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Title: Relationships Between Fish Species Distribution and Habitat in the Willamette River Drainage in Western Oregon

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The objectives of this study were to (1) describe physical environmental conditions and species composition at several sites along an upstream/downstream gradient in a number of tributaries of the Willamette River in western Oregon; and (2) identify possible relationships between species distributional patterns and physical habitat parameters using detrended correspondence analysis (DCA), graphical techniques, and contingency table analysis. Study sites that contained both pools and riffles were selected at various locations on seven streams. At each site 13 physical environmental parameters were measured, and fish species composition and abundance were determined by snorkeling and electroshocking techniques. Associations between environmental conditions and species composition and abundances were hypothesized using the results of DCA. The DCA analysis revealed three habitat gradients, each of which represents a composite of several physical habitat variables. Axis one was interpreted as a habitat gradient from pools to riffles based upon observations of temperature, depth, and percent gravel and bedrock. Axis two appeared to be a gradient of habitat cover types; instream cover (undercut banks, root wads and boles, woody debris, and rooted vegetation) typified one end of the axis and other cover types (riparian vegetation, large substrate composition, and swift water velocities) were indicative of the opposite end of the axis. Axis three seemed to be gradient of stream discharge. Species scores differed along each axis due to the variation in specific responses to these different physical habitat gradients. A three-dimensional graph of species scores for all three axes was used to predict fish community responses to potential human perturbations of the Willamette River drainage given known effects of these perturbations on the physical parameters underlying the three gradients.

Relationships Between Fish Species Distribution and Habitat in the Willamette River Drainage in Western Oregon

by

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This thesis is dedicated to my mother and father.

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INTRODUCTION

General Overview

The objectives of this study were to (1) describe physical environmental conditions and species composition at several sites along an upstream/downstream gradient in a number of tributaries of the Willamette River in western Oregon; and (2) identify possible relationships between species distributional patterns and physical habitat parameters using detrended correspondence analysis, graphical techniques, and contingency table analysis.

In overview, the following strategy was used to meet these objectives. Seven streams (six impounded and one non-impounded) in the Willamette River drainage were chosen for study. Study sites were located at various distances upstream and downstream (above and below the dams on the impounded streams). At each site a number of physical environmental parameters were measured, and fish species composition and abundance were determined by snorkeling and electroshocking techniques. Next, associations between environmental conditions and species composition and abundances were hypothesized using the results of detrended correspondence analysis. Graphical techniques and contingency table analysis were used to further investigate these hypotheses. Finally, predictions about impacts of human interventions (e.g., impoundment, logging, channelization) were made using knowledge about the changes in physical parameters that will occur from these activities and the ecological relationships between these parameters and the fish communities that were characterized in this analysis.

Brief Review of Theories about Stream Fish Assemblages

The association between fish species assemblages and stream habitats has been a major topic of study in the science of community ecology for many years. Very divergent schools of thought have been presented regarding the importance of physical and temporal variability of stream systems (unpredictable environmental changes) versus biological processes (predation, competition) in regulation and maintenance of stream fish communities (Grossman et al. 1982). Some researchers theorized that assemblages are generally in equilibrium and that predation, resource partitioning and competition maintain a persistent community (Schoener 1974, Fraser and Cerri 1982, Gorman and Karr 1978, Paine et al. 1982). In contrast, other researchers have emphasized the importance of physical and temporal variability of stream habitats in the regulation of stream fish assemblages (Grossman el.al. 1982, Layher and Maughan 1985, Lotich 1973, Platts 1979, Schlosser 1982). Other theories about the regulation of stream assemblages reflect a combination of biotic and abiotic factors (eg., Allen 1969, Baltz et al. 1982, Horwitz 1978, Moyle and Vondracek 1985, Schlosser 1987). This review focuses on the regulation of stream fish communities through physical habitat parameters and the effects of human activities (impoundment, logging) on the assemblages.

Vannote et al. (1980) proposed the idea that the network of streams within a river drainage is a continuum of physical environments and their associated biotic communities. Streams are viewed as a longitudinally linked system in which the downstream physical processes (cycling of organic material and nutrients, and ecosystem metabolism) are integrally linked to instream processes occurring upstream (introduction of organic material). The changes in physical habitat parameters from the headwaters to the downstream extent present a continuous gradient of conditions including width, depth, velocity, discharge and temperature. Biotic communities are distributed along these gradients according to their morphological and behavioral adaptations.

Longitudinal succession of species assemblages occurs within a stream system and between stream systems in a watershed or geographic region (Cummins 1974, Hughes et al.

1987, Schlosser 1987, Sheldon 1968). In fact, different stream habitat zones (e.g; headwaters, middle order sections, etc.) have been characterized by the occurrence of particular fish assemblages (Huet 1959, Lagler et al. 1962). One of the most widely-recognized classification schemes for these stream habitat zones was proposed by Huet (1959). He divided stream systems into four zones. Each was characterized by a particular combination of stream gradients, widths and velocities. The zones were named for the predominant fish species found in them. Huet determined that changes in species composition from the headwaters to the mouth of a stream were due to species addition, replacement, or changing relative abundances with respect to the changing physical characteristics of the streams.

In recent years theories on the biological processes occurring in stream ecosystems have evolved from consideration of stream sections as individual entities to consideration of the entire stream as an integrated continuous system (Vannote et al. 1980, Minshall et al. 1983). Previous research on stream systems centered on taxonomic inventories of the biological communities rather than taking a process-oriented or cause and effect approach.

Stream system processes change as a result of man-made disturbances (Karr 1981). Man-made disturbances may change physical characteristics of the stream enough to result in a change in the species assemblage. The amount of change in a species assemblage is related to the scale of the disturbance. Recent research has shown that man's activities in a watershed (i.e., logging, impoundment, etc.) can affect the entire stream system, not just a localized area (Petts 1984, Li et al. 1987). The perception of streams as integrated systems and the realization of man's influences on stream assemblages have resulted in a new approach to stream ecology research. This shift reflects a changing emphasis from descriptive studies to predictive studies (Minshall et al. 1985a). Further discussion of physical stream parameters, their influence on fish assemblages, and the impacts of man-made disturbances will be presented in the Discussion.

The Role of Statistics in Stream Ecology

Research techniques that can utilize either historic or current information on physical habitat characteristics and species composition from stream systems are necessary to predict possible impacts from proposed development projects. General, adaptable, and easily implemented methods for identifying relationships between fish assemblages and their habitats would be valuable management tools for predicting impacts of various activities that alter physical habitat parameters in known ways. That is, if the effects of logging, impoundment and channelization on the physical parameters of a stream (e.g., siltation, water temperature, canopy cover etc.) are understood, then a technique which can identify the ecological interrelationships (e.g., which species are associated with swift versus slow moving water or gravel versus bedrock substrate) can also be used to forecast changes in the fish community. Such a method would be of interest to resource agencies and private land use managers.

A number of statistical techniques are potential candidates for such purposes. Because of the numerous physical and environmental habitat parameters which interact to affect community composition, stream fish communities are best assessed using multivariate techniques (Gorman and Karr, 1978; Felley and Hill 1983). Statistical methods that treat only one, or a few variables at a time are impractical and ineffective treatments of multivariate data (Gauch 1982). The use of multivariate statistical techniques to analyze species-environment relationships in field studies is now common practice.

Review of Multivariate Statistical Approaches

There are three basic multivariate strategies used today: direct gradient analysis, ordination and classification. These three strategies can be combined to form a comprehensive, complementary analysis that characterizes the structure in complex ecological data sets, and can be used to reduce the number of explanatory variables to a manageable few (Strahler 1978, Carleton 1984). Data reduction often serves to increase the researcher's comprehension of the important ecological processes operating in the stream system (Gauch 1982).

The objective of direct gradient analysis is to associate the distribution of species with important environmental gradients. This technique incorporates both species and environmental data sets initially. Unlike gradient analysis, ordination and classification techniques use species data first, and later incorporate environmental data for interpretation. Classification is used in community ecology to assign the samples or species of large data sets to clusters or groups. The result is either a hierarchical or non-hierarchical arrangement of clusters of like samples or species. Many strategies and algorithms for forming clusters are available (see Gauch 1982 for an overview), and the appropriate choice is not always clear.

The purpose of ordination techniques is to represent species and sample relationships by producing a low-dimensional (typically one to three dimensions) ecological space from the input data. Ordination techniques are used to bridge the gap between field data, which is typically multi-dimensional, and human comprehension, usually limited to only low-dimensional summaries. Ordinations (e.g., weighted averages, polar ordination, principal components analysis, reciprocal averaging, etc.) are usually represented by a graph, in which similar samples or species or both are near each other and dissimilar entities are far apart. Ordination techniques have increased in mathematical complexity over the years. For a review of the historical development of ordination techniques the reader is referred to Orloci (1978) or Whittaker (1978).

Bray and Curtis (1957) devised an ordination technique, named polar ordination, that selects two samples as poles of an ordination axis. The goal of this technique was to map the species, samples or environmental factors in such a way that their relative proximity indicates the degree of association along a complex of factors (gradient). One limitation of polar ordination is that species and sample ordinations are calculated separately, thus having no mathematical relationship. Therefore, the two ordinations must be interpreted separately and may not have any straight forward relationship. In contrast, eigenvector-based ordination techniques (principal components analysis (PCA), reciprocal averaging (RA), and detrended correspondence analysis (DCA)), unify species and sample scores in one ordination space, thus allowing a more complete ecological interpretation of the data.

PCA (Goodall 1954) was the first ordination technique developed in which the ordination scores were derived from the data matrix alone; no weights, endpoints or other parameters are required. Strictly applied, PCA has several assumptions that must be met by the data set; the components must be normally distributed and uncorrelated. When PCA is used for descriptive purposes with field data sets, departures from ideal data structure are tolerable (Greig-Smith 1980). The function of PCA is to reduce points in a multi-dimensional space to fewer dimensions or axes. The first PCA axis lies in the direction of maximum variance. A second axis is then found that is orthogonal (perpendicular) to the first and accounts for a maximum of the remaining variance, and so on for the other axes. The result of PCA ordination is a series of axes of diminishing importance. The underlying model of PCA is unable to properly handle non-linear species response curves. This problem reduces the usefulness of PCA in analyzing community data and testing hypotheses. Currently the most common use of PCA is description and reduction of data sets that match the assumptions of the PCA model fairly well.

Reciprocal averaging (also known as correspondence analysis) is an ordination technique in which the species ordination scores are averages of the sample ordination scores and likewise the sample ordination scores are averages of the species ordination scores (Hill 1973, 1974). RA gives a clearer interpretation of the major environmental parameter affecting the species community than PCA, because it arranges the data set along a single or predominant gradient (Gauch 1981). This procedure can be extended to create several independent axes that each represent structure in the data set.

The intuitive appeal of RA is diminished by two major flaws. First, axes ends are compressed relative to the middle of the axis, which results in distortion of the distance of separation between species (or samples) on the axis. Ideally, an ordination would have species (or samples) appearing and disappearing at a steady rate along an axis. But with the compression of the axes ends it is difficult to know if the species has really reached the end of its range or whether its range has been truncated. PCA also has this characteristic flaw, but unlike RA, the arch may also be involuted causing opposite ends of a gradient to be brought close together (Gauch et al. 1977). This confounds axis interpretation. The second flaw of RA is the tendency for the first axis to be strongly related to the second (and sometimes higher axes). This is known as the arch effect (Gauch et al. 1977) and also often occurs in other ordination techniques, such as principal components analysis or non-metric multidimensional scaling (NMMS).

Detrended correspondence analysis (DCA) is derived from reciprocal averaging but differs from RA in two respects: the scaling of the axes and the way in which the second and higher axes are calculated (Hill 1973). DCA is designed primarily for ecologists who have collected data on the occurrence of species in a set of samples, and is used to identify possible relationships between species distribution patterns and physical parameters. DCA corrects one fault of RA, compression of axes ends, by removing any systematic relation between within-sample standard deviation and position along the gradient. This is accomplished by rescaling the expanded parts of the gradient where the standard deviation is low and contracting the parts where it is high (Hill 1979). DCA avoids the arch effect in RA by requiring that there be no correlation nor systematic relationship of any kind between axes.

DCA generally results in interpretable ordination axes for species and samples with each entity assigned a rank score for it's position on the axis. The ability of DCA to correct RA's faults becomes better appreciated upon acknowledging that these faults are present in most ordination techniques, including PO, PCA, NMMS, principal coordinates analysis, factor analysis and canonical correlation analysis (Gauch et al. 1981, Gauch 1982). Additionally, DCA performs well with data that is discrete but ordered, or grouped into intervals (i.e., categorical data). Because most of the species abundance and environmental data collected in this study are categorical and because of its other advantages discussed above, DCA was chosen as the primary analytical method in the analysis.

Contingency table analysis (CTA) was used to obtain a description of the relationships between the factors (e.g., environmental parameters and species abundances) in a table by ordering the importance of the interactions between the factors. These tables are appropriate for data that are categorical, such as much of the data collected in this study. This is similar to an analysis of variance (ANOVA) model except that the logarithm of the expected cell frequency replaces the expected value in the ANOVA model. The BMDP (1983) version P3F of this computer program was used in this analysis. This program is very flexible and allows specification of the variables to be tested and allows automatic addition or subtraction of the variables into the analysis based on their rank scores. This model tests for single or multiple order effects of variables. A more complete review of this technique is found in Dixon (1983).

METHODS

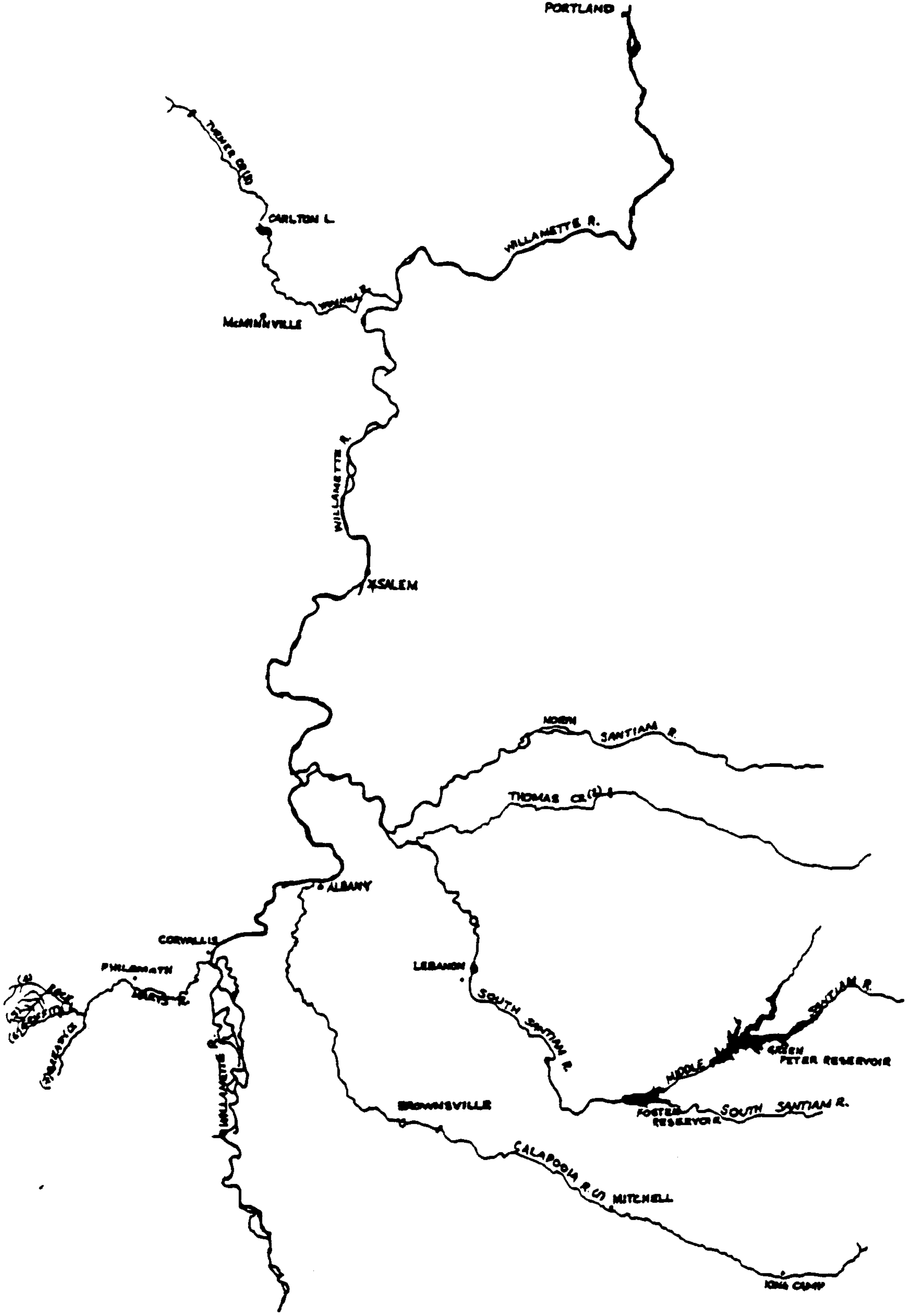
Selection of Streams and Study Sites

Seven streams were studied in this project: Calapooia River, Thomas Creek, North and South Forks of Rock Creek, Turner Creek, Griffith Creek and Greasy Creek (Figure 1). Study sites on each stream were located along a longitudinal gradient from the headwaters to the mouth. Several criteria were used to select the study sites; the presence of two representative patch types (usually a pool and a riffle), physical accessibility of the study site, acceptable water quality, and distance from Oregon State University. All sites on the Calapooia River and all but the farthest upstream site on Thomas Creek were sampled between July and September, 1982. All other streams were sampled between June and September, 1983.

The Calapooia River is a tributary of the Willamette River and originates in the Tid Bit Mountains of Linn County, Oregon. The Calapooia River is impounded approximately eight miles upstream of Brownsville, Oregon. The dam is a wood and concrete structure approximately three meters in height. The system is logged near its headwaters by King Camp and has been mined extensively for gold. Study sites on the Calapooia River were established 32180, 24140, 12870, 1600 and 4 m above the dam, and 10, 20, and 32 m below the dam. Study sites farther downstream

Figure 1. Location of seven streams chosen for study: Calapooia River, Thomas Creek, north and south forks of Rock Creek, Turner Creek, Griffith Creek, and Greasy Creek.

Figure 1.


PORTLAND
TURNER CR.(8)
CARLTON L.
YAMHILL R.
McMINNVILLE
WILLAMETTE R.
WILLAMETTE R.
SALEM
NORTH SANTIAM R.
THOMAS CR.(2)
ALBANY
CORVALLIS
PHILOMATH
MARYS R.
ROCK CR.
WILLAMETTE R.
LEBANON
SOUTH SANTIAM R.
MIDDLE SANTIAM R.
GREEN PETER RESERVOIR
FOSTER RESERVOIR
SOUTH SANTIAM R.
BROWNSVILLE
CALAPOOIA R.(1) MITCHELL
KING CAMP

from the dam could not be sampled using the established methods because of unacceptably high levels of fecal coliform in the water.

Thomas Creek is a tributary of the South Santiam River. It originates 5 miles northwest of Quartzville, Oregon and is impounded about 8 miles upstream of Scio, Oregon. The dam is a concrete structure with a small flow through an aperture approximately 2 m high with a 7 m bedrock drop immediately below the dam. Study sites on Thomas Creek were located 17700, 12900, 3200, 163, 150, 60 and 40 m above the dam, and 3, 30, 64, 500, 4800 and 12900 m below the dam.

The Rock Creek drainage is located five miles west of the city of Philomath, Oregon. Two forks of Rock Creek were examined, the north fork and the south fork. The south fork is impounded with a concrete diversion dam 0.5 m high. The north fork is impounded by a large earth-filled dam approximately 15 m high. Study sites on the south fork of Rock Creek were located 825 and 800 m above the dam and 5, 20, 40, 80 and 800 m below the dam. Study sites on the north fork of Rock Creek were located 1050 and 1000 m above the dam and 5, 20, 40, 1600 and 2400 m below the dam. The reservoir on this stream was approximately 1000 meters long and too large to effectively sample with the chosen techniques.

Griffith Creek is tributary of Greasy Creek in the Mary's River drainage system. It is impounded approximately one mile upstream of its confluence with Greasy Creek. The dam is a concrete structure approximately 0.5 m high. Study sites on Griffith Creek were located at 5, 13, 23, and 30 m above the dam. The stream bed below Griffith Creek is dry during summer low flow, which corresponded to the sample time period. Therefore no below-dam samples could be taken.

Greasy Creek is a tributary of the Mary's river and originates on the southern slope of Mary's Peak. It flows for approximately seven miles to its confluence with the Mary's River near Philomath, Oregon. Greasy Creek was the only unimpounded stream studied.

Turner Creek is a tributary of the Yamhill River in the Willamette River drainage. Turner Creek originates approximately one mile east of Neverstill, Oregon and is impounded at Yamhill Reservoir four miles upstream from Pike, Oregon. The dam is a concrete structure, four meters high. Study sites on Turner Creek were located 60 m and 5 m above the dam and 40 m and 80 m below the dam.

Data Collection Techniques

Data collection techniques for this study followed a hierarchical pattern beginning with the selection of study streams. Within each stream study sites were established.

Study sites contained different habitat types, called patches, which were visually categorized into one of four patch types; pool, riffle, run or other. Microhabitat patches are defined as homogeneous bodies with respect to substrate, current velocity, surface turbulence, and depth (Fraser and Sise 1980).

Waters deeper than 60 cm were sampled for fish species richness and abundance by visual observation using snorkeling techniques. This is a rapid, effective method that has minimal disruptive effects on fish behavior (Northcote and Wilkie 1963, Goldstein 1978). To assess fish abundance transects were established starting from the downstream boundary of the patch and swimming upstream parallel to stream flow. Each observer counted all fish in a designated area of his/her field of vision. Patches were snorkeled by one to three observers, depending on the stream width. Patches 5 m wide or less required one observer and one transect; patches 5 to 20 m wide required two observers and two transects; and patches over 20 m wide required three observers and three transects. Observers maintained even positions across the stream at all times during a dive. Numbers of fish observed during each pass through a patch were recorded on an underwater writing tablet. Each patch was sampled two or three times and abundances of all observed species were compared and averaged. Shallow patches (less than 60 cm) were sampled for fish species richness and abundance using the DeLury removal population estimate. Each patch was sampled three times with a Coefelt model BP-3 electroshocker. In narrow stream sections the downstream edge of the study site was blocked off with a seine. In wide stream sections nets were held below the electroshocker to catch stunned fish. Fish were counted after each pass, identified and held in separate buckets until sampling was complete. All fish were released back into the stream.

Physical habitat parameters were measured in each patch along transects perpendicular to stream flow and had specific data collection locations, or loci located 25%, 50% and 75% across the width of the stream. The number of transects in each patch varied from one to four, depending on the patch length; longer patches had more transects in order to adequately characterize the entire patch. At each loci the following physical parameters were measured; substrate composition, surface and mid-water velocity, surface turbulence, stream depth, and instream and overhead cover. Substrate composition was visually estimated for a 1 m^2 area at each locus using an Aquascope viewing box. Percent composition of substrates was estimated using the following categories: (1) sand, silt or clay; (2) small gravel (<2.5 cm diameter); (3) gravel (2.5-7.5 cm); (4)

cobble (7.5-15.0 cm); (5) rubble (15.0-30.0 cm); (6) boulders (>30.0 cm); and (7) bedrock. The presence or absence of woody debris, undercut banks, root wads, root boles and rooted vegetation was noted for each patch. Surface and mean velocity (0.4 m above the stream bottom) were measured with a Marsh McBirney electronic current meter, model 201. Surface turbulence was visually estimated using these categories: (1) mirror-like; (2) small riffles; (3) large riffles; (4) standing waves; (5) whitecaps; and (6) white foam. Stream depth was measured in centimeters with a graduated wooden dowel. The presence or absence of overhead cover, defined as riparian vegetation overhanging the stream bed, was recorded for each patch. Air temperature, dissolved oxygen, and water temperature were measured at each patch using a Yellow Springs temperature/oxygen meter, model 54A. All patches were sampled at mid-day (1000 and 1500 hr) to minimize fluctuations in dissolved oxygen, water temperatures, and amount of sunlight penetrating the streams.

Data Analysis

To examine habitat selection by each species, an adaptation of Strauss' (1979) linear index was calculated. First, the relative availability of each habitat type (p_i) was calculated as the number of sites of that type sampled divided by the total number of all sites sampled. For example, 26 of the 51 patches sampled were pools, the relative availability of pools (P_{pools}) was 0.51. Next, the relative use of each habitat type (r_i) for each species was calculated as the number of habitats of type i in which that species was sighted divided by the total number of sightings for that species. For example, squawfish were observed at 10 sites, and all of these were pools. The relative use of pools by squawfish was 1.00. Finally, the index of selection was calculated as the relative use minus the relative availability. For squawfish, the habitat selection index for pools was 1.00-0.51 = 0.49. Positive values indicate selection for that habitat type and negative values indicate selection against that habitat type. Variance of the index was calculated according to Strauss (1979).

For detrended correspondence analysis raw fish counts were transformed in several ways; densities, natural logarithm of densities, grouped densities (low, medium, and high), biomass, natural logarithm of biomass, and grouped biomass (low, medium, and high). Density values for each species in each patch were calculated by dividing the estimated number of individuals in that patch by the size of the patch (m^2). It seemed appropriate to define low, medium and high density categories differently for schooling species and non-schooling species. For example, redside shiners were sometimes present in numbers exceeding several hundred fish, while rainbow trout rarely exceeded ten in one patch. Boundaries for the three abundance categories for the schooling and non-schooling fishes were established to roughly correspond to the lower, middle, and upper 33 percentiles of density values for those species. Low, medium and high densities were defined as follows. For speckled dace (Rhinichthys osculus), and redside shiners (Richardsonius balteatus) the density categories were low, <3.24 m^{-2}; medium, between 3.25-5.24 m^{-2}; and high, >5.25 m^{-2}. For adult and juvenile cutthroat trout (Salmo clarki), squawfish (Ptychocheilus oregonensis), largescale sucker (Catostomus machrocheilus), longnose dace (Rhinichthys cataractae), adult and juvenile torrent sculpins (Cottus rhotheus), and adult and juvenile rainbow trout (Salmo gairdneri) the groupings were low, <1.49 m^{-2}; medium, 1.50-3.49 m^{-2}; and high, >6.10 m^{-2}. Biomass values for each species in each patch were calculated by multiplying the average weight of an individual fish by the number of individuals and then dividing by the area of the patch. Average weight was calculated from field estimates of mean length and published length-weight relationships (Table 1). The boundaries for low, medium and high values of biomass

Table 1. Observed mean length and estimated mean weight from length-weight relationships for each species used to calculate biomass. Information sources are: (1) Carlander (1969); and (2) Scott and Crossman (1973). SL denotes standard length, FL denotes fork length and TL denotes total length.

Species name	Life stage	Length (in)	Weight (g)	Length type	Information source
Cutthroat trout	adult	6.5	26.8	FL	1
Cutthroat trout	juvenile	2.5	3.2	FL	1
Squawfish	adult	10.0	129.0	FL	1
Suckers	adult	10.0	252.0	FL	1
Redside shiners	adult	3.5	6.0	TL	1
Speckled dace	adult	2.5	1.2	FL	1
Longnose dace	adult	3.0	4.5	FL	1
Torrent sculpins	adult	3.0	4.5	FL	2
Torrent sculpins	juvenile	1.5	2.3	FL	2
Rainbow trout	adult	10.0	151.0	SL	1
Rainbow trout	juvenile	2.5	3.4	SL	1
Sculpin spp.	adult	3.0	4.5	FL	2

were equal to the boundaries chosen for density multiplied by the average weight of each species.

Detrended correspondence analysis was applied to all types of transformations of the fish counts and the raw data. Procedures for effective use of DCA were followed (Hill and Gauch 1980) using the computer program DECORANA (Hill 1979). A second round of DCA runs was completed using an octave scale to reduce the effect of dominant species. The rare species (Mountain whitefish, Prosopium williamsoni), sand roller (Percopsis transmontana), western brook lamprey (Lampetra richardsoni), and largemouth bass (Micropterus salmoides) were then deleted as suggested by Hill and Gauch (1980), and final runs of DCA were made with the reduced species data set. Rare species were defined to be those that occurred only once in the data set, and were eliminated.

The amount of variability explained by each axis for each data transformation was determined by dividing its eigenvalue by the sum of all eigenvalues for all axes. Only axes that accounted for significant variability in the data (>15%) were considered for interpretation. To aid interpretation of these DCA axes, tables and figures were constructed in which summary statistics of the habitat characteristics for each species were ordered according to the species score for each DCA axis. Specifically, the following summary statistics of each environmental variable for each species were calculated: (1) mean value of each environmental variable averaged over all patches at which the species occurred; (2) mean values averaged over all patches at which the species was absent; and (3) the difference in means at patches of species occurrence and species absence, i.e., (2) minus (3). Trends in these three statistics were used to decipher potential underlying environmental gradients that could be used to explain the species scores along each DCA axis. The difference between the mean of each environmental variable averaged over sites of species occurrence and the mean at sites of species absence was viewed as a measure of the preference of the species for particular environmental conditions. For example, the average water temperature in patches containing redside shiners was 20.5 C while the average at patches in which they were absent was 15.7 C. The difference, +4.8 C, was an index of the preference of redside shiners for warmer temperatures. Significant differences between means for all environmental variables over sites of occurrence and sites of absence were tested using t-tests. Only environmental variables showing distinct linear trends along each axis were considered to be potentially meaningful.

The results of the DCA analysis (axis ordinations and scatter plots of species/sample scores) and trends in physical parameters associated with species scores were used to generate hypotheses about the major factors involved in regulating stream fish communities and individual members (species) in the community. The resulting hypotheses were further investigated with an observed frequency table analysis. The observed contingency table analysis did not constitute a true statistical test of the hypotheses in part because the same data were used in both DCA and CTA. However, CTA did offer an alternative method of further evaluating the species-habitat relationships. Observations were transformed into binary data for analysis. Fish abundance was transformed into presence/absence, habitat into pool/riffle, cover into instream cover/substrate cover and streamflow into low/high discharge. Observed frequency tables were constructed for all species/habitat gradient combinations. The Pearson goodness-of-fit statistic (Chi-square) was used to test for significant differences in the observed frequency tables. The Yates correction was not used, based upon Remington and Shork's (1970) view that this correction is overly conservative and that the corrected chi-square statistic fails to reject the null hypothesis as often as it should. It was hoped that a multiway contingency table analysis could have been used to explore second or third order models, but small sample sizes prohibited a meaningful analysis.

RESULTS

Summary of Species and Environmental Data

Species composition and physical habitat characteristics varied between streams (Table 2-8). Discharge patterns for Thomas Creek and the Calapooia River were influenced by adjacent land uses (irrigation). This resulted in a large variation in discharge between study sites. The total number of species present in the larger stream systems (Thomas Creek, Calapooia River and Greasy Creek) was much higher than in the smaller systems. Access was very limited in several streams (Turner Creek, Griffith Creek, north and south fork of Rock Creek) and few study sites could be sampled. Cutthroat trout and sculpins were present in all streams, but were the only species present in Turner Creek and Griffith Creek. Rainbow trout was the only additional species found in the north and south fork of Rock Creek. The remaining species were present in Greasy Creek, Thomas Creek and the Calapooia River (Table 2-8).

Fish species assemblages varied with patch type for each stream (Table 9). Significant differences between the average species richness for pools and riffles were tested using the t-test. Only Thomas Creek and the Calapooia River were tested due to small sample sizes for the other streams. There was no significant difference for the Calapooia River, but there was a significant difference for

Table 2. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at 17 study sites on Thomas Creek during July - September 1982 (sites 5-17) and July - August 1983 (sites 1-4). Low numbered sites are upstream and high numbered sites are downstream. The dam is located at site number 9.

a. Physical Characteristics

									Substrate Composition (%)				
Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Fines	Gravel	Cobble & Rubble	Boulder	Bedrock
1	pool	18	139	37	8.10	17	0	0	0	17	47	37	0
2	riffle	18	48	49	4.23	13	0	0	2	15	17	68	0
3	pool	23	91	39	6.66	14	0	0	2	13	26	6	52
4	riffle	22	53	50	5.94	14	12	0	4	22	45	29	0
5	pool	18	130	1	0.33	18	33	1	24	5	14	0	69
6	riffle	14	18	81	0.18	20	0	0	0	25	75	0	0
7	pool	15	127	5	1.05	29	0	1	43	6	28	23	0
8	riffle	10	16	41	0.63	18	0	0	0	37	63	0	0
9	pool	18	790	4	2.94	18	8	1	80	18	2	0	0
10	cascade	6	116	11	0.78	20	0	0	0	0	0	0	100
11	pool	9	148	12	1.29	20	100	1	16	2	0	20	62
12	riffle	20	45	85	8.10	21	17	0	7	17	33	43	0
13	pool	18	180	27	9.42	21	0	1	20	17	17	20	27
14	run	24	61	36	5.37	17	17	0	1	22	52	25	0
15	pool	21	61	51	7.11	20	0	1	1	35	27	0	38
16	riffle	24	43	52	5.94	20	0	0	1	26	57	3	13
17	backwater	36	60	10	2.58	20	0	1	67	0	0	0	33

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	pool	-	-	-	-	-	-	+	+	-
2	riffle	-	-	-	-	-	-	+	+	-
3	pool	-	-	+	-	+	-	+	+	+
4	riffle	-	-	-	-	-	-	+	+	-
5	pool	+	+	+	+	+	-	+	-	+
6	riffle	+	-	-	-	+	+	+	-	+
7	pool	+	+	-	+	+	-	+	-	+
8	riffle	+	-	-	+	+	+	+	-	+
9	pool	+	-	+	+	+	-	+	-	+
10	cascade	+	-	+	+	+	-	-	-	-
11	pool	+	+	+	+	+	-	-	-	-
12	riffle	+	-	-	-	+	-	+	-	-
13	pool	+	+	+	+	+	-	+	-	+
14	run	-	-	-	+	+	-	+	+	+
15	pool	-	+	-	-	+	-	+	+	+
16	riffle	-	-	-	-	+	+	+	+	+
17	backwater	-	+	+	-	-	-	-	-	-

Table 3. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at five study sites on Turner Creek during July - August 1983. Low numbered sites are upstream and high numbered sites are downstream. The dam is located at site number 2.

a. Physical Characteristics

									Substrate Composition (%)				
Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Fines	Gravel	Cobble & Rubble	Boulder	Bedrock
1	riffle	4	15	15	0.96	11	83	1	9	33	36	22	0
2	pool	12	108	1	0.39	12	30	1	92	8	0	0	0
3	pool	7	55	2	0.09	13	2	1	4	2	0	0	93
4	riffle	5	14	10	0.09	12	8	1	18	45	45	8	0
5	riffle	5	12	23	0.15	12	82	1	9	5	14	0	68

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	riffle	+	-	-	-	-	-	+	-	+
2	pool	+	-	-	-	-	-	-	-	+
3	pool	+	-	-	-	-	-	-	-	-
4	riffle	+	-	-	-	-	-	+	-	+
5	riffle	+	-	-	-	-	-	+	-	+

Table 4. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at four study sites on the south fork of Rock Creek during July - August 1983. Low numbered sites are upstream and high numbered sites are downstream. The dam is located between site number 2 and 3.

a. Physical Characteristics

Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Substrate Composition (%) Fines	Gravel	Cobble & Rubble	Boulder	Bedrock
1	riffle	5	34	20	0.33	13	63	1	4	29	18	48	0
2	pool	6	39	7	0.30	12	85	1	11	8	5	20	55
3	riffle	8	19	24	0.33	13	72	1	4	25	29	24	18
4	pool	4	92	5	0.15	15	38	1	53	17	7	0	0

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	riffle	+	-	-	-	-	-	+	+	+
2	pool	+	-	-	-	-	-	-	-	-
3	riffle	+	-	-	-	-	-	+	-	+
4	pool	+	-	-	-	-	-	+	+	+

Table 5. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at five study sites on the north fork of Rock Creek during July - August 1983. Site one is above the reservoir, and sites two, three and four are below the dam. The reservoir was not sampled.

a. Physical Characteristics

									Substrate Composition (%)				
Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Fines	Gravel	Cobble & Rubble	Boulder	Bedrock
1	riffle	5	19	13	0.12	11	0	1	9	47	36	2	7
2	riffle	3	11	16	0.03	15	100	1	18	65	8	0	0
3	pool	7	40	6	0.12	14	100	1	18	31	13	7	27
4	riffle	6	17	17	0.18	14	87	1	4	28	29	5	31

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	riffle	+	-	-	-	-	-	+	-	+
2	riffle	+	-	-	-	-	-	-	+	+
3	pool	+	-	-	-	+	-	+	-	+
4	riffle	+	-	-	-	-	-	+	-	+

Table 6. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at 16 study sites on the Calapooia River during July - September 1982. Low numbered sites are upstream and high numbered sites are downstream. The dam is located at site number 12.

a. Physical Characteristics

									Substrate Composition (%)				
Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Fines	Gravel	Cobble & Rubble	Boulder	Bedrock
1	run	22	55	23	2.79	15	0	0	0	10	90	0	0
2	riffle	25	67	43	7.20	15	0	1	5	11	30	12	42
3	pool	17	163	3	0.83	16	0	0	28	7	25	3	33
4	riffle	26	23	59	2.40	11	0	0	0	50	50	0	0
5	pool	13	223	5	1.44	16	0	1	27	0	37	3	33
6	pool	21	62	20	2.64	27	4	0	23	17	47	0	23
7	riffle	20	27	56	2.91	27	0	0	2	18	83	0	0
8	run	14	39	48	2.64	24	0	0	10	63	27	0	0
9	pool	9	81	37	2.73	23	0	0	17	0	3	13	67
10	pool	12	93	16	2.25	24	30	0	14	3	16	33	33
11	pool	17	95	22	3.60	24	0	0	12	68	15	5	0
12	reservoir	40	2400	3	28.80	22	0	1	90	5	5	0	0
13	pool	22	40	14	1.29	17	0	0	80	20	0	0	0
14	pool	23	93	23	5.70	17	5	1	0	20	0	22	57
15	riffle	15	47	40	2.25	17	0	0	0	2	17	80	0
16	chute	14	73	70	8.10	17	0	0	0	17	47	37	0

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	run	+	-	+	-	-	-	-	-	-
2	riffle	+	-	-	-	-	-	+	+	+
3	pool	-	-	+	-	-	-	-	-	-
4	riffle	-	-	-	-	+	+	+	-	-
5	pool	+	+	+	+	+	-	-	-	-
6	pool	-	-	-	-	+	+	+	-	-
7	riffle	-	-	+	-	+	+	+	-	-
8	run	-	-	-	+	-	-	+	-	-
9	pool	-	-	-	+	+	-	-	+	-
10	pool	-	-	-	+	+	-	-	-	-
11	pool	+	+	+	+	+	-	+	-	+
12	reservoir	-	-	-	-	-	-	-	-	-
13	pool	-	-	-	-	-	-	-	-	+
14	pool	+	+	+	+	+	-	+	+	-
15	riffle	-	-	+	+	+	+	+	+	+
16	chute	-	-	-	-	-	+	+	-	-

Table 7. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at five study sites on Greasy Creek during July - August 1983. Low numbered sites are upstream and high numbered sites are downstream. Greasy Creek is not impounded.

a. Physical Characteristics

									Substrate Composition (%)				
Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Fines	Grevel	Cobble & Rubble	Boulder	Bedrock
1	riffle	5	20	19	0.15	18	58	0	13	68	15	6	0
2	riffle	6	26	12	0.15	17	100	1	29	42	0	0	0
3	pool	11	68	5	0.36	17	100	1	52	28	5	0	0
4	pool	13	47	9	0.33	17	82	1	53	43	5	0	0
5	riffle	14	25	10	0.30	17	67	1	17	82	1	0	0

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	riffle	-	-	-	-	-	-	+	-	+
2	riffle	+	-	-	-	-	-	+	-	+
3	pool	+	+	+	+	-	-	+	-	+
4	pool	+	-	-	-	-	-	-	-	+
5	riffle	+	-	-	+	+	-	+	+	+

Table 8. Summary of (a) physical characteristics and (b) species composition ('+' = presence and '-' = absence) at three study sites on Griffith Creek during July - September 1983. Low numbered sites are upstream and high numbered sites are downstream. The dam is located at site number 3.

a. Physical Characteristics

									Substrate Composition (%)				
Site No.	Habitat Type	Mean Width (m)	Mean Depth (cm)	Mean Vel. (cm/s)	Discharge (m3/s)	Water Temp. (C)	% Canopy Cover	Pres. (1) or Abs. (0) of Instream Cover	Fines	Gravel	Cobble & Rubble	Boulder	Bedrock
1	pool	2	19	16	0.06	14	100	1	2	42	39	21	0
2	riffle	2	5	39	0.06	14	100	1	0	47	40	13	0
3	pool	3	39	4	0.06	14	6	1	11	52	5	3	0

b. Species Composition

Site No.	Habitat Type	Cutthroat Trout	Squawfish	Largescale Suckers	Redside Shiners	Speckled Dace	Longnose Dace	Torrent Sculpin	Rainbow Trout	Sculpin spp.
1	pool	-	-	-	-	-	-	-	-	+
2	riffle	-	-	-	-	-	-	-	-	+
3	pool	+	-	-	-	-	-	-	-	+

Table 9. Average number of fish species found by habitat type in all streams. The numbers in parentheses are the number of pools, riffles or reservoirs sampled. The reservoir of the north fork of Rock Creek was not sampled and Greasy Creek is not impounded.

	Stream Name						
Habitat	Calapooia	Thomas	Turner	North Rock	South Rock	Griffith	Greasy
Pool	2.7 (9)	6.8 (8)	1.5 (2)	4.0 (1)	2.5 (2)	1.5 (2)	4.0 (2)
Riffle	4.3 (4)	4.7 (7)	3.0 (3)	3.0 (3)	3.5 (2)	1.0 (1)	3.7 (3)
Reservoir	0.0 (1)	6.0 (1)	2.0 (1)	--- (0)	4.0 (1)	2.0 (1)	--- (0)

Thomas Creek ($t = 2.202$, $p < 0.05$, df = 12). There was no significant difference when data for both streams were combined. By comparing the total number of habitats available and habitat use by each species (Table 10), Strauss' (1979) linear index of habitat selection was calculated (Table 10b) to reveal species preferences for a particular habitat type. For example, squawfish were exclusively found in pools, while longnose dace were almost always found in riffles. Both rainbow and cutthroat trout were evenly distributed between pools and riffles. Suckers and redside shiners were generally found in pools.

Detrended Correspondence Analysis

The results of all final DCA runs are presented in Table 11. Comparisons of species rankings along each axis permitted an assessment of the effects of data transformations on DCA results. The order of species along an axis varied with the type of data transformation and changed between axes. Along axis one several species had nearly identical ranks for all data transformations; squawfish, cutthroat trout juveniles and adults, largescale suckers, speckled dace, and sculpin spp. The rankings for adult and juvenile torrent sculpins varied the most. The species ranking along axis two for logarithmic transformations of density values were often different from

Table 10. (a) Number of patches sampled (percentages in parentheses) and number of species sightings by habitat type. The percentage of sightings for any single species by habitat is shown in parentheses. For example, 50% of cutthroat trout sightings occurred in pools. (b) A linear index of habitat selection developed from Strauss (1979) using methods described in text and calculated from the values in (a). The variances are presented in parentheses.

a. Number of patches sampled and species sightings

No. of patches by habitat	Fish Species								
	Cutthroat trout	Squawfish	Suckers	Redside shiners	Speckled dace	Longnose dace	Torrent sculpins	Rainbow trout	Sculpin spp.
Pool	16	10	13	9	14	1	13	7	15
26 (51%)	(50)	(100)	(68)	(69)	(58)	(13)	(36)	(47)	(45)
Riffle	15	0	4	3	8	7	21	7	16
22 (43%)	(47)	(0)	(21)	(23)	(33)	(87)	(58)	(47)	(52)
Run	1	0	2	1	2	0	2	1	1
3 (6%)	(3)	(0)	(11)	(8)	(8)	(0)	(6)	(6)	(3)

b. Linear index of habitat selection developed from Strauss (1979)

Habitat type	Fish Species								
	Cutthroat trout	Squawfish	Suckers	Redside shiners	Speckled dace	Longnose dace	Torrent sculpins	Rainbow trout	Sculpin spp.
Pool	-0.01	0.49	0.17	0.18	0.07	-0.38	-0.15	-0.04	-0.06
	(0.013)	(0.0004)	(0.012)	(0.017)	(0.011)	(0.015)	(0.007)	(0.017)	(0.008)
Riffle	0.04	-0.43	-0.22	-0.20	-0.10	0.44	0.15	0.04	0.09
	(0.013)	(0.004)	(0.014)	(0.018)	(0.014)	(0.019)	(0.012)	(0.021)	(0.013)
Run	-0.03	-0.06	0.05	0.02	0.02	-0.06	0.00	0.00	-0.03
	(0.002)	(0.0004)	(0.006)	(0.007)	(0.004)	(0.001)	(0.003)	(0.005)	(0.002)

Table 11. Ranked species scores for the first three axes of all DCA runs with rare species removed. The largest positive score was assigned rank 1 and the most negative score was assigned rank 12. Because DECORANA sometimes produced axes (gradients) with the same interpretation but with species scores in the reverse order, ranks are also shown (in parentheses) where the largest positive score was assigned rank 12 and the most negative score was assigned rank 1. Non-meaningful axes (representing less than 15% of the total variability in the data) are denoted 'NA'.

		Density			Biomass	
Species	Raw numbers	Raw	Logarithmic transformed	Grouped logarithmic transformed	Raw	Grouped
			a. Axis 1			
cutthroat (adults)	6 (7)	8 (5)	7 (6)	6 (7)	8 (5)	6 (7)
cutthroat (juv.)	9 (4)	4 (9)	4 (9)	9 (4)	4 (9)	10 (3)
squawfish	1 (12)	11 (2)	12 (1)	1 (12)	11 (2)	1 (12)
suckers	2 (11)	10 (3)	10 (3)	2 (11)	10 (3)	3 (10)
redside shiners	3 (10)	12 (1)	11 (2)	3 (10)	12 (1)	2 (11)
speckled dace	5 (8)	9 (4)	9 (4)	5 (8)	9 (4)	5 (8)
longnose dace	4 (9)	7 (6)	8 (5)	4 (9)	7 (6)	4 (9)
torrent sculpin (adult)	7 (6)	5 (8)	6 (7)	7 (6)	3 (10)	7 (6)
torrent sculpin (juv.)	11 (2)	6 (7)	3 (10)	11 (2)	6 (7)	12 (1)
rainbow (adult)	12 (1)	3 (10)	2 (11)	12 (1)	1 (12)	11 (2)
rainbow (juv.)	10 (3)	2 (11)	1 (12)	10 (3)	2 (11)	9 (4)
sculpins	8 (5)	1 (12)	5 (8)	8 (5)	5 (8)	8 (5)

Table 11. Continued.

		Density			Biomass	
Species	Raw numbers	Raw	Logarithmic transformed	Grouped logarithmic transformed	Raw	Grouped
			b. Axis 2			
cutthroat (adults)	12 (1)	1 (12)	7 (6)	12 (1)	10 (3)	12 (10)
cutthroat (juv.)	11 (2)	2 (11)	5 (8)	11 (2)	11 (2)	11 (2)
squawfish	10 (3)	6 (7)	4 (9)	10 (3)	8 (5)	9 (4)
suckers	8 (5)	7 (6)	1 (12)	8 (5)	6 (7)	7 (6)
redside shiners	5 (8)	5 (8)	6 (7)	5 (8)	7 (6)	6 (7)
speckled dace	6 (7)	4 (9)	9 (4)	6 (7)	4 (9)	5 (8)
longnose dace	1 (12)	12 (1)	8 (5)	1 (12)	1 (12)	1 (12)
torrent sculpin (adult)	4 (9)	9 (4)	11 (2)	4 (9)	2 (11)	4 (9)
torrent sculpin (juv.)	9 (4)	8 (5)	12 (1)	9 (4)	3 (10)	10 (3)
rainbow (adult)	3 (10)	10 (3)	2 (11)	3 (10)	9 (4)	3 (10)
rainbow (juv.)	2 (11)	11 (2)	3 (10)	2 (11)	5 (8)	2 (11)
sculpin spp.	7 (6)	3 (10)	10 (3)	7 (6)	12 (1)	8 (5)

Table 11 continued.

		Density			Biomass	
Species	Raw numbers	Raw	Logarithmic transformed	Grouped logarithmic transformed	Raw	Grouped
			c. Axis 3			
cutthroat (adults)	8 (5)	6 (7)	12 (1)	NA	7 (6)	9 (4)
cutthroat (juv.)	3 (10)	2 (11)	11 (2)	NA	9 (4)	6 (7)
squawfish	4 (9)	5 (8)	9 (4)	NA	1 (12)	10 (3)
suckers	6 (7)	8 (5)	8 (5)	NA	3 (10)	7 (6)
redside shiners	5 (8)	4 (9)	6 (7)	NA	11 (2)	5 (8)
speckled dace	9 (4)	7 (6)	5 (8)	NA	2 (11)	8 (5)
longnose dace	11 (2)	12 (1)	1 (12)	NA	10 (3)	1 (12)
torrent sculpin (adult)	10 (3)	9 (4)	2 (11)	NA	8 (5)	4 (9)
torrent sculpin (juv.)	12 (1)	1 (12)	4 (9)	NA	12 (1)	2 (11)
rainbow (adult)	1 (12)	10 (3)	7 (6)	NA	4 (9)	11 (2)
rainbow (juv.)	2 (11)	11 (2)	3 (10)	NA	5 (8)	12 (1)
sculpin spp.	7 (6)	3 (10)	10 (3)	NA	6 (7)	3 (10)

the rankings produced from all other data transformations. The raw biomass data transformation appears to vary from the other data transformation rankings in that rainbow trout tend not to occur at the end of the axis. With the exception of the logarithmic transformations of density, the species that were ranked most consistently relative to other species were adult and juvenile cutthroat trout, largescale suckers, redside shiners, longnose dace, and adult and juvenile rainbow trout. Along axis three the species rankings for the various data transformations varied significantly. Only longnose dace and juvenile torrent sculpins had fairly uniform rankings.

Because the resultant order of species along axes was similar for most data transformations, many DCA runs suggested identical environmental gradients. For example, a DCA run using log transformed densities showed interpretable patterns for depth, temperature, percent gravel and percent bedrock on axis one; width, instream cover, percent sand, silt and clay and percent boulder on axis two; and none on axis three. For the DCA run which used grouped values of log transformed densities, interpretable patterns for depth, temperature, and percent gravel were on axis one; velocity, instream cover, percent sand, silt and clay, and percent boulder were on axis two; but no interpretable variables on axis three. Using biomass values, interpretable patterns were found for depth, percent gravel and percent bedrock on axis one; width and percent cobble and rubble on axis two; and no interpretable parameters on axis three. Using grouped values of biomass, the parameters with interpretable patterns were depth, temperature, percent gravel and percent bedrock on axis one; width, velocity, percent canopy cover, instream cover, percent sand, silt and clay and percent boulder for axis two; and discharge for axis three.

Despite the similar results from many of the data transformations, it was useful to select only one data transformation for all further analyses. Biomass values (g/m^2), are a better estimator of productivity in a patch than density ($abundance/m^2$), because density considers only the absolute number of fish cited there. For example, abundance is not a particularly useful measure of productivity when comparing large trout to small trout. Also, grouping was believed to be a useful transformation given the inaccuracy of enumeration techniques due to the difficulty of obtaining exact counts with visual observations. At times it was difficult to count exact numbers of fish while snorkeling. For example, the number of redside shiners in a school may have been estimated as 350, while the true number could have been 300-400. The sculpin species were also difficult to quantify. They were either very cryptic (reticulate sculpin) or less vulnerable to electroshocking (torrent sculpin); in either case their vulnerability to sampling was less than the other species.

Based upon the interpretive value of biomass for productivity comparisons and the magnitude of enumeration errors for schooling fishes and cryptic species, grouped biomass data was used for all subsequent analyses. Because there were no major differences between the DCA results for grouped biomass and the other data transformations, it is unlikely that subsequent analyses and discussion are specific to the choice of data transformation.

For each species the mean value of each environmental variable was calculated for (1) all patches of occurrence and (2) all patches of absence. Next, the difference in means (1) and (2) was calculated. Then, values (1), (2) and (3) were ordered by species score along the three DCA axes generated from the grouped biomass data. Mean values for all physical habitat parameters with significant patterns are presented (Table 12, Fig. 2-4). A pattern was defined as significant if there was a clear gradient from negative to positive values with the allowable exception of at most one value out of place, by sign (not magnitude). T-tests were performed on all variables showing patterns from the three interpretable axes to test for statistically significant differences.

Table 12. Mean values for the physical habitat parameters both averaged over patches where individual species were found and where they were not found, and the difference between the two mean values. Values are shown only for physical parameters having a pattern of positive differences at one end of the DCA axis to negative differences at the other. The symbol '*' denotes significant differences using the t-test at the 5% significance level. The numbers in parentheses represent the number of patches in which individual species were present or absent.

Axis 1

a. Temperature

			Mean Temperature (C)		
Ranked Score	Species Number	Species Name	Where Present (P)	Where Absent (A)	Difference P-A
1	3	Squawfish	20.4 (11)	16.3 (43)	4.1*
2	5	Redside shiners	20.5 (16)	15.7 (38)	4.8*
3	4	Largescale suckers	19.6 (17)	16.0 (37)	3.6*
4	7	Longnose dace	20.1 (10)	16.4 (44)	3.7*
5	6	Speckled dace	20.1 (23)	14.8 (31)	5.3*
6	1	Cutthroat trout (a)	16.5 (26)	17.6 (28)	-1.1
7	8	Torrent sculpin (a)	17.1 (34)	17.1 (20)	0.0
8	12	Sculpin spp.	16.2 (33)	18.5 (21)	-2.3
9	11	Rainbow trout (j)	15.6 (9)	17.4 (45)	-1.8
10	2	Cutthroat trout (j)	15.8 (17)	17.7 (37)	-1.9
11	10	Rainbow trout (a)	15.8 (12)	17.5 (42)	-1.7
12	9	Torrent sculpin (j)	15.2 (10)	17.5 (44)	-2.3

b. Depth

			Mean Depth (cm)		
Ranked Score	Species Number	Species Name	Where Present (P)	Where Absent (A)	Difference P-A
1	3	Squawfish	170.0 (11)	106.1 (43)	63.9
2	5	Redside shiners	131.0 (16)	114.1 (38)	16.9
3	4	Largescale suckers	135.0 (17)	111.8 (37)	23.2
4	7	Longnose dace	46.3 (10)	135.6 (44)	-89.3
5	6	Speckled dace	111.2 (23)	125.0 (31)	-13.8
6	1	Cutthroat trout (a)	97.0 (26)	140.0 (28)	-43.0
7	8	Torrent sculpin (a)	73.0 (34)	197.5 (20)	-124.5
8	12	Sculpin spp.	74.8 (33)	188.7 (21)	-113.9
9	11	Rainbow trout (j)	61.7 (9)	130.6 (45)	-68.9
10	2	Cutthroat trout (j)	93.1 (17)	131.1 (37)	-38.0
11	10	Rainbow trout (a)	59.8 (12)	136.0 (42)	-76.2
12	9	Torrent sculpin (j)	39.1 (10)	137.3 (44)	-98.2

Table 12. Continued.

Axis 1 continued

c. Gravel

Ranked Score	Species Number	Species Name	Mean Gravel (%) Where Present (P)	Mean Gravel (%) Where Absent (A)	Difference P-A
1	3	Squawfish	18.1 (11)	26.0 (43)	-7.9
2	5	Redside shiners	20.5 (16)	26.0 (38)	-5.5
3	4	Largescale suckers	16.2 (17)	28.1 (37)	-11.9*
4	7	Longnose dace	23.0 (10)	24.7 (44)	-1.7
5	6	Speckled dace	22.8 (23)	25.5 (31)	-2.7
6	1	Cutthroat trout (a)	24.3 (26)	24.4 (28)	-0.1
7	8	Torrent sculpin (a)	28.7 (34)	17.1 (20)	11.6*
8	12	Sculpin spp.	31.2 (33)	13.7 (21)	17.5*
9	11	Rainbow trout (j)	29.1 (9)	23.4 (45)	5.7
10	2	Cutthroat trout (j)	26.0 (17)	23.6 (37)	2.4
11	10	Rainbow trout (a)	30.7 (12)	22.6 (42)	8.1
12	9	Torrent sculpin (j)	31.5 (10)	22.8 (44)	8.7

d. Bedrock

Ranked Score	Species Number	Species Name	Mean Bedrock (%) Where Present (P)	Mean Bedrock (%) Where Absent (A)	Difference P-A
1	3	Squawfish	35.1 (11)	13.8 (43)	21.3*
2	5	Redside shiners	25.9 (16)	14.9 (38)	11.0
3	4	Largescale suckers	28.5 (17)	13.4 (37)	15.1
4	7	Longnose dace	10.6 (10)	19.9 (44)	-9.3
5	6	Speckled dace	24.7 (23)	13.3 (31)	11.4
6	1	Cutthroat trout (a)	23.6 (26)	13.1 (28)	10.5
7	8	Torrent sculpin (a)	11.8 (34)	28.9 (20)	-17.1*
8	12	Sculpin spp.	10.6 (33)	30.0 (21)	-19.4*
9	11	Rainbow trout (j)	11.4 (9)	19.5 (45)	-8.1
10	2	Cutthroat trout (j)	13.6 (17)	20.2 (37)	-6.6
11	10	Rainbow trout (a)	12.1 (12)	19.9 (42)	-7.8
12	9	Torrent sculpin (j)	12.0 (10)	19.5 (44)	-7.5

Table 12. Continued.

Axis 2

a. Stream width

Ranked Score	Species Number	Species Name	Mean width (m) Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	17.1 (10)	13.2 (44)	3.9
2	11	Rainbow trout (j)	18.8 (9)	13.1 (45)	5.7
3	10	Rainbow trout (a)	16.8 (12)	13.2 (42)	3.6
4	8	Torrent sculpins (a)	14.1 (34)	13.9 (20)	0.2
5	6	Speckled dace	16.2 (23)	12.4 (31)	3.8
6	5	Redside shiners	14.9 (16)	13.6 (38)	1.3
7	4	Largescale suckers	18.4 (17)	12.0 (37)	6.4*
8	12	Sculpins spp.	11.4 (33)	18.1 (21)	-6.7*
9	3	Squawfish	17.5 (11)	13.1 (43)	4.4
10	9	Torrent sculpin (j)	8.1 (10)	15.4 (44)	-7.3*
11	2	Cutthroat trout (j)	10.7 (17)	15.6 (37)	-4.9*
12	1	Cutthroat trout (a)	11.2 (26)	16.6 (28)	-5.4*

b. Average velocity

Ranked Score	Species Number	Species Name	Mean velocity (cm/s) Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	48.5 (10)	19.5 (44)	29.0*
2	11	Rainbow trout (j)	38.1 (9)	22.3 (45)	15.8*
3	10	Rainbow trout (a)	33.3 (12)	22.5 (42)	10.8
4	8	Torrent sculpins (a)	30.8 (34)	14.9 (20)	15.9*
5	6	Speckled dace	30.9 (23)	20.5 (31)	10.4
6	5	Redside shiners	21.6 (16)	26.3 (38)	-4.7
7	4	Largescale suckers	22.5 (17)	26.0 (37)	-3.5
8	12	Sculpins spp.	21.6 (33)	30.1 (21)	-8.5
9	3	Squawfish	15.5 (11)	27.3 (43)	-11.8
10	9	Torrent sculpin (j)	22.9 (10)	25.4 (44)	-2.5
11	2	Cutthroat trout (j)	17.2 (17)	28.5 (37)	-11.3
12	1	Cutthroat trout (a)	17.2 (26)	32.0 (28)	-14.8*

Table 12. Continued.

Axis 2 continued

c. Canopy cover

Ranked Score	Species Number	Species Name	Mean canopy cover (%) Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	3.4 (10)	35.3 (44)	-31.9*
2	11	Rainbow trout (j)	17.7 (9)	31.7 (45)	-14.0
3	10	Rainbow trout (a)	27.8 (12)	29.9 (42)	-2.1
4	8	Torrent sculpins (a)	28.1 (34)	31.8 (20)	-3.7
5	6	Speckled dace	15.3 (23)	39.9 (31)	-24.6*
6	5	Redside shiners	22.5 (16)	32.3 (38)	-9.8
7	4	Largescale suckers	14.5 (17)	36.3 (37)	-21.8
8	12	Sculpins spp.	40.4 (33)	12.1 (21)	28.3*
9	3	Squawfish	22.4 (11)	31.2 (43)	-8.8
10	9	Torrent sculpin (j)	50.3 (10)	24.7 (44)	25.6
11	2	Cutthroat trout (j)	40.7 (17)	24.2 (37)	16.5
12	1	Cutthroat trout (a)	41.6 (26)	18.1 (28)	23.5*

d. Instream cover

Ranked Score	Species Number	Species Name	Index of instream cover Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	0.10 (10)	0.68 (44)	-0.58*
2	11	Rainbow trout (j)	0.33 (9)	0.62 (45)	-0.29
3	10	Rainbow trout (a)	0.50 (12)	0.60 (42)	-0.10
4	8	Torrent sculpins (a)	0.50 (34)	0.70 (20)	-0.20
5	6	Speckled dace	0.44 (23)	0.68 (31)	-0.24
6	5	Redside shiners	0.50 (16)	0.61 (38)	-0.11
7	4	Largescale suckers	0.53 (17)	0.60 (37)	-0.07
8	12	Sculpins spp.	0.70 (33)	0.38 (21)	0.32*
9	3	Squawfish	0.82 (11)	0.52 (43)	0.30
10	9	Torrent sculpin (j)	0.80 (10)	0.53 (44)	0.27
11	2	Cutthroat trout (j)	0.88 (17)	0.43 (37)	0.45*
12	1	Cutthroat trout (a)	0.81 (26)	0.36 (28)	0.45*

Table 12. Continued.

Axis 2 continued

e. Sand, silt and clay

Ranked Score	Species Number	Species Name	Mean sand, silt & clay (%) Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	4.1 (10)	22.1 (44)	-18.0*
2	11	Rainbow trout (j)	4.3 (9)	21.3 (45)	-17.0*
3	10	Rainbow trout (a)	11.7 (12)	20.8 (42)	-9.1
4	8	Torrent sculpins (a)	13.5 (34)	27.8 (20)	-14.3
5	6	Speckled dace	14.0 (23)	22.3 (31)	-8.3
6	5	Redside shiners	18.6 (16)	18.8 (38)	-0.2
7	4	Largescale suckers	20.5 (17)	18.0 (37)	2.5
8	12	Sculpins spp.	20.8 (33)	15.6 (21)	5.2
9	3	Squawfish	28.6 (11)	16.2 (43)	12.4
10	9	Torrent sculpin (j)	16.3 (10)	19.3 (44)	-3.0
11	2	Cutthroat trout (j)	23.6 (17)	16.5 (37)	7.1
12	1	Cutthroat trout (a)	20.8 (26)	16.9 (28)	3.9

f. Boulder

Ranked Score	Species Number	Species Name	Mean boulder (%) Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	15.3 (10)	12.1 (44)	3.2
2	11	Rainbow trout (j)	26.4 (9)	9.9 (45)	16.5
3	10	Rainbow trout (a)	16.8 (12)	11.5 (42)	5.3
4	8	Torrent sculpins (a)	15.4 (34)	8.1 (20)	7.3
5	6	Speckled dace	11.7 (23)	13.3 (31)	-1.6
6	5	Redside shiners	15.1 (16)	11.6 (38)	3.5
7	4	Largescale suckers	28.5 (17)	13.4 (37)	15.1
8	12	Sculpins spp.	11.5 (33)	14.4 (21)	-2.9
9	3	Squawfish	8.1 (11)	13.8 (43)	-5.7
10	9	Torrent sculpin (j)	8.2 (10)	13.7 (44)	-5.5
11	2	Cutthroat trout (j)	7.5 (17)	15.0 (37)	-7.5
12	1	Cutthroat trout (a)	8.8 (26)	16.2 (28)	-7.4

Table 12. Continued.

Axis 3

a. Discharge

Ranked Score	Species Number	Species Name	Mean discharge (m^3/s) Where Present (P)	Where Absent (A)	Difference P-A
1	7	Longnose dace	3.4 (10)	2.7 (44)	0.7
2	9	Torrent sculpin (j)	1.2 (10)	3.2 (44)	-1.3
3	12	Sculpin spp.	1.8 (33)	4.5 (21)	-2.7
4	8	Torrent sculpin (a)	2.7 (34)	3.1 (20)	-0.4
5	5	Redside shiners	2.6 (16)	2.9 (38)	-0.3
6	2	Cutthroat trout (j)	1.0 (17)	3.7 (37)	-2.7*
7	4	Largescale suckers	3.3 (17)	2.6 (37)	0.7
8	6	Speckled dace	3.2 (23)	2.6 (31)	0.6
9	1	Cutthroat trout (a)	1.9 (26)	3.7 (28)	-1.8
10	3	Squawfish	3.2 (11)	2.8 (43)	0.4
11	10	Rainbow trout (a)	4.3 (12)	2.4 (42)	1.9
12	11	Rainbow trout (j)	4.9 (9)	2.4 (45)	2.5

Figure 2. Significant environmental gradients for detrended correspondence analysis axis one. Mean values of (a) temperature; (b) depth; (c) gravel; and (d) bedrock where individual species were present are plotted according to the ranked order of species along axis one. Species numbers are (1) cutthroat trout adults; (2) cutthroat trout juveniles; (3) squawfish; (4) largescale suckers; (5) redside shiners; (6) speckled dace; (7) longnose dace; (8) torrent sculpin adults; (9) torrent sculpin juveniles; (10) rainbow trout adults; (11) rainbow trout juveniles; and (12) sculpin spp.

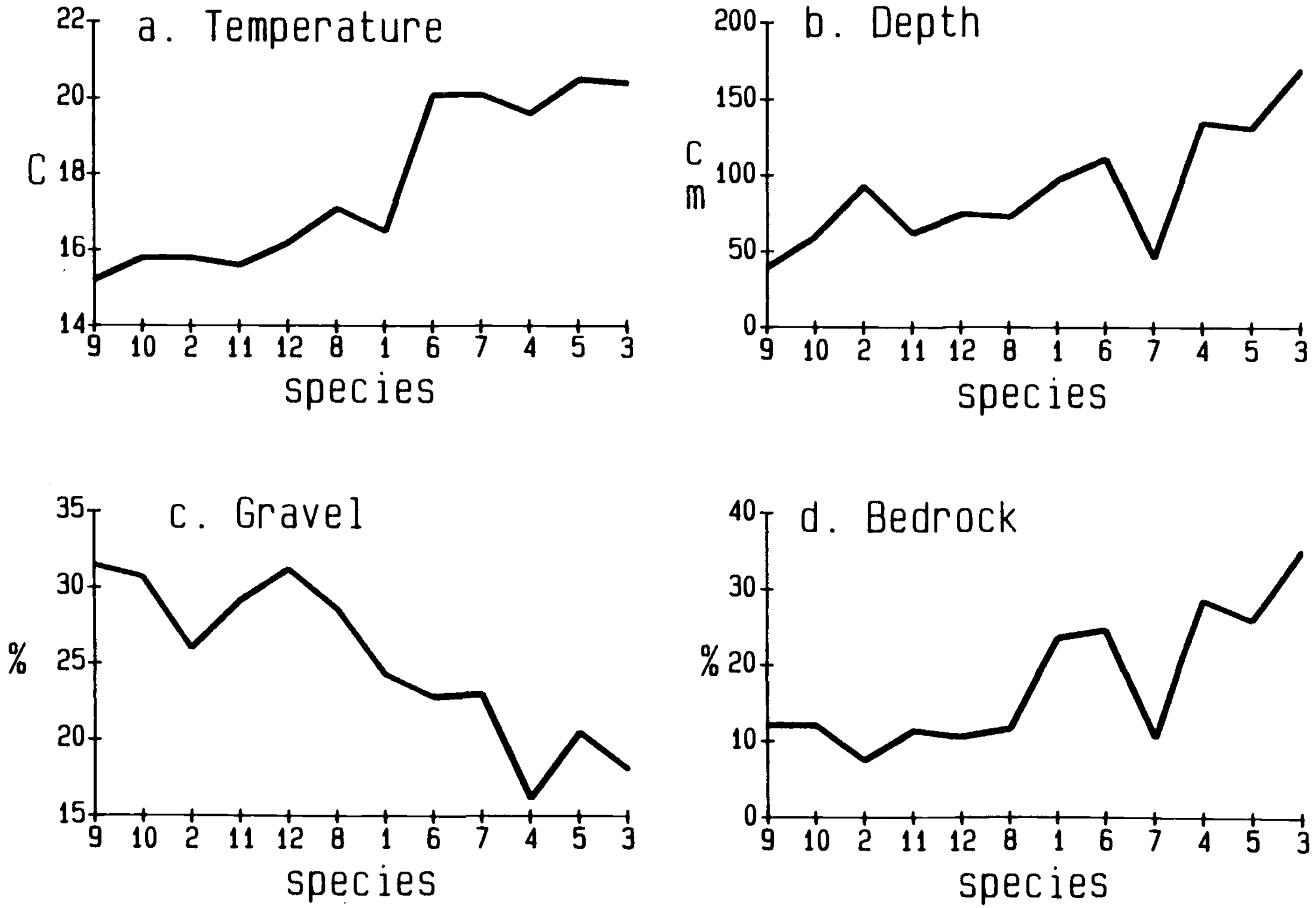
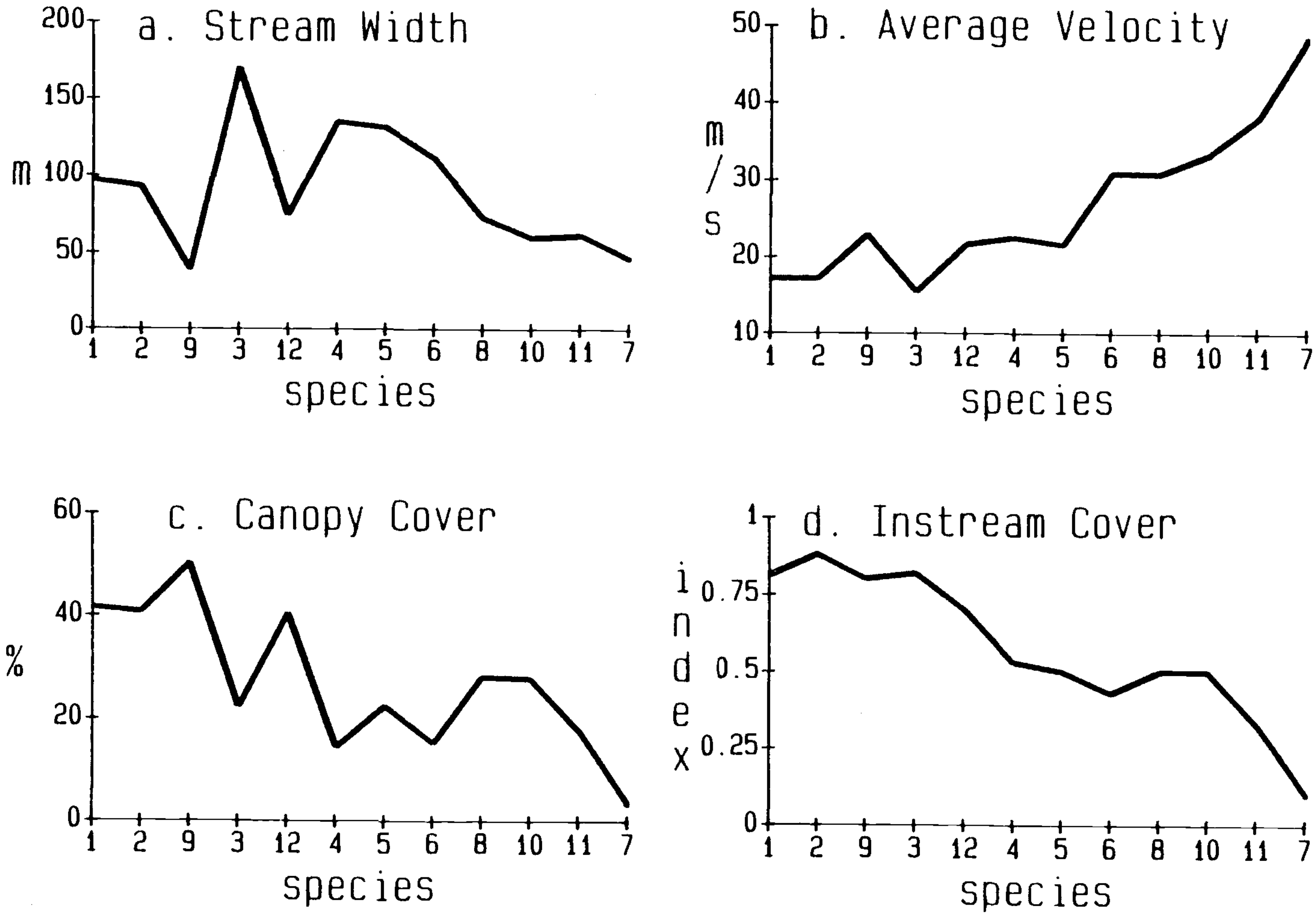

a. Temperature
22
20
C 18
16
14
9 10 2 11 12 8 1 6 7 4 5 3
species
b. Depth
200
150
cm
100
50
0
9 10 2 11 12 8 1 6 7 4 5 3
species
c. Gravel
35
30
%
25
20
15
9 10 2 11 12 8 1 6 7 4 5 3
species
d. Bedrock
40
30
% 20
10
0
9 10 2 11 12 8 1 6 7 4 5 3
species

Figure 2.

Figure 3. Significant environmental gradients for detrended correspondence analysis axis two. Mean values of (a) stream width; (b) velocity; (c) canopy cover; (d) instream cover; (e) sand, silt, and clay; and (f) boulders where individual species were present are plotted according to the ranked order of species along axis two. Species numbers are (1) cutthroat trout adults; (2) cutthroat trout juveniles; (3) squawfish; (4) largescale suckers; (5) redside shiners; (6) speckled dace; (7) longnose dace; (8) torrent sculpin adults; (9) torrent sculpin juveniles; (10) rainbow trout adults; (11) rainbow trout juveniles; and (12) sculpin spp.



a. Stream Width

b. Average Velocity

c. Canopy Cover

d. Instream Cover

Figure 3.

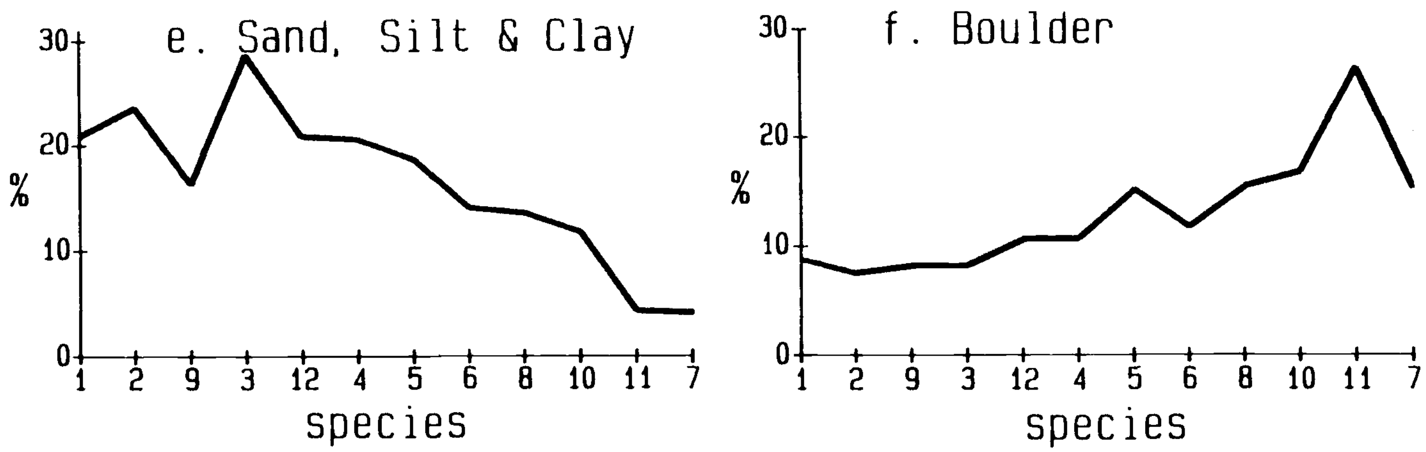


Figure 3. Continued.

Figure 4. The only significant environmental gradient for detrended correspondence analysis axis three. Mean values of discharge where individual species were present are plotted according to the order of species along axis three. Species numbers are (1) cutthroat trout adults; (2) cutthroat trout juveniles; (3) squawfish; (4) largescale suckers; (5) redside shiners; (6) speckled dace; (7) longnose dace; (8) torrent sculpin adults; (9) torrent sculpin juveniles; (10) rainbow trout adults; (11) rainbow trout juveniles; and (12) sculpin spp.

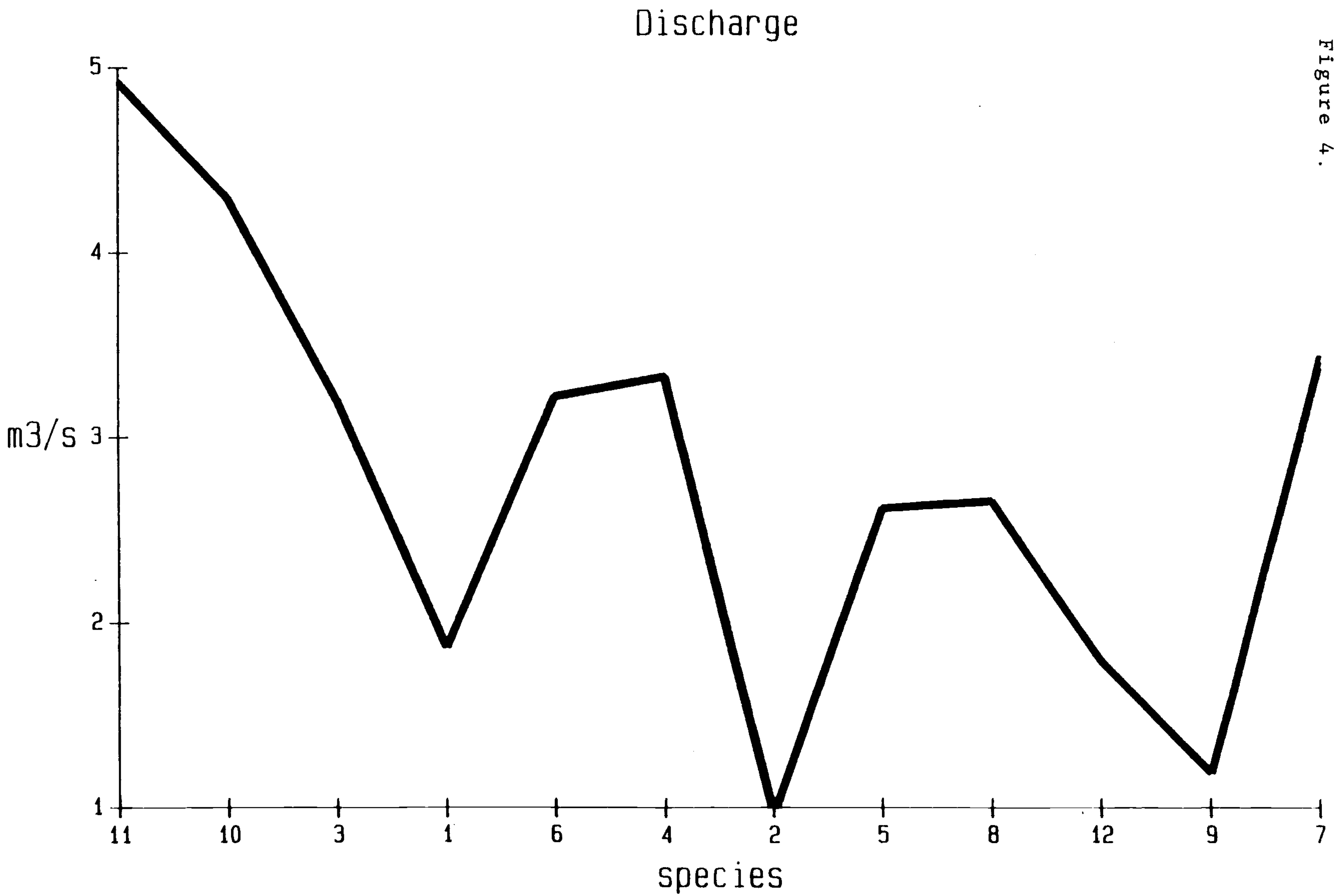


Figure 4.

Axis one describes a habitat that goes from warm to cool, deep to shallow, less gravel to more gravel, and more bedrock to less bedrock. This axis explains 40.1 percent of the variability. These physical parameters seem to describe a habitat gradient from pools to riffles. The species ranking also grades from species that typically are found in pools (squawfish, redside shiners and largescale suckers) to species that are typically found in riffles (torrent sculpins, rainbow trout and cutthroat trout).

Axis two parameters appear to represent different types of habitat cover. This axis shows a habitat that grades from wide to narrow, fast to slow, less canopy cover to more canopy cover, less instream cover to more instream cover, less sand, silt, and clay to more sand, silt, and clay, and more to less boulders. This axis explains 31.5 percent of the variability. Individual fish species often are found in habitats that are characterized by specific types of cover. Cover types may range from water velocity and larger substrate composition, overhanging canopy cover, undercut banks, woody debris and root wads and boles. Longnose dace, rainbow trout, and torrent sculpins, which are grouped on one end of axis two, are most often found in sections of streams where the currents are faster and the substrate composition was composed of mostly cobble, rubble and boulders. These species utilize the interstitial spaces created by large substrate and swift flows as cover. Cutthroat trout, which were on the opposite end of the axis, were most often found in areas further upstream that were narrower, shallower with more overhead cover, undercut banks, root wads and boles and woody debris. Therefore, it appears that axis two represents a gradient from white water and boulder cover to canopy cover, undercut banks, root boles and woody debris. An upstream-downstream interpretation of axis two can also be generated, but cover type appeared to have more explanatory power.

The only physical parameter with an interpretable pattern on the third axis was discharge. This axis explained 18.9 percent of the variability. Axis three reflects the selection by certain species (rainbow trout and squawfish) for deeper, wider stream areas where the discharge volume is greater. Species on the opposite end of the axis (longnose dace and sculpins) are found in shallower areas where the discharge volume is lower. However, depth alone did not reveal a clear trend for axis three.

A three-dimensional diagram of the species scores along the three DCA axes offered a method of viewing the species scores from the three axes (Figure 5). A three-dimensional structure is revealed that was not apparent from an examination of each axis separately. Species 10

Figure 5. Three dimensional plot of species scores along detrended correspondence analysis axis one, two and three. Species numbers are (1) cutthroat trout adults; (2) cutthroat trout juveniles; (3) squawfish; (4) largescale suckers; (5) redside shiners; (6) speckled dace; (7) longnose dace; (8) torrent sculpin adults; (9) torrent sculpin juveniles; (10) rainbow trout adults; (11) rainbow trout juveniles; and (12) sculpin spp.

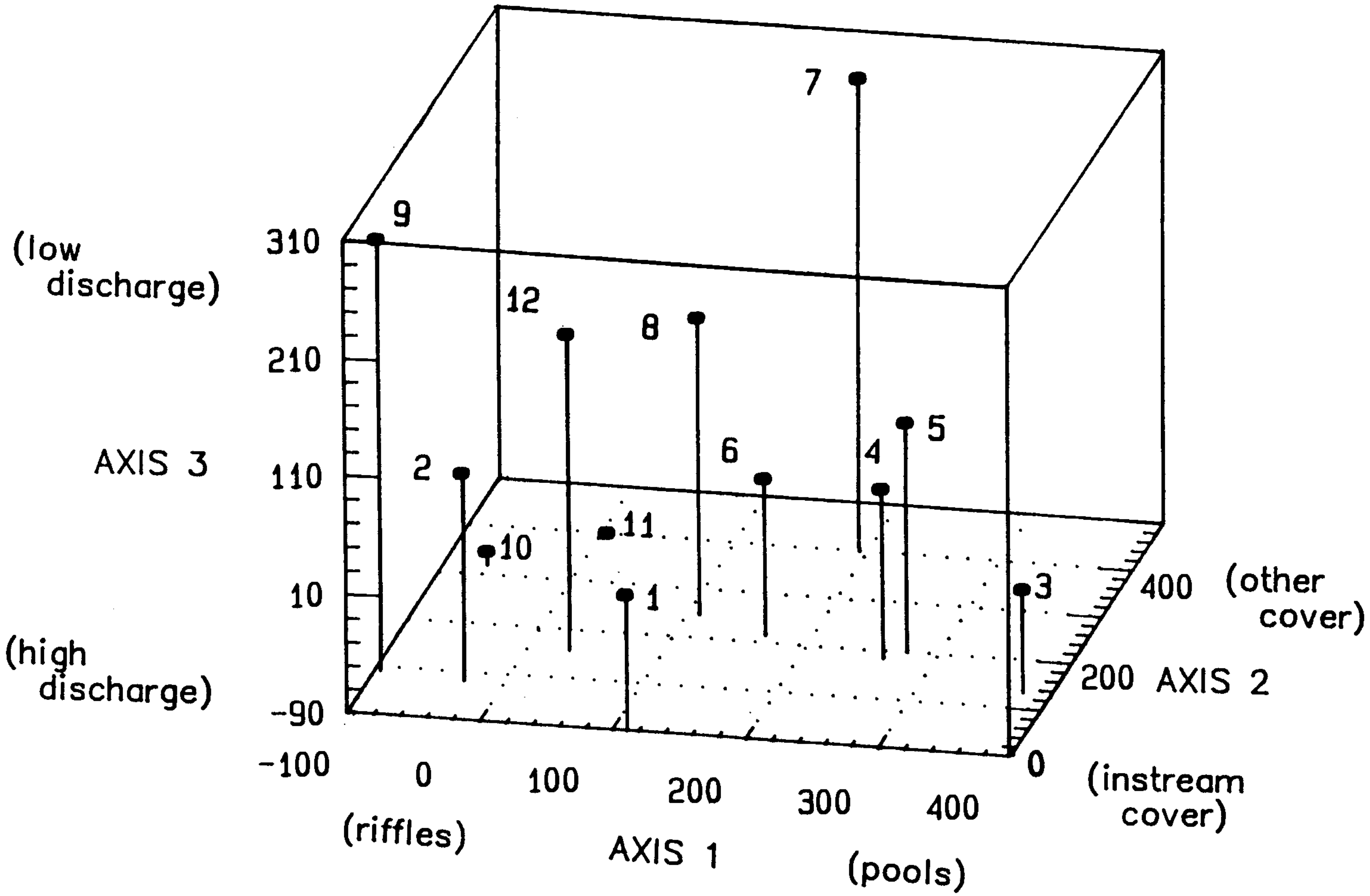

(low discharge)
310
210
AXIS 3
110
10
(high discharge)
-90
-100
0
100
200
300
400
(riffles)
AXIS 1
(pools)
0
200
400
AXIS 2
(other cover)
(instream cover)
1
2
3
4
5
6
7
8
9
10
11
12

Figure 5.

(adult rainbow trout) and 11 (juvenile rainbow trout) were found in areas of high discharge and white water cover. Species 9 (juvenile torrent sculpins), 12 (sculpins spp.), 8 (adult torrent sculpins) and 7 (longnose dace) appeared along a ridge in Figure 5 and were generally found in areas of high discharge associated with riffles and swift, shallow pools. They also tended to occur over a range of cover types from gravel to boulder. Lastly, species 2 (juvenile cutthroat trout), 1 (adult cutthroat trout), 6 (speckled dace), 4 (largescale suckers), 5 (redside shiners), and 3 (squawfish) were generally found in deeper areas with more instream cover (root wads and boles, and woody debris).

Observed Frequency Contingency Table Analysis

The results of the observed frequency contingency table analysis were supportive of the interpretations rendered for the three DCA axes earlier (Table 13). Species with significant ($P<0.05$) differences from expected frequencies tended to be those which occurred at opposite ends of the DCA axes. Species with significant associations with pools (squawfish and largescale suckers) scored low on DCA axis one, while torrent sculpins were significantly associated with riffles and scored high on DCA axis one. The contingency table analysis indicated that longnose dace

Table 13. Results of the observed frequency table analysis for all species. Species rank scores from the DCA axes are shown for comparison. An asterisk (*) represents a significant ($P<0.05$) difference from expected frequencies. Abbreviations for the effects are: (1) habitat, P = pool and R = riffle; (2) cover, I = instream and S = substrate; and (3) discharge, L = low and H = high. For the DCA axis one, lower scores on the first axis are pools and higher scores are riffles. The lower scores on the second axis represent the "substrate cover" end of the axis, while higher scores indicated instream cover. Lower scores on the third axis corresponded to lower discharge.

	Habitat		Cover		Discharge		DCA Axis scores		
							1	2	3
Species	P	R	I	S	L	H			
Cutthroat trout (a)			*				6	12	9
Cutthroat trout (j)			*				10	11	6
Squawfish	*						1	9	10
Largescale suckers	*						3	7	7
Redside shiners							2	6	5
Speckled dace							5	5	8
Longnose dace				*			4	1	1
Torrent sculpin (a)		*					7	4	4
Torrent sculpin (j)		*					12	10	2
Rainbow trout (a)						*	11	3	11
Rainbow trout (j)						*	9	2	12
Sculpin spp.							8	8	3

were associated with substrate cover (cobble/rubble and white water) and that cutthroat trout were associated with instream cover (undercut banks, root wads and boles). These results are consistent with the low score of longnose dace and the high score of cutthroat trout along DCA axis two. Only adult and juvenile rainbow trout were significantly associated with high discharge based upon the contingency table analysis, and this result is consistent with their extremely high scores on DCA axis three.

DISCUSSION

The DCA analysis revealed three habitat gradients that can be used to explain the distribution of species in each stream, and contingency table analyses were supportive of these interpretations. Axis one and two were not single factor gradients, but a composite of several physical habitat variables. This suggests that species assemblages respond to a complex combination of physical factors. A gradient interpreted as pools versus riffles explained the most variation in species assemblages (40.1%), and formed the first DCA axis. However, pools and riffles could not be defined by a single environmental factor, but rather by a combination of temperature, depth, gravel and bedrock. The type of habitat cover also explained much variability in the data set (31.5%), but no one type of cover was dominant in effect. The combination of instream (undercut banks, root wads and boles, woody debris, and rooted vegetation) and other cover (riparian vegetation, large substrate composition, and swift water velocities) were necessary to interpret patterns. Lastly, discharge had some interpretive value, but even this gradient is a function of depth, width and current speed.

Results of other stream research are generally consistent with the relationships between species assemblages and physical habitat variables inferred from detrended correspondence analysis here. However, these other studies offer some interesting contrasts and provide further insight into the patterns observed. In this study DCA allowed us to interpret the distribution of species assemblages along three physical habitat gradients. This three-dimensional decomposition of the original 13 physical variables contrasts with commonly used methods of presenting results from similar ecological studies based upon multiple regression analysis (e.g., Lewis 1969), perturbation of physical parameters, (e.g., Boussu 1954), and step-wise discriminant analysis (e.g., Baltz et al. 1987). All of these studies can lead to similar interpretations of the responses of each fish species to particular physical parameters of the stream. However, provided that the axes are interpretable (and they usually are interpretable, Gauch 1982), detrended correspondence analysis allows for a clearer presentation of the relationships of species to one another and with respect to multiple physical habitat gradients simultaneously. Additionally, the conceptualization of relationships between species assemblages and habitat gradients in multidimensional space (e.g., figure 5) allows prediction of fish community responses to human perturbations (e.g., logging, impoundment, etc.), if the effects of these impacts on the habitat gradients are known.

To focus the remainder of this discussion on the points just raised, a brief summary of relationships among species assemblages with respect to the three physical habitat gradients is presented. Then, these results are compared to results of other research on similar streams. The similarities and contrasts of the methods and results of these published studies to this study are highlighted. Lastly, speculation about the impacts of human perturbations based on the results of detrended correspondence analysis is provided.

In this study one species assemblage (squawfish, largescale suckers, redside shiners and speckled dace) was most often found in pools, and another assemblage (longnose dace, and juvenile and adult torrent sculpins) was found in riffles. The species rankings in the "pool" assemblage had low scores on DCA axis one, and those in the "riffle" assemblage had high scores on DCA axis one with one exception. Longnose dace were ranked along axis one closest to the members of the pool species assemblage; this apparent anomaly is discussed below. The ranking of rainbow and cutthroat trout on this axis was also of interest. My field observations revealed a preference by these species for cooler stream areas with smaller substrate and depths of two to three feet.

The species rankings on DCA axis two are very different from axis one. The squawfish assemblage is now in the middle of the gradient. Longnose dace and rainbow trout are grouped at the opposite end from cutthroat trout. Field observations revealed that cutthroat trout were found in narrower stream sections that had more canopy and instream cover, slower flows and smaller substrate size than rainbow trout. Longnose dace were found in shallow, swift flowing areas with larger substrate (cobble/rubble and boulders) and very little overhead canopy. The DCA results for axis two show that cutthroat trout have a significant preference for areas with both instream and canopy cover. The DCA results show that longnose dace prefer areas with swifter currents and a lack of both instream and canopy cover, and very fine substrate. However, none of these associations was significant (Table 12).

The species rankings for DCA axis three show a longnose dace, sculpin grouping on one end of the discharge gradient and a squawfish, trout grouping on the other. Cutthroat trout juveniles had the only significant relationship on this axis. Discharge was calculated using the values for width, depth and area (m^2) in each study patch. It is possible that the individual species ranking on the habitat gradients for stream width and depth in axis one and two influenced their rank on axis three. Cutthroat trout showed a significant preference for the narrower study site sections, while longnose dace and rainbow trout were ranked at the opposite end of the gradient. There were no significant relationships on the depth gradient. Yet, on axis three longnose dace and rainbow trout are ranked at opposite ends of the gradient. It appears that the species ranking on the width gradient has influenced the species ranking on the discharge gradient, but the interpretation is unclear.

Several researchers have shown an association between specific species distributions and physical habitat parameters (i.e.; Boussu 1954, Gorman and Karr 1978, Hawkins et al. 1982). The effects of physical variables such as streamflow, water temperature, depth, cover type and availability, and substrate composition on the distribution of numerous species and assemblages has been well documented. Moyle and Baltz (1985) conducted a study on the microhabitat use of stream fish in Deer Creek, a tributary of the Sacramento River in California, using electivities for mean velocity, total depth and substrate. They found that a species assemblage composed of adult rainbow trout, adult Sacramento suckers (Catostomus occidentalis), adult speckled dace and adult and juvenile riffle sculpin (Cottus gulosus) showed a preference for faster water (mean surface velocities > 40 cm/sec). Adult Sacramento squawfish (Ptychocheilus grandis) preferred slower water (mean surface velocities < 33 cm/sec.). The deeper parts of the stream were favored by juvenile and adult rainbow trout and Sacramento squawfish, while shallower stream sections were used by Sacramento suckers, speckled dace and riffle sculpins. Moyle and Baltz did not consider cover type and availability in their study.

There is a lot of similarity in the species and assemblage distributions detected by the DCA analysis and those described by Moyle and Baltz. The axis one "pool" assemblage corresponds well to the species found in deeper, warmer water by Moyle and Baltz. The axis one "riffle" assemblage differs from the species found in shallower, cooler water by Moyle and Baltz because trout were found in shallower patches (approximately 75 cm) than reported in Moyle and Baltz's work (approximately 100-120 cm). However, the difference in depth is not very great. The species assemblages distributed along the velocity gradient in axis two and species described by Moyle and Baltz that occurred in both swift and slow water correlate well. Both analyses showed that rainbow trout, dace and sculpins were in faster stream areas, while suckers and squawfish were in slower stream areas.

Baltz et al. (1987) also found that temperature, water velocity, and substrate influence the distribution of rainbow trout, Sacramento suckers, and Sacramento squawfish in a California stream. Rainbow trout occurred in shallower, swifter and cooler areas of the stream than either the suckers or squawfish. All rainbow trout were found in areas of 20 C or less, squawfish and suckers were generally observed in areas exceeding 20 C. Analogously, in the Willamette River drainage studied here, rainbow and cutthroat trout generally occurred at sites with cooler temperatures (<17 C), small substrate, and depths of 2-3 feet. Squawfish and suckers occurred at deeper sites with temperatures of 20 C or greater and bedrock substrate. Thus, DCA axis one is comparable to the gradient of physical variables that Baltz et at. (1987) found to be important.

Baltz et al. (1987) concluded that temperature gradients may be very important in some species' distributions. Temperature appears to be a major influencing factor in the distribution of longnose dace in this study. Longnose dace were ranked with the "pool" species assemblage on axis one even though they prefer swift shallow stream areas with larger substrate composition (cobble/rubble). It is possible that one very strong habitat preference may influence the DCA ranking algorithm and result in the placement of a species on an axis that is not easily interpretable. One possible explanation for this apparent inconsistency may come upon closer examination of the values of the habitat gradients for species presence and absence in Table 12. Temperature was the only significant preference shown by longnose dace on axis one. Perhaps the strong preference shown by longnose dace for warmer stream areas outweighed the ranking power of the depth parameter. Recent work by Bond et al. (1988) analyzed 229 sightings of longnose dace and found a significant Chi-square value ($P < 0.001$) for the association of longnose dace with warmer water. An alternative interpretation of axis one may be as a physiological response by individual species to a temperature gradient.

The effect of different types of cover on stream fish species distribution has been studied extensively. Boussu (1954) showed that abundance and growth rates of rainbow trout in Trout Creek, Montana increased in stream areas with either natural or added instream cover (brush bundles and undercut banks) versus stream areas where instream cover had been removed. Research conducted by Lewis (1969) used a multiple regression with six physical parameters; pool surface area, volume, mean depth, mean current velocity, percent cover, and total cover to explain the variation in rainbow trout abundance (N= 247) in 19 pools. The regression explained 70 percent of the variation, with current velocity and total cover accounting for 59 percent of the total.

Recent studies on the effects of instream cover on stream fish distribution and abundance in artificial stream channels (Wilzbach 1985), showed salmonids were strongly influenced by the amount of cover available. Wilzbach (1985) visually observed that cutthroat trout used areas with instream cover when food abundances were high. She concluded that cutthroat trout occur most often in stream areas with instream cover when food is plentiful and water temperatures are warm. DCA axis two shows a gradient of species preferences' for cover types. Cutthroat trout have a significant preference for stream areas with instream and canopy cover while on the opposite end of the axis rainbow trout and longnose dace prefer stream areas with less instream and canopy cover. DCA analysis is particularly informative in situations like this where the effects of more than one environmental factor (temperature and cover type) on species distributions are being examined. DCA allows the examination of both the combined and individual effects of temperature and cover type on species distributions to be examined, which contributes to a clearer understanding of the species responses to these parameters.

The interpretation of the DCA results is useful on two levels. The first is the relative importance of a single habitat parameter on the distribution of a species. The second and more interesting is the combined effect of all significant habitat parameters for all species on the three axes and the ability to group species into assemblages that respond similarly. The use of a three dimensional diagram (Figure 5) allows for clearer visualization of the relative influence of the three gradients on each species through the depiction of each species as a point in space. It also effectively displays species groupings. The technique of displaying the DCA axes gradients and species scores in a three dimensional plot provides the ability to qualitatively predict the reaction of a species or assemblage to a change in habitat.

Much research has been conducted to examine the effects of human perturbations in watersheds (i.e.; logging, impoundment, etc.) on resident fauna. Logging around streams can have both beneficial and detrimental effects on fish populations, depending upon the species considered, the extent of changes to the stream habitat and the time scale of interest. An increase in the amount of light reaching the stream after canopy removal can stimulate growth of aquatic vegetation and in turn result in an increase in invertebrate and fish densities (Murphy and Hall 1981, Hawkins et al. 1982). Fish growth rates may increase after logging due to warmer stream temperatures (Scrivener and Andersen 1984). Hawkins et al. (1983) noted that streams with little or no riparian shading had more abundant salmonid and sculpin populations than similar, but shaded streams. They attributed this difference to the higher autotrophic production in streams without canopy cover and resultant greater invertebrate abundance. Detrimental impacts of logging may also cause declines in salmonid populations. Examples of deleterious impacts would include increased sedimentation, collapsed stream banks, decreased channel stability, loss of large woody debris, less dissolved oxygen and elevated temperatures (Ringler and Hall 1975, Scrivener and Brownlee 1982, and Bisson and Sedell 1984).

Probable changes in fish communities in the Willamette River drainage can be estimated from these logging impacts using figure 5. Because autotrophic production and invertebrate abundance were not measured in this study, it is not possible to predict the impact of this effect directly. However, because increased food production is a result of loss of canopy cover, we can use this variable as a proxy for food production. If logging resulted in a reduction of canopy cover then there may be an initial increase in the abundance of salmonid populations due to increased food availability. However, if siltation increased and the substrate composition of the stream were effected there may be an ultimate decrease in the salmonid population. Table 12 shows that rainbow trout prefer habitat patches with gravel substrates that have a very low percentage of fines. If siltation occurs, use of the area by rainbow trout could be reduced. If logging resulted in a decrease in the amount of undercut banks or large woody debris, cutthroat trout use of the area may be reduced due to their strong association with instream cover (Table 12 and Figure 5). If stream temperatures become elevated, species that prefer warmer water (i.e., longnose dace, Table 12) may increase in abundance while species that prefer cooler temperatures (i.e., rainbow and cutthroat trout, Table 12) may decrease (Figure 5).

Much research has been conducted on the effects of impounding river systems. The severity of the impacts depend on the number and type of impoundment and their locations on the river (Petts 1984, Canter 1985). Small scale dams on stream systems similar in size to those of this study may cause a variety of changes to water chemistry and the physical environment. Impoundments may cause thermal stratification in the reservoir. This occurs when the cooler bottom waters do not mix with the warmer upper water. A progressive depletion of oxygen in the lower water layer may result. Thermal stratification usually occurs in deep reservoirs (20-30 feet), but shallow reservoirs can stratify, particularly when cool tributary streams or springs maintain low temperatures on the bottom. Even in impounded systems that do not completely stratify, some thermal gradient may be found in the reservoir (Kelly 1980).

Water temperature affects the rate of biochemical processes occurring within the stream and the solubility of gases. Oxygen is less soluble in warmer water. Warming of the water both upstream and downstream of a dam is particularly a problem during summer low flows. The combination of temperature elevation and oxygen depletion can alter the species composition in the dam area (Spence and Hynes 1971, Lehmkuhl 1972, Geen 1974). Impoundments also cause increased sedimentation and accumulation of pollutants and allochthonous nutrient materials in the reservoir. Sedimentation of the substrate can alter benthic conditions and macroinvertebrate assemblages, which in turn affects higher order species (Ward 1976, Kaster and Jacobi 1978).

Figure 5 can again be used to estimate the effects that an impoundment would have on the distribution of species assemblages. If the thermal regime increases and dissolved oxygen levels in the stream decrease then the species most sensitive to these parameters (salmonids) would be affected first (Table 12). These water chemistry changes could result in a decrease in the abundance of salmonids close to the impoundment and an increase in more tolerant species such as squawfish and suckers. Sedimentation of natural substrate and reductions of flows close to impoundments may result in a decrease in abundance of species (i.e., longnose dace, sculpins and salmonids, Table 12) that show strong associations with these parameters. Species that are strongly affected by discharge, axis three (longnose dace and torrent sculpins, Table 12) could decrease in abundance (Figure 5).

It is difficult to compare the differences, if any, in species composition near and far from the dams on the six impounded streams in this study because they vary greatly in size and species assemblage composition. Also, gaps in the data set resulting from limitations in field sampling restrict comparisons. Thomas Creek and Calapooia River were comparable in discharge, species composition and reservoir size. However, definitive statements about changes in species assemblage upstream and downstream of the reservoir on the Calapooia River cannot be made due to lack of samples below the dam as a result of poor water quality conditions. Even on Thomas Creek, where these problems did not occur, it is difficult to relate species distributions to the impoundment because of subtle changes in the assemblages upstream and downstream.

On Thomas Creek more species were present in the study sites that were located in the mid-reaches of Thomas Creek than in the furthermost upstream or downstream study sites (Table 2). Minor differences were found between the species composition of the Thomas Creek reservoir (study site 9) and the pools both upstream (study site 7) and downstream (study site 11). Squawfish occurred in these two pools, but not in the reservoir. The sculpin species were present in study site 7 and the reservoir, but not in study site 11. Largescale suckers were present in the reservoir and study site 11, but not study site 7. Similar difference inspecies composition can be seen between the closest riffles upstream of the reservoir (study sites 6 and 8) and downstream of the reservoir (study site 12). Redside shiners occurred in study site 8, but not 6 or 12. Longnose dace occurred in study site 6 and 8, but not 12. Much more sampling would be needed to determine if these species changes were merely an artifact of the sampling techniques or a response to changes in the physical habitat from the impoundment. That determination was outside of the scope of this project.

The remaining impounded streams were sampled only in close proximity to the dams. Comparisons of species assemblages above and below the dams are only possible on Turner Creek (Table 3) and the south fork of Rock Creek (Table 4). Turner Creek had a very simple species assemblage of cutthroat trout and sculpins. Species distributions were similar above and below the dam. The only notable difference at any of the sites was that torrent sculpins did not occur in pools. The species assemblage on the south fork of Rock Creek consisted of cutthroat and rainbow trout and sculpins. In this system sculpins did not occur in the reservoir and rainbow trout were not found in the immediate vicinity of the dam. Due to the small sample sizes it is impossible to know if the impoundments affected the species distributions on these stream systems.

The multivariate analyses used in this study discern which environmental gradients affect the distribution of specific species assemblages. These analyses provide insights into the critical characteristics of the habitat utilized by species assemblages. As just shown, from this information we may infer that major changes to critical habitat types through human perturbations could greatly alter species composition both on a local scale and throughout the stream system. Understanding the possible impacts of a development proposal could be useful in estimating the costs on stream fauna and benefits of a future project.

However, there are limitations to the approach presented here. For example, impacts of water pollution were not considered, because water quality was not measured. Hughes and Gammon (1987) attribute differences in fish assemblages in the mainstem Willamette River between 1945 and 1986 largely to changes in the quality of the physical habitat and water. They found that point sources of pollution affected fish assemblages less than gradual changes in water quality from the headwaters to the mouth of the river. Impacts of such a gradient in water quality are not discernable by the DCA analyses presented here. Li et al. (1987) stated that man-made disturbances have affected the fauna of the Willamette River basin-wide through alteration of the physical habitat. However, they warn that the presence or absence of a species in a given stream may not be due entirely to changes in physical gradients, but may be influenced by events elsewhere in the river system. As with water quality, the analysis presented in this study cannot detect these events nor their impacts, unless they resulted in measurable changes in the physical variables measured at the sites sampled.

REFERENCES

Allen, K. R. 1969. Distinctive aspects of the ecology of stream fishes: a review. Journal of the Fisheries Research Board of Canada 26:1429-1438.

Baltz, D.M., P.B. Moyle and N.J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, (Cottus gulosus), and speckled dace, (Rhinichthys osculus). Canadian Journal of Fisheries and Aquatic Sciences. 39:11:1502-1511.

Baltz, D.M., B. Vondracek, L.R. Brown and P.B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Transactions of the American Fisheries Society 116:12-20.

Bisson, P.A., and J.R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. p. 121-129. In W.R. Meehan, T.R. Merrell, Jr. and T.A. Hanley (ed.). Fish and wildlife relationships in old-growth forests, proceedings of a symposium held April 1982, Juneau, Alaska. American Institute of Fisheries Research Biologists, Juneau, Alaska.

Bond, C.E., E. Rexstad and R.M. Hughes. 1988. Habitat use of twenty-five common species of Oregon freshwater fishes. Oregon State University, unpublished manuscript.

Boussu, M. F. 1954. Relationship between trout populations and cover on a small stream. Journal of Wildlife Management 18:229-239.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325-349.

Canter, L. 1985. Environmental impact of water resources projects. Lewis Publishers, Inc. Chelsea, Michigan 352 p.

Carlander, K.D. 1969. Handbook of freshwater fishery biology. Volume 1. The Iowa State University Press, Ames, Iowa. 751 p.

Carleton, T.J. 1984. Residual ordination analysis; a method for exploring vegetation-environment relationships. Ecology 65:469-477.

Cummins, K.W., 1974. Structure and function of stream ecosystems. Bioscience 24:631-641.

Dixon, W.J., ed. 1983. BMDP statistical software, 1983 printing with additions. University of California Press. Berkley, California. 734 p.

Fraser, D.S. and R.D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. Ecology 63: 307-313.

Fraser, D.S. and T.E. Sise. 1980. Observations on stream minnows in a patchy environment: a test of a theory of habitat distribution. Ecology 6:790-797.

Felley, J.D. and L.G. Hill. 1983. Multivariate assessment of environmental preferences of cyprinid fishes of the Illinois River, Oklahoma. The American Midland Naturalist 109:209-221.

Gauch, H.G., 1981. Hierarchical classification of community data. Journal of Ecology. 69:135-152.

Gauch, H.G., 1982. Multivariate analysis in community ecology. Cambridge University Press. 298 p.

Gauch, H.G., R.H. Whittaker and T.R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. Journal of Ecology 65:157-174.

Gauch, H.G., R.H. Whittaker and S.B. Singer. 1981. A comparative study of non-metric ordinations. Journal of Ecology 69:135-152.

Geen, G.H. 1974. Effects of hydroelectric development in western Canada on aquatic ecosystems. Journal of Fisheries Research Board of Canada 31: 913-927.

Goldstein, R. M. 1978. Quantitative comparison of seining and underwater observation for stream fishery surveys. Progressive Fish Culturist 40(3) 108-111.

Goodall, D.W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. Australian Journal of Botany 1:39-63.

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

Greig-Smith, P. 1980. The development of numerical classification and ordination. Vegetatio 42:1-9.

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 120:423-454.

Hawkins, C.P., M.L. Murphy and N.H. Anderson. 1982. Effects of canopy, substrate composition and gradient on the structure of macroinvertebrate communities in Cascade range streams of Oregon. Ecology 63:1840-1856.

Hawkins, C.P., M.L. Murphy, N.H. Anderson and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-1185.

Hill, M.O. 1973. Reciprocal averaging; an eigenvector method of ordination. Journal of Ecology 65:157-174.

Hill, M.O. 1974. Correspondence analysis: a neglected multivariate method. Journal of Applied Statistics 23:340-354.

Hill, M.O. 1979. DECORANA- a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University. Ithaca, New York.

Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis; an improved ordination technique. Vegetatio 42:47-58.

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: 155-163.

Hughes, R.M., and J.R. Gammon. 1987. Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. Transactions of the American Fisheries Society 116:196-209.

Hughes, R.M., E. Rexstad and C.E. Bond. 1987. The relationship of aquatic ecoregions, river basins and physiographic provinces to the ichthyogeographic regions of Oregon. Copeia 2:423-432.

Karr, J.R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6(6):21-26.

Kaster, J.L. and G.Z. Jacobi. 1978. Benthic macroinvertebrates of a fluctuating reservoir. Freshwater Biology 8:28-290.

Kelly, J.A. 1980. Potential environmental effects of small-scale hydroelectric development on Oregon. Water Resources Research Institute, Oregon State University. 51 p.

Lagler, K.F., J.E. Bardach, R.R. Miller and D.R. May Passino. 1977. Ichthyology, second edition. John Wiley and Sons. New York, NY. 506 p.

Layher, W.G. and O.E. Maughan. 1985. Relations between habitat variables and channel catfish populations in prairie streams. Transactions of the American Fisheries Society 114:771-781.

Lehmkuhl, D.M. 1972. Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. Journal of Canadian Fisheries Research Board 29: 1329-1332.

Lewis, S.T. 1969. Physical factors influencing fish populations in pools of a trout stream. Transactions of the American Fisheries Society 98:14-19.

Li, H.W., C.B. Schreck, C.E. Bond and E. Rexstad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams pp. 193-202. <u>In</u> Community and evolutionary ecology of North American stream fishes. Edited by W.J. Matthews and D.C. Heins. University of Oklahoma Press.

Lotrich, V.A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. Ecological Monographs 43:377-397.

Minshall, G.W., R.C. Petersen, K.W. Cummins, T.L. Bott, J.R. Sedell, C.E. Cushing, and R.L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs 53:1-25.

Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Bruns, J.R. Sedell, and R.L. Vannote. 1985a. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences. 42:1045-1055.

Minshall, G.W., R.C. Petersen and C.F. Nimz. 1985b. Species richness in streams of different size from the same drainage basin. The American Naturalist 125:16-38.

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

Murphy, M.L. and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137-145.

Northcote, T.G., and D.W. Wilkie. 1963. Underwater census of stream fish populations. Transactions of the American Fisheries Society 92:146-151.

Orloci, L. 1978. Multivariate analysis in vegetation research. Junk, The Hauge.

Paine, M.D., J.J. Dodson, and G. Power. 1982. Habitat and food resource partitioning among four species of darters (Percidae: Etheostoma) in a southern Ontario stream. Canadian Journal of Zoology 60:1635-1641.

Petts, G.E., 1984. Impounded rivers- perspectives for ecological management. Wiley and Sons. New York, NY. 326 p.

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

Remington, R.D. and M. A. Schork. 1970. Statistics with applications to the biological and health sciences. Prentice-Hall Inc. Englewood Cliffs, NJ.

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

Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monograms 52:398-414.

Schlosser, I.J. 1987. Conceptual framework for fish communities in small warmwater streams pp. 17-24. In Community and Evolutionary Ecology of North American Stream Fishes. W.J. Matthews and D.C. Heins, editors. University of Oklahoma Press.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-37.

Scott, W.B. and E.J. Crossman. 1973. Freshwater fishes of Canada. Bulletin No. 171. Fisheries Research Board of Canada, Ottawa, Canada. 966 p.

Scrivener, J.C., and B.C. Andersen. 1984. Logging impacts and some mechanisms that determine the size of spring and summer population of coho salmon fry (Oncorhynchus kisutch) in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 41:1097-1105.

Scrivener, J.C., and M.J. Brownlee. 1982. An analysis of Carnation Creek gravel-quality data, 1973 to 1981, p. 154-176 In G.F. Hartman (ed.) Proceedings of the Carnation Creek Workshop: a ten-year review, Feb. 24-26, 1982. Pacific Biological Station, Nanaimo, British Columbia.

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

Spence, J.A., and H.B.N. Hynes. 1971. Differences in benthos upstream and downstream of an impoundment. Journal of Fisheries Research Board of Canada 28:35-43.

Strahler, A.H. 1978. Binary discriminant analysis; a new method for investigating species-environment relationships. Ecology 59:108-116.

Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344-352.

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.

Ward, J.V.. 1976. Effects of flow patterns below large dams on stream benthos: a review. In J.F. Orsborn and C.H. Allman (ed.) Instream flow needs, volume II. Western division of the American Fisheries Society, Bethesda, Maryland.

Whittaker, R.H. 1978. Direct gradient analysis. _In_ Ordination of Plant Communities, R.H. Whittaker (ed.) pp. 7-50.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (Salmo clarki). Canadian Journal of Fisheries and Aquatic Sciences 42:1668-1672.