MULTIVARIATE ANALYSIS OF FISH ASSEMBLAGE COMPOSITION AND ENVIRONMENTAL CORRELATES IN A HIMALAYAN RIVER - NEPAL'S

KALI GANDAKI/NARAYANI

By

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DEDICATION

This study is dedicated to the people of Nepal, and to their preservation, conservation, and wise use of the country's natural resources.

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INTRODUCTION

A major goal of community ecology is to describe the patterns of nature and to generalize explanations for their causal processes (Wiens 1984). Ecologists have long noted that fish assemblages exhibit patterns of longitudinal zonation in rivers and streams (reviews in Hynes 1970. Hawkes 1975, Fisher 1983). However, investigation of causal mechanisms of zonation continues to be an active area of study (e.g., Matthews 1986, Hughes and Gammon 1987, Schlosser 1987). In this paper, I test for spatial and temporal patterns and environmental correlates of the structure of fish assemblages in the Kali Gandaki/Narayani River of Nepal.

The Kali Gandaki/Narayani River forms the deepest gorge in the world as it flows through the Himalaya Mountains on its way from headwaters on the Tibetan Plateau to a lowland, subtropical confluence with the Ganges River. The Oriental and Palearctic biogeographic realms interdigitate in the Gandaki basin, thus the river lies at the zoogeographic center of Asia. The Kali Gandaki Valley may have the greatest abundance and variety of flora and fauna on the Asian continent. More than 65% of the 182 fish species known to occur in Nepal inhabit the Kali Gandaki/Narayani River (Edds 1986). The diversity of the ichthyofauna, and the tremendous altitudinal and ecological gradients of the drainage make the Kali Gandaki/Narayani system ideal as a case-study in longitudinal zonation of fish assemblage structure. Superimposed on the relatively static physiographic features of the drainage are dramatic changes associated with the monsoon season. Thus, I also test for seasonal changes in assemblage structure. Relatively little is known of the distribution and ecology of fishes in the Himalaya Mountains and lowlands of Nepal. Published records include brief notes by Regan (1907), Hora (1937a) and Menon (1949), and the annotated species lists and accounts of DeWitt (1960), Shrestha (1981), Rajbanshi (1982) and Edds (1985, 1986, 1987).

I also present a comparison of the results obtained from analyses by direct and indirect gradient methods, two commonly used multivariate approaches to community analysis. The indirect approach is a two-step process: first, exploratory multivariate techniques such as principal components analysis (PCA), reciprocal averaging (RA) or detrended correspondence analysis (DCA) are used to ordinate samples of community composition (Gauch 1982). Associations between ordination scores and environmental variables are then examined by correlation and multiple

regression analyses (e.g., Chang and Gauch 1986. Matthews and Robison 1988).

Direct gradient analysis relates species occurrence directly to the environment (Gauch 1982, Ter Braak 1986, Ter Braak and Prentice 1988). This technique searches for the patterns of variation in assemblage structure that are most closely associated with variation in measured environmental variables. While the ordination axes obtained by the indirect approach are, by definition, orthogonal, there may be other axes that are better related to the environmental parameters. Direct ordination techniques extract axes of assemblage structure that are both orthogonal and constrained to be maximally associated with linear combinations of environmental variables. For direct gradient analysis, I used canonical correspondence analysis (CCA) and detrended canonical correspondence analysis (DCCA), direct gradient analysis techniques developed by Ter Braak (1986, 1987, 1988a, 1988b) that allow interpretation of the response of individual species as well as species assemblages to environmental gradients.

STUDY AREA

The Kali Gandaki/Narayani River lies between the latitudes 27° 20' and 29° 30' N and longitudes 83° 20' and

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84° 30' E. The river traverses the Himalaya Mountains, with intrusions into the Tibetan Plateau to the north and the Gangetic Plain to the south (Fig. 1). Four major mountain ranges cross the drainage and divide the river basin into at least nine geographic zones (Anonymous 1979). These zones are, from north to south: 1) the Tibetan Plateau, with average altitudes > 5000 m; 2) the Tibetan Marginal Mountains which rise to 7000 m; 3) the Inner Himalaya Zone, consisting of desert-like high mountain valleys, with elevations > 3000 m; 4) the Great Himalaya Range, having snow-covered peaks to 8137 m and deep narrow gorges and glacial valleys; 5) the Midland Zone, or lowlying hills and valleys with relatively smooth topography and altitudes between 600 and 2500 m; 6) the Mahabharat Range, steep and rugged mountains ranging to 2200 m; 7) the Dun valleys, low-gradient wide valleys with steep sides and elevations to 1500 m; 8) the Churia Hills, a low-lying range with altitudes to 1000 m; and 9) the Tarai, the Nepalese section of the Great Gangetic Plain, with elevations as low as 50 m above sea level. Herein, I group these zones into five regions: trans-Himalaya (zones 1-3), mountain (zone 4), high hills (zones 5-6), low hills (zones 7-8), and lowlands (zone 9) (Fig 1).

The ecology of all zones south of the Great Himalaya Range is greatly influenced by the summer monsoon from the Bay of Bengal. Much of the Gandaki basin receives more

than 250 cm of rain during the June - September rainy season. Two other distinct seasons occur in this area: a cool and dry season from October - January, and a hot and dry season from February - May.

The headwaters of the Kali Gandaki River flow approximately 60 km southward before collecting the Chalunga River to become a fourth-order stream north of the Great Himalaya Range. The Kali Gandaki then traverses this mountain range at a riverbed elevation of about 2500 m near Kalapani and flows 80 km before joining the Myagdi at Beni to become a fifth-order stream. Near Ridi Bazar, the Kali Gandaki meets the Badigarh River and is a sixth-order stream that flows nearly 200 km to the east before joining the Trisuli. At the confluence with the Trisuli, the river becomes a seventh-order stream and is known as the Sapta (seven) Gandaki, or Narayani River. The Narayani flows south and then west with a low gradient before breaking through the Churia Hills to spill south onto the Gangetic Plain (Fig. 1).

River gradients vary between 0.1% and 0.5% for the Narayani. The slope of the Kali Gandaki in its middle zones ranges between 0.5% and 5%, with the highest gradients occurring near the Great Himalaya Range. Gradients may exceed 10% where the river cuts through the Himalayas. Stream gradients are only about 1% in the trans-Himalayan region (Fig. 2).

SAMPLING METHODS

I made 172 samples at 85 sites along the Kali Gandaki/Narayani River from March 1984 to May 1986. Fourteen sites were sampled in each of the three seasons (Fig. 1). Sample sites were chosen so as to adequately sample all geographic zones. However, sampling was limited in some areas due to difficulties of access. Fishes were collected by a variety of methods, including seine, cast net, gill net, and backpack electrofisher. Choice of method at individual sites was based on the need to sample all distinct microhabitats (riffle, pool, raceway, backwaters, etc.). Collections from each type of microhabitat were maintained separately.

Specimens were preserved in 10% formalin. Identification of species followed Hamilton (1822), M'Clelland (1839), Day (1878), Hora (1921a, 1937b, 1935), Shaw and Shebbeare (1937), Roberts (1980, 1983), Shrivastava (1980), Jayaram (1981), Shrestha (1981) and Rainboth (1983). Problematical specimens were identified by comparison with collections housed at the Nepal Natural History Museum, California Academy of Sciences, Chicago Field Museum of Natural History, National Museum of Natural History, American Museum of Natural History, and Philadelphia Academy of Natural Sciences. Higher taxonomy herein follows Nelson (1984) except for the

Cobitoidea, which is after Sawada (1982). Voucher specimens were deposited in the Nepal Natural History Museum, Kathmandu and the Oklahoma State University Department of Zoology Collection of Vertebrates, Stillwater.

At each site I measured 37 environmental variables which I have grouped into five categories: geography, water quality, season, substrate, and vegetation (see Appendix A for values of variables at each site). Geographic factors included: altitude, measured from 1:250,000 U.S. Army Corps of Engineers maps and a Thommen 2000 altimeter; percent gradient of the riverbed, calculated from map and altimeter readings; river kilometer, or distance from the source of the Kali Gandaki, also measured from these maps; stream order, determined from these 1:250,000 maps and concomitant ground-truth studies which verified the smallest tributaries as first-order streams, streams formed by the joining of two first-order streams as second-order, streams formed by the joining of two second-order streams as third-order, etc.; predominantly exposed geological strata at the site, from Sharma (1977a), coded from 1 to 5 in order of geologic age, from Pleistocene to Precambrian (Appendix A); estimated maximum width of stream; and natural region, including trans-Himalaya, mountain, hill, lowland valley, and lowland plain, coded sequentially from 1 to 5.

Water quality factors included current speed (measured with a Teledyne Gurley pygmy current meter no. 625 at 60% depth) and stream depth. I measured both depth and current at 10 locations spaced at 1 m intervals in 3 to 5 transects across each microhabitat and calculated means of these measurements to arrive at an estimate of average depth and current speed for each site. Other water quality factors were: surface temperature, water clarity, and the following parameters measured with a Hach kit (model AL-36B): dissolved oxygen (mg/L), dissolved carbon dioxide (mg/L), pH, free acidity and total acidity (grains/gallon calcium carbonate -- gpg CaCO₃), free alkalinity and total alkalinity (gpg CaCO₃), and total hardness (gpg CaCO₃).

Substrate parameters were quantified with a modification of the Wentworth scale (Cummins 1962, Hynes 1970) by estimating the percent comprised of mud (< ca. 0.0625 mm), sand (ca. 0.0625-1 mm), gravel (ca. 2-16 mm), stone (ca. 16-64 mm), rubble (ca. 64-256 mm), and boulder (> ca. 256 mm), and by noting the dominant substrate and total number of substrate types at each site.

Vegetation was measured as percent of the site covered by filamentous algae, submerged vegetation, emergent vegetation, floating vegetation, debris, and detritus, and by noting the dominant vegetation, number of vegetation types, and percent of each site covered by vegetation.

ANALYTICAL METHODS

Twenty-two collections were not considered in the analysis. These included sixteen collections that were qualitative only and/or had no environmental parameters measured and six collection efforts that produced no fish. Two collections having only two and four specimens eventually were excluded because they were outliers in the ordination analysis. Three environmental variables, free acidity, free alkalinity, and percent floating vegetation, were effectively invariant and were also excluded. Thus my results are based on 34 environmental variables measured for each of 148 collections at 73 sites (Fig. 1, Appendix B).

Fifty-two of the 120 fish species I collected are included in the analysis. The remaining 68 species occurred in less than 5% of the samples and were eliminated following Gauch (1982). Species abundances were coded for each collection on a scale of 0-4, with 0 = absent, 1 = 1-5 individuals, 2 = 6-10, 3 = 11-20, and 4 = > 20. Only adult fishes were included. Coded abundances improved normality of fish species distributions, but further transformation to log of coded abundance resulted in no improvement (Kolomogorov D-test, PROC UNIVARIATE, SAS Institute 1985a). Therefore, coded

abundances were used as the raw data for final analysis.

Transformation of environmental variables to $\log_{10}(x + 1)$, or to arcsin \sqrt{x} for percentage data, markedly improved normality (reduced skewness and kurtosis) for 21 variables, including: altitude, percent stream gradient, stream width, dissolved CO₂, total alkalinity, total hardness, percent substrate comprised of mud, percent sand, percent gravel, percent stone, percent rubble, percent boulder, dominant substrate type, percent of cover by filamentous algae, percent submerged vegetation, percent emergent vegetation, percent detritus, percent debris, percent total cover by vegetation, number of vegetation types, and stream depth. These transformed variables were used in all subsequent analyses, while the remaining 13 variables were input as untransformed values. Transformation of non-normal data allows a closer approximation to the normality assumption on which correlation and regression analyses are based. and also decreases the chance that analyses will be unduly affected by extreme but infrequent values (Sokal and Rohlf 1981).

Indirect gradient analysis included initial DCA ordination of the fish collections on the basis of species abundances. Two different algorithms were used to obtain DCA ordinations: the DECORANA program of Hill (1979a) and the CANOCO procedures of Ter Braak (1988a).

DCA ordination axes were subsequently compared with environmental parameters by correlation analysis (PROC CORR, SAS Institute 1985a) and stepwise multiple regression (PROC STEPWISE, SAS Institute 1985b). Mallows' C_p statistic (Mallows 1964) was used as the criterion for selecting a regression model.

Two other indirect multivariate ordination techniques, PCA and RA, were also performed but DCA provided more interpretable results. Linear ordination methods, such as PCA and redundancy analysis are appropriate if the range of sample scores along the length of the first axis, ordinated by reciprocal averaging (RA), is less than about 1.5 SD (Gauch et al. 1977; Ter Braak and Prentice 1988). However, where gradients are longer and where species have unimodal (Gaussian) responses along the gradient, nonlinear methods like RA, DCA, CCA, and DCCA more consistently and accurately recover the structure of data (Gauch et al. 1977; Peet 1980; Pielou 1984; Ter Braak and Prentice 1988).

DCA is a variance maximization method of ordination based on RA, which is itself similar to PCA (Hill 1973). PCA is based on a Euclidean distance matrix, and the correlation matrix between all variables is decomposed using eigenvector analysis; standardized data are then projected onto the first few resulting axes. These linear, orthogonal axes typically account for a large

portion of the residual variance. RA is algebraically similar, except that it decomposes an association matrix based on the chi-square distance metric.

DCA corrects for the two major faults of RA, which can cause difficulties in attempts to interpret the axes: the arch effect, caused by a quadratic relationship of axis 2 on axis 1 (Hill and Gauch 1980); and distortion of ecological distances along the axes (Hill 1979a). DCA also aids interpretation by scaling the axes (gradient length) to average standard deviation units (SD) of species turnover, where 1 SD = half change and 4 SD = total change in species composition. DCA also calculates separate sample scores and species scores that can be superimposed on the same figure, providing an approximation of species' optima along the axes.

In DECORANA, the arch effect of RA is removed by an ad-hoc DCA algorithm known as detrending by segments. DCA has been criticized by Pielou (1984) as "overzealous" and by Wartenberg et al. (1987) as "without theoretical justification". However, others, using real and simulated data, have found it to give useful and ecologically correct interpretations (Gauch 1982; Peet et al. 1988). DCA is the ordination method presently favored by the majority of ecologists for nonlinear data from a variety of organisms (e.g., Chang and Gauch 1986; Leland et al. 1986; Ben-Shahar and Skinner 1988), including fishes (e.g., Rahel 1984; Larsen et al. 1986; Hughes and Gammon 1987; Hughes et al. 1987; Matthews and Robison 1988; Meffe and Sheldon 1988; Townsend and Peirson 1988; Ibarra and Stewart 1989). Ter Braak and Prentice (1988) developed a less "brute-force" algorithm for DCA, available in CANOCO, known as detrending by polynomials, which eliminates systematic relations between axes by making subsequent axes orthogonal not only to axes already extracted, but also to quadratic, cubic, and quartic functions of those axes.

RA and DCA axes are obtained by a converging sequence of weighted averaging regressions and calibrations such that sample axes are linear combinations of weighted mean species scores with the constraint that successive axes are uncorrelated with previous ones. Direct ordination methods of CCA and DCCA impose the additional constraint that ordination axes based on species abundances be linear combinations of supplied environmental variables (Ter Braak 1986; Ter Braak and Prentice 1988). Thus, these methods produce community ordinations with an environmental basis (Ter Braak 1986; 1987). In resulting ordination diagrams, sites and species are represented by points, and environmental variables are represented by arrows. Thus, the axes can be interpreted directly from the pattern of community variation along environmental gradients. Also visible in these biplots are the approximate distributions of species

with respect to plotted variables. Eigenvalues measure the separation of species distributions along these environmental axes.

I performed direct gradient analysis with the CCA and DCCA algorithms provided by the CANOCO package. The downweighting option, which supplies lesser weights to rare species, was employed in all direct and indirect ordinations. The species-environment correlation (Ter Braak 1986, 1988a) is equal to the correlation between site scores that are weighted mean species scores and site scores that are linear combinations of the environmental variables. CANOCO provides a facility for testing statistical significance of the canonical axes with a Monte Carlo permutation test (Ter Braak 1988a). It allows an overall test of the effect of the environmental variables on the species, as well as significance tests on individual axes. The fraction of variance accounted for by an axis, i.e., variance in the weighted averages of fish species with respect to environmental variables, can be expressed as a percentage, and is calculated by dividing the eigenvalue of the axis by the sum of all canonical eigenvalues (the trace). It is important to remember that 100% is not expected, since part of the total variance is due to noise. Also, the percent accounted for depends on the number of variables (= the number of canonical axes extracted) in the analysis. Thus, for example, with only

three environmental variables in an analysis, three canonical axes explain 100% of the variance, whether or not the result is ecologically meaningful. The importance of an axis is better judged by its eigenvalue and a Monte Carlo significance test (Ter Braak 1988a).

RESULTS

Appendix C shows, for each collection, coded abundance of the 52 species included in my analysis. Seventy-one percent (37) are cypriniforms (Cyprinidae, Cobitidae, Homalopteridae) and 15% (8) are siluriforms (Schilbeidae, Amblycipitidae, Sisoridae). Other orders represented are Cyprinodontiformes (Belonidae) 2% (1) and Perciformes (Centropomidae, Gobiidae, Channidae, Mastacembelidae) 12% (6).

Longitudinal succession of species is evident in the Kali Gandaki/Narayani, with the number of species increasing steadily from upper reaches of the river to the downstream areas (r = 0.69, P < .0001; Fig. 3). No fish were captured in first or second order streams, and only one species, <u>Schizothorax richardsoni</u>, was present in the trans-Himalayan portion of the Kali Gandaki. Proceeding downstream, numbers of species ranged from one to four per site in the mountain region ($\bar{x} = 1.9$; SD = 0.9), 3 to 18 ($\bar{x} = 7.8$; SD = 4.1) in the high hills,

4 to 18 ($\bar{x} = 10.7$; SD = 4.4) in the low hills, and 6 to 33 ($\bar{x} = 15.6$; SD = 6.1) in the lowlands.

Indirect Gradient Analysis

Plots of the first two axes from both the PCA and the RA computations showed an uninterpretable horseshoe or arch effect. DCA from DECORANA provided better results; however, its detrending by segments algorithm produced a systematic relation between axes. Scores on axes 1 and 3 (r = 0.206, P = 0.0116), axes 1 and 4 (r = -0.257, P = 0.0015), and axes 3 and 4 (r = -0.273, P = 0.0007) were significantly correlated. CANOCO's DCA with detrending by fourth-order polynomials produced more desirable uncorrelated axes and the most interpretable ordination; consequently, this technique was used in all subsequent indirect gradient analyses.

<u>Axis 1</u>

DCA axis 1 (DCA 1) displays an extremely long gradient, more than 10 SD, from the mountains to the lowlands. Samples from the high hills showed the greatest variability in DCA 1 scores (Fig. 4). Mountain samples formed a discrete cluster widely separated from the remaining samples. Samples from the high hills and low hills were completely separated in the biplot of DCA 1 versus DCA 2. Samples from the low hills and the lowlands overlapped broadly on both DCA 1 and DCA 2. DCA 1 scores for samples from the low hills were shifted somewhat toward those for the high hills.

DCA 1 represents the tremendous altitudinal gradient of the Kali Gandaki/Narayani, with scores most highly and significantly correlated with major geographic factors (Table 1). Pearson product-moment correlations with DCA 1 scores are highest for stream gradient, stream order, altitude and natural region. Highly significant correlations also occur between DCA 1 scores and some water quality, substrate, and vegetation factors, such as stream depth, total hardness, percent substrate comprised of boulders, and percent cover by debris (Table 1).

Results of stepwise multiple regression analysis also suggest a geographic interpretation for DCA 1. The following multiple regression equation provided the best predictive model for DCA 1 scores:

DCA 1 = -3110.18 + 1402.115G - 75.61G + 16.62RK+ 108.68SW + 216.05TH + 972.93A + 176.96D (R² = 0.93; df = 140)

where SG = stream gradient, G = geology, RK = riverkilometer, SW = stream width, TH = total hardness,

A = altitude, and D = debris (Table 2).

Fishes having the highest scores on DCA 1 (and thus = "mountain" fishes) were <u>Schizothorax richardsoni</u>, <u>Euchiloglanis hodgarti</u>, and <u>Noemacheilus rupecula</u>. Highest negative loadings were for <u>Rasbora daniconius</u>, <u>Channa punctatus</u>, <u>Mastacembelus pancalus</u>, <u>Puntius</u> <u>guganio</u>, and <u>Chela cachius</u>, species which occurred only in the lowlands (Fig. 4).

<u>Axis 2</u>

Patterns of sample scores along DCA 2 are less conspicuous by inspection (Fig. 4). Gradient length is 3 SD, with greatest variability in the lowlands. DCA 2 scores are most highly correlated with season, water clarity, water temperature, and dissolved oxygen (Table 1), suggesting an association with the seasons. Stepwise regression results (Table 2) also point to a seasonal effect. The model best predicting DCA 2 scores is:

DCA 2 = 268.90 - 27.26S + 91.76SV + 82.70SW + 55.47B - 70.73NV + 122.69D + 1.05WC - 134.71TH - 30.85SO + 55.12FA + 18.63M (R² = 0.46; df = 136)

where S = season, SV = submerged vegetation, B = boulders,

NV = number of vegetation types, WC = water clarity, SO = stream order, FA = filamentous algae, M = mud, and other terms are as above. Several variables retained in the regression model for DCA 2 scores are expected to change seasonally: e.g., percent of habitat covered by submerged vegetation, stream width, number of vegetation types, percent cover by debris, water clarity, total hardness, percent cover by filamentous algae, and percent of substrate comprised of mud.

Fishes loading high on axis 2 are <u>Rasbora</u> <u>daniconius</u>, <u>Puntius guganio</u>, <u>Danio devario</u>, <u>Esomus</u> <u>danricus</u>, <u>Barilius tileo</u>, and <u>Puntius ticto</u>. Species with the largest negative scores include <u>Glyptothorax</u> <u>telchitta</u>, <u>Barilius barila</u>, <u>Clupisoma garua</u>, <u>Crossocheilus latius</u>, <u>Tor tor</u>, <u>Garra gotyla</u>, and <u>Tor</u> putitora (Fig. 4).

Axis 3

DCA 3 spans 3 SD, with greatest variability in the lowlands. Plots of DCA 3 versus DCA 1 and DCA 2 showed no obvious patterns in samples or species. Pearson productmoment correlations between DCA 3 and environmental variables are significant for current speed, three substrate factors, and three vegetation factors (Table 1), suggesting a possible current and related substrate/ vegetation component. This interpretation is supported by stepwise multiple regression analysis (Table 2), which provides the model:

DCA 3 =
$$568.21 - 91.75SW + 0.48C - 143.96A - 22.31G$$

+ $71.34D + 94.63Z - 127.41SA - 86.44ST$
- $76.21M - 58.67B$
(R² = 0.45; df = 137)

where C = current speed, Z = stream depth, SA = sand, ST = stone, and other terms are as above.

Fishes with highest scores on DCA 3 include <u>Labeo</u> <u>dero</u>, <u>Botia lohachata</u>, <u>Chela cachius</u>, <u>Pseudecheneis</u> <u>sulcatus</u>, <u>Glyptothorax kashmirensis</u>, <u>Chanda baculis</u>, <u>Mastacembelus armatus</u>, and <u>Garra gotyla</u>. Species with lowest scores are <u>Noemacheilus scaturigina</u>, <u>Semiplotus</u> <u>semiplotus</u>, <u>Chagunius chagunio</u>, <u>Barilius bola</u>, and <u>Aspidoparia jaya</u>.

Ordination without mountain samples

To better differentiate high hills, low hills and lowland samples, I removed the distinctive mountain collections and reordinated the remaining samples, leaving 120 collections at 59 sites. Separation of disjunct sample sets allows a more critical analysis of the relationship between environmental parameters and fish assemblage structure outside the extreme mountain zone (e.g., Peet 1980, Green 1980, Gauch 1982).

<u>Axis 1</u>

Without the mountain samples, the axis 1 eigenvalue, a measure of separation of species' distributions along the axis, is considerably smaller than when mountain samples are included in the ordination (0.76 vs. 0.43). However, even without these collections, DCA axis 1 displays a dominant geographic component, spanning nearly 5.5 SD from high hills to lowlands (Fig. 5). Correlation coefficients remain most significantly correlated with geographic factors such as river kilometer, stream order, altitude, geology, stream gradient and natural region (Table 3). Highly significant correlations with DCA 1 scores also occur for some water quality, substrate and vegetation factors (e.g., water temperature, dominant substrate type, percent cover by submerged vegetation, and current speed) (Table 3).

The results of stepwise multiple regression analysis also demonstrate the geographic component of DCA 1 (Table 4). The model best predicting axis 1 scores without mountain samples is: DCA 1 = 518.70 - 4.62RK - 64.78SO + 62.60NR - 60.39SV - 34.55FA - 3.42WT - 75.73D - 73.98B ($R^2 = 0.88$; df = 111)

where NR = natural region, WT = water temperature, and other terms are as above.

Species loading highest on the DCA 1 obtained without mountain samples are <u>Euchiloglanis hodgarti</u>, <u>Schizothorax</u> <u>richardsoni</u>, <u>S</u>. progastus, <u>Acrossocheilus hexagonolepis</u>, and <u>Noemacheilus shebbearei</u>. Fishes with highest negative loadings on DCA 1 include <u>Rasbora daniconius</u>, <u>Puntius</u> <u>guganio</u>, <u>Mastacembelus pancalus</u>, <u>Channa punctatus</u>, <u>Puntius</u> <u>ticto</u>, <u>Barilius tileo</u>, <u>Danio devario</u>, <u>Chela cachius</u>, and <u>Lepidocephalus guntea</u> (Fig. 5).

<u>Axis 2</u>

Environmental interpretation of DCA 2 without mountain samples is not obvious from Fig. 5. Scores span 3 SD, with lowland samples most variable. Scores are most highly correlated with current speed, season, and water temperature (Table 3), suggesting a seasonal effect. Stepwise regression results also support a seasonal interpretation (Table 4). The model best predicting axis 2 scores without mountain samples is: DCA 2 = 670.12 + 21.99S + 0.51C - 199.61A - 151.55SW - 100.75M - 93.46ST + 138.88Z - 144.49SA - 78.59B - 18.91G (R² = 0.62; df = 109)

where terms are as above.

Fish species with highest scores on DCA 2 without mountain samples are <u>Labeo dero</u>, <u>Botia lohachata</u>, <u>Glyptothorax telchitta</u>, <u>Pseudecheneis sulcatus</u>, and <u>Glyptothorax trilineatus</u>, followed by <u>Chanda baculis</u>, <u>Glyptothorax kashmirensis</u>, <u>Clupisoma garua</u>, <u>Barilius</u> <u>barila</u>, <u>Crossocheilus latius</u>, and <u>Garra gotyla</u>. Highest negative loadings on DCA 2 are for <u>Semiplotus semiplotus</u>, <u>Rasbora daniconius</u>, <u>Esomus danricus</u>, <u>Puntius sophore</u>, <u>Barilius bola</u>, <u>Chagunius chagunio</u>, and <u>Barilius tileo</u> (Fig. 5).

<u>Axis 3</u>

Plots of the DCA 3 obtained without mountain samples showed no readily discernable patterns. However, Pearson product-moment correlations between DCA 3 scores and environmental variables are highly significant for percent cover by detritus and number of vegetation types (Table 3). Correlations were also significant for current speed, percent substrate composed of gravel, and percent cover by vegetation, suggesting a currentrelated substrate/vegetation component to DCA 3. Multiple regression results are similar (Table 4). DCA 3 scores are best predicted by the equation:

DCA 3 =
$$-106.77 + 276.70$$
DET + 0.95C + 50.83NV
+ 49.18GR -14.26 S + 3.41WT
(R² = 0.39; df = 113)

where DET = detritus, GR = gravel, and other terms are as above.

Species loading high on DCA 3 without mountain samples are <u>Noemacheilus shebbearei</u>, <u>Tor putitora</u>, <u>T. tor</u>, <u>Semiplotus semiplotus</u>, and <u>Acrossocheilus</u> <u>hexagonolepis</u>. Highest negative loadings on DCA 3 are for <u>Glyptothorax telchitta</u>, <u>Osteobrama cotio</u>, <u>Clupisoma garua</u> and <u>Chanda ranga</u>.

Direct Gradient Analysis

<u>Axis 1</u>

A plot of canonical correspondence analysis axis 1 versus axis 2 showed an uninterpretable arch effect, thus I used detrended canonical correspondence analysis for all direct gradient analyses, with detrending by fourth-order polynomials.

The overall ordination and the first DCCA axis (DCCA 1) are both highly significant (P < 0.001), with DCCA 1 explaining 34% of the variability in species scores. DCCA 1 spans 8.7 SD and displays a gradient from mountains to lowlands (Fig. 6), with mountain samples quite distinctive, as in the DCA ordination. Correlations between environmental variables and DCCA 1 (= "intra-set correlations"; Ter Braak 1986, 1988a) again suggest a geographic component. DCCA 1 scores are most highly and significantly correlated with stream gradient, stream order, altitude, geology, natural region, and river kilometer (Table 5). DCCA 1 is also highly correlated with certain water quality and substrate factors, including stream depth, current speed, total hardness, water temperature, total alkalinity, percent substrate comprised of boulders, dominant substrate type, percent gravel, and percent mud.

The species-environment correlation for DCCA 1 of 0.951 shows the extracted variation in assemblage composition is well explained by the measured environmental variables. Multiple regression of site scores for DCCA 1 on the environmental variables demonstrates the geographic basis of DCCA 1 (Table 6). Variables making significant contributions to the model explaining DCCA 1 scores include

stream gradient, river kilometer, altitude, and geology.

Environmental variables are represented by arrows on the species-environment biplot of DCCA scores (Fig. 6). Trajectory and length of arrows represent the direction and magnitude of correlations between environmental variables and assemblage composition along the gradient (Ter Braak 1988a, Ter Braak and Prentice 1988). Thus, the arrows in Fig. 6 demonstrate the importance of stream gradient, altitude, stream order, and river kilometer on DCCA 1. The approximate distribution of fish species with respect to these environmental gradients can be inferred from their position along these arrows.

Fishes loading highest on DCCA axis 1 are <u>Euchiloglanis hodgarti</u>, <u>Schizothorax richardsoni</u>, and <u>Noemacheilus rupecula</u>. Fishes with highest negative loadings on DCCA 1 include <u>Mastecembelus pancalus</u>, <u>Chela</u> <u>cachius</u>, <u>Puntius ticto</u>, <u>P. guganio</u>, <u>Channa punctatus</u>, <u>Chanda baculis</u>, <u>Danio devario</u>, and <u>Esomus danricus</u> (Fig. 6).

<u>Axis 2</u>

DCCA 2 (Fig. 6) is highly significant (P < 0.01) and explains 7.6% of the variability in the species scores. DCCA 2 scores are most variable in the lowlands and are

most highly correlated with season, water temperature, dissolved oxygen, water clarity, and current speed (Table 5), again supporting a seasonal interpretation. The species-environment correlation is 0.874. A multiple regression model incorporates stream width, percent cover by submerged vegetation, water temperature, geology, river kilometer, percent filamentous algae, season, and stream order to predict DCCA 2 scores (Table 6). The arrows for environmental variables on Fig. 6 indicate the effect of seasonal factors on fish assemblage composition.

Fishes with highest scores on DCCA axis 2 are <u>Glyptothorax telchitta</u>, <u>Labeo dero</u>, <u>Clupisoma garua</u>, and <u>Barilius barila</u>. Species with highest negative loadings on DCCA 2 include <u>Rasbora daniconius</u>, <u>Esomus danricus</u>, <u>Danio devario</u>, <u>Puntius guganio</u>, and <u>Barilius tileo</u> (Fig. 6).

<u>Axis 3</u>

DCCA 3 is statistically significant (P < 0.05) and is also most variable in the lowlands. It explains 4.2% of the variance in the species data; however, plots of DCCA 3 showed no obvious pattern in samples or species. DCCA 3 scores are most highly correlated with vegetation factors, including number of vegetation types, percent cover by vegetation, percent filamentous algae, percent
detritus, and percent submerged vegetation (Table 5). Significant correlations also occur with the substrate factors, percent rubble and percent boulders; thus DCCA 3 could be interpreted as a vegetation/substrate gradient. The species-environment correlation is 0.777. The multiple regression model for scores on DCCA 3 incorporates eight vegetation/substrate factors: percent cover by detritus, percent substrate comprised of stone, number of vegetation types, percent filamentous algae, percent mud, percent submerged vegetation, percent cover by vegetation, and percent sand (Table 6).

Species loading highest on DCCA 3 are <u>Labeo dero</u>, <u>Tor tor</u>, and <u>Pseudecheneis sulcatus</u>. Fishes with highest negative loadings include <u>Glyptothorax telchitta</u>, <u>Clupisoma</u> <u>garua</u>, and <u>Osteobrama cotio</u>.

Ordination without mountain samples

<u>Axis 1</u>

As with indirect gradient analysis, I removed the distinctive mountain collections and reordinated the remaining samples in an attempt to better differentiate fish assemblage composition and its environmental basis in the high hills, low hills, and lowlands (Fig. 7). The overall ordination and DCCA 1 are both highly significant

(P < 0.001). DCCA 1 maintains extremely high correlations with all geographic variables and concomitant correlations with water quality, substrate, and vegetation variables (Table 7). The species-environment correlation is 0.959.

The strength of the relationship between geographic factors and DCCA 1 scores is indicated by the arrows in Fig. 7. DCCA 1 explains 28.5% of the variation in species data. Multiple regression analysis shows that three geographic factors (river kilometer, stream order, and natural region) explain the greatest portion of variance in a model predicting DCCA 1 scores (Table 8).

Fishes with highest scores on DCCA 1 without mountain samples include <u>Euchiloglanis hodgarti</u>, <u>Schizothorax richardsoni</u>, <u>S. progastus</u>, <u>Acrossocheilus</u> <u>hexagonolepis</u>, <u>Noemacheilus shebbearei</u>, <u>Glyptothorax</u> <u>kashmirensis</u>, and <u>Pseudecheneis sulcatus</u>. Highest negative loadings are for <u>Rasbora daniconius</u>, <u>Mastacembelus</u> <u>armatus</u>, <u>Osteobrama cotio</u>, <u>Puntius guganio</u>, <u>Channa</u> <u>punctatus</u>, and <u>Barilius tileo</u> (Fig. 7).

<u>Axis 2</u>

DCCA 2 is highly significant (P < 0.01) and scores are most variable in the lowlands (Fig. 7). Highest correlations between axis 2 scores and environmental variables are with season, water temperature, dissolved

oxygen, current speed and water clarity (Table 7), again suggesting a seasonal interpretation for axis 2. The species-environment correlation is 0.884.

DCCA 2 explains 10.7% of the variance in species data. Arrows of environmental factors on Fig. 7 highlight the seasonal component. A multiple regression model predicting DCCA 2 scores includes stream width, stream depth, percent substrate comprised by sand, percent mud, percent stone, season, and current speed as variables explaining the greatest portion of variance in fish assemblage composition along DCCA 2 (Table 8).

Species scoring high on DCCA 2 include <u>Glyptothorax</u> <u>telchitta</u>, <u>Labeo dero</u>, <u>Botia lohachata</u>, <u>Chanda baculis</u>, <u>Clupisoma garua</u>, <u>Crossocheilus latius</u>, <u>Pseudecheneis</u> <u>sulcatus</u> and <u>Barilius barila</u>. Fishes with highest negative loadings on DCCA 2 are <u>Semiplotus semiplotus</u>, <u>Rasbora daniconius</u>, <u>Esomus danricus</u>, and <u>Puntius sophore</u> (Fig. 7).

<u>Axis 3</u>

DCCA 3 is also statistically significant (P < 0.05) and explains 5.1% of the variation in the species data. The species-environment correlation is 0.790, but plots of DCCA 3 scores showed no obvious patterns in samples or species. DCCA 3 is most highly correlated with vegetation factors, including percent cover by detritus, number of vegetation types, and percent cover by vegetation (Table 7). Multiple regression analysis further supports the association between DCCA scores and percent detritus and number of vegetation types (Table 8).

Fishes having highest scores on DCCA 3 are <u>Tor tor</u>, <u>Semiplotus semiplotus</u>, <u>Acrossocheilus hexagonolepis</u>, and <u>Tor putitora</u>. Species with highest negative loadings on DCCA 3 include <u>Clupisoma garua</u>, <u>Osteobrama cotio</u>, and <u>Glyptothorax telchitta</u>.

Comparison of DCA and DCCA

Indirect and direct gradient methods lead to similar results and interpretations in the analysis of fish assemblage data and environmental gradients in the Kali Gandaki/Narayani River. Plots of the ordination of species and site scores are similar for the two methods. The relative importance and statistical significance of correlation coefficients between environmental variables and ordination axes are also similar for indirect and direct methods for data sets with and for those without mountain samples, though magnitudes differ for some variables. Comparison of multiple regression analyses of environmental variables on ordination scores also shows the

similarity of the two techniques for these data.

Eigenvalues of the first three axes are similar for DCA and DCCA in analyses both with and without mountain samples. Species-environment correlations of the first three axes are all high for both data sets (Table 9). The fraction of variance accounted for by the axes is nearly the same for DCA and DCCA both with and without mountains (Table 9). Such similarity between the results of direct and indirect gradient analyses indicates that the measured environmental variables are sufficient to explain a major portion of the variation in fish assemblage composition (Ter Braak 1986).

Analysis of seasonal and stream order effects

Indirect and direct gradient analyses both show a seasonal component for axis 2. Extended periods of heavy rains during the monsoon season (June - September) result in greatly increased river discharge and turbidity (Sharma 1977b). For example, mean monthly discharges for the Kali Gandaki River at Setibeni in 1976 ranged from 45 m³/s in March to 904 m³/s in August (Anonymous 1984). Such increases in discharge coincide with increased movement and upriver spawning migrations of many adult fishes (personal observation, personal communication with local fishermen). Similar spawning migrations occur with increased discharge

of rivers in Africa and South America (Lowe-McConnell 1975, and references therein).

The seasonality hypothesis just described predicts that the abundance of individual species loading heavily on axis 2 should show an added variance component attributable to season. To test this hypothesis, I subjected the coded abundances of the ten species having the highest absolute scores for DCCA 2 to a two-way analysis of variance (ANOVA -- Sokal and Rohlf 1981) in which the independent variables were biogeographic zone (mountains, high hills, low hills, and lowlands) and season (hot, wet monsoon; cool, dry; and hot, dry). The intent of this analysis was to assess temporal effects independently of spatial variation (c.f., Lewis 1978, Matthews 1989 - manuscript submitted).

Five of the 10 species -- <u>Barilius barila</u>, <u>Crossocheilus latius</u>, <u>Danio devario</u>, <u>Puntius quganio</u>, and <u>Rasbora daniconius</u> -- exhibited statistically significant temporal variation (.01 \leq P \leq .04; 3.39 \leq F \leq 6.30, 2 df). (Three of those five were among the six species having the highest scores on DCA 2.) Thus, as predicted, the abundances of individual species loading heavily on DCCA 2 are associated with seasonality.

I also examined the distribution of fishes in the Kali Gandaki/Narayani for "faunal breaks" (sensu Matthews 1986), or distinct areas of faunal change. Presenceabsence data for species in each collection were used to compare species similarity among sites and to investigate the correspondence between faunal change and stream order. Morisita's index (Morisita 1959) was employed to test for sharp differences in species composition between adjacent sites. Calculated values of Morisita's index indicate that as much variation exists within zones and even at given sites over different seasons as occurs between sites where stream order increases. Thus, while stream order was highly significantly correlated with scores on the first ordination axis (Tables 1, 3, 5, 7) and was often retained as a significant independent variable in regression models for ordination scores (Tables 2, 4, 6, 8), it alone does not sufficiently explain a high proportion of the variance in fish assemblage composition in the Kali Gandaki/Narayani. Rather, my results indicate that a combination of synergistic and related physiochemical parameters, mainly components of "stream hydraulics" (Statzner and Higler 1986), are the abiotic factors that best predict longitudinal zonation in fish assemblage structure in the Kali Gandaki/Narayani River.

Mesohabitat patterns of assemblage composition

Insight into fish assemblage structure along the length of the Kali Gandaki/Narayani is provided by an

examination of "mesohabitat" trends (sensu Meffe & Sheldon 1988); i.e., the relative abundance of species in riffles, pools and runs from region to region. To investigate such possible trends, I performed separate DCA ordinations on species captured in riffles, pools and runs throughout the river. I included only those sites at which separate samples were made in all three mesohabitats, i.e., in riffle(s), pool(s), and run(s).

To further increase the validity of comparisons among such divergent macrohabitat types, I eliminated all sites where gill netting or electrofishing sampling methods were employed, and used only those sites where seining (hauls or riffle kicks) and cast netting were used for sampling. (See Edds (1986) for a more qualitative treatment of assemblage composition that includes all sites and species. Pool and run assemblages at sites were found to be very similar throughout the river. Thus, I later combined individuals from these two mesohabitats at each site for comparison with the distinctive riffle fish assemblages.

Longitudinal patterns in riffle DCA 1 scores are evident along the length of the Kali Gandaki/Narayani (Fig. 8). Scores for collections made in mountain riffles are particularly distinctive compared with those of other zones. On average, scores for riffle collections made in the high hills are intermediate between those made in the

mountains and those made in the low hills and lowlands. Riffle collections from the low hills and lowlands exhibit similar scores on DCA 1. A parallel pattern exists for the collections from pool/run assemblages (Fig. 9). The small differences in DCA 1 scores between low hills and lowlands for both riffles and pool/runs is in part due to inclusion of the highly divergent data for mountain samples, and is not entirely indicative of the degree of similarity in species composition between low hills and lowlands. Some of the overlap between zones is also due to seasonal effects, since species composition at a given site may vary greatly among seasons.

Along the length of the Kali Gandaki/Narayani, riffle-dwelling fishes are mainly cyprinids, homalopterid loaches and sisorid sucker catfishes, with the loaches and sucker catfishes becoming the most common fishes in the riffles of the hill and lowland zones. The cyprinid <u>Schizothorax richardsoni</u> is dominant in mountain riffles while the loach <u>Noemacheilus shebbearei</u> is the most common riffle-dweller in the high hills. The loaches <u>N</u>. <u>scaturigina</u>, <u>N</u>. <u>rupecula</u>, and the sucker catfishes <u>Glyptothorax pectinopterus</u> and <u>G</u>. <u>kashmirensis</u> are the most common riffle-dwellers in the low hills. In the lowlands, the loaches <u>N</u>. <u>scaturigina</u>, <u>N</u>. <u>rupecula</u>, <u>N</u>. <u>corica</u>, <u>N</u>. <u>beavani</u> and <u>Botia lohachata</u> form a major portion of the fish assemblage in riffles.

Pool/run assemblage composition is dominated by <u>Schizothorax richardsoni</u> in the mountain zone, but the congeneric species <u>S</u>. <u>progastus</u> and other cyprinids dominate in the high hills. Cyprinids and homalopterids are important members of the pool/run mesohabitat in the high hills, low hills and lowlands. The greatest number of species inhabits the lowland pool/runs, where, in addition to the cyprinids and homalopterids that are most abundant, two cobitid loaches, two chandid glassfishes, two mastacembelid spiny eels, one schilbeid catfish, one belonid needlefish, and one gobiid goby are important members of the pool/run assemblage of fishes.

Mountains

In the mountain zone, riffles and pool/runs are both dominated by the cyprinid <u>Schizothorax richardsoni</u> (Table 10). The sisorid catfish <u>Euchiloglanis hodgarti</u> also is a major component of the fish assemblage in mountain riffles. The homalopterid loach <u>Noemacheilus rupecula</u> also occurs in both riffles and pool/run mesohabitats in the mountains (Table 10).

<u>High hills</u>

The riffle fish-assemblage in the high hills

comprises cyprinids (5 species), homalopterids (3), and sisorids (2), the most common being the homalopterid loaches <u>Noemacheilus shebbearei</u> and <u>N. rupecula</u>, the cyprinids <u>Barilius bendelisis</u>, <u>B. vagra</u>, and <u>Schizothorax</u> <u>progastus</u>, and the sisorid <u>Euchiloglanis hodgarti</u> (Table 11).

Pool/run habitats are dominated by cyprinids (10), with one homalopterid and one sisorid also occurring periodically. <u>Schizothorax progastus</u> is the most common fish in high hills pool/runs, along with <u>Barilius</u> <u>bendelisis</u> and <u>B. vagra</u>. The cyprinids <u>B. shacra</u>, <u>Schizothorax richardsoni</u> and <u>Acrossocheilus hexagonolepis</u> also occur in many pool/run collections in this zone (35-53%). Less abundant members of this assemblage include the cyprinids <u>Tor putitora</u>, <u>Crossocheilus latius</u>, and <u>Garra gotyla</u> and the loach <u>Noemacheilus corica</u> (Table 12).

Low hills

The riffle fish-assemblage in the low hills comprises mainly cyprinids (8), homalopterids (4), and sisorids (4), one cobitid loach, one amblycipitid catfish, and one mastacembelid spiny eel (Table 12). The major components are the cyprinids <u>Barilius vagra</u> and <u>B. bendelisis</u>, the sisorid <u>Glyptothorax pectinopterus</u>, and the homalopterid <u>Noemacheilus scaturugina</u>, all of which occur in 38-50% of the collections. The cobitid loach <u>Botia</u> <u>lohachata</u> and the sisorids <u>Glyptothorax</u> <u>kashmirensis</u> and <u>Pseudecheneis</u> <u>sulcatus</u> are also present at many sites (19%).

Pool/run assemblages are dominated by cyprinids (18) and homalopterid loaches (5), with one cobitid loach, one schilbeid catfish, two sisorids, and one belonid also occurring (Table 13). The cyprinid <u>Barilius vagra</u> occurred in all 25 pool/run collections from the low hills. The cyprinids <u>B. bendelisis</u>, <u>B. shacra</u>, <u>B. barna</u> and <u>Schizothorax progastus</u> are also common, and the loaches <u>Noemacheilus corica</u> and <u>Noemacheilus scaturigina</u> form another major component of pools and runs in the low hills (Table 12).

Lowlands

Lowland riffles had 13 species of cyprinids, six homalopterid loaches, five sisorid catfishes, two cobitid loaches, one amblycipitid catfish, one chandid glassfish and one mastacembelid spiny eel (Table 13). The most common species are the homalopterids <u>Noemacheilus</u> <u>scaturigina</u>, <u>N. rupecula</u>, <u>N. corica</u>, <u>N. beavani</u>, <u>N. botia</u> and <u>N. shebbearei</u>, the cyprinids <u>Barilius bendelisis</u>, <u>B</u>. <u>vagra</u>, and <u>Garra gotyla</u>, the cobitid <u>Botia lohachata</u>, the amblycipitid <u>Amblyceps mangois</u>, and the sisorid <u>Glyptothorax pectinopterus</u>.

Lowland pool/runs are inhabited by 28 cyprinid species, five homalopterids, two cobitids, two sisorids, two chandids, two mastacembelids, one schilbeid, one amblycipitid, one belonid, one chandid glassfish, and one gobiid goby (Table 14). The most common fishes in lowland pool/runs are the cyprinids <u>Barilius barna</u>, <u>B. bendelisis</u>, <u>B. shacra</u>, <u>B. vagra</u>, <u>B. barila</u>, <u>Puntius conchonius</u>, <u>P. ticto</u>, <u>Chaqunius chaqunio</u>, <u>Aspidoparia jaya</u>, <u>A. morar</u> and <u>Danio devario</u>, the homalopterids <u>Noemacheilus corica</u> and <u>N. botia</u>, the needlefish <u>Xenentodon cancila</u> and the glassfish <u>Chanda baculis</u> (Table 13).

Intra-generic zonation

Patterns of longitudinal zonation are evident among species of four different genera. <u>Schizothorax richardsoni</u> dominates in the mountains, but is replaced by <u>S</u>. <u>progastus</u> in the high hills. Species of another cyprinid genus, <u>Barilius</u>, also demonstrate a longitudinal progression of occurrence in the Kali Gandaki/Narayani: 1) <u>B</u>. <u>bendelisis</u> is widespread, occurring from the high hills to the lowlands; 2) <u>B</u>. <u>bendelisis</u> and a second species, <u>B</u>. <u>vagra</u> dominate the high hill and low hill portions of the river; 3) <u>B</u>. <u>shacra</u> and <u>B</u>. <u>barna</u> become more common downstream in the low hills and lowlands; 4) these four species are joined by <u>B</u>. <u>bola</u> and <u>B</u>. <u>tileo</u> in the lowlands.

<u>Noemacheilus rupecula</u> is the most wide ranging of all the fishes of the Kali Gandaki/Narayani. It occurs from the mountains to the lowlands, and is the only loach in the mountains. <u>N. shebbearei</u> is the most common loach in the high hills, whereas <u>N. scaturigina</u> and <u>N. corica</u> are the most common members of the genus in the low hills and lowlands. Among the Sisoridae, <u>Euchiloglanis hodgarti</u> is the only species of the family in the mountains and is the most abundant sisorid in high hills riffles. In the low hills, <u>E. hodgarti</u> is replaced other sisorids, including <u>Glyptothorax pectinopterus</u>, <u>G. kashmirensis</u>, and <u>Pseudecheneis sulcatus</u>; these are joined in lowland riffles by <u>G. telchitta</u> and <u>G. trilineatus</u>.

DISCUSSION

Longitudinal zonation and distribution of Himalayan fishes

The general distribution pattern of fishes throughout the Himalaya mountain range has been addressed by Hora (1951, 1952) and Menon (1954, 1962, 1974). These accounts were based primarily on ichthyofauna surveys done in India in the Eastern Himalaya (e.g., Hora 1921b, 1935, Shaw and Shebbeare 1937) and the Western Himalaya (e.g., Silas 1960, Sehgal 1971). However, relatively little

information has been published on the distribution of fishes in the Central Himalaya, i.e., between about 80 and 87 degrees east longitude in Nepal.

G.E. Hutchinson outlined a scheme of fish species
zonation in his 1939 monograph on fishes of the extreme
northwestern Himalaya. His zones included: 1) headwater
streams inhabited by rheophilic species of <u>Noemacheilus</u>;
2) large streams with schizothoracines and <u>Noemacheilus</u>
species; 3) rapid, turbid rivers with rheophilic species of
<u>Schizothorax</u> and <u>Noemacheilus</u>; and 4) slow rivers and
lacustrine swamps inhabited by limnadophil species of

Jhingran and Sehgal (1978) designated three fish zones in torrential Himalayan streams: 1) the "loach" or "headwater zone", inhabited by noemacheiline loaches and the sucker catfish <u>Glyptosternum</u>; 2) the "snow trout" (Cyprinidae, Schizothoracinae) or "rapid clear water zone", the most torrential reaches of which are inhabited by one schizothoracine species (less rapid reaches of this zone are frequented by other schizothoracines); and 3) the "rapid turbid water zone", inhabited mainly by rheophilic schizothoracines and loaches.

Menon (1954) recognized six categories of Himalayan fishes according to their various morphological and behavioral adaptations to the types of waters they inhabit: 1) fishes that live at the bottom of deep, swift

waters, cylindrical in form and possessing powerful muscular bodies like <u>Schizothorax</u>, <u>Tor</u> and <u>Semiplotus</u>; 2) fishes that attach themselves to bare rocks in torrential waters, including Euchiloglanis and Pseudecheneis; 3) fishes that live among the stones at the bottom of shallower, less forceful waters, including Noemacheilus, Botia and Amblyceps; 4) fishes having ventrally placed adhesive disks that are used to attach the fish to bare rocks in comparatively slower waters, (e.g., <u>Glyptothorax</u> and <u>Garra</u>); 5) fishes modified for a burrowing habit and which bury themselves in the substrate to avoid the force of rushing waters, (e.g., Mastacembelus and Psilorhynchus); and 6) fishes inhabiting shallow, clear waters at the base of hills, "without any striking adaptive characters" for high current speeds, (e.g., Bagarius and Gagata). Sehgal (1983) also includes Barilius and Puntius in the latter group.

My study is the first to document fish species distribution from first-order streams to lower mainstream in a major Himalayan river. The fish assemblage of the Kali Gandaki/Narayani exhibits a pattern of macrohabitat zonation from the trans-Himalaya plateau, through the mountains into the high hills, low hills and finally the lowland plains. Although zonal boundaries are not sharply defined, certain fishes dominate each region, and can be considered indicator species in the following description

of fish assemblage zonation in central Nepal.

1. Schizothorax richardsoni zone: In the trans-Himalaya region, up to and including fourth-order waters, I collected only one species, namely Schizothorax richardsoni, a stenothermal cyprinid having a ventral mouth surrounded by a sucker-like disk used to cling to the substrate in torrential waters (Edds 1986). In the mountains, S. richardsoni remained by far the most common fish species, both in terms of frequency of occurrence and number of individuals. However, I also found Euchiloglanis hodgarti and Noemacheilus rupecula, both of which possess anatomical and behavioral adaptations to torrents. Thus, the stretch of the river upstream from the fifth-order portion, and including both the mountain and trans-Himalayan regions, can be called the Schizothorax richardsoni zone, after its most common member, which dominates both riffle and pool/run mesohabitats.

2. <u>Schizothorax progastus</u> zone: In the fifth-order portion of the Kali Gandaki/Narayani, <u>S</u>. <u>richardsoni</u> is gradually replaced by its congener <u>S</u>. <u>progastus</u>, a species having a suckerless, terminal mouth and a terete, streamlined body which aids in exploitation of the water column in the less torrential waters it inhabits. <u>S</u>. <u>progastus</u> inhabits both pool/run and riffle mesohabitats,

and is the most frequently encountered species in the high hills (Table 11). The cyprinids <u>Barilius bendelisis</u> and <u>B</u>. <u>vagra</u> also commonly occur in pools and runs of this zone, as well as in the riffle mesohabitat with <u>Noemacheilus shebbearei</u>, <u>N</u>. <u>rupecula</u>, and <u>Euchiloglanis</u> <u>hodgarti</u>.

3. <u>Barilius vagra</u> zone: The low hills fish assemblage is dominated by several laterally compressed species of cyprinids whose body shape presumably facilitates swimming in deeper, slower waters. <u>B. vagra</u> is by far the most common fish in the low hills, and the only species that occurred in every collection I made in a region. It is the most common species in the pool/run mesohabitat, along with <u>B. bendelisis</u>, <u>B. shacra</u> and the loach <u>Noemacheilus corica</u>. <u>B. vagra</u> is also the most common fish species in low hill riffles, along with <u>Glyptothorax pectinopterus</u>, <u>B bendelisis</u>, <u>Noemacheilus</u> <u>scaturigina</u> and <u>N. rupecula</u>.

4. <u>Barilius barna zone</u>: <u>Barilius barna</u> is the most abundant fish species in the lowlands, along with its congeners <u>B</u>. <u>bendelisis</u>, <u>B</u>. <u>shacra</u> and <u>B</u>. <u>vagra</u>. However, many other fishes are also common in this area of broad slow waters and diverse microhabitats. Besides these four barils, this zone is also characterized by the following fishes all of which occurred in at least 50% of my lowland collections: two cyprinid detritivores <u>Aspidoparia jaya</u>

and <u>A</u>. <u>morar</u>, two omnivorous cyprinids, <u>Chagunius chagunio</u> and <u>Puntius conchonius</u>, the carnivorous homalopterid <u>Noemacheilus corica</u> and the belonid predator <u>Xenentodon</u> <u>cancila</u>. The lowland riffle mesohabitat also supports a great number of species, including <u>Barilius bendelisis</u>, and the loaches <u>Botia lohachata</u>, <u>Noemacheilus scaturigina</u>, <u>N. corica and N. rupecula</u>.

Comparison with studies from other areas

Fish species distribution in the Kali Gandaki/Narayani differs somewhat from that reported in the other Himalayan studies mentioned above. Both Hutchinson (1939) and Jhingran and Sehgal (1978) noted that headwaters on the southern slopes of the Western Himalaya were inhabited by rheophilic noemacheiline loaches. In contrast, my extensive sampling revealed no loaches above the fourthorder mountain region of the Kali Gandaki. The longitudinal pattern of fish species distribution in the Kali Gandaki River roughly corresponds to the morphological/behavioral categories described by Menon (1954). Although Menon's classification was not necessarily meant to describe zonation, his general categories parallel many of the fish assemblages in this river. Dominance of upstream areas by a schizothoracine rather than by noemacheiline rheophiles

may be due in part to zoogeographic factors. While the great majority of Himalayan fish genera dispersed from the Oriental realm after the early Tertiary upheavals that created these mountains, many Central Asiatic Schizothoracinae were able to populate trans-Himalayan rivers like the Kali Gandaki during interglacial periods of the Pleistocene (Menon 1954, 1955).

Moyle and Herbold (1987) concluded that Pleistocene events also played a large role in structuring fish assemblages in Europe and eastern and western North America. These investigators found the fish faunas of Europe and western North America more similar to each other than to those of eastern North America in terms of various life history characteristics, and attributed this in part to the harsh conditions of the Ice Age. In northern parts of Europe and western North America, drainages were covered with continental glaciers, and southern portions of these areas experienced extremely adverse conditions. However, in eastern North America, fishes found refuge in the vast Mississippi-Missouri River drainage. For the fishes of Nepal, the extensive Ganges River drainage could have provided similar refuge, resulting in the present-day fish fauna which is more similar to that of eastern North America than to western North America or Europe in terms of species richness, body size, reproductive traits, migratory patterns and trophic specialization.

The structure of headwater fish assemblages is much the same in Europe, northern Asia, eastern North America, and western North America (Moyle and Herbold 1987). This is the "Trout Zone" of Huet (1949, 1959), the exact composition of which varies from place to place. Assemblage structure in the Schizothorax richardsoni zone of the Kali Gandaki bears some resemblance to that of other mountain fish communities (Hutchinson 1939, Burton and Odum 1945, Moyle and Herbold 1987). In North America, this zone is generally inhabited by trout (Salmonidae), sculpins (Cottidae), suckers (Catostomidae) and dace (Cyprinidae); in northern Europe by trout, sculpins, loaches, (Homalopteridae, mainly Noemacheilus) and minnows (Cyprinidae). In this zone of the Central Himalaya, comparable ecological equivalents can be found, including the "snow trout" Schizothorax (Cyprinidae), Euchiloglanis (Sisoridae, morphologically similar in general aspect to sculpins), Noemacheilus and drift-feeding cyprinids (Barilius).

While humans have long recognized that fishes inhabit different zones along the length of rivers and streams, the search for a universal classification scheme has proved unfruitful, perhaps sometimes even misguided. The general scheme proposed by Illies (1961) is, however, the most widely applicable, and can be compared to the zones described in the Kali Gandaki/Narayani. The rhithron, or

the portion from the headwaters downstream to the point where mean monthly temperature reaches 20 degrees Celsius (Illies 1961) is represented in the Kali Gandaki from first-order streams down to where it changes to a sixthorder stream (Ridi Bazar); downstream from that point, the river can be characterized as potamon. Such a division of the Kali Gandaki/Narayani corresponds to the break between high hills and low hills and between the <u>Schizothorax</u> <u>progastus</u> and <u>Barilius vagra</u> zones as well as between fifth-order and sixth-order portions.

Illies and Botosaneanu (1963) added a headwater zone, the crenon, and further divided the rhithron and potamon into epi-, meta-, and hypo- zones. In the Kali Gandaki/Narayani the crenon consists of the fishless first- and second-order headwater streams, while the epirhithron corresponds to the trans-Himalaya region, the metarhithron to the remainder of the <u>Schizothorax</u> <u>richardsoni</u> mountain zone, and the hyporhithron to the fifth-order <u>Schizothorax</u> progastus zone. The epipotamon is the sixth-order <u>Barilius vagra</u> zone, the metapotamon is the seventh-order lowland composite zone, and the hypopotamon likely lies in northern India, upstream from the river's confluence with the Ganges.

Comparison of analytical methods

The ordinations produced by direct and indirect gradient analyses yielded essentially the same interpretations and conclusions. That is, geographic, water quality, and factors of stream hydraulics such as current speed, stream depth and substrate type are the major abiotic factors influencing fish assemblage structure in the Kali Gandaki/Narayani River. Seasonal changes have a substantial, but secondary effect.

Exclusion of the distinctive mountain samples does not fundamentally alter the main patterns of correspondence between measured environmental parameters and fish species distribution. Rather, it allows a closer examination of the overlap of ordination scores between high hills, low hills and lowland zones. Removal of mountain samples leads to minor differences in correlations between ordination scores and environmental parameters as well as the regressions predicting axis scores, but does not change interpretation of the major abiotic factors affecting fish assemblage structure in the Kali Gandaki/Narayani.

DCCA performed as well or better than DCA in obtaining an effective ordination. The DCCA speciesenvironment biplot simultaneously displays environmental vectors on the ordinations along with sites and species. This provides a diagrammatic view of associations between species abundances and environmental variables. The biplot provides not only an indication of how community composition changes, but also how selected species vary along the environmental gradients. Thus, direct gradient analysis simplifies interpretation of species-environment relationships, compared to the two-step process of indirect gradient analysis which requires an initial ordination and subsequent correlation and multiple regression analyses.

CANOCO also facilitates significance testing. The Monte Carlo test expedites analysis of the cumulative effects of measured environmental variables on assemblage structure by testing overall significance of the ordination. CANOCO also performs Monte Carlo tests of significance on individual axes. The program allows the investigator to partial out the effects of particular environmental variables (including extracted axes) to consider the residual variation in the species data.

DCA from DECORANA, which uses a detrending by segments algorithm, produced a systematic relation between axes 1 and 3, 1 and 4, and 3 and 4. Though the correlation coefficient between axes was small (absolute value of r =0.206 - 0.273), it was nevertheless significant (P = 0.0007 - 0.0116). CANOCO'S DCA, with the detrending by polynomials option produced uncorrelated axes; thus this method rectifies at least some of the suggested

imperfections of DCA (c.f., Wartenberg et al. 1987, Peet et al. 1988).

Comparison of the results of direct and indirect gradient analysis allows further examination of the effects of measured environmental variables on assemblage composition. If conclusions drawn from the two techniques are divergent, then the measured environmental parameters account for less conspicuous directions of variation in the assemblage data or they account for no variation at all. However, if conclusions are in agreement then the measured environmental variables are sufficient to explain much of the variation in assemblage structure (Ter Braak 1986). The high degree of similarity between results of the two methods in my analysis probably would not occur in analyses of regions showing less extreme physiographic differences from headwaters to tailwaters. Such congruence testifies to the profound influence exhibited on the fish assemblage of the Kali Gandaki/Narayani by the physiochemical factors associated with the extreme environmental gradients in a river system draining the highest mountain range on Earth.

TABLES

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TABLE 1

CORRELATION COEFFICIENTS (r) BETWEEN ENVIRONMENTAL FACTORS AND DCA AXES (n = 148). EIGENVALUES OF AXES ARE GIVEN IN PARENTHESES^a.

Environmental Factor	DCA 1 (.761)	DCA 2 (.221)	DCA 3 (.186)
Geography			
Altitude	.853****	.000	124
Stream gradient	.875****	.081	.022
River kilometer	786****	052	.097
Stream order	867****	074	.015
Stream width	662****	077	123
Natural region	832****	050	.080
Geology	787****	.054	.037
Water Quality			
Dissolved oxygen	290***	.321****	065
Dissolved CO ₂	.097	026	.107
pH	134	.157	.121
Total acidity	.174*	.040	.028
Total alkalinity	.471****	.044	.067
Total hardness	.657****	.067	.000
Temperature	452****	369****	.106
Water clarity	430****	.410****	.050
Current speed	.375****	137	.272***
Stream depth	536****	.025	.122
Seasonal			
Season	.304***	481****	.062

TABLE	1 (continued)

Environmental Factor	DCA 1 (.761)	DCA 2 (.221)	DCA 3 (.186)
Substrate			
Dominant substrate	.404****	.025	.191*
Number types substrate	.224**	.012	122
Percent mud	410****	.239**	.033
Percent sand	334****	121	174*
Percent gravel	.460****	130	.010
Percent stone	.332****	091	019
Percent rubble	.145	.069	146
Percent boulder	.559****	.134	161*
Vegetation (veg.)			
Dominant vegetation	.129	039	043
Number vegetation types	.004	.130	.189*
Percent cover by veg.	121	.195*	.171*
Percent detritus	090	.092	081
Percent filamentous alga	e .167*	.268***	.179*
Percent submerged veg.	171*	.196*	.100
Percent emergent veg.	.030	193*	080
Percent debris	.275***	.230**	.153

 Correlation coefficient significant at * P < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001. RESULTS OF STEPWISE MULTIPLE REGRESSION ANALYSIS OF ENVIRONMENTAL VARIABLES ON DCA AXES (n = 148).

Variables in Model	Partial	R² P	Model R ²
DCA 1			
Stream gradient	.766	.0001	.766
Geology	.109	.0001	.875
River kilometer	.027	.0001	.902
Stream width	.013	.0001	.915
Total hardness	.006	.0047	.921
Altitude	.005	.0071	.926
Percent debris	.003	.0094	.929
DCA 2			
Season	.231	.0001	.231
Submerged vegetation	.051	.0016	.282
Stream width	.031	.0046	.313
Percent boulder	.027	.0122	.340
Number vegetation types	.024	.0098	.364
Percent debris	.023	.0235	.387
Water clarity	.018	.0378	.405
Total hardness	.018	.0372	.423
Stream order	.018	.0359	.441
Percent filamentous algae	.014	.0546	.455
Percent mud	.008	.1269	.463

Variables in Model		Partial	R₂ p	Model R ²
DC	2A 3			
Stream width		.079	.0002	.079
Current speed		.074	.0008	.153
Altitude		.062	.0015	.215
Geology		.050	.0019	.265
Percent debris		.035	.0039	.300
Stream depth		.034	.0053	.334
Percent sand		.034	.0119	.368
Percent stone		.032	.0100	.400
Percent mud		.030	.0110	. 430
Percent boulder		.016	.0692	. 446

TABLE 2 (continued)

TABLE 3

CORRELATION COEFFICIENTS BETWEEN ENVIRONMENTAL FACTORS AND DCA AXES WITHOUT MOUNTAIN SAMPLES (n=120). EIGENVALUES OF AXES ARE GIVEN IN PARENTHESES^a.

Environmental Factor	DCA 1 (.423)	DCA 2 (.197)	DCA 3 (.135)
Geography			
Altitude	.817****	233*	.029
Stream gradient	.790****	020	016
River kilometer	868****	.182*	048
Stream order	864****	.059	077
Stream width	672****	065	055
Natural region	706****	.208*	069
Geology	811****	.029	009
Water Quality			
Dissolved oxygen	.010	233*	202*
Dissolved CO ₂	.023	.094	.132
pH	110	.042	.001
Total acidity	.097	017	136
Total alkalinity	.284**	.002	.079
Total hardness	.149	095	.119
Temperature	593****	.297***	.207*
Water clarity	139	195*	.043
Current speed	.330***	.346****	.206*
Stream depth	174	.169	114
Seasonal			
Season	115	.332***	.022

Environmental Factors	DCA 1 (.423)	DCA 2 (.197)	DCA 3 (.135)
Substrate			
Dominant substrate	.443****	.141	.098
Number types substrate	.303***	159	.072
Percent mud	348****	064	004
Percent sand	128	099	155
Percent gravel	.316***	.073	.189*
Percent stone	.220*	025	.071
Percent rubble	.346****	.111	.145
Percent boulder	.401****	282**	065
Vegetation (veg.)			
Dominant vegetation	080	.031	.098
Number vegetation types	362****	.132	.283 **
Percent cover by veg.	445****	.062	.193*
Percent detritus	064	138	.401****
Percent filamentous algae	255**	002	.103
Percent submerged veg.	451****	.032	.081
Percent emergent veg.	160	.062	.048
Percent debris	157	.117	.117

Correlation coefficient (r) is significant at * P < 0.05,
 ** P < 0.01, *** P < 0.001, **** P < 0.0001.

TABLE 4

RESULTS OF STEPWISE MULTIPLE REGRESSION ANALYSIS OF ENVIRONMENTAL VARIABLES ON DCA AXES WITHOUT MOUNTAIN SAMPLES (n = 120).

Variables in Model	Partial R ²	Р	Model R ²
DCA 1	2 Manuar (M. 17. o princip and going	•	
River kilometer	.754	.0001	.754
Stream order	.055	.0001	.809
Natural region	.032	.0001	.841
Percent submerged vegetation	.019	.0001	.860
Percent filamentous algae	.007	.0124	.867
Temperature	.007	.0183	.874
Percent debris	.006	.0272	.880
Percent boulder	.005	.0276	.885
DCA 2			
Season	.120	.0001	.120
Current speed	.120	.0001	.240
Altitude	.119	.0001	.359
Stream width	.054	.0037	.413
Percent mud	.050	.0008	.463
Percent stone	.038	.0022	.501
Stream depth	.036	.0060	.537
Percent sand	. 036	.0071	.573
Percent boulder	.022	.0155	.595
Geology	.021	.0171	.616

Variables in Model	Partial R ²	Ρ	Model R ²
DCA 3			
Percent detritus	.161	.0001	.161
Current speed	.087	.0003	.248
Number vegetation types	.049	.0054	. 297
Percent gravel	.039	.0111	.336
Season	.027	.0270	.363
Temperature	.026	.0347	. 389

TABLE 4 (continued)

TABLE 5

INTRA-SET CORRELATION COEFFICIENTS (r) BETWEEN ENVIRONMENTAL VARIABLES AND DCCA AXES (n = 148). EIGENVALUES OF AXES ARE GIVEN IN PARENTHESES^a.

Environmental Factor	DCCA 1 (.684)	DCCA 2 (.153)	DCCA 3 (.084)
Geography			
Altitude	.733****	118	.097
Stream gradient	.945****	030	007
River kilometer	686****	.119	097
Stream order	805****	.045	.036
Stream width	519****	085	197*
Natural region	691****	.126	084
Geology	700****	061	023
Water Quality			
Dissolved oxygen	129	528****	202*
Dissolved CO ₂	.100	.138	.103
pH	102	066	.104
Total acidity	.228**	098	052
Total alkalinity	.329****	103	.223**
Total hardness	.448****	137	.145
Temperature	372****	.619****	.166*
Water clarity	251**	459****	.073
Current speed	.305***	.388****	.045
Stream depth	428****	.133	252**
Seasonal			
Season	.124	.641****	142

Environmental Factor	DCCA 1 (.684)	DCCA 2 (.153)	DCCA 3 (.084)
Substrate			
Dominant substrate	.357****	.116	.079
Number types substrate	.180*	211**	103
Percent mud	299***	308***	028
Percent sand	258**	.125	069
Percent gravel	.349****	.086	.022
Percent stone	.244**	071	090
Percent rubble	.141	.148	.281***
Percent boulder	.515****	237**	225**
Vegetation (veg.)			
Dominant vegetation	.027	.013	.061
Number vegetation types	063	.039	.573***
Percent cover by veg.	152	094	.442***
Percent detritus	055	185*	.351***
Percent filamentous algae	121	171*	.430***
Percent submerged veg.	190*	057	.339***
Percent emergent veg.	011	.177*	122
Percent debris	.127	205*	.265**

TABLE 5 (continued)

 Correlation coefficient significant at * P < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001.
RESULTS OF WEIGHTED MULTIPLE REGRESSION ANALYSIS SHOWING ENVIRONMENTAL VARIABLES EXPLAINING THE GREATEST PORTION OF VARIANCE IN THE SPECIES DATA, ORDINATED BY DCCA, WITH STUDENT'S t-VALUE FOR SIGNIFICANCE TESTS OF CANONICAL COEFFICIENTS (TER BRAAK 1988a) (n = 148).

Variables in Model	t	P <	
DCCA 1			
Stream gradient	9.55	.0001	
River kilometer	5.11	.0001	
Altitude	4.38	.0001	
Geology	2.20	.025	
DCCA 2			
Stream width	4.38	.0001	
Percent submerged vegetation	3.97	.0001	
Temperature	3.05	.005	
Geology	2.88	.005	
River kilometer	2.79	.005	
Percent filamentous algae	2.72	.005	
Season	2.55	.01	
Stream order	2.55	.01	
Dissolved CO2	2.50	.01	
Stream gradient	2.32	.025	
Percent debris	2.24	.025	

Variables in Model	t	P <
DCCA 3		
Percent detritus	4.27	.0001
Percent stone	3.55	.0005
Number vegetation types	3.46	.0005
Percent filamentous algae	3.37	.0005
Temperature	3.15	.005
Percent mud	3.02	.005
Percent submerged vegetation	2.89	.005
Stream order	2.87	.005
Season	2.83	.005
Natural region	2.39	.01
Percent cover by vegetation	2.30	.025
Percent sand	2.21	.025

TABLE 6 (continued)

INTRA-SET CORRELATION COEFFICIENTS (r) BETWEEN ENVIRONMENTAL VARIABLES AND DCCA AXES, WITHOUT MOUNTAIN SAMPLES (n = 120). EIGENVALUES OF AXES ARE GIVEN IN PARENTHESES^a.

Environmental Factor	DCCA 1 (.386)	DCCA 2 (.145)	DCCA 3 (.068)
Geography			
Altitude	.784****	205*	012
Stream gradient	.818****	.037	051
River kilometer	866****	.144	023
Stream order	881****	027	055
Stream width	620****	184*	278**
Natural region	711****	.161	.021
Geology	805****	087	006
Water Quality			
Dissolved oxygen	001	493****	166
Dissolved CO ₂	.027	.014	.112
pH	103	.212*	.179*
Total acidity	.096	069	070
Total alkalinity	.301***	086	.074
Total hardness	.145	162	.270**
Temperature	551****	.529****	.138
Water clarity	151	365****	.196**
Current speed	.434****	.410****	056
Stream depth	.221****	.156	242**
Seasonal			
Season	100	.541****	236**

Environmental factor	DCCA 1 (.386)	DCCA 2 (.145)	DCCA 3 (.068)
Substrate			
Dominant substrate	.450****	.148	.065
Number types substrate	.278**	259**	044
Percent mud	326***	235**	.089
Percent sand	237**	.092	.005
Percent gravel	.353****	.087	.055
Percent stone	.251**	132	097
Percent rubble	.380****	.134	.199*
Percent boulder	.378****	352****	256**
Vegetation (veg.)			
Dominant vegetation	143	008	.132
Number vegetation types	386****	.114	.446**
Percent cover by veg.	435****	001	.374**
Percent detritus	019	183*	.677**
Percent filamentous algae	e206*	062	.196*
Percent submerged veg.	461****	.083	.148
Percent emergent veg.	166	.090	049
Percent debris	160	027	. 107

Correlation coefficient significant at * P < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001.

RESULTS OF WEIGHTED MULTIPLE REGRESSION ANALYSIS SHOWING ENVIRONMENTAL VARIABLES EXPLAINING THE GREATEST PORTION OF VARIANCE IN THE SPECIES DATA WITHOUT MOUNTAIN SAMPLES, ORDINATED BY DCCA, WITH STUDENT'S t-VALUE FOR SIGNIFICANCE TESTS OF CANONICAL COEFFICIENTS (TER BRAAK 1988a) (n = 120).

Variables in Model	t	P <
DCCA 1		200 2 1-200 000 000 1100 01-100 00
River kilometer	5.07	.0005
Stream order	4.65	.0005
Natural region	3.23	.001
Percent submerged vegetation	2.46	.01
Temperature	2.37	.01
Dominant substrate	2.36	.01
Geology	2.18	.025
DCCA 2		
Stream width	4.33	.0005
Stream depth	3.43	.0005
Percent sand	3.20	.001
Percent mud	2.70	.005
Percent stone	2.64	.005
Season	2.44	.01
Current speed	2.23	.025

Variables in Model	t	P <
DCCA 3		
Percent detritus	5.54	.0005
Number vegetation types	3.63	.0005
Temperature	3.34	.001
Season	2.93	.005

TABLE 8 (continued)

RESULTS OF DCA AND DCCA FOR FISH SPECIES AND ENVIRONMENTAL DATA INCLUDING AND EXCLUDING MOUNTAIN SAMPLES: EIGENVALUES, SPECIES-ENVIRONMENT CORRELATION COEFFICIENTS, AND FRACTION OF TOTAL VARIANCE ACCOUNTED FOR BY THE FIRST S AXES, WHERE S = 1,2,3. SUM OF ALL CANONICAL EIGENVALUES (TRACE) = 2.015 FOR WITH AND 1.352 FOR WITHOUT MOUNTAINS.

Axis 1 Axis 2 Axis 3 With mountains Eigenvalues DCA 0.761 0.221 0.186 DCAA 0.684 0.153 0.084 Correlation coefficients DCA 0.944 0.827 0.786 DCCA 0.951 0.874 0.777 Fraction of variance accounted for DCA 0.336 0.412 0.469 DCCA 0.339 0.416 0.457

	Axis	1 Axis	2 Axis 3	3
	Wi	thout mov	<u>untains</u>	
		Eigenvalu	les	
DCA	0.423	0.197	0.135	
DCAA	0.386	0.14	5 0.068	
,	Correla	tion coer	fficients	
DCA	0.948	0.829	9 0.712	
DCCA	0.959	0.884	4 0.790	
	Fraction of	variance	accounted	for
DCA	0.282	0.382	0.432	
DCCA	0.285	0.392	0.443	

MOUNTAIN FISH SPECIES DISTRIBUTION IN RIFFLE (n = 17) AND POOL/RUN (n = 11) HABITATS, SHOWING PERCENT FREQUENCY OF OCCURRENCE, RANGE (IN PARENTHESES) AND MEAN \pm 1 SD OF CODED ABUNDANCE OF SPECIES OCCURRING IN AT LEAST 5% OF ALL COLLECTIONS, WHERE 0 = NONE, 1 = 1-5, 2 = 6-10, 3 = 11-20, AND 4 = > 20 INDIVIDUALS.

SPECIES	RIFFLE	POOL/RUN
Cyprinidae		
<u>Schizothorax</u> progastus	6 (0-1) 0.1 <u>+</u> 0.2	
<u>S.</u> <u>richardsoni</u>	82 (0-4) 2.2 ± 1.5	100 (1-4) 3.3 ± 1.2
Homalopteridae		
<u>Noemacheilus</u> rupecula	35 (0-4) 0.5 ± 0.8	9 (0-2) 0.2 ± 0.6
Sisoridae		
<u>Euchiloglanis</u> <u>hodgarti</u>	71 (0-4) 1.5 \pm 1.5	

HIGH HILLS FISH SPECIES DISTRIBUTION IN RIFFLE (n = 13) AND POOL/RUN (n = 17) HABITATS, SHOWING PERCENT FREQUENCY OF OCCURRENCE, RANGE (IN PARENTHESES) AND MEAN ± 1 SD OF CODED ABUNDANCE, AS IN TABLE 10.

	SPE	CIES	RIFFLE	POOL/RUN
Cyprinidae	;			
	Acr	ossocheilus <u>hexagonolepis</u>		53 (0-3) 0.8 ± 1.0
	<u>Bar</u>	ilius bendelisis	38 (0-4) 0.8 <u>+</u> 1.2	82 (0-4) 2.9 ± 1.6
	<u>B</u> .	shacra		35 (0-4) 0.7 ± 1.2
	<u>B</u> .	vagra	31 (0-2) 0.4 <u>+</u> 0.6	82 (0-4) 2.5 ± 1.6
	Cro	ssocheilus <u>latius</u>		12 (0-1) 0.1 ± 0.3
	<u>Gar</u> :	ra <u>gotyla</u>	8 (0-1) 0.1 <u>+</u> 0.3	12 (0-1) 0.1 ± 0.3
	<u>Sch</u>	izothorax progastus	31 (0-3) 0.5 ± 1.0	88 (0-4) 2.6 ± 1.5
	<u>s</u> .	<u>richardsoni</u>	8 (0-1) 0.1 ± 0.3	47 (0-3) 0.8 ± 1.0
	Tor	putitora		18 (0-2) 0.2 <u>+</u> 0.6
	<u>T</u> .	tor		6 (0-1) 0.1 ± 0.2
Homalopter	rida	e		
	Noei	<u>macheilus</u> <u>corica</u>	8 (0-1) 0.1 ± 0.3	23 (0-1) 0.2 <u>+</u> 0.4
	<u>N</u> .	rupecula	31 (0-1) 0.3 <u>+</u> 0.5	
	<u>N</u> .	shebbearei	46 (0-4) 1.4 + 1.7	6 (0-1) 0.1 ± 0.2

	SPECIES	RIFFLE	POOL/RUN
Sisoridae			
	<u>Euchiloglanis</u> <u>hodgarti</u>	38 (0-1) 0.4 ± 0.5	
	<u>Glyptothorax</u> <u>kashmirensis</u>	8 (0-1) 0.1 ± 0.3	6 (0-1) 0.1 ± 0.2

LOW HILLS FISH SPECIES DISTRIBUTION IN RIFFLE (n = 16) AND POOL/RUN (n = 25) HABITATS, SHOWING PERCENT FREQUENCY OF OF OCCURRENCE, RANGE (IN PARENTHESES) AND MEAN ± 1 SD OF CODED ABUNDANCE, AS IN TABLE 10.

	<u>SPE</u>	CIES	RIFFLE	POOL/RUN
Cyprinidae				
	Acr	ossocheilus hexaqonolepis		16 (0-3) 0.2 ± 0.7
	<u>Asp</u>	<u>idoparia jaya</u>		8 (0-1) 0.1 ± 0.3
	<u>A</u> .	morar		8 (0-1) 0.1 ± 0.3
	<u>Bar</u>	<u>ilius</u> <u>barila</u>		tr*(0-4) 0.2 ± 0.8
	<u>B</u> .	<u>barna</u>	12 (0-3) 0.2 ± 0.8	44 (0-4) 1.0 ± 1.5
	<u>B</u> .	<u>bendelisis</u>	38 (0-2) 0.5 ± 0.7	88 (0-4) 2.5 <u>+</u> 1.6
	<u>B</u> .	bola		12 (0-1) 0.1 ± 0.3
	<u>B</u> .	<u>shacra</u>	12 (0-1) 0.1 ± 0.3	80 (0-4) 2.0 ± 1.5
	<u>B</u> .	vagra	50 (0-3) 0.6 ± 0.8	100 (1-4) 2.8 ± 1.3
	<u>Cha</u>	<u>gunius</u> <u>chagunio</u>		24 (0-4) 0.4 ± 0.9
	<u>Cro</u>	<u>ssocheilus latius</u>	19 (0-1) 0.2 ± 0.4	20 (0-2) 0.3 ± 0.7
	<u>Gar</u>	ra gotyla	12 (0-1) 0.1 ± 0.3	16 (0-3) 0.2 ± 0.7
	<u>Pun</u>	tius conchonius		12 (0-2) 0.2 ± 0.5

	SPECIES	RIFFLE	POOL/RUN
	<u>Schizothorax</u> progastus	6 (0-1) 0.1 ± 0.2	32 (0-4) 0.8 ± 1.5
	<u>S. richardsoni</u>	6 (0-1) 0.1 ± 0.2	8 (0-1) 0.1 ± 0.3
	<u>Semiplotus</u> <u>semiplotus</u>		20 (0-3) .0.3 ± 0.7
	Tor putitora		$\begin{array}{ccc} 20 & (0-4) \\ 0.5 & \pm & 1.0 \end{array}$
	<u>T</u> . <u>tor</u>		20 (0-3) 0.4 ± 0.9
Cobitidae			
	<u>Botia lohachata</u>	19 (0-1) 0.2 ± 0.4	8 (0-1) 0.1 ± 0.3
Homalopter	idae		
	<u>Noemacheilus</u> <u>beavani</u>		20 (0-3) 0.3 ± 0.7
	<u>N</u> . <u>corica</u>	$\begin{array}{c} 12 & (0-4) \\ 0.5 & \pm & 1.4 \end{array}$	64 (0-4) 1.3 ± 1.4
	<u>N</u> . <u>rupecula</u>	31 (0−1) 0.3 ± 0.5	4 (0-1) tr* \pm 0.2
	<u>N</u> . <u>scaturigina</u>	38 (0-4) 0.6 ± 1.1	28 (0-3) 0.5 ± 0.9
	<u>N. shebbearei</u>	12 (0-3) 0.2 ± 0.8	$ 8 (0-1) \\ 0.1 \pm 0.3 $
Schilbeida	e		
	<u>Clupisoma</u> garua		8 (0-1) 0.1 ± 0.3
Amblycipit	idae		
	<u>Amblyceps</u> <u>manqois</u>	6 (0-1) 0.1 ± 0.2	

TABLE 12 (continued)

	SPECIES	RIFFLE	POOL/RUN
Sisoridae			
	<u>Glyptothorax</u> <u>kashmirensis</u>	19 (0-1) 0.2 ± 0.4	
	<u>G</u> . <u>pectinopterus</u>	50 (0-2) 0.6 ± 0.6	4 (0-1) tr* ± 0.2
	<u>G</u> . <u>trilineatus</u>	6 (0-1) 0.1 ± 0.2	4 (0-1) tr* ± 0.2
	<u>Pseudecheneis</u> <u>sulcatus</u>	19 (0-1) 0.2 <u>+</u> 0.4	
Belonidae			
	<u>Xenentodon</u> <u>cancila</u>		4 (0-1) tr* ± 0.2
Mastacembe	lidae		
	<u>Mastacembelus</u> <u>armatus</u>	$ \begin{array}{c} 6 & (0-1) \\ 0.1 & \pm & 0.2 \end{array} $	

tr* = trace = < 0.5%

LOWLAND FISH SPECIES DISTRIBUTION IN RIFFLE (n = 26) AND POOL/RUN (n = 62) HABITATS, SHOWING PERCENT FREQUENCY OF OCCURRENCE, RANGE (IN PARENTHESES) AND MEAN \pm 1 SD OF CODED ABUNDANCE, AS IN TABLE 10.

SPECIES	RIFFLE	POOL/RUN
Cyprinidae		
<u>Acrossocheilus</u> <u>hexagonolepis</u>		3 (0-1) tr* ± 0.2
<u>Aspidoparia</u> jaya		55 (0-4) 1.5 <u>+</u> 1.7
<u>A</u> . <u>morar</u>	8 (0-1) 0.1 ± 0.3	56 (0-4) 1.1 ± 1.3
<u>Barilius</u> <u>barila</u>	8 (0-3) 0.2 ± 0.6	45 (0-4) 0.9 <u>+</u> 1.3
<u>B</u> . <u>barna</u>	12 (0-1) 0.1 ± 0.3	84 (0-4) 2.6 ± 1.6
<u>B</u> . <u>bendelisis</u>	38 (0-3) 0.7 <u>+</u> 1.0	85 (0-4) 2.1 ± 1.5
<u>B</u> . <u>bola</u>		40 (0-3) 0.5 ± 0.7
<u>B</u> . <u>shacra</u>	12 (0-2) 0.2 <u>+</u> 0.5	81 (0-4) 2.2 ± 1.5
<u>B</u> . <u>tileo</u>		16 (0-3) 0.2 ± 0.5
<u>B</u> . <u>vagra</u>	23 (0-1) 0.2 ± 0.4	73 (0-4) 1.8 <u>+</u> 1.6
<u>Chagunius</u> <u>chagunio</u>	4 (0-1) tr* ± 0.2	69 (0-4) 1.8 ± 1.6
<u>Chela</u> <u>cachius</u>		18 (0-4) 0.4 <u>+</u> 1.0
<u>Crossocheilus</u> <u>latius</u>	8 (0-1) 0.1 <u>+</u> 0.3	24 (0-4) 0.3 ± 0.7

TABLE	13	(continued)

SPECIES	RIFFLE	POOL/RUN
<u>Danio</u> <u>devario</u>		31 (0-4) 0.7 ± 1.3
<u>Esomus</u> <u>danricus</u>		16 (0-4) 0.4 ± 1.0
<u>Garra</u> gotyla	19 (0-4) 0.3 ± 0.8	13 (0-4) 0.2 <u>+</u> 0.6
Labeo dero		3 (0-1) tr* ± 0.2
<u>Osteobrama</u> <u>cotio</u>		13 (0-4) 0.2 \pm 0.7
<u>Puntius</u> <u>conchonius</u>	8 (0-1) 0.1 <u>+</u> 0.3	69 (0-4) 1.9 <u>+</u> 1.7
<u>P</u> . <u>guganio</u>		26 (0-4) 0.5 ± 1.1
<u>P</u> . <u>sophore</u>		18 (0-4) 0.3 <u>+</u> 0.7
<u>P</u> . <u>ticto</u>	4 (0-1) tr* ± 0.2	35 (0-4) 0.7 ± 1.2
<u>Rasbora</u> <u>daniconius</u>		19 (0-4) 0.4 ± 0.9
<u>Salmostoma</u> <u>bacaila</u>		15 (0-3) 0.2 <u>+</u> 0.5
<u>Schizothorax</u> progastus	8 (0-1) 0.1 ± 0.3	5 (0-4) 0.1 <u>+</u> 0.5
<u>Semiplotus</u> <u>semiplotus</u>	4 (0-1) tr* <u>+</u> 0.2	5 (0-1) tr* <u>+</u> 0.2
<u>Tor</u> <u>putitora</u>		15 (0-3) 0.2 <u>+</u> 0.5
<u>T</u> . <u>tor</u>		11 (0-4) 0.2 <u>+</u> 0.7

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	SPECIES	RIFFLE	POOL/RUN
Cobitidae	\$		
	<u>Botia</u> <u>lohachata</u>	35 (0-4) 0.5 <u>+</u> 0.9	11 (0-4) 0.3 ± 0.9
	Lepidocephalus guntea	8 (0-2) 0.1 ± 0.4	19 (0-3) 0.3 ± 0.6
Homalopte	eridae		
	<u>Noemacheilus</u> <u>beavani</u>	27 (0-3) 0.3 <u>+</u> 0.7	15 (0-4) 0.2 ± 0.6
	<u>N</u> . <u>botia</u>	19 (0-3) 0.3 <u>+</u> 0.7	35 (0-2) 0.4 <u>+</u> 0.5
	<u>N</u> . <u>corica</u>	35 (0-1) 0.3 ± 0.5	55 (0-4) 1.2 ± 1.5
	<u>N</u> . <u>rupecula</u>	35 (0-2) 0.4 ± 0.6	3 (0-2) tr* ± 0.3
	<u>N</u> . <u>shebbearei</u>	15 (0-1) 0.2 ± 0.4	
	<u>N. scaturigina</u>	42 (0-4) 0.7 ± 1.0	15 (0-4) 0.2 ± 0.6
Schilbeid	lae		
	<u>Clupisoma</u> garua		$\begin{array}{ccc} 10 & (0-4) \\ 0.1 & \pm & 0.6 \end{array}$
Amblycipi	tidae		
	<u>Amblyceps</u> mangois	19 (0-2) 0.2 ± 0.5	5 (0-1) tr* ± 0.2

TABLE 13 (continued)

SPECIES		RIFFLE	POOL/RUN
Sisoridae			
	<u>Glyptothorax</u> <u>kashmirensis</u>	8 (0-1) 0.1 ± 0.3	
	<u>G</u> . <u>pectinopterus</u>	15 (0-1) 0.2 ± 0.4	
	<u>G</u> . <u>telchitta</u>	8 (0-1) 0.1 ± 0.3	3 (0-2) tr* ± 0.3
	<u>G</u> . <u>trilineatus</u>	12 (0-1) 0.1 ± 0.3	2 (0-1) tr* ± 0.1
	<u>Pseudecheneis</u> <u>sulcatus</u>	8 (0-1) 0.1 ± 0.3)	
Belonidae			
	<u>Xenentodon</u> <u>cancila</u>		50 (0-4) 1.0 <u>+</u> 1.3
Channidae			
	Channa punctatus		11 (0-1) 0.1 ± 0.3
Chandidae			
	<u>Chanda</u> baculis	4 (0-1) tr* ± 0.2	29 (0-4) 0.7 <u>+</u> 1.3
	<u>C</u> . <u>ranga</u>		13 (0-4) 0.2 ± 0.7
Gobiidae			
	<u>Glossogobius</u> giuris		23 (0-2) 0.2 ± 0.5

TABLE 13 (continued)

SPECIES	RIFFLE	POOL/RUN
Mastacembelidae		
<u>Mastacembelus</u> <u>armatus</u>	12 (0-2) 0.2 <u>+</u> 0.5	8 (0-1) 0.1 <u>+</u> 0.3
<u>M</u> . <u>pancalus</u>		10 (0-2) 0.1 <u>+</u> 0.4

tr* = trace = < 0.5%

FIGURES

















(QS) F SIXA


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APPENDIXES

APPENDIX A

VALUES OF ENVIRONMENTAL PARAMETERS AT EACH SITE

collection number, number of species, longitudinal position (x 6.5 = river kilometer), water temperature (°C), water clarity (in inches), dominant substrate type (1 = mud, 2 = sand, 3 = gravel, 4 = stone, 5 = rubble, 6 = boulder), number of substrate types, dominant vegetation type (1 = filamentous algae, 2 = submerged, 3 = emergent, 4 = floating, 5 = detritus, 6 = debris), number of vegetation types, **\$** cover by vegetation, width (1 = 0-25 m, 2 = 26-50 m, 3 = 51-75 m, 4 = 76-100 m, 5 = 101-150 m, 6 = 151-200 m, 7 = 201-300 m, 8 = 301-400 m , 9 = 401-500 m, 10 = > 500 m), altitude (m), dissolved oxygen (mg/L), pH, carbon dioxide (mg/L), total hardness (grains per gallon (gpg) CaCO₃), total acidity (gpg CaCO₃), total alkalinity (gpg CaCO₃), mean current velocity (/ 30 = feet per second), mean depth (inches), percent gradient, natural region (1 = trans-Himalaya, 2 = mountains, 3 = hills downstream from Beni, 4 = lowland valley downstream from Devghat, 5 = lowland plains downstream from Tribeni Barrage), stream order, season (1 = Oct.-Jan., 2 = Feb.-May, 3 = June-Sept.), geologic stratum (1 = Pleistocene-Recent, 2 = Tethysian, 3 = Arenaceous Cambrian-Precambrian, 4 = Argillaceous Cambrian-Precambrian, 5 = Calcarous Cambrian-Precambrian), % mud, % sand, % gravel, % stone, % rubble, % boulder, % detritus, % filamentous algae, % submerged vegetation, % emergent vegetation, % floating vegetation, % debris.

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APPENDIX B

SAMPLE SITES, IN ORDER FROM HEADWATERS DOWNSTREAM: SAMPLE NUMBER, LOCATION, AND DATE. "KGR" = KALI GANDAKI RIVER, "NR" = NARAYANI RIVER. "*" = SITES NOT INCLUDED IN PRESENT ANALYSIS.

KGR AT CHUSANG, MUSTANG 14 SEPT 85 1 2 KGR ABOVE KAGBENI, MUSTANG 10 SEPT 84 з KGR AT JOMSOM, MUSTANG 11 SEPT 84 KGR AT JOMSOM, MUSTANG 10 SEPT 85 4 KGR AT LARJUNG, MUSTANG 5 JUNE 84 5 KGR AT LARJUNG, MUSTANG 6 12 SEPT 84 7 KGR AT LARJUNG, MUSTANG 18 FEB 85 8 KGR AT LARJUNG, MUSTANG 30 MAY 85 KGR AT LARJUNG, MUSTANG 9 SEPT 85 9 KGR AT LARJUNG, MUSTANG 12 FEB 86 10 KGR BELOW BAKSHI R. CONFLUENCE, DOWNSTREAM FROM 11 LARJUNG, MUSTANG 30 MAY 85 KGR AT KALAPANI, MUSTANG 30 MAY 85 12 13 KGR AT PAHIROTHAPLA, MUSTANG 13 SEPT 84 14 KGR AT RUPCHE CHARA, MYAGDI 28 MAY 85 KGR AT MRISTI R. CONFLUENCE, MYAGDI 15 26 MAY 85 KGR AT TATOPANI, MYAGDI 14 SEPT 84 16 16 FEB 85 17 KGR AT TATOPANI, MYAGDI KGR AT TATOPANI, MYAGDI 18 27 MAY 85 19 KGR AT TATOPANI. MYAGDI 8 SEPT 85 20 KGR AT TATOPANI, MYAGDI 10 FEB 86 21 KGR AT TATOPANI, MYAGDI 21 MAY 86 KGR AT GHAR R. CONFLUENCE, 2 KM DOWNSTREAM FROM 22 TATOPANI, MYAGDI 27 MAY 85 KGR AT MOHABIR, MYAGDI 15 SEPT 84 23 KGR AT BEG KHOLA, MYAGDI 25 MAY 85 24 KGR AT SANSAR R. CONFLUENCE, 3 KM DOWNSTREAM FROM 25 BEG KHOLA, MYAGDI 15 FEB 85 KGR AT BENI, MYAGDI 15 FEB 85 26 27 KGR AT BENI, MYAGDI 24 MAY 85 28* KGR AT BENI, MYAGDI 6 SEPT 85 29 KGR AT BENI, MYAGDI 9 FEB 86 30 KGR AT SIMAA, MYAGDI 27 MAY 84

KGR AT AT KHANIYA GHAT, PARBAT 31 14 FEB 85 32* KGR AT SHASADARA, PARBAT 24 MAY 85 KGR AT RITHE R. CONFLUENCE, ARMADI, PARBAT 33 13 FEB 85 34 KGR AT MODI R. CONFLUENCE, KUSMA, PARBAT 23 MAY 85 KGR AT BAGLUNG BALEYA, BAGLUNG 23 JAN 85 35 KGR AT JYAMRI GHAT, BAGLUNG 22 JAN 85 36 KGR AT SUMSA GHAT (="BINAMARE"), BAGLUNG 37 25 MAY 84 38 KGR AT SUMSA GHAT, BAGLUNG 22 JAN 85 KGR AT SUMSA GHAT, BAGLUNG 23 MAY 85 39 40 KGR AT SUMSA GHAT, BAGLUNG 23 AUG 85 41* KGR AT SUMSA GHAT, BAGLUNG 23 JAN 86 42* KGR AT BELBAGAR, BAGLUNG 21 JAN 85 KGR AT GAUNDI R. CONFLUENCE (="GUMTI"), GULMI 43 20 JAN 85 44 KGR AT GAUNDI R. CONFLUENCE, GULMI 22 MAY 85 45 KGR AT GAUNDI R. CONFLUENCE, GULMI 22 AUG 85 46 KGR AT GAUNDI R. CONFLUENCE, GULMI 21 JAN 86 47 KGR AT SETI BENI, PARBAT 19 JAN 85 KGR AT PAHADI, SYANGJA 18 JAN 85 48 KGR AT BADIGARH R. CONFLUENCE AT RUDRABENI, GULMI 49 19 AUG 84 KGR AT RIDI BAZAR, GULMI 50 22 MAY 84 KGR AT RIDI BAZAR, GULMI 51 18 AUG 84 52 KGR AT RIDI BAZAR, GULMI 17 JAN 85 53 KGR AT RIDI BAZAR, GULMI 20 MAY 85 54 KGR AT RIDI BAZAR, GULMI 19 AUG 85 KGR AT RIDI BAZAR, GULMI 55 19 JAN 86 KGR AT RANI GHAT, PALPA 56 16 JAN 85 KGR AT RAMDI, PALPA 1 MAY 85 57 KGR AT NIMA, SYANGJA (5 KM FROM GYALANG) 4 MAY 84 58 KGR AT NIMA, SYANGJA 59 21 AUG 84 60 KGR AT NIMA, SYANGJA 6 JAN 85 KGR AT NIMA, SYANGJA 2 MAY 85 61 62 KGR AT NIMA, SYANGJA 20 AUG 85 KGR AT NIMA, SYANGJA 6 JAN 86 63 KGR AT NAU GAUN, PALPA 5 JAN 85 64 65 KGR AT KHORIYA GHAT, PALPA 4 JAN 85 66 KGR AT RAMPUR, PALPA (="RAMPUR-POKHARA") 1 MAY 84 67 KGR AT KELADI GHAT, PALPA 3 JAN 85 KGR AT PUTTAR GHAT, TANAHUN 2 JAN 85 68 KGR AT BAUNDI R. CONFLUENCE, DERGAON, NAWALPARASI 69 1 JAN 85 70 KGR AT HADAHA, NAWALPARASI 29 APRIL 84

KGR AT SPRING FEEDER CONFLUENCE, BULING, NAWALPARASI 71 31 DEC 84 72 KGR AT LADI R. CONFLUENCE, SANO TADI, NAWALPARASI 30 DEC 84 73 KGR AT KHALTE, TANAHUN 27 APRIL 84 74 KGR AT CHERANGA R. CONFLUENCE, TANAHUN 29 DEC 84 75 KGR AT BHATYARI, TANAHUN 28 DEC 84 76 KGR AT KALIKATAR, TANAHUN 25 APRIL 84 77 KGR AT KALIKATAR, TANAHUN 10 AUG 84 78 KGR AT KALIKATAR, TANAHUN 27 DEC 84 KGR AT KALIKATAR, TANAHUN 79 21 APRIL 85 KGR AT KALIKATAR, TANAHUN 13 AUG 85 80 81 KGR AT KALIKATAR, TANAHUN 28 DEC 85 82 KGR AT DEUTI R. CONFLUENCE, 2 KM N OF DEV GHAT, 9 DEC 84 TANAHUN 83 NR AT DEV GHAT, CHITAWAN 9 DEC 84 84 NR AT NARAYANGARH, CHITAWAN 1 APRIL 84 85 NR AT NARAYANGARH, CHITAWAN 18 JULY 84 86 NR AT NARAYANGARH, CHITAWAN 10 DEC 84 87 NR AT NARAYANGARH, CHITAWAN 13 JAN 85 88 10 FEB 85 NR AT NARAYANGARH, CHITAWAN 89 NR AT NARAYANGARH. CHITAWAN 12 MAR 85 90 NR AT NARAYANGARH, CHITAWAN 19 APRIL 85 NR AT NARAYANGARH, CHITAWAN 18 MAY 85 91 92 NR AT NARAYANGARH, CHITAWAN 11 JUNE 85 93 NR AT NARAYANGARH, CHITAWAN 18 JULY 85 94 NR AT NARAYANGARH, CHITAWAN 14 AUG 85 NR AT NARAYANGARH, CHITAWAN 20 SEPT 85 95 96 NR AT NARAYANGARH, CHITAWAN 17 OCT 85 97 NR AT NARAYANGARH, CHITAWAN 10 NOV 85 NR AT NARAYANGARH, CHITAWAN 10 DEC 85 98 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 99 4 APRIL 84 17 JULY 84 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 100 6 DEC 84 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 101 102 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 3 APRIL 85 17 JULY 85 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 103 7 DEC 85 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 104 NR BELOW BRIDGE AT NARAYANGARH, CHITAWAN 105 3 APRIL 86 NR AT KHARKHARE GHAT, NAWALPARASI, 13 KM W OF 106 NARAYANGARH 21 APRIL 84 NR AT KHARKHARE GHAT, NAWALPARASI 19 JULY 84 107 10 MAY 84 108* NR AT KHARKHARE GHAT, NAWALPARASI NR AT KHARKHARE GHAT, NAWALPARASI 8 DEC 84 109 NR AT KHARKHARE GHAT, NAWALPARASI 20 APRIL 85 110

19 JULY 85 111 NR AT KHARKHARE GHAT, NAWALPARASI 112 NR AT KHARKHARE GHAT, NAWALPARASI 8 DEC 85 113* NR AT SIKRAULI GHAT, NAWALPARASI, 7 AUG 84 NR AT PIPARA (3 KM S OF RAJAHAR), NAWALPARASI 114 17 DEC 84 115 NR AT BHUSARE GHAT, NAWALPARASI 15 MAR 85 NR UPSTREAM FROM TIGER TOPS TENTED CAMP, NAWALPARASI 116 5 APRIL 85 117* NR AT RAPTI R. CONFLUENCE, CHITAWAN 5 MAY 86 NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI 118 R. CONFLUENCE, CHITAWAN 7 APRIL 84 NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI 119 R. CONFLUENCE, CHITAWAN 6 AUG 84 120 NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI R. CONFLUENCE, CHITAWAN 12 DEC 84 121* NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI R. CONFLUENCE, CHITAWAN 12 DEC 84 - 15 FEB 85 NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI 122 R. CONFLUENCE, CHITAWAN 4 APRIL 85 NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI 123 R. CONFLUENCE, CHITAWAN 10 AUG 85 124* NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI R. CONFLUENCE, CHITAWAN 11 AUG 85 NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI 125 R. CONFLUENCE, CHITAWAN 11 DEC 85 126* NR AT GHARIAL CONSERVATION PROJECT CAMP, BELOW RAPTI R. CONFLUENCE, CHITAWAN 10 DEC 85 NR AT AMALTARI GHAT, CHITAWAN 5 APRIL 85 127 128 NR AT LAINDA GHAT, NAWALPARASI 13 DEC 84 . 129 NR ABOVE ARUNG R. CONFLUENCE, NAWALPARASI 13 DEC 84 130 NR AT ARUNG R. CONFLUENCE, NAWALPARASI 21 JULY 85 131 NR AT BINAI R. CONFLUENCE, NAWALPARASI 22 JULY 85 132 NR 4 KM DOWNSTREAM FROM MATYARI (= "MATERI"), CHITAWAN 14 DEC 84 NR 2 KM UPSTREAM FROM KANAHA R., CHITAWAN 133 14 DEC 84 134 NR AT CONFLUENCE WITH KANAHA R., CHITAWAN 14 DEC 84 135 NR AT KANAHA R. CONFLUENCE, CHITAWAN 8 MAR 85 NR 1 KM BELOW CONFLUENCE WITH KANAHA R., CHITAWAN 136 14 DEC 84 NR AT TRIBENI, NAWALPARASI 137* 25 - 29 MAR 85 138* NR AT TRIBENI, NAWALPARASI 25 MAR 86 NR AT TRIBENI GHAT, NAWALPARASI (ABOVE BARRAGE) 139 3 AUG 84 NR AT TRIBENI GHAT, NAWALPARASI (ABOVE BARRAGE) 140 15 DEC 84

NR AT TRIBENI GHAT, NAWALPARASI (ABOVE BARRAGE) 141 7 MAR 85 NR AT TRIBENI GHAT, NAWALPARASI (ABOVE BARRAGE) 142 7 AUG 85 143 NR AT TRIBENI GHAT, NAWALPARASI (ABOVE BARRAGE) 15 DEC 85 144 NR AT TRIBENI GHAT, NAWALPARASI (ABOVE BARRAGE) 13 MAR 86 145* NR AT CONFLUENCE WITH FEEDER CREEK, TRIBENI, NAWALPARASI 9 MAR 85 146 NR AT CONFLUENCE WITH NEPALI CANAL, TRIBENI, NAWALPARASI 9 MAR 85 147 NR AT CONFLUENCE WITH GANDAK WESTERN CANAL, TRIBENI, NAWALPARASI 9 MAR 85 148 NR JUST BELOW TRIBENI BARRAGE, NAWALPARASI 3 AUG 84 NR JUST BELOW TRIBENI BARRAGE, NAWALPARASI 149 15 DEC 84 150 NR JUST BELOW TRIBENI BARRAGE, NAWALPARASI 7 MAR 85 NR JUST BELOW TRIBENI BARRAGE, NAWALPARASI 7 AUG 85 151 NR JUST BELOW TRIBENI BARRAGE, NAWALPARASI 152 15 DEC 85 153 NR JUST BELOW TRIBENI BARRAGE, NAWALPARASI 13 MAR 86 NR BETWEEN TRIBENI AND NARSAI, AT #6 PIER, 154 NAWALPARASI 6 MAR 85 NR NEAR NARSAI, NAWALPARASI, AT PIER # 10 THROUGH 155 # 13, DOWNSTREAM FROM TRIBENI 27 FEB 86 NR AT NARSAI, NAWALPARASI PIER #12 6 MAR 85 156 157 NR ACROSS FROM NARSAI, NAWALPARASI AT PIER #13 12 APRIL 86 NR BELOW NARSAI, NAWALPARASI AT PIER #15 158 12 APRIL 86 159 NR AT SEMARI TARAINI, NAWALPARASI AT PIER #2 13 APRIL 86 NR 5 KM N OF TADI GHAT, NAWALPARASI AT PIER #5 160 13 APRIL 86 NR 2 KM N OF TADI GHAT, NAWALPARASI 15 MAR 84 161

APPENDIX C

CODED ABUNDANCE OF SPECIES (ROWS) AT SITES (COLUMNS) ARRANGED BY TWINSPAN (HILL 1979b). SEE APPENDIX D FOR KEY TO SPECIES' ABBREVIATIONS.

		11111111111111111111111111111111111111
Esce	dan	
Rasb	dan	-2
Bari	til	
Punt	gug	-2222
Sale	bac	*22
Punt	t10	
Lepi	gun	
nast L. J	pan rar	
Dani	dev	22-2227-2447-2547-2-2-2-242
61yo	Cav	
6105	giu	22-22-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-2-
Chan	pun	
Oste	cat	-222
Chad	pac	-22332-24
Noen	bot	222-242-22-2-22222-222222-22-22-322
A201	ean	-2
runt	500	<u>ZZZ-</u> <u>-</u>
Kast	are	
Asoi	eor	777
Clup	car	
61yp	tel	2
Chad	ran	3
Bari	bol	
Punt	CON	-2-2-27-25245345342555544-255-25-5754-2453522-55452-25-3522-44-225
Chag	cha	22222-3-2-54-3525-244-452-5-4524-4-3224252542354255-25-5522-52
Xene	can	-2-222
Pari	Jery hal	
Bari	han	
' Tor	tor	
61yp	tri	2-
Seai	sen	-2
Noen	sca	
Boti	loh	4-2-4322-52222222222222-
ler_	put	72-72-72-72-72-72-72-72-72-72-72-72-72-7
LIOS	Iat	22
Nace	bea	
Rari	cha	
Nces	COL	
Bari	bed	
Bari	vag	2-455-425352222-225222245452-4532372725-4-22-5-545555555555555555555555555
Pseu	sul	
Glγp	kas	-3
Acro	hex	
Noen	she	
61yp	pec	
Schi	110	
Noce	anti gun	
- HITA	DO	La uppears J Té J TJ

APPENDIX D

ALPHABETICAL LISTING OF SPECIES' ABBREVIATIONS

- Acro hex = Acrossocheilus hexagonolepis
- Ambl man = Amblyceps mangois
- Aspi jay = <u>Aspidoparia</u> jaya
- Aspi mor = <u>Aspidoparia</u> <u>morar</u>
- Bari bal = <u>Barilius</u> <u>barila</u>
- Bari ban = <u>Barilius</u> <u>barna</u>
- Bari bed = <u>Barilius</u> <u>bendelisis</u>
- Bari bol = Barilius bola
- Bari sha = Barilius shacra
- Bari til = <u>Barilius</u> <u>tileo</u>
- Bari vag = <u>Barilius</u> vagra
- Boti loh = Botia lohachata
- Chad bac = Chanda baculis
- Chad ran = Chanda ranga
- Chag cha = Chagunius chagunio
- Chan pun = Channa punctatus
- Chel cac = <u>Chela</u> <u>cachius</u>
- Clup gar = <u>Clupisoma</u> garua
- Cros lat = <u>Crossocheilus</u> <u>latius</u>
- Dani dev = Danio devario

- Esom dan = Esomus danricus
- Euch hod = Euchiloglanis hodgarti
- Garr got = Garra gotyla
- Glos giu = <u>Glossogobius</u> giuris
- Glyp kas = Glyptothorax kashmirensis
- Glyp pec = Glyptothorax pectinopterus
- Glyp tel = Glyptothorax telchitta
- Glyp tri = Glyptothorax trilineatus
- Labe der = <u>Labeo</u> <u>dero</u>
- Lepi gun = Lepidocephalus guntea
- Mast arm = Mastacembelus armatus
- Mast pan = <u>Mastacembelus</u> pancalus
- Noem bea = <u>Noemacheilus</u> <u>beavani</u>
- Noem cor = <u>Noemacheilus</u> <u>corica</u>
- Noem rup = Noemacheilus rupecula
- Noem sca = Noemacheilus scaturigina
- Noem she = <u>Noemacheilus</u> <u>shebbearei</u>
- Oste cot = Osteobrama cotio
- Pseu sul = <u>Pseudecheneis</u> <u>sulcatus</u>
- Punt con = Puntius conchonius
- Punt gug = Puntius guganio
- Punt sop = Puntius sophore
- Punt tic = <u>Puntius</u> <u>ticto</u>

- Rasb dan = Rasbora daniconius
- Salm bac = <u>Salmostoma</u> <u>bacaila</u>
- Schi pro = <u>Schizothorax</u> progastus
- Schi ric = <u>Schizothorax</u> <u>richardsoni</u>
- Semi sem = <u>Semiplotus</u> <u>semiplotus</u>
- Tor put = <u>Tor putitora</u>
- Tor tor = Tor tor
- Xene can = Xenentodon cancila

VITA

David Ray Edds

Candidate for the Degree of

Doctor of Philosophy

- Thesis: MULTIVARIATE ANALYSIS OF FISH ASSEMBLAGE COMPOSITION AND ENVIRONMENTAL CORRELATES IN A HIMALAYAN RIVER - NEPAL'S KALI GANDAKI/NARAYANI
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