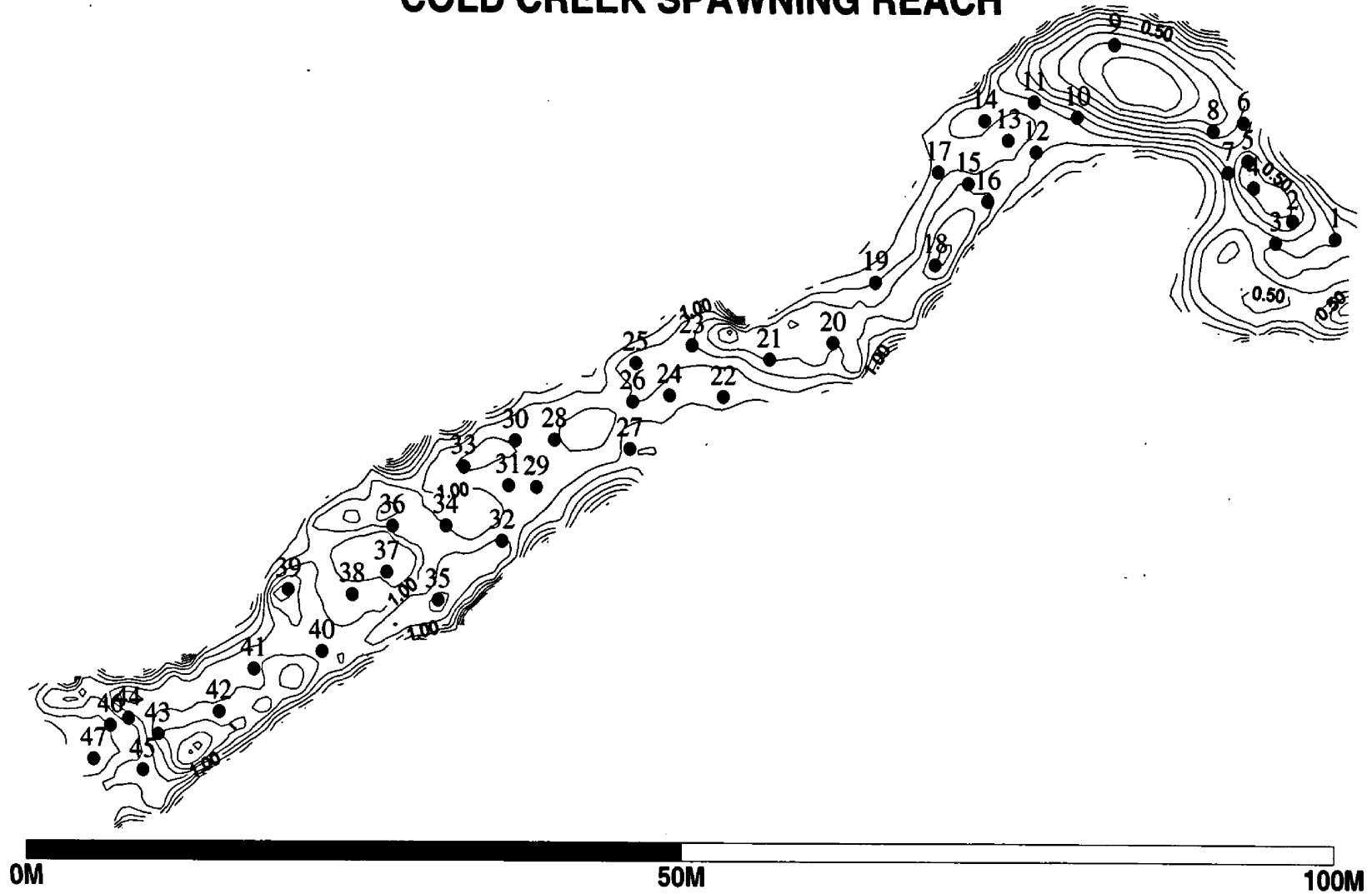
APPENDIX 3B

VHG, PERMEABILITY, AND FLOW DATA
FROM PEIZOMETERS LOCATED IN THE MAPPED SPAWNING REACH OF
COLD CREEK

Peizometer Number	Northing	Easting	VHG	K (cm/sec)	Q (cm³/sec)
1	16.165	-4.249	0.035	0.009203	0.000364
2	12.932	-3.003	0.0238095	0.1695222	0.004561
3	11.644	-4.545	0.0421053	0.0304465	0.0014486
4	9.962	-0.66	0.0181818	0.0176137	0.0003619
5	9.529	1.218	0.0090909	0.0196072	0.0002014
6	9.1651	3.88578	-0.007856	0.1082158	0.0009607
7	8.019	0.391	0	0.1182873	0
8	6.875	3.306	-0.004762	0.0279091	0.0001502
9	-0.649	9.342	-0.023256	0.0308573	0.0008109
10	-3.49	4.248	0.0269231	0.1799366	0.0054742
11	-6.781	5.288	0.0321429	0.1205327	0.0043779
12	-6.608	1.786	0.012	0.0260098	0.0003527
13	-8.717	2.603	0.0377358	0.1066169	0.0045463
14	-10.509	3.985	0.0384615	0.0031576	0.0001372
15	-11.714	-0.45	-0.052	0.1501118	0.0088206
16	-10.253	-1.692	-0.055	0.0004736	2.943E-05
17	-14.0179	0.350917	-0.05	0.1099664	0.0062131
18	-14.261	-6.19	0.0407407	0.0004674	2.152E-05
19	-18.824	-7.431	0.0041667	0.0596959	0.0002811
20	-22.081	-11.739	0.0244898	0.0451688	0.00125
21	-26.913	-12.937	0.0133333	0.0009728	1.466E-05
22	-30.443	-15.599	0.027451	0.0406741	0.0012617
23	-32.81	-11.963	0	0.0279719	0
24	-34.541	-15.505	0.1115385	0.00282	0.0003554
25	-37.131	-13.224	0	0.0626205	0
26	-37.375	-15.953	0.0384615	0.1673919	0.0072751
27	-37.606	-19.296	0.0301887	0.1152973	0.0039332
28	-43.364	-18.679	-0.065385	0.0284627	0.002103
29	-44.775	-22.039	0.0436364	0.127227	0.0062734
30	-46.351	-18.747	-0.008	0.0229432	0.0002074
31	-46.9	-21.934	0	0.0975727	0
32	-47.411	-25.874	-0.085714	0.2119038	0.0205244
33	-50.285	-20.629	0.0078431	0.0242504	0.0002149
34	-51.697	-24.819	0.0464286	0.0075242	0.0003948
35	-52.319	-30.097	0.0188679	0.0010939	2.332E-05
36	-55.784	-24.808	0.0192308	0.0010317	2.242E-05
37	-56.243	-28.085	-0.095652	0.1420047	0.0153489
38	-58.868	-29.685	-0.004762	0.133192	0.0007167
39	-63.73	-29.365	0.0321429	0.0044012	0.0001599
40	-61.221	-33.727	0.0241379	0.0320791	0.000875
41	-66.434	-34.981	0.0036364	0.0724994	0.0002979
42	-69.113	-38.012	0.04	0.0211569	0.0009563
43	-73.735	-39.625	0.0153846	0.0052888	9.194E-05

APPENDIX 3B
(continued)

Peizometer Number	Northing	Easting	VHG	K (cm/sec)	Q (cm^3/sec)
44	-75.975	-38.521	0.0150943	0.0158077	0.0002696
45	-74.925	-42.185	-0.05	0.0030011	0.0001696
46	-77.363	-39.015	-0.085714	0.2222215	0.0215237
47	-78.664	-41.411	0.0105263	0.0172073	0.0002047

COLD CREEK SPAWNING REACH

Appendix 3B. The locations and point numbers of peizometer sites in the mapped spawning reach of Cold Creek.