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UNIVERSITY OF ALBERTA

BOREAL STREAM FISH ASSEMBLAGE STRUCTURE:
A LANDSCAPE APPROACH

BY

DAVID ALAN HALSTEAD ©

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE.

DEPARTMENT OF GEOGRAPHY

Edmonton, Alberta

Spring 1993

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **BOREAL STREAM FISH ASSEMBLAGE STRUCTURE: A LANDSCAPE APPROACH** submitted by **DAVID ALAN HALSTEAD** in partial fulfilment of the requirements for the degree **MASTER OF SCIENCE** in **GEOGRAPHY**.

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Dated 16 April 92.

ABSTRACT.

Fish species presence-absence data, collected from 38 stream locations in Alberta's northernmost eastern slopes, were evaluated in combination with environmental variables at the site and watershed scales of analysis to determine the most appropriate scale for describing stream fish assemblage structure. Fish assemblage species included: Arctic grayling (*Thymallus arcticus*); bull trout (*Salvelinus confluentus*); mountain whitefish (*Prosopium williamsoni*); slimy sculpin (*Cottus cognatus*); longnose sucker (*Catostomus catostomus*); and lake chub (*Couesius plumbeus*). Canonical correspondence analysis (CCA) attributed the majority of variation in fish species occurrence to the watershed scale. Environmental gradients were identified in relation to watershed size (combination of sub-basin area and elevation) and potential stream power (combination of sub-basin relief, orientation and stream order). Multiple logit regression was used in conjunction with CCA to derive probability of occurrence surfaces for each stream fish population. This analysis confirmed the statistical and ecological significance of identified environmental gradients and produced a model of stream fish assemblage structure that was relevant for all fish species. Comparisons of fish presence-absence data at sites resampled over three years of study suggests that the relationships identified by this analysis are stable over time. Identification of a gradient related to watershed size, with demonstrated significance for all fish species, supports theoretical assumptions of the river continuum concept. Conformity with the river continuum concept is also inferred by a persistent distributional structure capable of compensating variations in energy flow by fluctuations in fish abundance. Size-related differences in physical habitat requirements within fish populations are hypothesized to account for the apparent stability of occurrence data. This study provides a new approach for viewing and analyzing stream fish assemblages. Practical applications include prediction of fish habitat suitability at specific streamlength locations or over broad regional expanses. The study approach may also be useful for detecting cumulative watershed impacts or as an ecological context for more conventional methods of fish and fish habitat prediction at the fish population level.

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I. INTRODUCTION

Background

Considerations of scale figure prominently in the detection of ecological patterns and underlying processes. Scale is particularly relevant to the study of stream fish assemblages where several potential environmental gradients have been proposed for relating fish distribution and abundance to habitat variation. Some of these gradients involve variations in habitat that are observable at the stream reach or site-specific scale. These gradients are sensitive to short term climatic changes and undergo considerable daily and seasonal variation (Horwitz 1978). Important habitat variables used to describe these gradients include measures of stream depth, velocity, substrate, cover, pool-riffle ratios and habitat diversity (Gorman and Karr 1978; Baker and Ross 1981; Schlosser 1982).

Environmental gradients are also observable at the scale of the watershed sub-basin. These gradients are established over geologic time and are considered relatively stable (Frissel et al. 1986). Shelford (1911) originally described stream fish occurrence in the context of an evolving watershed landscape by relating patterns of fish distribution to inferred geologic age of the stream channel. Subsequent studies have related fish distribution and abundance to variations in several watershed parameters including watershed size, watershed relief, stream order, and streambed slope (Burton and Odum 1945; Huet 1959; Platts; 1974; 1979; Swanston et al. 1977; Lanka et al. 1987).

Scale also varies with respect to numerical resolution of the biological response being measured (Rahel 1990). Absolute measures of abundance (e.g. biomass) are sensitive to small scale spatial and temporal variations in environmental conditions. Abundance rankings are less sensitive to environmental change and are often preferred for the purpose of reducing sampling errors. Presence-absence data are the most persistent biological measure and may be appropriate for analyzing community stability over evolutionary time.

The range of interpretations available from different scales of numerical resolution have contributed to controversies regarding the persistence of stream fish assemblages over time (Heins and Matthews 1987; Rahel 1990). Grossman et al. (1982) provided much of the stimulus for this controversy when they reported a "total lack" of persistence in species abundance rankings during a 12 year study of an Indiana stream fish assemblage. This lack of persistence was attributed to stochastic variation in physico-chemical habitat conditions. Without the environmental stability necessary to establish equilibrium conditions, species abundances were considered products of environmental change rather than biological interactions (Rahel et al. 1984). Conversely, Moyle and Vondracek (1985) reported a deterministic stream fish assemblage based on five years of rank species abundance and presence-absence data collected from a small California stream. This deterministic structure was attributed to morphological diversity and habitat segregation arising from competitive interactions.

Both of these studies yield contrary results when examined at different numerical resolutions. Yant et al. (1984) evaluated the fish species abundance data of Grossman et al. (1982) in terms of presence-absence. At this coarser level of resolution, the stream fish community was judged to be stable. The results of Moyle and Vondracek (1985) were also re-evaluated after it was discovered that a contingency table analysis had been misinterpreted (Rahel 1990). Upon review, it was reported that fish presence-absence data was stable, but species abundance rankings were not (Rahel 1990). Similar conflicting interpretations of persistence have been reported for studies involving multiple scales of spatial (Sale 1980; Anderson et al. 1981; Wiens 1986) and temporal resolution (Davis and van Blaricom 1978; in Rahel 1990).

Environmental scale and the persistence of ecological structure are important elements of process explanations. Scales of analysis should be compatible in order to avoid the kinds of inconsistencies described by Wiens (1984) whereby global patterns of species distributions are determined by processes operating at the level of the individual. Fine-grained observations (e.g. at the stream or stream reach level) are necessary for detecting high frequency behaviours of populations and their response to changing resource scenarios at local and contemporary scales of analysis (Hoekstra et al. 1984; Allen et al. 1984). Coarse-grained observations (e.g. at the regional scale) are more appropriate for low frequency behaviours of communities and their response to broad scale environmental processes such as climatic, geomorphic, and evolutionary change (Allen et al. 1984; Hoekstra et al. 1984).

These considerations of scale have not been formally recognized by gradient related studies of stream fish assemblage structure. As a consequence, several studies have attempted to relate geomorphic change at the scale of the watershed sub-basin with measures of stream fish abundance (Platts: 1974; 1979: Swanston et al. 1977; Lanka et al. 1987), while other studies have attempted to relate changes in physical habitat at the site-specific scale with fish presence-absence (Matthews 1985). These studies have identified many important trends with respect to ecological patterns and processes, but their long term relevance may be compromised by an inconsistency in scale. One way of extending their relevance may be to equilibrate levels of persistence among cause and effect mechanisms by employing long term averages. Another way is to select environmental gradients and scales of numerical resolution that already display compatible rates of change.

In this thesis, I apply these considerations of scale in deriving a model of stream fish assemblage structure in northwestern Alberta. My objective was to derive a model at a coarse level of analysis involving fish presence-absence so that stable ecological relationships among fish and fish habitat could be identified and used as a context for evaluating finer levels of spatial, temporal, and numerical resolution. An assemblage-defined homogenous area was used as the geographical context for this model because such models can be expected to perform better than single species models built for large heterogenous areas (Hawkes et al. 1986).

Before developing this model, it was first necessary to establish the scale of environmental analysis most compatible with changes in fish presence-absence. Patterns of fish occurrence either reflect long-term adaptations to geomorphological gradients at the scale of the watershed sub-basin (e.g. Shelford 1911; Burton and Odum 1945; Huet 1959), or short-term responses to physical habitat change at some finer scale of resolution (e.g. Gorman and Karr 1978; Baker and Ross 1981; Schlosser 1982). To determine the appropriate scale of analysis and to satisfy the objectives of this study, I related fish presence-absence data from headwater streams in northwestern Alberta to simultaneous measures of site and watershed-specific habitat variables. Three alternative hypotheses were anticipated from this analysis: 1) variations in fish occurrence could be attributed to site-specific differences in fish habitat, implying that stream fish assemblage structure responds to conventional (fine-scale) habitat gradients of depth, velocity, substrate etc.; 2) variations in fish occurrence could be attributed to a combination of site and watershed-specific habitat variables, implying that stream fish assemblage structure responds to gradients at different spatial and temporal scales, or; 3) variations in fish occurrence could be attributed to habitat variation at the scale of the watershed sub-basin, implying that stream fish assemblage structure responds to gradients of changing geomorphic conditions.

Study Area

The study area is located in west central Alberta adjacent to the Alberta-British Columbia boundary (Figure 1). A comprehensive description of the region is given by Archibald et al. (1984). They describe the area as physiographically diverse, encompassing parts of the Wapiti Plains, Western Alberta Plains, Rocky Mountain Foothills and Rocky Mountain Physiographic Regions. Both continental and Cordilleran glaciers covered the area during the Pliestocene epoch and morainal, glacio-fluvial and glaciolacustrine deposits are predominant. These deposits have been re-worked and more recent colluvial, fluvial, eolian, and organic deposits are also significant.

The landscape falls within six ecoregions: Boreal Mixedwood, Boreal Foothills, Boreal Upland, Subalpine, Alpine, and a variant of the Montane (Strong and Legatt 1981). Gradients of decreased temperature and increased precipitation accompany increased elevation towards the southwest. Vegetative sequences correspond to these climactic gradients with deciduous aspen forest at low elevations in the Boreal Mixedwood, grassland and deciduous forest in the Montane, coniferous forests in the Boreal Upland and Subalpine, and heather and shrublands in the Alpine.

Mean daily temperatures in the growing season range from 7.6°C to 12.2°C. Winter temperatures range from -11.5°C to -23°C in the low lying Wapiti Plains, to between -7°C and -12°C at treeline where higher topography deflects cold Arctic air from the north. Slope and aspect influence regional patterns of temperature and moisture in areas of high relief. A slope of 30%, for example, results in a difference of 20-25% more solar energy received for southwest facing slopes compared to northeast-facing slopes. Precipitation during the growing season accounts for about 60-70% of annual totals and varies between 220 mm and 602 mm depending on location. Mean winter precipitation ranges from 180 mm to 360 mm water equivalent.

The area represents a headwater source of Arctic Ocean drainage via the Wapiti, Smoky, Peace, Slave, and Mackenzie River systems. Streams range from first to sixth order in magnitude. Discharge data indicate the timing of peak flow is variable with peak river discharges generally being recorded at a later date for rivers originating in the Rocky Mountains than rivers originating in the Western Alberta Plains. All of the rivers are prone to flooding especially at times of intense summer rainfall. Silt loads of streams in the area are considered relatively high.

Fish production and population densities tend to be lower than elsewhere along Alberta's eastern slopes because of a more northerly latitude, cooler climate and shorter growing season. Resident sportfish species include: Arctic grayling, *Thymallus arcticus* (Pallas); bull trout, *Salvelinus confluentus* (Suckley); and mountain whitefish, *Prosopium williamsoni* (Girard). Forage species include: slimy sculpin, *Cottus cognatus* Richardson; longnose sucker, *Catostomus catostomus* (Forster); and lake chub, *Couesius plumbeus* (Agassiz). Less frequent inhabitants include: northern pike, *Esox lucius* Linnaeus; white sucker, *Catostomus commersoni* (Lace pe'de); largescale sucker, *Catostomus macrocheilus* Girard; longnose dace, *Rhinichthys* *cataractae* (Valenciennes); redside shiner, *Richardsonius balteatus* (Richardson); trout perch, *Percopsis omiscomaycus* (Walbaum); and burbot, *Lota lota* (Linnaeus).

II. METHODS

Field Sampling

I obtained data for this study from fisheries investigations I conducted as a participant of the Deep Basin Research Project. The Deep Basin Research Project was initiated by Scientific and Engineering Services of Alberta Energy and Natural Resources to address environmental concerns associated with an anticipated increase in exploration and development of oil and gas resources on trout producing watersheds of northwestern Alberta. Part of the mandate of this three year study was to acquire baseline fisheries inventory data for streams and rivers of the Grande Prairie Forest. Data used for the present study were collected during the final year of study in 1984. These data are presented in Appendices I - III. Intense rainfall and record flooding restricted sampling and affected the quality of results during the two previous years.

Field sampling procedures were aimed at obtaining simultaneous measures of fish occurrence and fish habitat variables over a broad geographic range of habitat. Each site was visited once so that regional variation could be summarized by the maximum number of sites. Site sampling was performed between 17 July and 30 August 1984. This timing coincides with the late summer critical flow period for fish production. Fish populations are relatively sedentary and at their highest concentrations during this time. In addition, fish sampling is most effective due to shallow depths, high solute concentrations, and high water clarity.

Forty five sites (Figure 1) distributed among 35 watershed sub-basins were assessed in total. Sites were selected on the basis of Ecological Land Classification maps (Strong and Leggat 1981), 1:50 000 NTS maps, 1:250 000 Forestry Series Access Maps, and Alberta Forestry Service input. Logistics and accessibility also affected site selection. A permanent field camp was established in the central portion of the study area to help minimize these constraints and to afford maximum flexibility in response to changing road and weather conditions. Two field crews consisting of two persons each were involved in sampling operations. Access was facilitated by four wheel drive trucks, all-terrain cycles, and helicopters.

Sampling procedures were initiated at each site by the collection of water quality information. Two one litre water samples were obtained for detailed water analysis by the Edmonton laboratory of the Energy Resources Conservation Board. Analysis was performed for routine parameters including major ions and total dissolved solids. An additional 500 ml water sample was collected for analysis by the Alberta Forest Service. Suspended sediment, turbidity, pH, and conductivity were assessed by A.F.S. personnel using a glass microfilter, Hach turbidimeter, pH meter and portable conductivity meter.

Physical habitat characteristics were measured using a modified transect method (Dunham and Herrington 1967). Transects were oriented perpendicular to the direction of flow and spaced at 30 m intervals over a maximum site length of 300

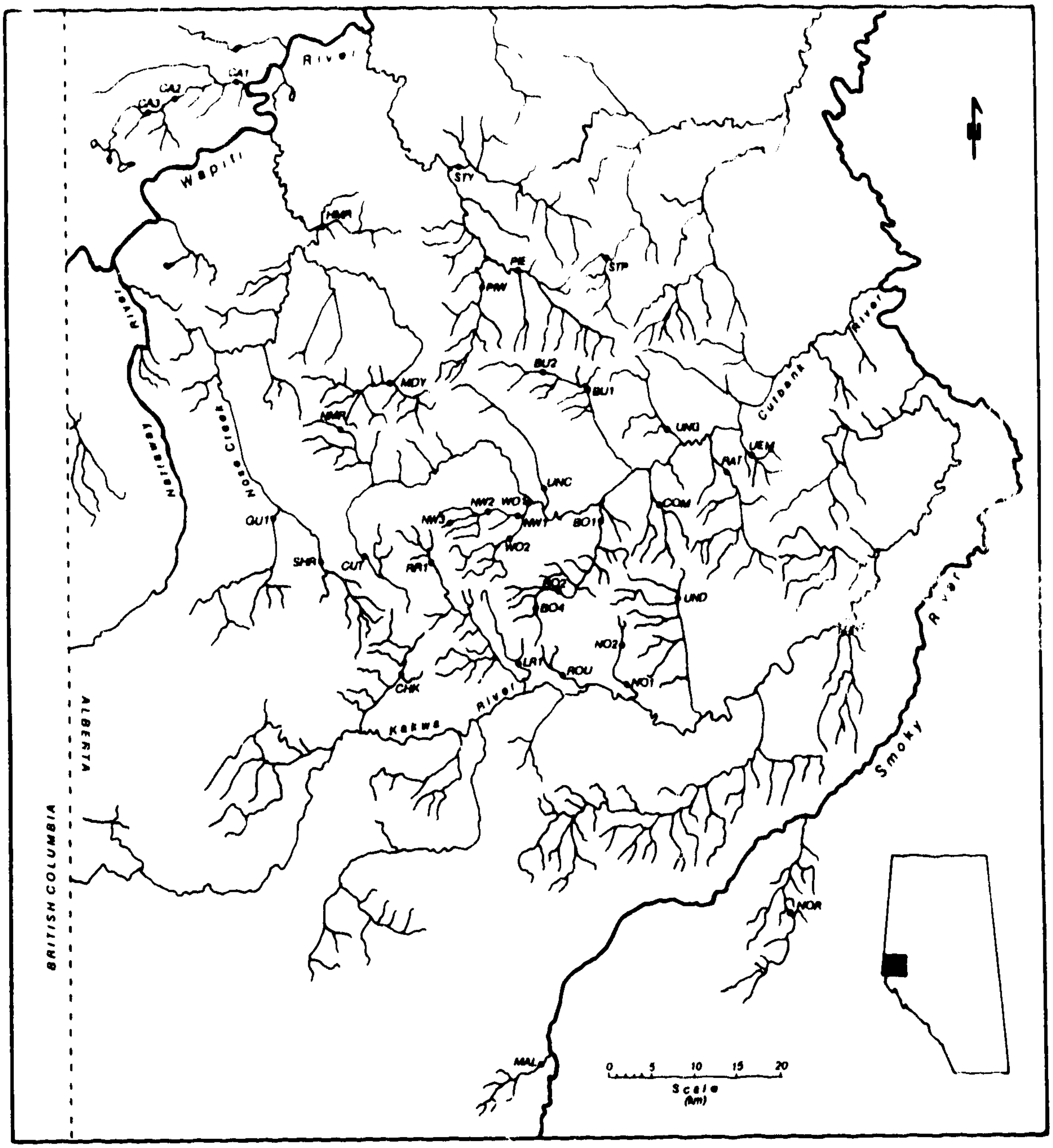

Figure 1. Study area and sample site locations. Sample site abbreviations are as follows: BO1, BO2, BO4 = Boulder Creek; BU1, BU2 = Bull Creek; CA1, CA2, CA3 = Calahoo Creek; CHK = Chicken Creek; COM = Comeau Creek; CUT = Cutbank River; GU1 = Gunderson Creek; HMR = Hammer Creek; LR1 = Little Redrock Creek; MAL = Malcolm Creek; MDY = Muddy Creek; NOR = Norris Creek; NW1, NW2, NW3 = North Wolf Creek; PIE, PIW = Pinto Creek; RAT = Rat Creek; RR1 = Redrock Creek; ROU = Route Creek; SHR = Shetler Creek; STP = Steep Creek; STY = Stony Creek; WO1, WO2 = Wolf Creek; NO1, NO2, NMR, UNA, UNC, UND, UEM, UNG = Unnamed Creeks.

m. The first transect was placed 15 m above the downstream end of the site to reduce possible bias associated with initial transect placement. This arrangement resulted in a maximum of ten transects with the last transect situated 15 m below the upstream end of the site. Sample site length was occasionally reduced due to extremes in depth or instream debris. In these instances fewer transects were used but transect intervals were maintained at 30 m.

Stream width was measured at each transect location and used to calculate depth measurement stations at five equal intervals (i.e. 0.17, 0.33, 0.5, 0.67, and 0.83) along the transect width. Depth measurements were obtained to the nearest cm. Substrate composition was visually estimated for the transect, or examined for texture, on the basis of Wentworth's classification of particle size (Orth 1983; Hynes 1970). Substrate classes and their particle size intervals included percent boulder (>256 mm), rubble (64-256 mm), gravel (2-64 mm), sand (0.06 - 2 mm), silt (0.004 - 0.06 mm), organic matter (various sizes), and clay (<0.0039 mm). Streambank stability, height, and angle were estimated for the left and right streambanks and riparian vegetation was classified according to percent coniferous, deciduous, grass, or open vegetation conditions. Calculations of mean site depth and substrate characteristics were area-weighted to account for stream width variation by the following formula:

$$\bar{d}_w = \frac{\sum_{i=1}^{n} (\bar{d}_i w_i)}{\sum_{i=1}^{n} w_i} \tag{1}$$

where $\bar{d}_w$ = weighted mean depth of site, $\bar{d}_i$ = mean depth for transect i, and w_i = width of transect i, and;

$$\bar{s}_{jw} = \frac{\sum_{i=1}^{n} (s_{ij} w_i)}{\sum_{i=1}^{n} w_i} \tag{2}$$

where $\bar{s}_{jw}$ = weighted mean substrate proportion for substrate class j (j = 1 - 7), s_{ij} = proportion for substrate class j along transect i, and w_i = width of transect i.

Discharge measurements were conducted at the most suitable location within the site. A shallow u-shaped channel with smooth bottom characteristics was generally preferred. Ten velocity measures were obtained at equal intervals across the stream width using a Pygmy type current meter. Shallow stream conditions (< 0.76 m) permitted one reading at 0.6 of the distance from water surface to substrate (Orth 1983). In deeper waters (> 0.76 m), velocity measures were averaged from readings taken at 0.2 and 0.8 of the distance from water surface to substrate (Orth 1983).

Mean site velocity and hydraulic variability were calculated to provide relative measures of streamflow conditions. Mean site velocity was calculated by dividing discharge by the area of an average stream cross section derived from the mean depths at each of the five transect depth measurement locations and the mean transect width. A measure of hydraulic variability was used to describe the extent to which velocity and related habitat conditions varied at the constant discharge along the site. This variable was estimated by the coefficient of variability (Zar 1974) applied to stream width measurements.

Surface water characteristics were averaged for the site according to visual estimates of the proportions of pool, riffle, and run habitat in each 30 m section between transects (the two 15 m sections below and above the first and last transect were combined to form one of these 30 m sections). Pools function as resting and feeding areas for fish and are an important source of fish cover (Platts et al. 1983). Pool areas were defined by overhead cover and reduced flows relative to other portions of the stream channel. These conditions were generally associated with increases in stream depth or habitat volume, and were qualitatively enhanced by overhanging vegetation and instream debris.

Riffles serve as food production and fish spawning areas (Platts et al. 1983). They were identified by a broken or undulating water surface flowing over a shallow flat or convex stream bottom. Coarse substrate materials and high water velocity relative to other portions of the stream channel were also indicative of riffle habitats.

Runs represent the transition between pool and riffle habitat. They were identified as low gradient stream sections with uniform channel dimensions, non-turbulent flow characteristics, and a relatively flat unbroken water surface. Runs also included stream channels with imperceptible flow characteristics often referred to as glides (Platts et al. 1983).

Fish Collection

A Smith-Root Type VII electrofisher and hand held net were used to facilitate fish capture during an upstream and downstream pass of the sample site length. Movement into or out of the site was deterred by the installation of upstream and downstream blocking nets prior to sampling. The nets consisted of a 0.5 cm juvenile mesh downstream and a 2.5 cm stretch gill net mesh upstream. The objective of fish collection was to determine fish species occurrence, however; efforts were made to capture all fish observed during sampling. Cumulative fishing effort, recorded by the electrofisher when the circuit through the water is complete, ranged from twenty minutes to one hour depending on site conditions. Captured fish were placed in a large pail and released upstream or downstream of the site at the conclusion of each pass. Before being released each fish was identified to species, examined for evidence of sex and reproductive condition, and measured to the nearest mm of fork length.

Sub-basin Mapping

Watershed sub-basins were delineated on 1:50 000 scale NTS topographic mapsheets by outlining the height of land separating site drainage from adjacent watershed drainages. These maps provided the basis for deriving thirteen morphometric parameters previously identified as potential environmental correlates of fish abundance (Swanston Meehan and McNutt, 1977; Platts 1979). After some initial data screening, the number of watershed morphometric parameters was reduced to five. These variables include: sub-basin area; stream order; elevation; relief; and orientation. Sub-basin area (km^2) was measured directly from the 1:50 000 scale maps using an electronic planimeter. Stream order was determined by designating each permanent unbranched tributary within the sub-basin as stream order 1 (Strahler 1957). Higher order stream channels were identified whenever two or more tributaries of the same order converged. This process continued downstream until stream order of the site was established. Site elevation was estimated from the 1:50 000 scale NTS maps by interpolating between elevation contours intersecting the stream channel above and below the site. Sub-basin relief was calculated as the difference between site elevation and maximum elevation within the sub-basin. Sub-basin orientation was rated from 1 to 9 according to stream channel orientation. Drainages flowing north were rated 1; drainages flowing east or west were rated 5, and; drainages flowing south were rated 9. Drainages with intermediate compass orientations were rated accordingly.

Data Analysis

Persistence of the stream fish assemblage was assessed by between year comparisons of fish presence-absence at sites that were resampled during the three year Deep Basin study. This analysis was performed to determine the reliability over time of the ordination analyses discussed below. The formula used to calculate persistence was:

$$2n/(n_1 + n_2) \tag{3}$$

where n = the number of times fish species occurrences corresponded between years for all resampled sites, and n_1 and n_2 = the number of fish species occurrences at resampled sites in years 1 and 2. Data used to assess persistence are included in Appendix IV.

Canonical correspondence analysis (CCA) was used to investigate the separate and combined influences of site and watershed variables affecting stream fish assemblage structure. Canonical correspondence analysis is an ordination method for direct gradient analysis of biological data assumed to exhibit unimodal distributions (ter Braak 1986; 1987a). The CCA algorithm selects linear combinations of environmental variables that maximize dispersion of species scores along unrelated axes (ter Braak 1987b). To account for different units of measure, all variables are first standardized to zero mean and unit variance.

Input data for the CCA ordination consisted of fish presence-absence information and site and watershed sub-basin environmental data. The combined spatial scales of environmental data were analyzed to determine if the majority of explained variance in fish occurrence could be attributed to site or watershed factors. Fish presence-absence data were reduced prior to analysis to ensure a continuous spatial association among fish species pairs. This reduction was achieved by removing the less frequently occurring members of fish species pairs that had no occurrences in common. A continuous association among species increases the likelihood of identifying environmental correlations at higher levels of ecological organization (May 1972; in Herbold 1984). In addition, this reduction effectively removes rare species which can obscure interpretation of the results without adding significantly to the result (Gauch 1982). Three species of fish (northern pike [*Esox lucius*], white sucker [*Catostomus commersoni*], and longnose dace [*Rhinichthys cataractae*]) were removed in total, accounting for 6% of sampled fish species occurrences.

Environmental data were also reduced prior to analysis. Four sites were eliminated because fish were not observed during sampling. An additional three sites were eliminated because of environmental impact or inadequate sampling due to extreme water depth. Variables for the remaining sites were inspected for serious departures from normality (Zar 1974; Jager and Looman 1987) and analyzed in an untransformed state. The statistical program SPSS (Norusis 1986) was used to perform data inspection. Proportional data were treated as pseudo-independent measures by eliminating one or more mutually dependent classifications from analysis. Thus, runs were eliminated from among classes of surface water characteristics, grass and open classifications were eliminated from riparian vegetation types, and gravel was eliminated from among classes of substrate. Fine sediments (sand, silt, organic matter, and clay) were combined into one substrate class to emphasize the distinction between erosional and depositional environments.

The computer program CANOCO (ter Braak 1987a) was used to perform the CCA ordination. A species-environment biplot produced by the analysis provided a graphical summary of site and watershed environmental variable weightings. Species points in the biplot correspond to the optima of bell-shaped response surfaces. Arrows relate the direction of maximum change for environmental variables. Output parameters include eigenvalues, expressing maximized species dispersions attained by each CCA axis, and species-environment correlations.

A Monte Carlo permutation test supplied with the CANOCO program (ter Braak 1987a) was used to assess statistical significance of the CCA ordination. The Monte Carlo test rearranges ordination data into pseudo-random data sets and compares the first eigenvalue or the sum of all eigenvalues (ie. the trace) derived from trial ordinations to the current analysis result (ter Braak 1987a). The current ordination is significant at the 0.05 level if its eigenvalues exceed ninety five percent of the eigenvalues produced by the trial ordinations (ter Braak, 1987a).

Multiple logit regression was used to verify distributional relationships identified by CCA, and determine the extent to which stream fish assemblage structure could be predicted on the basis of watershed data alone. Logit regression is a generalized linear model for relating presence-absence data to quantitative explanatory variables using nonlinear probability models (Aldrich and Nelson 1987). Models may vary in complexity depending on the number of parameters needed to describe behaviour of the response variable. Parameters are added in an iterative manner, and compared against previous models by the deviance test (ter Braak and Looman 1987).

The application of multiple logit regression was preceded by a second CCA ordination involving fish presence-absence and watershed environmental data only. A stepwise multiple logit procedure (Harrel 1980) was then used to relate probability of fish occurrence to CCA sample scores and their squared values. The analysis initially tests whether probabilities of occurrence significantly depart from a null hypothesis model expressing no difference in the likelihood of fish presence-absence across the environmental space defined by the first two CCA axes. Subsequent steps refine the shape of each species response surface by testing sigmoid and Gaussian logit models. A significance level of 0.1 was specified for inclusion and retention of variables selected by the stepwise procedure. The Logist procedure (Harrel 1980) supplied with the mainframe version of SAS (Statistical Analysis System) was used to perform the analysis.

III. RESULTS

Stability of Fish Occurrence Data

Six fish species comprised the stream fish assemblage after non-associated species were removed. Of the 38 sites selected for analysis, Arctic grayling (*Thymallus arcticus*), bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*) occurred at 25, 23, and 11 sites respectively. Slimy sculpin (*Cottus cognatus*), longnose sucker (*Catostomus catostomus*) and lake chub (*Couesius plumbeus*) occurred at 29, 18, and 11 sites respectively. Maximum number of species recorded at any one site was 5. Average number of species was 3.

A comparison of fish occurrences at sites revisited during the three year Deep Basin Research Project suggests an acceptable level of persistence with regard to fish occurrence data. Of 17 sites sampled during 1983 and 1984, 14 sites demonstrated complete agreement in fish species occurrence, and three sites differed by one species. In these latter three cases, fish species changes were caused by the addition or subtraction of a bull trout individual. Overall, concordance in fish species occurrence for 1984 and 1983 was 94.7%. This value is significant because of markedly different climatic conditions between 1984 and 1983. Drought like conditions prevailed in 1984, while 1983 was a year of near record levels of precipitation. In addition, this value accounts for sampling error.

Comparisons between 1984 and 1982 are even more striking because of two devastating floods, representing a 1 in 100 year and 1 in 75 year flood event (Golding and Wilkinson 1982), experienced during the height of the 1982 sampling season. Of 12 sites sampled in both 1982 and 1984, 7 displayed complete agreement in species occurrence, 4 differed by a single species, and one site registered a difference of 2 species. Again, differences between years were primarily due to the addition or subtraction of individual fish. Concordance in fish species occurrences for 1984 and 1982 was 90.2 %.

Comparisons between 1983 and 1982 offer the most dramatic evidence of the effects of flooding prior to recovery. Seven out of 12 consistently sampled sites displayed no change in fish species occurrence, three sites differed by one species, and two sites differed by two species. Concordance in fish species occurrence for 1982 and 1983 was 86%. Average concordance for all possible pairwise comparisons was 90.3% (sd=4.35, n=3).

Ordination Analysis

Canonical correspondence analysis of the combined fish occurrence, site, and watershed data accounted for 95.7% of the variation in the species data on the first four axes. The sum of canonical eigenvalues was 0.66. Distribution of the explained variation in fish species data among CCA axes was 53.2% for CCA 1, 20.5% for CCA 2, 11.5% for CCA 3, and 10.5% for CCA 4. Monte Carlo test results indicate the first eigenvalue to be significant ($P=0.01$). A maximum variance inflation factor of 8.14 (for fine sediments) indicates a low to moderate degree of multicollinearity among environmental variables (ter Braak 1987a).

Interpretation of the CCA analysis was limited to the first two axes comprising 73.7% of the variation in the species data. Biplot scores of environmental variables are graphically illustrated in Figure 2 and presented in Table 1. In Figure 2, the overall importance of environmental variables is indicated by their distance from the origin. The position of environmental variables relative to CCA 1 and CCA 2 indicates their correlation with these axes (ter Braak 1987a).

The majority of variation in the species data was ascribed by CCA to environmental variables at the watershed scale. This is indicated by the position of watershed variables at the extreme ends of each axis (Figure 2), and by the absolute value of their biplot scores (Table 1). The first CCA axis demonstrates a species-environment correlation of $R=0.952$, and was interpreted as a stream gradient related to watershed size. Environmental variation extended from downstream sites draining large watershed sub-basins to high elevation sites draining small sub-basins. Interpretations at the site-specific scale reflect a corresponding gradient from deep turbid sites with a high proportion of pools and fine sediment substrates to shallow high velocity sites with rocky substrates and riffles. Lake chub, longnose suckers, and to a lesser extent Arctic grayling were the dominant species occurring in downstream sites. Slimy sculpin and mountain whitefish received scores corresponding to intermediate size streams. Bull trout were identified with headwater sites.

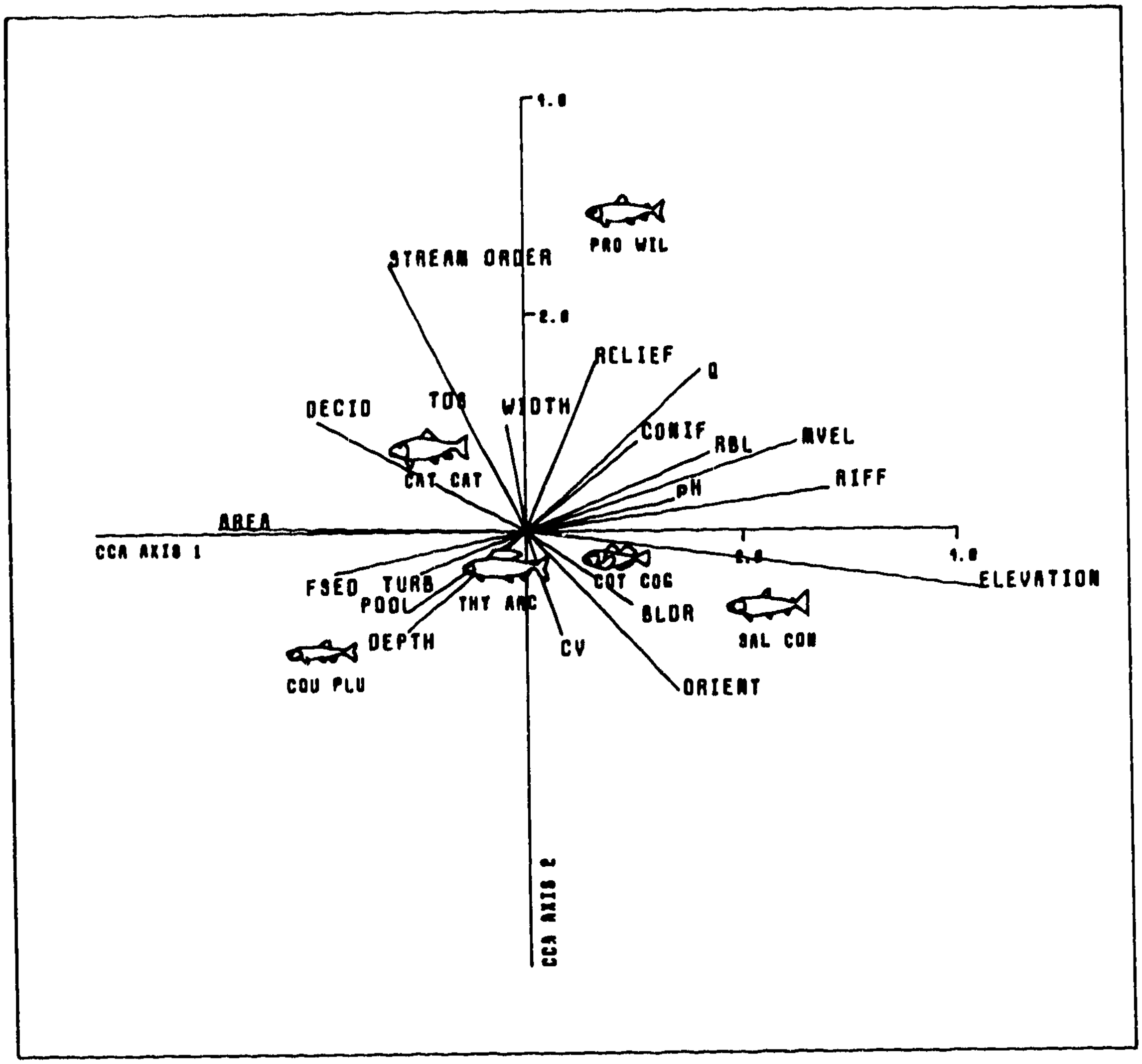

Figure 2. Species-environment biplot from CCA ordination of fish presence-absence data, site and watershed variables. Fish species include: bull trout (SAL CON), Arctic grayling (THY ARC), mountain whitefish (PRO WIL), slimy sculpin (COT COG), longnose sucker (CAT CAT), and lake chub (COU PLU). Environmental variables are: sub-basin area (AREA), orientation (ORIENT), and relief (RELIEF); deciduous (DECID) and coniferous (CONIF) riparian vegetation; stream width (WIDTH), depth (DEPTH), discharge (Q), and velocity (MVEL); riffle (RIFF) and pool (POOL) habitat; boulder (BLDR), rubble (RBL), and fine sediment (FSED) substrates; width variability (CV); turbidity (TURB) and total dissolved solids (TDS). Ordination statistics are given in Table 1. Scale = species scores x 1, environmental scores x 10.

Table 1. Species and environmental scores produced by CCA ordination of fish presence-absence data, site and watershed environmental variables.

	CCA 1	CCA 2	CCA 3	CCA 4
EIGENVALUE	0.35	0.14	0.08	0.07
CUMULATIVE VARIANCE (%)	53.2	73.7	85.2	95.7
SPP./ENV. CORRELATION	0.95	0.84	0.69	0.80
SPECIES SCORES (*)				
Bull trout (SAL CON)	1.82	-0.72	0.90	-0.78
Mountain whitefish (PRO WIL)	0.57	2.93	0.77	1.06
Arctic grayling (THY ARC)	-0.59	-0.35	-1.25	0.13
Slimy sculpin (COT COG)	0.49	-0.28	-0.69	0.85
Lake chub (COU PLU)	-2.25	-1.11	2.11	1.12
Longnose suckers (CAT CAT)	-1.27	0.75	-0.06	-1.89
SITE VARIABLE SCORES (*)				
Mean velocity (MVEL)	0.257	0.079	0.015	0.072
Discharge (Q)	0.169	0.140	0.033	0.085
Mean Depth (DEPTH)	-0.146	-0.107	0.009	0.056
Mean Width (WIDTH)	-0.020	0.109	0.069	0.107
Coniferous veg. (CONIF)	0.106	0.085	0.017	0.030
Turbidity (TURB)	-0.133	-0.054	0.038	-0.156
Rubble substrate (RBL)	0.175	0.072	0.041	0.037
Boulder substrate (BLDR)	0.100	-0.060	-0.019	-0.010
Fine sediments (FSED)	-0.204	-0.056	-0.024	-0.008
Width variation (CV)	0.029	-0.114	0.008	-0.097
Riffles (RIFF)	0.287	0.040	-0.039	0.015
Pools (POOL)	-0.153	-0.073	0.054	-0.027
pH (pH)	0.138	0.033	0.058	0.001
Total Diss. Solids (TDS)	-0.088	0.115	-0.008	-0.019
Deciduous veg. (DECID)	-0.202	0.109	-0.009	-0.004
WATERSHED VARIABLE SCORES (*)				
Sub-basin area (AREA)	-0.284	0.005	0.110	0.053
Sub-basin relief (RELIEF)	0.064	0.155	0.106	0.010
Site elevation (ELEVATION)	0.421	-0.055	-0.043	0.021
Stream order (STREAM ORDER)	-0.124	0.246	-0.044	0.074
Sub-basin orientation (ORIENT)	0.138	-0.148	-0.057	-0.027

* abbreviations used in Figure 2.

The second CCA axis has a species-environment correlation of R=0.837 and was interpreted as a gradient related to potential stream power. Stream order and sub-basin relief were both highly correlated with this axis indicating a complex association independent of sub-basin size. Sub-basin orientation was also highly correlated with CCA 2, suggesting the involvement of different watershed snow retention and runoff capabilities associated with this variable. At the site-specific scale, CCA 2 describes a gradient from low discharge sites with diverse hydraulic characteristics to high discharge sites with wide and uniform stream channel dimensions. Species scores (Table 1) identify lake chub, bull trout, Arctic grayling, and slimy sculpin with low stream power habitats. Scores for longnose suckers and mountain whitefish correspond to intermediate and high stream power habitats respectively. The rank order of species scores along CCA 2 suggests no evidence for the arch effect (ter Braak 1987b). CCA 2 is therefore likely to represent a "true underlying gradient" rather than a modified form of CCA 1 (ter Braak 1987b).

A second CCA ordination, involving fish presence-absence and watershed variables only, indicates that stream fish assemblage structure can essentially be summarized in terms of geomorphology. The reduced set of environmental variables accounted for 99.6% of the variation in the fish species data on the first four axes. The sum of canonical eigenvalues (0.45) was lower than the first CCA ordination. Distribution of the explained variation in species data increased, however, to 88.9% on the first two axes indicating only a minor loss of information as far as interpretations of these two axes are concerned. Monte Carlo test results indicate the first eigenvalue to be significant ($P = 0.01$). Significant reductions were realized in terms of multicollinearity among environmental variables as evidenced by a maximum variance inflation factor of 1.6. The species-environment biplot produced by the second CCA ordination is presented in Figure 3, and species and environmental variable scores are shown in Table 2. Environmental variables retained the same relative position with respect to CCA 1 and CCA 2 as described in the first analysis (Figure 2). Species-environment correlations were $R = 0.902$ for CCA 1 and $R = 0.644$ for CCA 2. The comparable species-environment correlation for CCA 1 underscores the importance of watershed variables for describing stream fish occurrence along this axis. The reduced species-environment correlation for CCA 2 indicates that at least two site variables, discharge and the coefficient of width variability (expressing habitat diversity), may have contributed to its environmental explanation. Overall, species and environmental relationships were retained relative to the first analysis. Moreover, concordance between the two analyses suggests that environmental interpretations of the first CCA may be equally applicable to the second.

Multiple Logit Regression

Probability of occurrence curves ($P < 0.1$) were independently derived for all six fish species using multiple logit regression. These curves are presented in

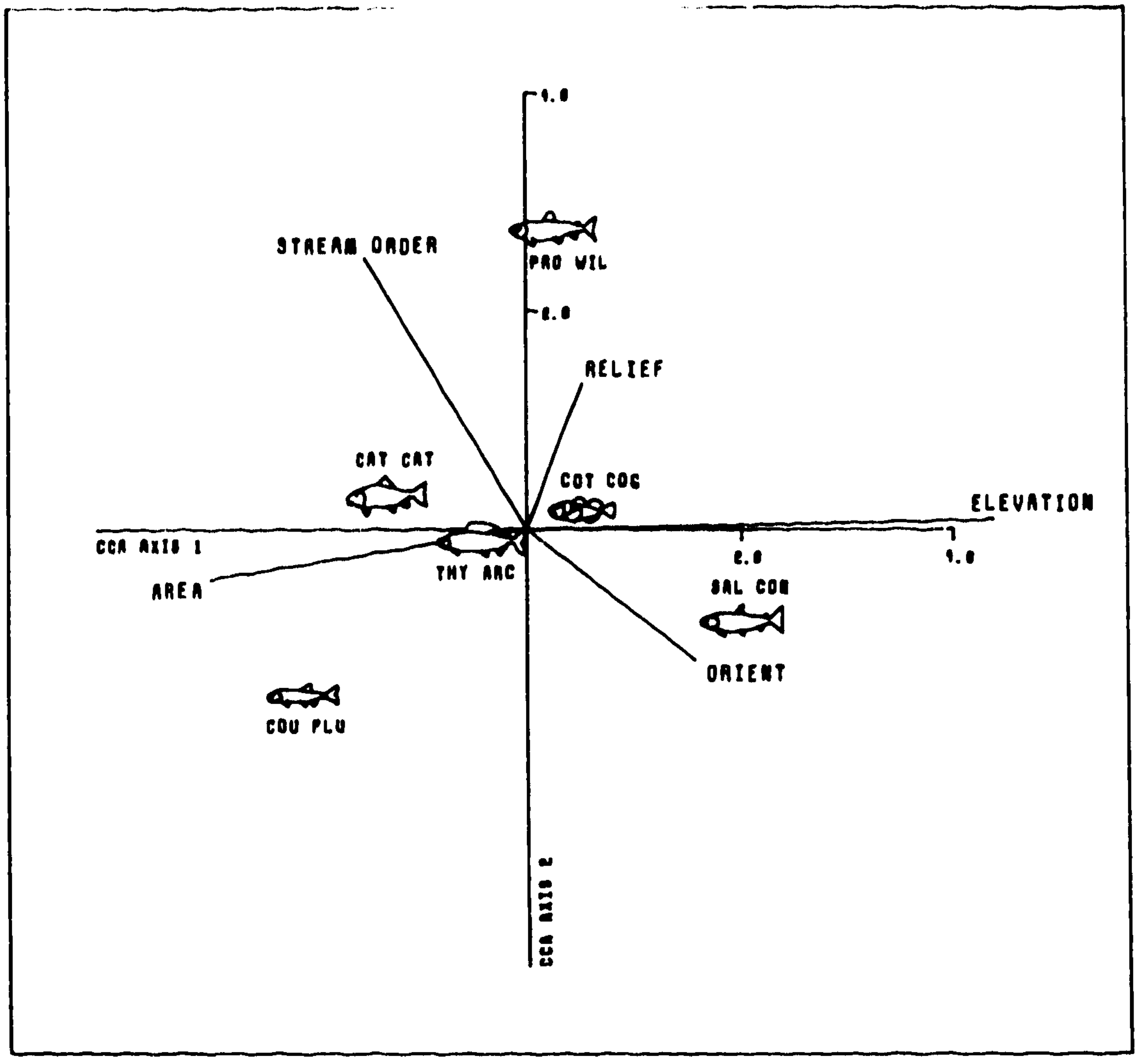

Figure 3. Species-environment biplot from CCA of fish presence-absence data and watershed variables only. Fish species include: bull trout (SAL CON), Arctic grayling (THY ARC), mountain whitefish (PRO WIL), slimy sculpin (COT COG), longnose sucker (CAT CAT) and lake chub (COU PLU). Environmental variables at the watershed scale include: stream order (STREAM ORDER), sub-basin area (AREA), sub-basin orientation (ORIENT), sub-basin relief (RELIEF) and site elevation. Ordination statistics are given in Table 2. Scale = species scores x 1, environmental scores x 10.

Table 2. Species and environmental scores produced by CCA ordination of fish presence-absence data and watershed environmental variables.

	CCA 1	CCA 2	CCA 3	CCA 4
EIGENVALUE	0.31	0.09	0.04	0.01
CUMULATIVE VARIANCE (%)	69.1	88.9	97.1	99.6
SPP./ENV. CORRELATION	0.90	0.64	0.54	0.32
SPECIES SCORES (*)				
Bull trout (SAL CON)	1.84	-0.89	0.75	0.67
Mountain whitefish (PRO WIL)	0.21	2.74	1.61	-0.42
Arctic grayling (THY ARC)	-0.44	-0.11	-0.87	-0.35
Slimy sculpin (COT COG)	0.46	0.15	-0.91	-0.84
Lake chub (COU PLU)	-2.10	-1.52	1.78	-1.14
Longnose sucker (CAT CAT)	-1.33	0.29	-0.34	1.94
WATERSHED VARIABLE SCORES (*)				
Sub-basin area (AREA)	-0.293	-0.046	0.107	-0.051
Sub-basin relief (RELIEF)	0.051	0.133	0.151	0.032
Site elevation (ELEVATION)	0.437	0.009	-0.033	-0.027
Stream order (STREAM ORDER)	-0.149	0.249	0.018	-0.028
Sub-basin orientation (ORIENT)	0.156	-0.120	-0.081	-0.007

* abbreviations used in Figure 3.

Figure 4. Estimated parameters and regression statistics are included in Table 3. General form for the regression model involving all possible coefficients is:

$$p = [\exp(b_0+b_1x_1+b_2x_1^2+b_3x_2+b_4x_2^2)]/[(1+\exp(b_0+b_1x_1+b_2x_1^2+b_3x_2+b_4x_2^2)] \qquad (4)$$

where x_1 and x_2 are CCA 1 and CCA 2 sample site scores, respectively.

For bull trout, probability of occurrence was significantly related to sample site scores on CCA 1, but not CCA 2. The regression model indicates a sigmoid response curve ($P < 0.01$) with optimum habitat at the margin of the sampled habitat range. Based on interpretations obtained from CCA, probability of occurrence can be described as a response to sub-basin size and elevation.

At a more refined level of analysis, bull trout population data indicated an upstream to downstream progression of habitat use for different life history functions. To test whether this trend had any significance for the present analysis, I proposed a null hypothesis of no difference in mean bull trout length (mm fork length) along CCA 1. This hypothesis was rejected by linear regression analysis ($r^2=0.29$; d.f. = 21; $0.01 < P < 0.05$). Intra-population differences in habitat use cannot be discounted with respect to probability of bull trout occurrence along CCA 1. Rearing populations of bull trout were common at sites with high CCA 1 scores (headwater regions), and mean bull trout length demonstrated a progressive increase towards the negative CCA 1 direction (downstream reaches).

Probability of occurrence for Arctic grayling was described by a sigmoid response curve ($P < 0.01$) in relation to interpretations of sub-basin size and elevation on CCA 1, and by a Gaussian logit response curve ($P < 0.05$) in relation

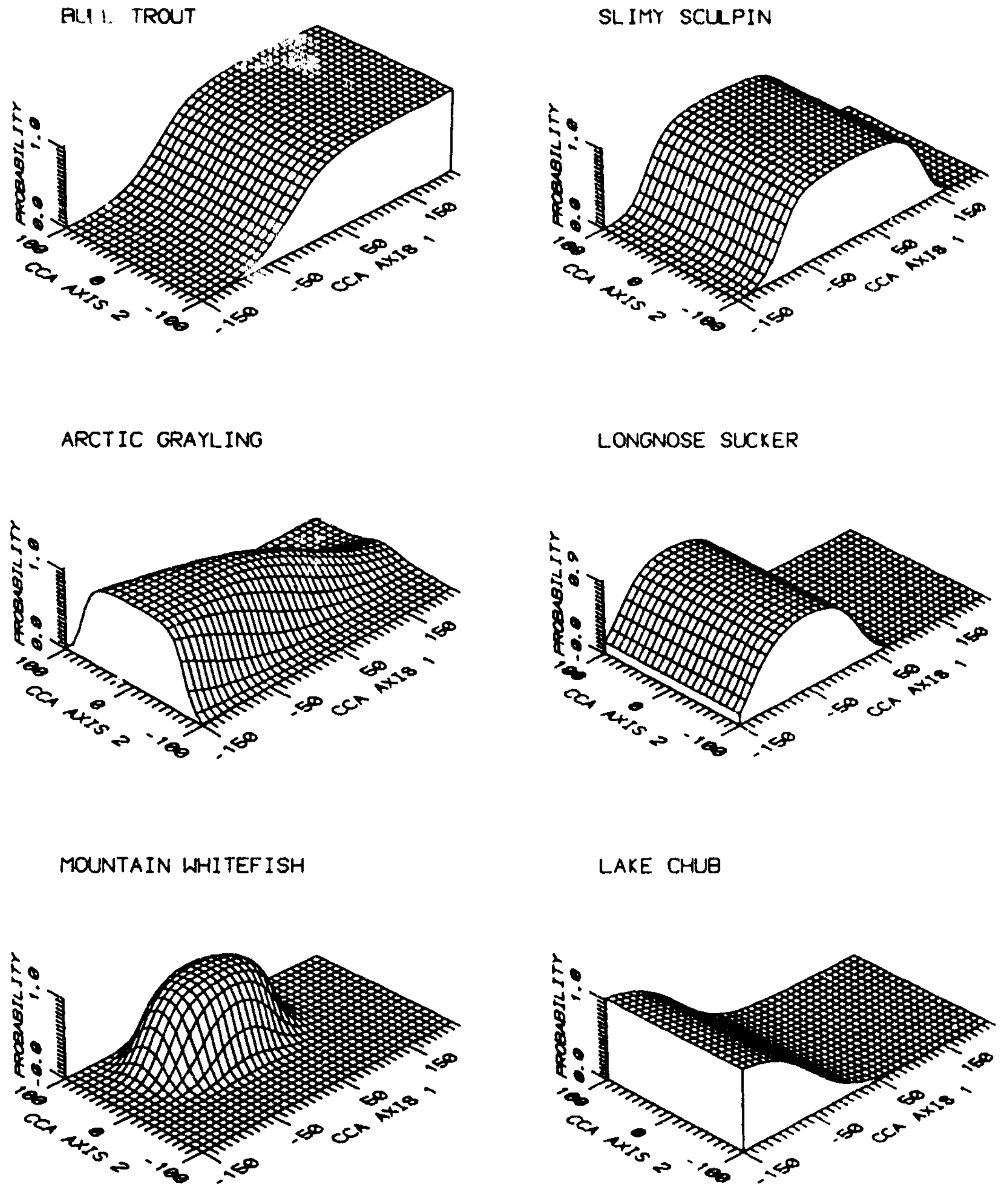

Figure 4. Fish species probability of occurrence for the multivariate habitat space defined by CCA 1 and CCA 2. Curves were derived by multiple logit regression analysis. General form of the regression model is: $p = [\exp(b_0+b_1x_1+b_2x_1^2+b_3x_2+b_4x_2^2)]/[(1+\exp(b_0+b_1x_1+b_2x_1^2+b_3x_2+b_4x_2^2)]$ where x_1 and x_2 are CCA 1 and CCA 2 sample site scores respectively.

Table 3. Estimated parameters and regression statistics for multiple logit regression of fish presence absence and CCA site scores.

	VARIABLE		ESTIMATE	S.E.	CHI-SQUARE	P
BULL TROUT						
$X^2 = 27.02_{(1)}$	constant	b_0	0.76387	0.56943	1.80	0.1789
$P < 0.0001$	CCA1	b_1	0.03890	0.01212	10.29	0.0013
$R^2 = 0.49$						
ARCTIC GRAYLING						
$X^2 = 15.67_{(2)}$	constant	b_0	2.04323	0.69564	8.63	0.0033
$P < 0.0005$	CCA1	b_1	-0.01867	0.00699	7.11	0.0077
$R^2 = 0.24$	$CCA2^2$	b_4	-0.00087	0.00040	4.72	0.0298
MOUNTAIN WHITEFISH						
$X^2 = 25.79_{(3)}$	constant	b_0	0.87518	0.92443	0.90	0.3438
$P < 0.0001$	$CCA1^2$	b_2	-0.00046	0.00022	4.40	0.0360
$R^2 = 0.43$	CCA2	b_3	0.10530	0.04305	5.98	0.0144
	$CCA2^2$	b_4	-0.00122	0.00072	2.85	0.0913
SLIMY SCULPIN						
$X^2 = 16.04_{(2)}$	constant	b_0	3.60477	1.11158	10.52	0.0012
$P < 0.0005$	CCA1	b_1	0.01351	0.00685	3.89	0.0485
$R^2 = 0.29$	$CCA1^2$	b_2	-0.00034	0.00012	7.34	0.0068
LONGNOSE SUCKER						
$X^2 = 25.05_{(2)}$	constant	b_0	0.98683	0.62525	2.49	0.1145
$P < 0.0001$	CCA1	b_1	-0.04035	0.01671	5.83	0.0158
$R^2 = 0.40$	$CCA1^2$	b_2	-0.00039	0.00020	3.82	0.0505
LAKE CHUB						
$X^2 = 19.78_{(1)}$	constant	b_0	-1.60975	0.67532	5.68	0.0171
$P < 0.0001$	CCA1	b_1	-0.03342	0.01148	8.48	0.0036
$R^2 = 0.39$						

X^2 = Model chi-square(d.f.); P = probability; R^2 = R^2 value for the model (Harrell 1980).

to interpretations of potential stream power on CCA 2. Habitat suitability, as defined by the optimum, increased towards the margin of the sampled habitat range on CCA 1, and is located near the midpoint (i.e. optimum was non-significant) of CCA 2. The Gaussian logit curve of CCA 2 permits estimation of tolerance (a measure of ecological amplitude analogous to standard deviation) and maximum probability of occurrence. These two parameters were estimated to be 23.97 and 0.89 respectively. At the population level of analysis, joint optima for CCA 1 and CCA 2 roughly correspond with field assessments of Arctic grayling spawning and rearing habitats. Linear regression analysis failed to detect any further size related trends in habitat use for either CCA 1 ($r^2 = 0.05$, d.f. = 21, $0.2 < P < 0.5$) or CCA 2 ($r^2 = 0.05$, d.f. = 21, $0.2 < P < 0.5$).

Mountain whitefish displayed a narrow distributional range in comparison to other analyzed fish species. Probability of occurrence was described by Gaussian logit curves in relation to both CCA 1 and CCA 2. For CCA 1, the optimum was located near the mid-point of the axis (i.e. optimum was non-significant) and the tolerance was estimated as 32.97. For CCA 2, the optimum was 4.[illegible] and the tolerance 20.24. Maximum probability of occurrence was equal to 0.96. At the population level, joint optima of CCA 1 and CCA 2 response curves correspond with field assessments of mountain whitefish rearing habitat. Linear regression analysis identified a marginal, but non-significant, relationship between mean mountain whitefish length and sample site scores on CCA 2 ($r^2 = 0.30$, d.f. = 9, $0.05 < P <$

0.1). Size related relationships were not apparent for CCA 1 ($r^2 = 0.13$, d.f. = 9, $0.2 < P < 0.5$).

Probability of occurrence was described for slimy sculpin by a Gaussian logit response curve on CCA 1. Significant relationships were not identified for CCA 2. The habitat optimum and tolerance of the CCA 1 response curve were estimated to be 19.87 and 38.34, respectively. Maximum probability of occurrence was estimated to be 0.98. Size related relationships were not evaluated for slimy sculpin or remaining species.

A similar distributional response was indicated for longnose sucker. Probability of occurrence was described by a Gaussian logit response curve on CCA 1, but no significant relationships were identified on CCA 2. The habitat optimum and tolerance were estimated to be -51.73 and 35.81 respectively. Maximum probability of occurrence was estimated to be 0.88.

Probability of occurrence was described for lake chub by a sigmoid response curve in relation to CCA 1. Significant relationships were not identified for CCA 2. The habitat optimum for lake chub lies near the margin of the sampled habitat range, in the negative (downstream) CCA 1 direction.

Combined Species Distributions

Stream fish assemblage structure is described by the combined response surfaces of all fish species in Figure 5. This model was evaluated for goodness of fit by comparing the sum of the residual deviance of extended models to the sum of the residual deviance of null hypothesis models and subtracting this ratio from one (ter Braak 1987b). The fraction of deviance in presence-absence data accounted for by the model was 0.45.

The stream fish assemblage depicted by Figure 5 indicates that most regions of the study area are highly suited for one or more species considered by this analysis. A possible exception refers to the dip in probability of occurrence associated with some habitats located in downstream reaches. Incidental fish species, excluded from the analysis, may account for a significant portion of this under-utilized habitat. Average site scores for sites inhabited by longnose dace were -43.0 on CCA 1 (s.d. = 41.03, n = 4) and -3 on CCA 2 (s.d. = 23.68, n=4). Northern pike occurred once at -108 on CCA 1 and -60 on CCA 2. White sucker also occurred once at -96 on CCA 1 and 26 on CCA 2.

Apart from illustrating habitat suitability, the combined response surfaces of Figure 5 also provide an ecological context for locating new sample sites using map-based watershed information. Regression equations of the CCA axes in their unstandardized form are as follows:

$$\text{CCA 1} = -0.2876z_1 + 0.1571z_2 + 0.3539z_3 - 19.1240z_4 + 3.6665z_5 - 338.4986 \qquad (5)$$

$$(R = 0.902)$$

$$\text{CCA 2} = -0.4669z_1 + 0.0214z_2 + 0.0159z_3 + 43.4917z_4 - 2.9681z_5 - 134.1268 \qquad (6)$$

$$(R = 0.644)$$

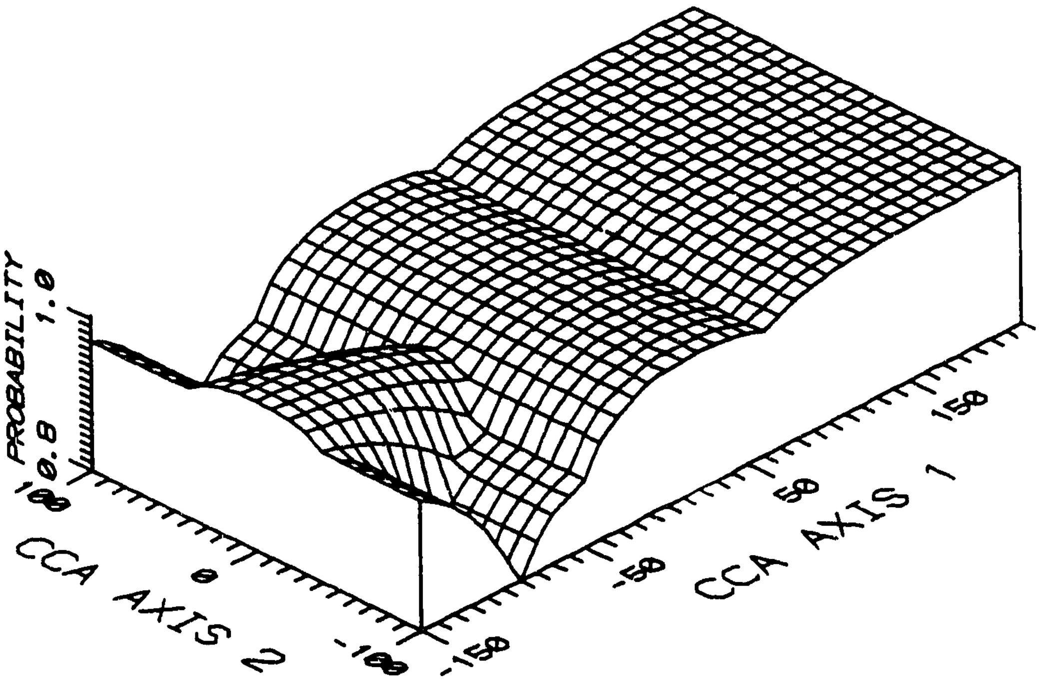

Figure 5. Combined fish species response surfaces in multivariate habitat space defined by CCA analysis of fish presence absence data and watershed environmental variables.

where, z_1 = sub-basin area (km^2), z_2 = sub-basin relief (m), z_3 = elevation (m), z_4 = stream order, and z_5 = orientation (N to S, 1 - 9): R = canonical coefficient.

These equations use variables derived from 1:50 000 scale NTS mapsheets. For any stream location, these variabies can be determined and used in conjunction with the above equations to identify CCA 1 and CCA 2 coordinates in multivariate habitat space. Habitat suitability is given by the probability of occurrence for each species corresponding to the calculated CCA 1 and CCA 2 coordinates. Habitat suitability can either be estimated by referring to the probability of occurrence surfaces in Figure 4, or it can be calculated using the coefficients in Table 3.

IV. DISCUSSION

Patterns of species occurrence contributing to boreal stream fish assemblage structure are relatively persistent and correlated with geomorphic processes at the scale of the watershed sub-basin. Persistence was indicated by 90% average concordance in fish presence-absence data over three years. This duration of study does not satisfy minimum recommendations of one complete turnover of assemblage members when assessing persistence (Connell and Sousa 1983; in Moyle and Vondracek 1985). Nevertheless, the three year study incorporates a wide range of environmental conditions including two major floods in the summer of 1982, excessive rainfall in 1983, and high temperatures and low amounts of precipitation in 1984. Discordant patterns of occurrence can be attributed to displacement due to flooding, foraging behaviour of large predatory bull trout, variation in sampling methods and sampling times between years, and sampling error. Timber harvesting and road construction may also have had some impact on fish and fish habitat in the region (Alberta Recreation, Parks and Wildlife 1978).

Stability of the stream fish assemblage in terms of abundance is unlikely. Low fish population densities were encountered after the flood events of 1982. Patterns of stream fish abundance are frequently destabilized by the effects of flooding and re-establishment may vary according to the survival and redispersal of adults, spawning success of different species at different times of the year, and recovery of physical habitat conditions (Matthews 1986; Finger and Stewart 1987). Fluctuations in stream fish abundance are also common under less catastrophic circumstances (Grossman et al. 1982; Platts and Nelson 1988; Rahel 1990). Platts and Nelson (1988) considered fluctuations in trout abundance from 93 sample years of time trend information collected during an 11 year study in Idaho, Nevada, and Utah. They reported an average fluctuation of 234% and a maximum fluctuation of 486% in bull trout (*Salvelinus confluentus*) numbers for a creek where bull trout were the only species present; and an average fluctuation of 198% and maximum fluctuation of 1,017% for a creek in which bull trout were part of a diverse assemblage of fish species. Comparable fluctuations in numerical abundance were reported for four other trout species and for total salmonids. Fluctuations in numerical abundance may be no less severe for boreal stream fishes exposed to the harsh climate of northwestern Alberta.

A persistent species assemblage, with respect to fish presence-absence but not relative abundance, was reported by Moyle and Vondracek (1985; see also Rahel 1990) after monitoring a California stream for five years. Their results invite comparison with my study because both investigations involve low diversity stream systems populated by morphologically and taxonomically distinct native fish species. Stream fish assemblages exhibiting these characteristics are assumed to have coevolved towards a state of reduced competition. Consequently, they are considered to be highly specialized, and near the deterministic end of the stochastic-deterministic spectrum (Connell 1980; in Moyle and Vondracek 1985). Typical inhabitants of these fish assemblages include native trout species (*Salmo* or *Salvelinus*), sculpin (*Cottus*), sucker (*Catostomus*), dace (*Rhinichthys*), and a drift feeding cyprinid (Moyle and Vondracek 1985). These genera are, for the most part, consistent with fish genera of the present study.

Persistence of stream fish assemblage structure is also indicated by environmental correlations at the watershed scale that surpass the explanatory value of site-specific habitat variables. The potentially obscuring effects of climate were considered minimal in this analysis. For example, turbidity was included among analyzed site variables because it was judged to be at base flow levels at all but one site that was affected by a minor precipitation event. Relationships of stream fish distribution to spatial differences in site-specific habitat should be most evident under these stable climatic conditions.

The persistence of occurrence data, combined with its more precise relationship with landscape variables, suggests that stream fish distribution conforms to "the mean state of the physical system" (Vannote et al. 1980) rather than to transitory physical habitat events. Ordination results further indicate that the physical system is largely defined by gradients related to watershed size and stream power. Numerous longitudinal zonation studies have described watershed-related gradients by assuming that fish species distributions along the streamlength persist through time but, as Meador and Matthews (1992) point out, this assumption has rarely been tested. Joint analysis of environmental variables at the site and watershed scale offers one approach for testing this assumption without the benefit of a long-term study.

Shelford (1911) is generally credited as being the first North American researcher to describe longitudinal zonation of fish species distributions along the streamlength. He incorporated watershed size and stream power gradients in his description of Illinois stream fish distributions by relating patterns of occurrence to geologic age of the stream channel and its associated sub-basin. Variables related to watershed size and stream power were also emphasized by Burton and Odum (1945) to account for the longitudinal distribution of fishes in five Virginia creeks. Huet (1959) classified Western European streams into four fish faunal zones on the basis of watershed slope expressed in terms of longitudinal stream profiles, and watershed size expressed in terms of stream valley cross section. Gradients of stream size and stream power may also be significant from a purely geomorphological perspective. Ebisemiju (1985) identified size and slope as the two most significant orthogonal dimensions of drainage basin morphology, regardless of spatial scale, from an analysis of 1244 drainage basins in eastern Nigeria.

In more recent studies, geomorphic variables have been used to derive estimates of stream fish abundance and productivity. These studies have identified many of the same variables used in my study to describe watershed size and stream power gradients including: stream order (Platts 1974; 1979; Swanston et al. 1977; Lanka et al. 1987); watershed area (Swanston et al. 1977; Lanka et al. 1987); sub-basin relief (Swanston et al. 1977; Lanka et al. 1987); elevation (Platts 1974; Lanka et al. 1987); and orientation (Swanston et al. 1977). Results of mine and other studies (e.g. Platts and Nelson 1988) suggest that relationships established between geomorphic predictors and fish abundance may be compromised over time by a disparity in scale. Fluctuations in fish abundance occur independently of watershed geomorphology and may therefore be more closely tied to nutrient concentrations or climatic influences (as discussed above). Differences in fish abundance between sites may be observable at the watershed scale, however, if long term averages are employed (Swanston et al. 1977) or if equilibrium conditions are established (Platts and Nelson 1988).

The statistical and ecological significance of the watershed size and stream power gradients was confirmed by multiple logit regression analysis. Significant relationships were described by probability of occurrence surfaces for all species in relation to the watershed size gradient while Arctic grayling and mountain whitefish were significantly related to the stream power gradient. These relationships approximate sigmoid and Gaussian response surfaces conforming to what would be expected for an ecological description of stream fish assemblage structure. Success of a species along an environmental gradient should generally correspond to a Gaussian or sigmoid curve depending on whether species maxima are located near the centre or the edge of the environmental range sampled (Beals 1973).

The probability of occurrence surfaces also permitted analysis of species-environment relationships at the population level. These analyses generally agree with standard life history references (Scott and Crossman 1973; Nelson and Paetz 1992). For bull trout, maximum probability of occurrence corresponded with fall and spring field assessments of spawning and rearing habitat in high elevation headwater streams. A preference for spawning in small headwater streams has also been noted for bull trout by Dietz (1971) in the Macleod River system of Alberta, and by Allan (1980) in the Clearwater system of Alberta. Bull trout are considered threatened due to low numbers and limited distributions (Johnson 1987; Nelson and Paetz 1992). Quantitative descriptions of spawning and rearing habitats in headwater areas may therefore be of special management concern for this species. Population level analysis also identified an increase in mean bull trout length towards downstream habitats. Platts and Partridge (1983) reported a similar relationship for bull trout populations in Idaho and were able to describe a related decrease in bull trout numbers with increasing stream width by linear regression analysis. The downstream movement of bull trout corresponds to a size related adjustment in diet. As bull trout mature they become increasingly predatory on other fish. Mountain whitefish (*Prosopium williamsoni*) have been identified as a favoured food item of bull trout in Alberta (Alberta Fish and Wildlife 1984).

Maximum probability of occurrence was described for Arctic grayling (*Thymallus arcticus*) by a sigmoid response surface that levelled off at intermediate watershed size locations and extended to the downstream limit of the sampled habitat range. In relation to the stream power gradient, maximum probability of occurrence displayed a Gaussian response with increasingly narrowed tolerance levels as watershed size was reduced. This reduced tolerance could be due to geomorphological considerations rather than species limitations. Field assessments conducted during the spring identified the largest concentration of spawning Arctic grayling at the downstream end of large watersheds. Scott and Crossman (1973) describe similar spawning habitat tendencies and a summer habitat preference for clear waters of large rivers, rocky creeks, and lakes. Bond and Machniak (1977) described spawning and summer habitat of adult migrant Arctic grayling to be in the lower ten kilometres of the Muskeg River in northeastern Alberta. A similar pattern of summer habitat use was described by Whitney et al. (1975) for the Sheep Creek drainage at the southern extent of my study area.

Mountain whitefish were represented by a Gaussian response surface in relation to both watershed size and stream power gradients. Maximum probability of occurrence corresponded with field assessments of spawning and rearing habitats conducted during the fall and spring seasons. These habitats were located near the mouth of intermediate to large watersheds. Whitney et al. (1975) described similar spawning habitat for mountain whitefish in Sheep Creek. A general habitat preference for larger streams and rivers has also been described by Scott and Crossman (1973) and Nelson and Paetz (1992).

Longnose suckers (*Catostomus catostomus*) displayed a Gaussian relation to the gradient describing watershed size. Maximum probability of occurrence corresponded with intermediate to large watersheds. Nelson and Paetz (1992) indicate that longnose sucker spawning usually takes place in creeks during spring. Whitney et al. (1975) identified spawning habitat at the lowermost segment of the Sheep Creek drainage on the basis of large numbers of sucker fry sampled at that location.

Slimy sculpin (*Cottus cognatus*) also displayed a Gaussian relation to the gradient describing watershed size and probability of occurrence extended over a relatively wider range of habitat. Spawning takes place in the spring under rocks or similar objects in cool rocky streams (Nelson and Paetz 1992). Whitney et al. (1975) and Bond and Machniak (1977) reported that slimy sculpin preferred clean gravel and rubble substrates of lower reaches of their respective study streams.

Lake chub (*Couesius plumbeus*) are often found in lentic habitats but also frequent the pools and slackwater habitats of streams and rivers (Scott and Crossman 1973). This preference for standing water habitat is consistent with a high probability of occurrence in the downstream reaches of large watersheds. Female lake chub in spawning condition were reported to occur throughout the Muskeg River during the early summer season (Bond and Machniak 1977). In comparison, there were no reports of lake chub in the Sheep Creek drainage of northwestern Alberta (Whitney et al. 1975). These two drainages differ substantially in terms of gradient suggesting that stream power may be an important determinant of habitat use. This suggestion was supported by the results of CCA, but not by the multiple logit regression analysis.

Additional interpretations at the fish population level suggest probability of occurrence curves are unaffected by most seasonal or age-related changes in habitat use. For large salmonid species, where seasonal variations in habitat use are most pronounced, maximum probability of occurrence generally coincides with field assessments of spawning and rearing habitat. Probability of occurrence should remain high regardless of whether the corresponding site is populated by developing embryos, rearing individuals, or spawning adults. However, overwintering habitats may be poorly represented by probability of occurrence curves as many of the smaller streams are subject to complete evacuation and freeze-up, and many of the fish will move to large rivers at the downstream extent of the sampled habitat range.

The identification of a common environmental gradient and different levels of persistence within and between probability of occurrence surfaces lends support to theoretical assumptions regarding the river continuum concept (Vannote et al. 1980). The river continuum concept was originally hypothesized as a means of relating functional attributes of invertebrate communities to changing streamlength conditions (Vannote et al. 1980). As far as fish communities are concerned, the river continuum concept has remained a loosely applied set of generalizations (Schlosser 1982). These generalizations are quantitatively and qualitatively enhanced by conformity of the boreal stream fish assemblage to a common environmental gradient related to watershed size. A second requirement of the river continuum concept is that community organization should be maintained in a consistent pattern of structure and function while retaining the ability to elicit rapid biological responses to fluctuations in energy flow (Vannote et al. 1980). These requirements are mutually exclusive of each other in the context of a strictly stochastic or deterministic explanation of stream fish assemblage structure as described by Grossman et. al (1982). Both are realizable, however, by a broad explanation of fish assemblage structure and function in the form of persistent distributional limits; and by a more refined and flexible definition of fish assemblage structure and function in the form of fluctuating patterns of abundance.

This correspondence with the river continuum concept can be used to relate the probable mechanisms contributing to persistence of the stream fish assemblage. For aquatic invertebrates, community structure and function are maintained along a streamlength gradient of changing resource states, and considerations of trophic function outweigh the physical habitat requirements of different taxa in determining broad-scale distributional limits (Vannote et al. 1980; Culp and Davies 1982). A reverse situation appears evident for boreal stream fishes, leading to the hypothesis that assemblage structure and function are maintained along a streamlength gradient of changing physical habitat conditions, and differences in physical habitat requirements among species outweigh considerations of trophic function in determining distributional limits. Furthermore, Vannote et al. (1980) attribute ecosystem stability in highly variable stream habitats to species diversity, or at least to a high complexity in species function. The low diversity of the boreal stream fish assemblage suggests an explanation involving high complexity in species function is more appropriate. This complexity is most likely provided by size-related differences in physical habitat requirements within populations. The importance of size-related differences in physical habitat requirements and life history function is well known and has been incorporated within several models designed to assess habitat suitability of stream fishes (e.g. Bovee 1978). In addition, Moyle et al. (1982; in Moyle and Vondracek 1985) hypothesized that in low diversity stream fish assemblages, juvenile fishes are sufficiently distinct in their ecological requirements from adults, that they may essentially function as a separate species. These size-related differences should be evident over space and time (Root 1967). In this way, habitats that undergo large amounts of variation may support a greater diversity of size-related physical habitat requirements. Also, statistical deviations away from average habitat conditions will work in the favour of one component of the population at the expense of another. Changes in abundance may arise, but fish species presence-absence will remain resistant to change. Similar relationships between fish and fish habitat diversity have been described at the species level (Gorman and Karr 1978; Schlosser 1987; Pearsons, Li, and Lamberti 1992).

In addition to supplying these theoretical considerations, my study provides a new approach for viewing stream fish assemblages. Spatial extent is defined at the level of the stream fish assemblage incorporating a broad range of fish habitat for the detection of environmental gradients. These environmental gradients are stable and statistically and ecologically relevant for all species. Maximum likelihood estimates supplied by multiple logit regression offer a means of quantifying occurrence data for purposes of assessing habitat suitability. These curves are stable over time and comply with ecological theory regarding animal distributions (Hutchinson 1957; Schoener 1974). Competition and predator prey interactions are incorporated within the model as quantifiable distances among species.

This approach offers many practical applications for managing the boreal stream fish assemblage evaluated by this study. The model derived by combined analyses of canonical correspondence analysis and multiple logit regression describes the stream fish assemblage in relation to landscape processes presumably decided over geological time. It may therefore serve as a benchmark for relating future changes in habitat use to natural and anthropogenic sources of disturbance. Many fisheries scientists are beginning to realize the significance of cumulative watershed impacts and their insidious effects on fish and fish habitat. These impacts may ultimately be quantifiable in terms of non-compliance with the present model. The usefulness of this approach will depend on the extent that the model reflects environmental relationships within a natural and undisturbed setting. The present model was derived at the onset of major timber harvesting and oil and gas developments in the region. Resampling sites used in my study could provide a test of assemblage stability in relation to major habitat disturbance.

The model also provides a means for inventorying and rating habitat over a broad geographical extent. Independent variables used to define the multivariate habitat space derived by CCA consist entirely of map-based watershed parameters. It is therefore possible to derive these parameters for any map-identified stream location and situate it with relative accuracy in relation to the watershed size and stream power gradients described by CCA axes 1 and 2. Habitat suitability is indicated by the probability of occurrence exhibited by each species at the specified location. Because the model is essentially mathematical, digital terrain modelling techniques may be employed for conducting automated inventories of large remote regions on the basis of relatively small data sets.

At more precise levels of analysis, probability of occurrence curves offer an ecological context for applying conventional methods of fish and fish habitat prediction at the population level. Present ecological methods are developed and applied at the fish species level for purposes of relating fish abundance and fish habitat suitability to microhabitat variables such as depth, velocity, and substrate. These methods include the habitat quality index (HQI; Binns and Eiserman 1979) and the instream flow methods developed by the U.S. Fish and Wildlife Service (IFIM; Bovee 1978; Milhaus et al. 1984). Models derived from these methods have been criticized for several reasons including their insensitivity to available habitat and the presence of other species (Moyle and Baltz 1985; Jowett 1992). These criticisms would no longer be valid if methods for predicting fish abundance and fish habitat suitability were applied in the context of this or similar stream fish assemblage models. Different probabilities of occurrence associated with different physical and biological circumstances could be acknowledged prior to the application of fish abundance and fish habitat suitability models by noting the location of the site in fish assemblage and multivariate habitat space.

V. CONCLUSIONS

Patterns of species occurrence contributing to boreal stream fish assemblage structure are relatively stable and correlated with broad-scale geomorphic processes at the scale of the watershed sub-basin. Stability was indicated by high levels of concordance in fish presence-absence at sites re-examined over three years of study, and by comparisons with the results of a similar study. Stability was also indicated by ordination results that attribute the majority of variation in fish distributional structure to the watershed scale. Confirmation of the ordination result was indicated by Monte Carlo testing.

The two most prominent environmental gradients affecting boreal stream fish assemblage structure are related to watershed size and stream power. The gradient related to watershed size is significant for all members of the fish assemblage and was described in terms of watershed area and site elevation. The gradient related to stream power is significant for grayling and mountain whitefish and was described in terms of sub-basin relief, stream order, and orientation. Probability of occurrence curves aligned along these gradients offered statistical and ecological confirmation of their significance.

Identification of a gradient related to watershed size, with demonstrated significance for all fish species, supports theoretical assumptions of the river continuum concept (Vannote et al. 1980). In addition, a stable stream fish assemblage, consisting of fluctuations in numerical abundance within fish population surfaces, corresponds to requirements of the river continuum concept for a consistent community structure with capabilities for rapid functional responses to changes in energy flow. Size-related functional responses at the fish population level are hypothesized to explain biological adjustments in energy flow while the apparent stability of the stream fish assemblage is maintained at coarse ecological levels of analysis.

The approach used by this study offers several advantages for analyzing stream fish assemblages. Spatially, ecologically, and numerically coarse levels of analysis contributed to a portrayal of stream fish assemblage structure resistant to change and applicable over broad geographical areas. Assessments can be performed at multiple levels of ecological organization. Habitats can be identified within multivariate habitat space on the basis of map-based information sources. Occurrence data are effectively quantified within this habitat space for purposes of illustrating stream fish distributions and describing habitat suitability. Disadvantages of this approach include the cost for initial data acquisition and the logistical difficulties of sampling large geographical areas. These disadvantages can be mitigated by using existing inventory data; however, the analyses used by this approach are sensitive to incorrect assessments of presence-absence.

Practical applications of this approach are extremely varied. Cumulative watershed impacts may be discerned by non-compliance with stream fish assemblage models. Habitat suitability can be assessed for specific streamlength locations or for broad geographical regions on the basis of map-based watershed parameters. Present quantitative models may be enhanced by the stream fish assemblage and fish habitat context offered by this approach. Ecological studies of predator prey interactions, competitive exclusion processes, and fish stocking suitability and success may also benefit.

Several questions regarding the mechanisms responsible for stream fish assemblage structure are raised by this study. Hypotheses are required to more firmly establish the reasons for distinct levels of stability at different spatial, temporal, and numerical scales of analysis. These hypotheses need to be tested over time and at the stream fish assemblage and individual fish population levels. Hypotheses are also needed to establish whether the principles and concepts identified here are applicable to other types of stream fish assemblages including large rivers and estuaries, and systems spanning the entire range of cold water and warm water stream fish habitats.

REFERENCES

Alberta Fish and Wildlife. 1984. Bull trout species management in Alberta. Prep. by Fisheries Branch. Fish and Wildlife Division. Energy and Natural Resources.

Alberta Recreation, Parks and Wildlife. 1978. Environmental effects of forestry operations in Alberta. Fish and Wildlife Division Concerns and Recommendations.

Aldrich, J.H. and F.D. Nelson. 1987. Linear Probability, Logit, and Probit Models. Sage Publications. Beverly Hills, London, New Delhi.

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

Allen, T.F.H., R.V. O'Neill, and T.W. Hoekstra. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 11 p.

Anderson, G., A. Ehrlich, P. Ehrlich, J. Roughgarden, B. Russel, and F. Talbot. 1981. The community structure of coral reef fishes. The American Naturalist 117:476-495.

Archibald, J.H., N.B. Ferguson, R.W. Haag, W.K. Hay, D.J. O'Leary. 1984. An integrated resource inventory of Deep Basin Area (NTS 83L). Vols I-III. Prep.

by Resource Inventory and Appraisal, Resource Evaluation and Planning, Alberta Energy and Natural Resources. ENR Report # T/78.

Baker, J.A. and S.T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1981:178-189.

Beals, E.W. 1973. Ordination: mathematical elegance and ecological naivete. Journal of Ecology 61:23-35.

Binns, N.A. and F.M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. Transactions of the American Fisheries Society 108:215-228.

Bond, W.A. and K. Machniak. 1977. Interim report on an intensive study of the fish fauna of the Muskeg River Watershed of Northeastern Alberta. Alberta Oil Sands Environmental Research Program. Aquatic Fauna Technical Research committee. Project AF 4.5.1

Bovee, K.D. 1978. The incremental method of assessing habitat potential for coolwater species, with management implications. American Fisheries Society Special Publication 11:340-346.

Burton, G.W. and E.P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology 26:182-194.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Connell, J.H. and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist 121:789-824.

Culp, J.M., R.W. Davies. 1982. Analysis of longitudinal zonation and the river continuum concept in the Oldman-South Saskatchewan River system. Canadian Journal of Fisheries and Aquatic Sciences. 39:1258-1265.

Davis, N., and G.R. van Blaricom. 1978. Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 23:417-427.

Dietz, K.G. 1971. The rainbow trout populations (*Salmo gairdneri*, Richardson) and other fish of three streams in the foothills of Alberta. MSc. Thesis. Dept. of Zoology, University of Alberta. Edmonton.

Dunham, D.K., and R.B. Herrington, 1967. A technique for sampling general fish habitat characteristics of streams. U.S. Forest Service Research Paper Int-41.

Ebisemiju, F.S. 1985. Spatial scale and drainage basin morphometric interaction. Catena 12:261-270.

Finger T.R. and E.M. Stewart. 1987. Responses of fishes to flooding regime in lowland hardwood wetlands. Pages 86-92 *in* Matthews W.J. and D.C. Heins, editors. Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press: Norman and London.

Frissel, C.A., W.J. Liss, C.E. Warren, M.D. Hurley. 1986. A hierarchial framework for stream habitat classification: viewing streams in a watershed context. Environmental Management Vol. 10, No. 2:199-214.

Gauch, H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge.

Golding B. and D. Wilkinson. 1982. Boulder Creek watershed assessment. Grande Prairie Forest. Alberta Forestry Service.

Gorman, O.T. and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59(3):507-515.

Grossman, G.D., P.B. Moyle, and J.O. Whitaker Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. The American Naturalist. 120(4):423-454.

Harrel, F. 1980. The LOGIST procedure. In: SAS supplemental library user's guide, 1980 Edition. SAS Institute Inc., Cary N.C., p. 83-89.

Hawkes, C.L., D.L. Miller, and W.G. Layher. 1986. Fish ecoregions of Kansas: stream fish assemblage patterns and associated environmental correlates. Environmental Biology of Fishes 17:267-279.

Heins, D.C. and W.J. Matthews. 1987. Historical perspectives on the study of community and evolutionary ecology of North American stream fishes. Pages 3-7 *in* Matthews W.J. and D.C. Heins, editors. Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press: Norman and London.

Herbold, B. 1984. Structure of an Indiana stream fish association: choosing an appropriate model. The American Naturalist 124(4):561-572.

Hoekstra, T.W., C.H. Flather, and G. Ironside. 1984. Theoretical basis for integrating wildlife resources in ecological land surveys. Occ. Paper. Lands Directorate, Environment Canada. 46 p.

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

Huet, M. 1959. Profiles and biology of western European streams as related to fish management. Transactions of the American Fisheries Society. 88:115-163.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia in Quantitative Biology 22:415-427.

Hynes, H.B.N. 1970. The Ecology of Running Waters. University of Toronto Press, Toronto, Ontario, Canada.

Jager, J.C. and C.W.N. Looman. 1987. Pages 10-28 *in* Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren editors. Data Analysis in Community and Landscape Ecology

Johnson, J.E. 1987. Protected Fishes of the United States and Canada. American Fisheries Society. Bethesda, Maryland.

Jowett, I.G. 1992. Models of abundance of large brown trout in New Zealand Rivers. North American Journal of Fisheries Management 12:417-432.

Lanka, R.P., W.A. Hubert, and T.A. Wesche. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society 116:21-28.

Matthews, W.J. 1985. Distribution of Midwestern fishes on multivariate environmental gradients, with emphasis on *Notropis lutrensis*. The American Midland Naturalist 113(2):225-237.

Matthews, W.J. 1986. Fish community structure in a temperate stream: Stability, persistence, and a catastrophic flood. Copeia 1986:388-397.

May, R.M. 1972. Will a large complex system be stable? Nature 238:413-414.

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

Milhaus, R. T., D.L. Wegner, and T. Waddle. 1984. Users guide to the physical habitat simulation system (PHABSIM). U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-81/43.

Moyle, P.B., and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Transactions of the American Fisheries Society. 114:695-704.

Moyle, P.B., J.J. Smith, R.A. Daniels and D. M. Baltz. 1982. Distribution and ecology of stream fishes of the Sacramento-San Joaquin drainage system. California. IV. A review. University of California Publications in Zoology 115:225-256.

Moyle, P.B., and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66(1):1-13.

Nelson, J.S. and M.J. Paetz. 1992. The Fishes of Alberta. University of Alberta Press, University of Calgary Press.

Norusis, M.J. 1986. SPSS/PC+. SPSS inc. Chicago, Illinois.

Orth, D.J., 1983. Aquatic habitat measurements *in* Nielsen L.A., D.L. Johnson, and S.S. Lampton editors. Fisheries Techniques. American Fisheries Society. Bethesda, Maryland.

Pearsons, T.N., H.W. Li, and G.A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society. 121:427-436.

Platts, W.S. 1974. Geomorphic and aquatic conditions influencing salmonids and stream classification with application to ecosystem classification. Surface Environment and Mining, U.S. Forest Service. 199 p.

Platts, W.S. 1979. Relationships among stream order, fish populations and aquatic geomorphology in an Idaho drainage. Fisheries 4(2):5-9.

Platts, W.S., W.F. Megahan, G.W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. Intermountain Forest and Range Experiment Station. Ogden, Utah. United States Department of Agriculture. General Technical Report INT-138.

Platts, W.S. and R.L. Nelson. 1988. Fluctuations in trout populations and their implications for land use evaluation. North American Journal of Fisheries Management 9:446-457.

Platts, W.S. and F.E. Partridge. 1983. Inventory of salmon, steelhead trout, and bull trout: South Fork Salmon River, Idaho. Intermountain Forest and Range Experiment Station. Ogden, Utah. United States Department of Agriculture. General Technical Report INT-324.

Rahel, F.J. 1990. The hierarchial nature of community persistence: a problem of scale. The American Naturalist. 136(3):328-344.

Rahel, F.J. , J.D. Lyons, and P.A. Cochran. 1984. Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. American Naturalist 124:583-589.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs, 37:317-319, 331-349.

Sale, P.F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 18:367-421.

Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological monographs 52(4):395-414.

Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *in* Matthews W.J. and D.C. Heins, editors. Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press: Norman and London.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science. 185:27-39.

Scott W.B. and E.J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin 184. Fisheries Research Board of Canada.

Shelford, V.E. 1911. Ecological succession: Stream fishes and the method of physiographic analysis. Biological Bulletin 21:9-35.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology: Trans. Am. Geophys. Union, vol 38, pp. 913-920.

Strong, W.L. and K.R. Leggat. Ecoregions of Alberta. 1981. Prep. by Resource Evaluation and Planning Division. Alberta Energy and Natural Resources. ENR Technical Report # T/4.

Swanston, D.N., W.R. Meehan, and J.A. McNutt. 1977. A quantitative geomorphic approach to predicting productivity of pink and chum salmon streams in southeast Alaska. USDA Forest Service Research Paper PNW-227, Pacific Northwest Forest and Range Experimental Station, Portland Oregon. 16 p.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

ter Braak, C.J.F. 1987a. CANOCO - a FORTRAN Program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis, Principal Component Analysis and Redundancy Analysis (Version 2.1). Agriculture Mathematics Group, Wageningan.

ter Braak, C.J.F. 1987b. Ordination. Pages 91-173 *in* Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren editors. Data Analysis in Community and Landscape Ecology.

ter Braak, C.J.F. and C.W.N. Looman. 1987. Regression. Pages 29-77 *in* Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren editors. Data Analysis in Community and Landscape Ecology.

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 Sciences 37:130-137.

Whitney, P., P.J. McCart, and A. Sekarak. 1975. Baseline Studies of the biology of streams and wildlife populations in the Sheep Creek Drainage, Alberta. Prep. by Aquatic Environments Limited. Crossfield Alberta.

Wiens, J.A. 1984. On understanding a non-equilibrium world: Myth and reality in community patterns and processes. Pages 439-457 *in* Strong, D.R. Jr, D. Simberloff, L.A. Abele, and A.B. Thistle editors. Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, New Jersey.

Wiens, J.A. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. Pages 154-172 *in* Diamond, J. and T.J. Case editors. Community Ecology. Harper & Row, Publishers, New York.

Yant, P.R., J.R. Karr, and P.L. Angermeier. 1984. Stochasticity in stream fish communities: an alternative interpretation. The American Naturalist 124(4):573-582.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Engelwood Cliffs N.J.

APPENDIX I

SITE-SPECIFIC PHYSICAL HABITAT DATA

SITE	MVEL (m/s)	Q (m^3/s)	DEPTH (m)	WIDTH (m)	BLDR (%)	RBL (%)	FSED (%)	POOL (%)	RIFF (%)	CV	pH	TDS (mg/l)	TURB (ntu)	CON. (%)	DEC. (%)
BO1	0.0960	0.132	0.24	6.78	17.5	12.6	55.3	25.0	15.8	23.4	8.3	340.0	1.0	11.0	52.0
BO2	0.0420	0.023	0.11	4.97	10.6	26.5	26.9	14.5		43.8	8.8	290.0	2.0	66.0	6.0
BO4	0.0140	0.007	0.61	1.35	0.0	4.3	89.6	76.7	15.6	86.0	8.8	230.0	3.0	18.0	0.0
WO1	0.0740	0.138	0.35	6.90	0.4	19.6	42.5	37.0	18.8	30.0	8.0	450.0	1.0	62.0	7.0
WO2	0.0340	0.017	0.09	5.31	17.5	30.6	27.1	28.5	58.3	39.3	8.1	480.0	1.0	3.0	22.0
NW1	0.0500	0.045	0.17	5.87	9.6	23.0	36.0	12.5	33.5	63.9	8.0	440.0	1.0	71.0	6.0
NW2	0.0900	0.032	0.11	3.64	7.2	36.7	32.7	14.3	50.3	28.3	8.1	380.0	1.0	26.0	1.0
NW3	0.0180	0.005	0.11	2.38	0.0	1.1	78.5	10.0	47.5	42.0	8.1	290.0	5.0	30.0	0.0
CA1	0.0100	0.003	0.10	4.00	24.8	24.2	40.2	22.3	31.3	52.0	8.2	490.0	11.0	29.0	9.0
CA2	0.0064	0.001	0.06	2.45	35.4	28.5	14.8	16.8	48.5	30.9	8.1	280.0	8.0	19.0	29.0
CA3	0.0005	0.001	0.64	4.52	0.0	0.0	89.9	100.	0.0	45.8	7.6	460.0	13.0	38.0	0.0
NO1	0.0280	0.023	0.22	4.46	13.8	25.8	46.7	19.5	50.3	61.7	8.1	410.0	3.0	20.0	0.0
NO2	0.2300	0.010	0.17	3.33	12.6	21.9	32.6	28.5	35.0	25.4	8.1	300.0	1.0	30.0	0.0
GU1	0.2280	0.248	0.17	6.43	20.1	29.9	16.8	3.5	54.0	26.3	8.3	80.0	2.0	69.0	0.0
RR1	0.0410	0.033	0.13	6.67	20.2	25.2	14.1	2.5	50.0	44.5	8.1	100.0	2.0	2.0	0.0
LR1	0.1140	0.064	0.15	4.12	32.6	29.9	18.6	25.3	56.5	28.2	8.3	240.0	3.0	60.0	0.0
BU1	0.0610	0.076	0.24	5.79	10.7	31.9	25.3	41.5	24.3	29.6	8.3	210.0	4.0	45.0	13.0
BU2	0.0042	0.010	0.50	6.29	11.1	0.4	72.8	79.0	21.0	46.8	7.7	300.0	1.0	53.0	2.0
PIE	0.0220	0.030	0.29	6.60	8.1	21.9	32.3	43.0	18.5	43.0	7.9	320.0	1.0	67.0	0.0
PIW	0.0220	0.026	0.27	5.47	24.8	23.9	28.8	29.0	25.0	20.0	8.1	280.0	8.0	20.0	24.0
HMR	0.0270	0.015	0.19	3.54	15.8	32.4	28.1	13.5	36.5	35.8	8.3	200.0	5.0	21.0	49.0
NMR	0.0280	0.008	0.09	3.58	40.6	47.9	1.1	4.5	68.3	31.3	8.7	250.0	2.0	58.0	1.0
MDY	0.0230	0.016	0.19	4.73	22.7	35.3	25.5	38.5	18.0	19.4	8.2	400.0	7.0	14.0	32.0
STP	0.0140	0.016	0.28	4.93	7.4	7.6	63.7	20.5	7.5	37.8	7.7	370.0	9.0	19.0	1.0
UNG	0.0250	0.024	0.20	5.27	4.1	19.6	40.0	49.0	24.3	71.4	8.4	310.0	5.0	14.0	10.0
SHR	0.2160	0.115	0.12	5.01	23.1	35.2	15.2	18.8	58.0	28.3	8.1	380.0	7.0	52.0	6.0
CUT	0.0740	0.117	0.19	7.86	33.3	28.6	19.0	11.5	54.0	47.5	8.1	100.0	4.0	57.0	0.0
UNC	0.0500	0.043	0.38	2.86	0.0	1.8	52.1	92.5	7.5	31.4	8.0	470.0	2.0	7.0	0.0
COM	0.0260	0.010	0.13	3.50	16.3	16.9	55.7	12.0	46.0	40.3	8.3	350.0	3.0	51.0	20.0
UEM	0.0320	0.014	0.18	3.29	19.6	10.9	61.7	29.8	36.0	46.1	8.0	230.0	5.0	29.0	20.0

RAT	0.0080	0.019	0.39	6.98	28.2	35.1	21.8	52.8	22.5	26.9	8.2	410.0	1.0	55.0	9.0
CHK	0.1880	0.214	0.20	6.27	17.6	31.5	22.9	1.3	54.0	32.6	8.3	420.0	6.0	22.0	0.0
UND	0.0180	0.012	0.51	1.79	0.4	7.1	62.4	0.0	14.3	51.0	7.5	320.0	1.0	0.0	0.0
ROU	0.0466	0.012	0.16	2.21	23.3	23.5	20.9	36.0	40.5	46.9	8.0	200.0	7.0	46.0	0.0
UNA	0.1525	0.120	0.13	6.25	17.3	20.8	30.2	4.0	72.5	0.5	8.1	500.0	2.0	56.0	8.0
NOR	0.1490	0.120	0.17	5.35	37.6	45.6	2.9	1.3	67.0	25.0	8.2	460.0	4.0	65.0	0.0
STY	0.0001	0.001	0.76	7.34	0.0	17.5	82.5	100.	0.0	23.1	7.7	120.0	3.0	29.0	0.0
MAL	0.2940	0.121	0.11	4.25	45.3	26.5	4.4	3.3	92.3	30.3	8.2	210.0	9.0	32.0	7.0

Site variables are explained as follows: MVEL = mean site velocity; Q = discharge; DEPTH = area weighted mean site depth; WIDTH = mean site width; BLDR = area weighted mean boulder substrate composition; RBL = area weighted mean rubble substrate composition; FSED = area weighted mean fine sediment substrate composition; POOL = mean percent pool habitat; RIFF = mean percent riffle habitat; CV = coefficient of width variability; pH = acidity in pH units; TDS = total dissolved solids; TURB = turbidity in nephelometric turbidity units; CON. = mean percent coniferous riparian vegetation; DEC. = mean percent deciduous riparian vegetation. Site codes are explained in Figure 1.

APPENDIX II

WATERSHED-SPECIFIC PHYSICAL HABITAT DATA

SITE	AREA (km^2)	RELIEF (m)	ELEV (m)	SO	ORIENT (1-9)
BO1	91.7	488.0	884.0	4.0	2.0
BO2	35.6	354.0	1076.0	4.0	3.0
BO4	6.9	141.0	1231.0	2.0	2.0
WO1	49.7	519.0	944.0	5.0	2.0
WO2	28.5	408.0	1055.0	4.0	3.0
NW1	29.8	487.0	946.0	4.0	6.0
NW2	11.6	348.0	1084.0	3.0	6.0
NW3	1.7	192.0	1241.0	1.0	3.0
CA1	153.1	345.0	696.0	3.0	4.0
CA2	78.7	267.0	774.0	3.0	4.0
CA3	49.5	218.0	823.0	3.0	4.0
NO1	29.9	252.0	1028.0	3.0	8.0
NO2	19.2	183.0	1097.0	3.0	9.0
GU1	86.2	671.0	975.0	4.0	2.0
RR1	36.8	123.0	1371.0	3.0	7.0
LR1	23.8	250.0	1183.0	3.0	8.0
BU1	64.5	292.0	927.0	4.0	6.0
BU2	31.9	213.0	1006.0	3.0	7.0
PIE	58.5	297.0	861.0	3.0	2.0
PIW	35.2	414.0	866.0	3.0	2.0
BMR	67.3	262.0	759.0	3.0	4.0
NMR	11.1	244.0	1250.0	2.0	7.0
MDY	31.0	454.0	963.0	3.0	3.0
STP	50.2	281.0	786.0	4.0	3.0
UNG	53.7	257.0	825.0	3.0	8.0

SHR	34.5	442.0	1143.0	3.0	3.0
CUT	40.1	298.0	1317.0	3.0	4.0
UNC	57.5	349.0	931.0	3.0	8.0
COM	31.1	358.0	876.0	4.0	2.0
UEM	19.9	198.0	823.0	3.0	3.0
RAT	93.2	370.0	849.0	4.0	2.0
CHK	42.9	366.0	1250.0	4.0	7.0
UND	23.2	126.0	1108.0	3.0	6.0
ROU	12.3	241.0	1131.0	2.0	8.0
UNA	64.7	427.0	861.0	4.0	2.0
NOR	47.2	396.0	1219.0	3.0	2.0
STY	135.4	304.0	747.0	3.0	4.0
MAL	26.6	1417.0	1066.0	3.0	4.0

Watershed variables are explained as follows: AREA = area of the watershed sub-basin; RELIEF = watershed sub-basin relief; ELEV = site elevation; SO = stream order; ORIENT = watershed sub-basin orientation. Site codes are explained in Figure 1.

APPENDIX III

FISH PRESENCE-ABSENCE DATA, 1984.

	BULL TROUT	MOUNTAIN WHITEFISH	ARCTIC GRAYLING	SLIMY SCULPIN	LAKE CHUB	LONGNOSE SUCKER
SITE						
BO1	0	1	1	1	1	1
BO2	1	1	1	1	0	1
BO4	1	0	0	1	0	0
WO1	0	1	0	1	0	1
WO2	1	1	1	1	0	1
NW1	1	1	1	1	0	1
NW2	1	1	1	1	0	0
NW3	1	0	0	0	0	0
CA1	0	0	1	0	1	1
CA2	0	0	1	0	0	1
CA3	0	0	1	0	0	1
NO1	1	0	1	1	0	0
NO2	1	0	1	1	0	0
GU1	1	1	1	1	0	0
RR1	1	0	1	1	0	0
LR1	1	0	1	1	0	0
BU1	1	1	1	1	0	1
BU2	0	0	1	1	0	0
PIE	1	0	0	1	1	1
PIW	0	0	1	1	1	1
HMR	0	0	1	1	1	1
NMR	1	0	0	1	0	0
MDY	1	1	1	1	0	1
STP	0	0	1	0	1	1
UNG	1	0	0	1	1	1
SHR	1	1	0	1	0	0
CUT	1	0	0	1	0	0

UNC	1	0	1	1	1	1
COM	0	0	1	1	1	1
UEM	0	0	1	1	0	1
RAT	0	0	1	1	1	0
CHK	1	0	0	1	0	0
UND	0	0	1	1	0	0
ROU	1	0	0	0	0	0
UNA	0	1	1	1	0	0
NOR	1	0	0	0	0	0
STY	0	0	0	0	1	0
MAL	1	0	0	0	0	0

1 = present; 0 = absent.

APPENDIX IV

FISH PRESENCE-ABSENCE DATA AT RESAMPLED SITES 1982, 1983, 1984.

SITE (yr)	SPECIES SAL CON	THY ARC	PRO WIL	COT COG	CAT CAT	COU PLU
GU1 '82	X	X	X	X	X	
GU1 '83	X	X	X	X		
GU1 '84	X	X	X	X		
WO1 '82	X	X	X	X	X	
WO1 '83			X	X	X	
WO1 '84			X	X	X	
WO2 '82	X	X	X	X		
WO2 '83	X	X	X	X		
WO2 '84	X	X	X	X		
NW1 '82	X	X	X	X		
NW1 '83	X	X	X	X		
NW1 '84	X	X	X	X		
NW2 '82		X	X	X		
NW2 '83	X	X	X	X		
NW2 '84	X	X	X	X		
NW3 '82	X					
NW3 '83	X					
NW3 '84	X					
BO1 '82	X	X	X	X	X	X
BO1 '83		X	X	X	X	X
BO1 '84		X	X	X	X	X
BO4 '82	X			X		
BO4 '83	X			X		
BO4 '84	X			X		

	SPECIES					
SITE (yr)	SAL CON	THY ARC	PRO WIL	COT COG	CAT CAT	COU PLU
NO1 '82	X	X		X		
NO1 '83	X	X		X		
NO1 '84	X	X		X		
NO2 '82	X	X		X		
NO2 '83	X	X		X		
NO2 '84	X	X		X		
CA1 '82		X		X		X
CA1 '83	X	X		X	X	X
CA1 '84		X		X	X	X
CA2 '82		X			X	
CA2 '83		X			X	
CA2 '84		X			X	
CA3 '83		X			X	
CA3 '84		X			X	
RR1 '83	X	X		X		
RR1 '84	X	X		X		
LR1 '83		X		X		
LR1 '84	X	X		X		
BU1 '83	X	X	X	X	X	
BU1 '84	X	X	X	X	X	
PIW '83	X	X		X	X	X
PIW '84		X		X	X	X

Species codes: SAL CON = bull trout; THY ARC = arctic grayling; PRO WIL = mountain whitefish; COT COG = slimy sculpin; CAT CAT = longnose sucker; COU PLU = lake chub. X denotes occurrence.