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Patterns in the distribution of freshwater fishes in rivers of Central Western Ghats, India and their associations with environmental gradients

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Abstract

The community ecology of freshwater fishes in four river systems (Sharavati, Aghanashini, Bedti and Kali) of the central Western Ghats (India) has been studied for the first time. Patterns of fish species distributions were analysed and important stream and environmental parameters determining the species richness and composition of this region were identified. Upstream–downstream trends in species richness and diversity as well as changes in stream characteristics were studied using univariate correlation analyses. Preliminary analyses on changes in species composition and feeding guilds showed the presence of a gradual species turnover along the stream gradient. There were associated changes in the major feeding guild compositions, with a higher proportion of insectivore and algivore/herbivore composition in the upper reaches shifting to a predominance of omnivores and carnivores downstream. Pearson's product–moment correlation analyses along with stepwise multiple regression analyses identified stream depth and altitude as the important parameters determining species richness. Canonical correspondence analysis was performed to study species associations with environmental parameters. The analysis showed a strong species–environmental correlation to the CCA axes, a high significance for the CCA axis 1 as well as for the overall test. The plots of the species and site scores on the CCA axes showed a clear segregation of species based on their relations with environmental and stream properties. This study is an important step in our understanding of the community structure of fish species of these rivers and would be helpful in future efforts on the conservation of aquatic communities and their habitats.

Introduction

One of the interesting aspects of community ecology studies has been that of patterns in assemblage structure and their relationships to biotic and abiotic factors. At the global scale, river size (surface area of the drainage basin and the mean annual river discharge) and the energy availability (net primary productivity) are two important factors influencing fish species richness patterns (Oberdorff et al., 1995). Species richness at local scales, however, are more dependent on biological factors like competition (Grossman, 1982; Ross et al., 1985) and predation (Moyle & Vondracek, 1985) as well as physical factors like habitat diversity (Gorman & Karr, 1978), water chemistry, flow regimes, temperature and channel morphology (Horwitz, 1978; Schlosser, 1982). Earliest studies on the relationship of community diversity to habitat diversity demonstrated an increase in community diversity with vegetation complexity (MacArthur, 1964; Rosenweig & Winakur, 1969; Pianka, 1967). For fish communities, substrate complexity, stream flow and water quality characteristics were found to be important in determining local richness (Gorman & Karr, 1978).

The River Continuum Concept, originally postulated for aquatic invertebrates, predicts that there is an upstream–downstream gradient of changing physical conditions and associated biotic changes (Vannote et al., 1980). Species assort themselves along environmental gradients like pH, temperature etc. and their diversity increases in going from upstream to downstream. From observations on tropical and temperate ecosystems, Lowe-McConnell (1975) explained this pattern as being related to habitat diversity which also increases along the upstream to downstream gradient. This, in addition to a greater richness of detritus and plankton downstream, could lead to greater diversity in the higher trophic levels.

Studies in temperate (Fausch et al., 1984; Belliard et al., 1997) and tropical systems like Western Africa (Hugeuny, 1989) and in the Lower Ntem River Basin of Cameroon (Kamdem Toham & Teugels, 1997, 1998) highlight the occurrence of a distinct pattern in the longitudinal zonation of species: they found a sequential shift in species composition together with an increase in species diversity along the stream gradient, influenced by environmental and physical characteristics of the stream like width, depth, current velocity and substrate type, as well as biotic characteristics like canopy cover and instream cover. Instream cover is known to influence habitat features like depth and stream current (Angermeier & Karr, 1983) and also enhance invertebrate production important for fish feeding (Benke et al., 1984). Wright & Li (2002), in studying the pattern of stream physical parameters and community distribution, developed a framework for using multivariate ordination techniques to integrate continuous and patchy patterns. Fish communities were found to be strongly correlated to large, landscape-scale physical gradients and were generally distributed along a continuous longitudinal gradient.

The Western Ghats (WG), located along the southwest coastline of the Indian subcontinent, is a biodiversity 'hotspot' (Myers et al., 2000) and is extremely rich in its fish diversity as well as endemicity (Bhat, 2003; Dahanukar et al., 2004). Very little, however, is known of the community ecology and distribution patterns of fish fauna in the streams and rivers of this region except for some isolated studies (parts of the Western and the Eastern Ghat hill streams) for fishes (Arunachalam, 2000) and invertebrates (Sivaramakrishnan et al., 1995). The main objective of this work is to study the patterns of species distribution in some rivers of the central Western Ghats. Some of the questions addressed here are as follows. What are the patterns of changes in important stream characteristics like width, depth and current along the streams in the Western Ghats? How does the community structure of fishes change along these longitudinal stream gradients? Are these similar to patterns found in other regions of the world, especially to those observed in other tropical streams? In answering them, we test the hypothesis that there is a gradation of species diversity as well as community structure characterized by species additions and replacements and that the compositions change markedly from upstream to downstream. Finally, what is the relationship of fish composition to varying environmental gradients along these rivers?

Materials and methods

Study area

The study was conducted in the Uttara Kannada district of Karnataka state, located in the central WG, a set of medium to low lying mountain ranges along the southwestern borders of the Indian peninsula (Fig. 1). The region consists of three topographically distinct regions – the higher elevation region (which continues towards the east into the Deccan Plateau), the steep ridge area (where the mountain ranges slopes west wards towards the coastline) and the plainer coastal zone on the west (which touches the Arabian Sea). The climate of the region is mainly tropical with a well defined rainy season between June and October, a very mild winter between December and February and a relatively dry pre-monsoon summer between March and May. There are a number of medium to small rivers and streams in this region, most of which originate in the higher elevation zones and flow westwards into the Arabian Sea. Four of the prominent rivers of the district are the Kali, Bedti, Aghanashini and Sharavati. While Aghanashini and Bedti are relatively undisturbed rivers, Sharavati and Kali have been subjected to severe alterations of their habitat and in some localities even deterioration of water quality due to the

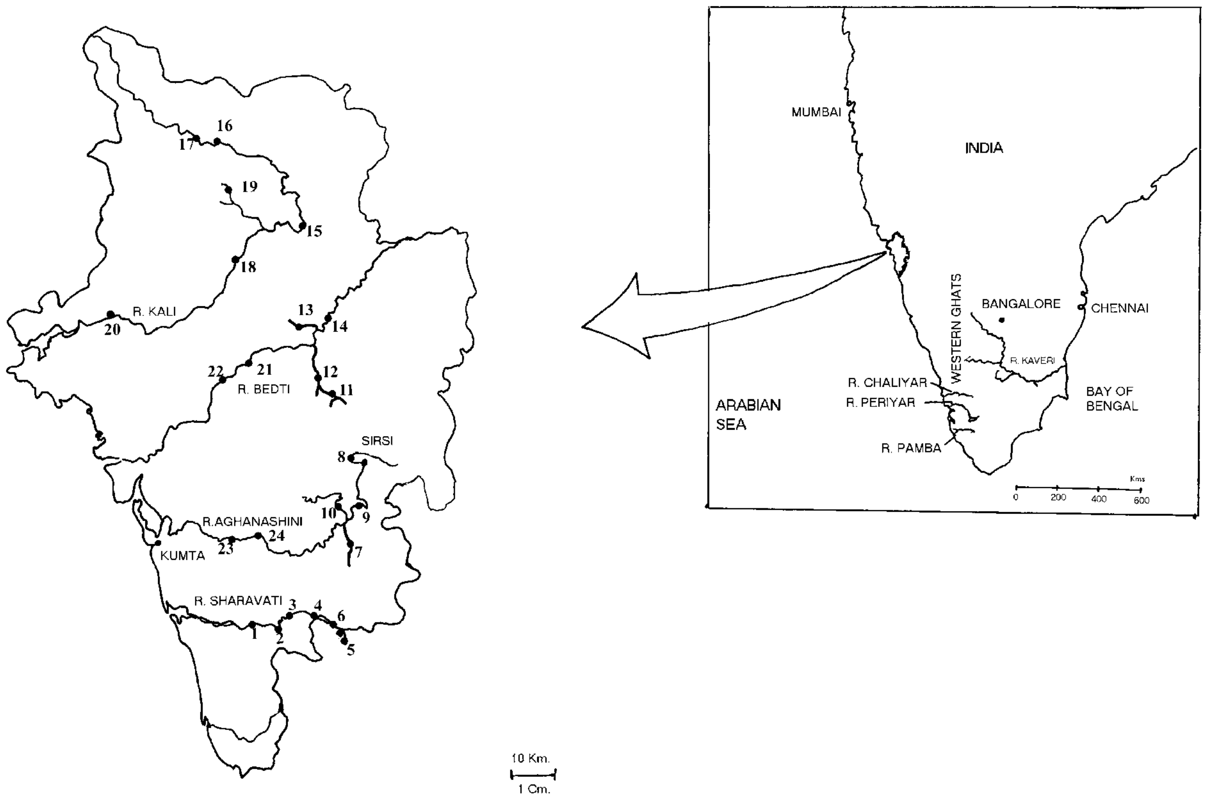

Figure 1. Map of the study region (Uttara Kannada) indicating the sampling sites (shown by a dot and the site code).

construction of dams and reservoirs as well as industries along the rivers (Bhat, 2002).

Sampling

The present study was conducted on the four river systems – Sharavati, Aghanashini, Bedti and Kali – details of the length, catchment areas and discharge are summarized in Table 1. Fishes were sampled regularly (using a variety of fishing nets of varying mesh sizes – gill nets, cast nets and dragnets) over a period of 2 years (January 1997–April 1999) on 24 sampling sites (details are tabulated in Appendix 1). Due to the specific topography of the Western Ghats, such that after a relatively gentle slope from the Western coastline, there is a steep rise in elevation at ≈250 m and further eastwards, these mountains join the Deccan Plateau (at ≈650 m), the sites were chosen such that each river had 6 sampling sites: three on the higher elevation zone (>250 m) and three on the mid and lower elevation zones (<250 m).

100–150 m stretches of the river at each site were sampled. For the study, a 'sample' is defined as the collection made at a particular habitat using a particular sampling tool (cast nets, gillnets or

Table 1. River lengths, catchment area, annual discharge, and other physical attributes

River	Total length (km)	Catchment area (km^2)	Annual discharge (million m^3)	No. of major dams	Pollution
Sharavati	128	2208	4545	2	Unpolluted
Aghanashini	75	2146	966	–	Unpolluted
Bedti	152	3902	4925	–	Minimal – some sewage discharged
Kali	184	5179	6537	4	Industrial effluents

dragnets). A total of 340 samples were collected from the entire study region (including all the 24 sites on the four rivers). The fishes were identified and some representative specimens were collected and preserved (in 4% formaldehyde solution). Identification was carried out based on keys (Jayaram, 1999; Talwar & Jhingran, 1991) and with the help of taxonomic expertise from the Regional Station of the Zoological Survey of India at Chennai. A detailed description of sampling methodology is presented in Bhat (2003).

Physical characteristics

At each site, the following physical parameters of the stream were measured at 4–5 points, each 25 m apart – (a) stream depth, measured at three separate parts of the stream – two measurements at 1/3 distance of the stream width from both sides of the bank and one at the centre of the stream, (b) stream width and (c) stream velocity at the point of maximum flow. The stream velocity was calculated by measuring the time taken for a cork to cover a unit distance. Data on the water temperature, pH (pH meter – Salvin Instruments, India), % canopy cover (based on a visual estimation of sky visible from the centre of the stream) and the type of riparian vegetation along the stream were also collected. The % canopy cover values were divided into five categories – 0–20% (category 1), 20–40% (category 2), 40–60% (category 3), 60–80% (category 4) and 80–100% (category 5). Altitudes for the areas closest to the sampling sites were noted with the help of 1:50 000 scale maps of the Geological Survey of India. Substrate types found in the sampling sites were divided into the following categories – (1) rocks, (2) pebbles and gravel and (3) sand and silt. A value of 0 or 1 was designated for the absence or presence of either of these variables at each of the sites.

Not much is known about the feeding ecology of most of the non-commercial native fishes in the Indian subcontinent. However, information on the major feeding habits of some of the species available in the literature (Talwar & Jhingran, 1991) was collected for interpretation of distribution patterns of feeding guilds. These guilds have been broadly categorised into seven divisions – algivore, herbivore, insectivore, larvivore, omnivore, carnivore and piscivore.

Data analyses

Total species richness at upstream and downstream reaches of the four rivers was measured by calculating the total number of species collected from the three sites on each stream reach. Species diversity at each stream reach was measured using the Shannon–Weiner index and differences in species composition across reaches were calculated as the Jaccard index of coefficient of species similarity (Ludwig & Reynolds, 1988). Comparison of species richness across upstream–downstream reaches was done after rarefaction of the data and calculation of mean species richness values for 200 randomised Monte Carlo simulations. This was done in order to remove any biases which can be encountered due to differences in sampling effort across sites (Colwell & Coddington, 1994). Spearman rank (non-parametric) correlations were used for studying changes in species richness and abiotic parameters along the river gradient while correlations between species richness and each abiotic parameter was done with Pearson's product–moment (parametric) correlation method.

Trends in upstream to downstream gradients

Mean values of the physical parameters were used in all the correlation analysis (Table 2). The location of a site on the stream gradient was determined by the stream order on which it was located as well as its elevation from sea level. Two measures of habitat quality were used for the analyses – (a) size measured by the mean width, current and depth and (b) variability, measured by the percentage coefficient of variation of width, current and depth. Percent coefficient of variation (% CV) is a measure of habitat variability and diversity (Gorman & Karr, 1978) and was included in the analyses to test for correlations between habitat diversity and species richness.

Fish communities in tropical streams are known to show a gradual species turnover along the gradient – due to addition of more species, replacement of a species by another occupying the same niche, or deletion of species (Kamdem Toham & Tuegels, 1998). Based on qualitative data from literature, changes in feeding guild structure of fish communities along gradients in rivers of WG were compared. As a preliminary study, the

Table 2. Mean values of stream width, depth, current velocity and altitude for each study site on Sharavati (S), Kali (K), Aghanashini (A) and Bedti (B)

Site	River	Width (m)	Depth (m)	Current (m/s)	Altitude (m)
Allanki	S	86.7	1.68	1.51	30
Gersoppa bate	S	123.2	–	2.86	40
Gersoppa nursery	S	183.3	–	1.00	40
Jog falls	S	17.20	0.43	0.65	496
Joginmatha	S	157.7	3.65	–	374
Chainagate	S	15.0	2.00	2.04	476
Balur	A	29.6	0.70	1.31	633
Bilgi	A	24.1	0.57	1.28	630
Manihole	A	25.7	0.67	0.86	603
Serkuli	A	15.3	0.68	2.48	500
Kirtigadde	A	79.5	0.77	1.88	38
Hulidevarakodlu	A	79.1	0.64	1.27	28
Pattnahole	B	19.5	0.40	1.71	472
Kumbri	B	41.1	0.89	1.08	428
Manchikeri	B	19.2	0.55	2.49	422
Ganeshpal	B	23.5	0.37	1.22	395
Ramanguli	B	69.8	0.46	1.24	60
Hoskambi	B	54.4	0.82	2.84	20
Bommanahalli	K	43.5	0.16	–	427
Dandelappa	K	57.5	–	1.25	440
Maulangi	K	121.6	0.66	0.88	460
Ganeshgudi	K	152.0	2.40	1.88	80
Nujji	K	27.9	0.76	1.03	560
Kadra	K	187.5	–	–	20

– indicated where readings could not be taken.

proportions for each feeding guild in the upstream and downstream reaches were calculated within Aghanashini and Bedti.

Multivariate analyses

Two methods of analyses were employed in calculating correlations and understanding the association of species richness and composition to the various environmental parameters. Multiple regression method using a stepwise selection of parameters was used to study correlation of multiple environmental parameters to species richness. A simplified model for species richness based on large-scale physical parameters was thus developed.

Ordination analysis with the direct gradient technique of the canonical correspondence analyses was performed to study the association of these environmental parameters to species composition. This method chooses the ordination axes on the basis of species and environmental data and determines locations for sites (samples) and species in ecological space assuming a Gaussian-type response of species to environmental gradients (Ter Braak, 1985, 1986). For this study, additional variables like the % canopy cover, pH value and the three categories of substrate types (rock, pebbles and sand) were also included along with the width, depth, current velocity and altitude parameters. Species abundance data was log transformed ($\ln(x)$) to obtain a more normal distribution. All the species collected from the 24 sampling sites were included in the analysis, after downweighting for rare species with less than 20 individuals. CCA was conducted with the forward selection procedure where the significance of each variable was tested with a Monte Carlo simulation algorithm (with 999 random permutations) before adding to the model. However, all the variables were included in the final model. The relative contribution of the ordination axes was evaluated by the canonical coefficients and interset correlations. The interset correlations are the correlation coefficients between the environmental variable and the ordination axes. The species–environment correlation is a measure of the association between species and the environmental variable (Ter Braak, 1988).

All the statistical analyses and generation of graphs were performed using the STATISTICA (Statsoft version 5.0) and CANOCO (version 3.12) software packages.

Results

10 771 individuals of 92 species belonging to 25 families and 45 genera were collected from the four rivers. Appendix 2 shows the names and codes for the most abundant species collected in this region.

Species richness and diversity

Total species richness as well as abundance was highest for Bedti upstream reaches (SR = 47) while the lowest was recorded for Sharavati downstream region (SR = 26). Within rivers, Aghanashini had the highest number of species shared between its two reaches (JI = 2.30) whereas Sharavati showed the least overlap of species between the reaches (JI = 0.46). Abundances and sampling efforts at each reach being

Table 3. Total species richness, abundance, rarefied species richness and Jaccard index of species similarity between upstream and downstream reach of each study river

	Total species richness	Individuals	Species richness for 500 individuals	Jaccard index
Sharavati upstream	36	905	28	0.46
Sharavati downstream	26	524	36	
Aghanashini upstream	37	1835	24	2.30
Aghanashini downstream	35	1129	25	
Bedti upstream	47	3117	23	0.62
Bedti downstream	36	1310	25	
Kali upstream	38	1196	27	1.36
Kali downstream	33	685	28	

Table 4. Results of the correlation analyses (Spearman's rank correlation) of environmental parameters with stream gradient (Panel A), (Pearson's product–moment correlation) of environmental parameters with species richness (SR) (Panel B)

Parameter	Aghanashini	Bedti	Sharavati	Kali
Panel A				
Mean width (m)	0.60	0.77	0.31	0.77
Mean depth (m)	0.37	0.60	−0.10	0.20
Mean current velocity (m/s)	0.25	0.25	0.20	0.80
% CV (width)	0.14	0.60	0.02	−0.20
% CV (depth)	0.02	−0.20	0.30	**0.90**
% CV (velocity)	−0.25	0.31	−0.30	0.20
Species richness (SR)	**0.88**	0.65	−0.40	0.30
Shannon's index	0.60	0.03	−0.60	−0.14
Panel B				
Mean width (m)	0.55	0.36	−0.24	0.48
Mean depth (m)	0.44	**0.88**	0.13	−0.34
Mean current velocity (m/sec)	0.70	0.18	−0.25	−0.42
% CV (width)	0.19	0.05	0.79	−0.24
% CV (depth)	0.18	0.49	0.55	−0.03
% CV (velocity)	−0.03	−0.26	−0.39	−0.92
Altitude (m)	**−0.92**	−0.15	0.47	0.10

Values of the correlation coefficient (*r*) are shown. Significant correlations ($p < 0.05$) indicated in bold. CV = Coefficient of variation.

Table 5. Species addition, substitution and deletion along *upstream*–downstream gradient on Aghanashini and Bedti

Code	Upstream sites			Downstream sites		
Aghanashini						
Na	+	–	–	–	–	–
Ps	+	+	+	+	–	–
Lp	+	+	+	+	–	–
Pn	+	+	+	+	+	–
Br	+	–	–	+	–	–
Path	+	+	–	+	+	–
Pfi	+	+	+	+	+	+
Pj	+	+	+	+	+	+
Pa	+	+	+	+	+	+
Rd	+	+	+	+	+	+
Da	+	+	+	+	+	+
Sb	+	+	+	+	+	+
Gg	+	+	+	+	+	+
Ma	+	+	+	+	+	+
Al	+	–	–	+	–	+
Nb	+	–	+	+	–	–
Np	+	–	–	+	–	–
Pt	+	–	–	+	+	+
Gd	–	+	–	–	–	–
Ba	–	+	–	–	–	–
Ga	–	+	+	–	–	–
Mc	–	+	+	+	–	–
Mm	–	+	+	+	+	+
Cn	–	+	+	+	+	+
Gk	–	–	+	+	+	+
Pss	+	–	–	+	+	+
Pf	–	–	+	–	–	–
Pso	–	–	–	+	+	+
Lk	–	+	+	+	–	–
Nr	–	–	+	–	+	–
Nd	–	–	+	–	–	–
Ns	–	–	–	+	–	–
Pv	–	–	–	+	–	–
Lt	–	–	–	+	–	–
Omb	–	–	–	+	–	+
Pb	–	–	–	+	–	+
Nan	–	–	–	–	+	–
Hl	–	–	–	–	+	–
Mcyp	–	–	–	–	+	–
Hb	–	–	–	–	+	–
Ic	–	–	–	–	+	+
Glg	–	–	–	+	+	
Pew	–	–	–	–	+	+

Table 5. (Continued)

Code	Upstream sites			Downstream sites		
Pek	–	–	–	–	+	+
Tk	–	–	–	–	+	+
Aghanashini						
Na	+	–	–	–	–	–
Xc	–	–	–	–	+	+
Tt	–	–	–	–	+	+
Ecan	–	–	–	–	+	+
Esur	–	–	–	–	–	+
Pc	–	–	–	–	–	+
Al	+	–	–	–	–	–
Bedti						
Pn	+	+	–	–	+	–
Nd	+	+	–	–	–	–
Ps	+	+	–	–	–	+
Pf	+	+	–	–	–	–
Pc	+	+	–	+	–	–
Br	+	–	–	–	–	–
Pa	+	+	+	+	+	+
Pj	+	+	+	+	+	+
Mm	+	+	+	+	+	+
Rd	+	+	+	+	+	+
Da	+	+	+	+	+	+
Gg	+	+	+	+	+	+
Omb	+	+	+	+	–	–
Cn	+	+	+	+	+	–
Path	+	+	+	+	–	+
Mc	+	–	+	+	–	–
Pss	+	–	+	+	–	–
Tk	–	+	+	+	–	–
Ga	–	+	–	–	–	–
Sw	–	–	+	–	–	–
Lt	–	–	+	–	–	–
Nbo	–	–	–	+	–	–
Lp	–	–	–	+	–	–
Pad	–	–	–	+	–	–
On	–	–	–	+	–	–
Np	–	–	–	+	–	–
Pt	–	–	+	+	–	–
Ma	–	–	+	+	+	+
Pb	–	–	+	+	+	+
Sbo	–	–	+	+	+	+
Gk	–	–	+	+	+	+
Glg	–	–	–	+	+	+
Pfi	–	–	–	+	+	+
Pew	–	–	–	–	+	–

Continued on p. 90

Table 5. (Continued)

Code	Upstream sites			Downstream sites		
Pek	–	–	–	–	+	–
Esur	–	–	–	–	+	+
Xc	–	–	–	–	+	+
Ob	–	–	–	–	+	+
Bedti						
Ic	–	–	–	–	+	–
Tt	–	–	–	–	+	+
Hl	–	–	–	–	+	+
Mcyp	–	–	–	–	–	+
Gers	–	–	–	–	–	+
Orm	–	–	–	–	–	+

Presence and absence (of most abundant species) indicated by + and –, respectively.

different, comparisons across reaches, based on rarefaction and Monte Carlo simulations show that, in general, for a given number of individuals sampled (e.g. 500 individuals, based on the least number of individuals sampled at a reach), downstream reaches were more diverse than upstream reaches (Table 3).

Patterns of species richness and abiotic parameters along longitudinal gradients

The Spearman rank correlation analyses for trends in species richness along the gradient show higher positive correlations in Aghanashini and Bedti as contrasted to Kali and Sharavati, which show weak positive and negative correlations, respectively. The Shannon index also shows similar trends (Table 4, Panel A). Mean width, depth, and current in Aghanashini Bedti and Kali increased downstream. However, mean depth in Sharavati seemed to decrease along the gradient. Variability in habitat structure (determined by % CV) was unclear for most parameters in these rivers (Table 4, Panel A).

Correlations between species richness and abiotic parameters

While species richness was positively correlated to mean values of the depth, width and current velocity parameters and negatively to altitude in Aghanashini and Bedti, its correlation to most of the parameters

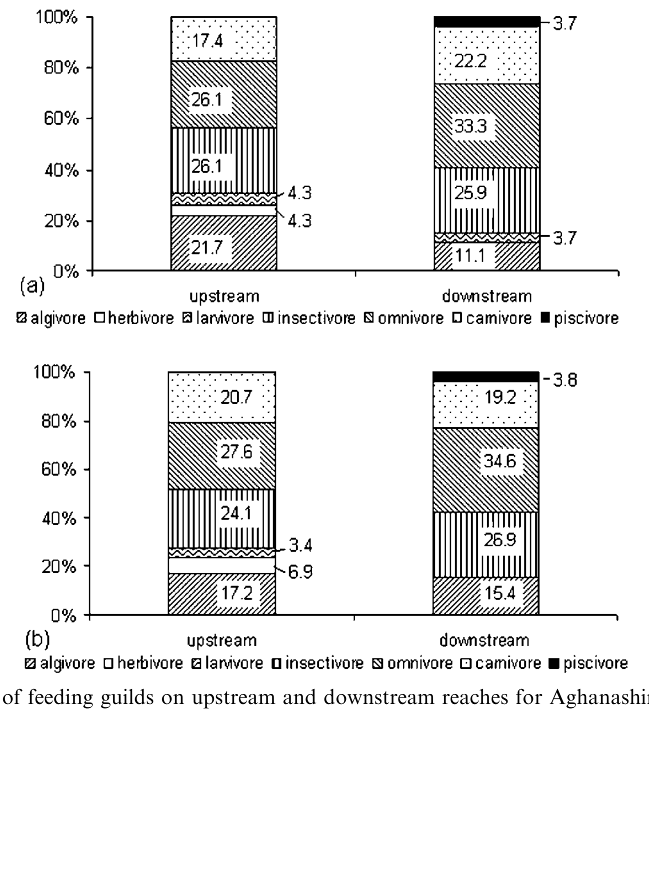

Figure 2. Relative proportions of feeding guilds on upstream and downstream reaches for Aghanashini (a) and Bedti (b).

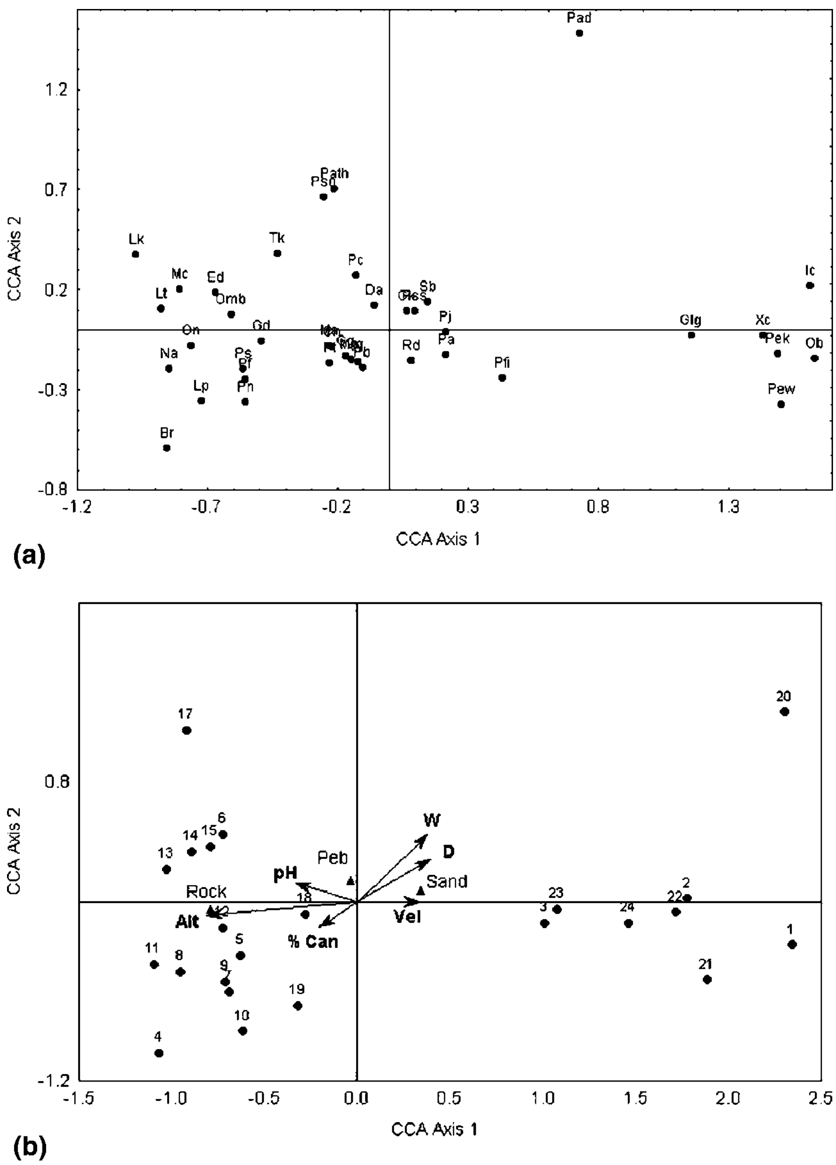

Figure 3. CCA plots showing species scores (a), site scores and environmental vectors and centroids (b). Names for site codes are given in Appendix 1 and full species names are given in Appendix 2. W = stream width; D = stream depth; Vel = stream velocity; Alt = altitude; % Can = % canopy cover; Peb = pebble substratum; Sand = sandy substratum; Rock = rocky substratum.

in Kali and Sharavati were negative (Table 4, Panel B). Its correlation with habitat variability, however, was found to be inconsistent for all four rivers.

Changes in species composition along stream gradient and pattern of distribution of feeding guilds

A gradual change in species composition and species abundance (consisting of addition, substitution and deletion of species) was observed along the upstream – downstream gradient (Table 5). Smaller sized cyprinids that are common in upper stretches (e.g. *Brachydanio rerio*, *Aplocheilus lineatus* and *Glyptothorax annadalei* which are characteristically present in swift moving runs or more turbulent habitats like riffles and rapids) were replaced by larger sized species which are common in slower moving habitats (e.g. *Puntius sarana*, *Labeo*

Table 6. Results of the canonical correspondence analysis. The total inertia is total variance in species abundance data

Axes	1	2	3	4	Total inertia
Eigenvalues	0.227	0.150	0.095	0.080	1.630
Species–environment correlations	0.959	0.927	0.948	0.944	
Cumulative percentage variance					
of species data	14.0	23.2	29.0	33.9	
of species-environment relation	28.6	47.5	59.5	69.5	
Test of significance					
CCA axis 1		F-ratio = 2.27, $p < 0.005$			
Overall test		F-ratio = 1.48, $p < 0.005$			

The species–environmental correlations scale the strength of the relationship between species and environment for the axes. F ratio statistics are listed for the first and for all the axes combined.

spp.) and some brackish-water dwelling species (*Arius caelutus*, *Tetrodon travancoria*, *Etroplus suratensis*, *Gerres* spp., etc.). Some generalist species were found to be distributed all along the rivers (*Garra gotyla stenorhynchus*, *Rasbora daniconius*, *Danio aequipinnatus*, *Puntius filamentosus*).

Insectivores were found to be evenly distributed along the gradient. Some common trends were observed: herbivores were seen to be present only in the upstream regions, while piscivores were present only in the downstream regions. While algivores decreased in numbers, carnivores as well as omnivores were found to increase downstream in both Aghanashini and Bedti (Fig. 2(a) and (b)). Most of the guilds were present all along the stream gradient and the species richness of most of the guilds increased downstream. However, the proportion of each guild category changed – upstream regions were characterized by a higher proportion of algivores (e.g. *Gonoproktopterus curmuca*, *Puntius dorsalis* and *Lepidocephalus thermalis*), herbivores (e.g. *Osteocheilus nashii* and *Labeo fimbriatus*) and larvivores (e.g. *Aplocheilus lineatus*), while this changed to an increased proportion of omnivores, carnivores (*Carangx ignobilis*, *Arius caelutus*, etc.) and even some piscivores (*Megalops cyprinoides*, *Nandus nandus*) downstream.

Multivariate analyses

The final model from the multiple regression analysis based on a forward stepwise selection, chose the depth and altitude parameters. This analysis showed a significant correlation between the chosen parameters (depth and altitude) and species richness ($R^2 = 0.58$, $R = 0.76$, $F = 6.46$; $p = 0.02$). Mean depth showed a highly significant positive correlation ($\beta = 0.59$, $p = 0.02$), while

Table 7. CCA regression/canonical coefficients (A) and Interset correlations (B) of environmental variables with CCA axes

Variable	CCA axis 1		CCA axis 2		CCA axis 3		CCA axis 4	
	A	B	A	B	A	B	A	B
Width	−0.25	0.43	0.03	0.28	−1.03	−0.02	−0.94	0.13
Depth	0.28	**0.41**	0.62	0.45	1.39	0.39	0.22	0.02
Velocity	−0.10	0.36	0.03	−0.002	0.20	0.09	−0.19	−0.29
Altitude	−0.06	**−0.88**	−1.50	−0.09	2.64	0.24	−0.49	−0.16
Sand	0.005	0.46	0.18	0.10	1.34	0.30	0.22	1.59
Pebble	−0.47	−0.04	2.38	0.15	−0.98	0.08	−0.20	−0.51
Rock	−1.03	−0.60	1.79	−0.04	−0.82	−0.27	1.39	0.27
pH	−0.88	−0.36	1.58	0.12	−2.13	0.26	0.01	0.18
Canopy	−0.44	−0.21	−0.32	−0.17	−0.96	0.22	−0.25	−0.44

Statistically significant values are in bold ($p < 0.05$).

altitude showed a negative correlation ($\beta = -0.40$, $p = 0.09$).

Association of species composition to stream environmental gradients

The plots of the species and site scores (on the first two axes) produced from CCA show the distribution of species and sites in ordination space (Figs. 3(a) and 3(b), respectively). Here, 40 of the most abundant species have been depicted, to provide insight into their composition and distribution. Species common to downstream sites (*Glossogobius giuris*, *Periophthalmus weberi* and *P. koelreuteri*, together with the brackish-water species, *Xenontodon cancila*, *Osteobrama bakeri* and *Ichthyocamus carci*) had higher scores on the CCA axis 1, while species common to upstream sites (*Brachydanio rerio*, *Puntius narayani* and *P. sahyadrensis*, *Aplocheilus lineatus*, *Osteocheilus nashi*, etc.) had more negative values on this axis. Species occupying both upstream and downstream regions (i.e. more widely distributed) were clustered in the centre (e.g. *Garra gotyla stenorhynchus*, *Rasbora daniconius*, *Danio aequipinnatus*, *Mystus malabaricus*, etc.).

The positions of the environmental vectors indicate their correlation to the axes as well as to each other (Fig. 3(b)). The species–environment correlation was high for both the axes (0.96 and 0.93, respectively) and the Monte Carlo tests for the first axis and the overall test were significant ($p < 0.01$). The canonical axes 1 and 2 (Eigenvalues = 0.22 and 0.15) explained 23.2% of the cumulative variance of the species data, while they explained 47.5% of the cumulative variance of the species–environment relation (Table 6). Out of the nine variables used in the model, two were found to be significant (depth and altitude; $p < 0.05$) accounting for 30% of the total 80% variance of the entire set of variables. Highest correlations are observed for altitude (−0.88 in the CCA axis 1), pebble substratum type (−0.51 in the CCA axis 4), rocky substratum (−0.60 in the CCA axis 1) and depth parameters (0.45 in the CCA axis 2) (Table 7).

Discussion

The Western Ghats, while being extremely rich in its fish biodiversity, has not so far been investigated with regards to species distributions and their interactions with environmental and physical parameters. This study is, therefore, the first of its kind for the Western Ghats; patterns observed and studied in detail for most temperate, and some tropical regions, have been tested and analyses for this region as well.

In general, fish communities displayed a continuous distribution, with a gradual increase in richness towards downstream regions. Univariate and regression analyses for correlations between species richness (SR) and environmental and stream characteristics showed that species richness is positively correlated to stream depth and width and negatively to altitude. Stream habitat complexity however, does not seem to contribute significantly to the increase in species numbers in the lower reaches. It is possible that other aspects of stream structural characteristics (e.g. greater stream living space and moderating environmental conditions) could influence fish communities (Rahel & Hubert, 1991; Reyes-Gavilan et al., 1996). In this study, the observed increase in SR downstream is likely to be due to an increase in stream size as well as to the influence of the adjacent marine environment. While diversity (as shown by species richness and the Shannon index) clearly increased downstream and was positively related to the abiotic parameters for Aghanashini and Bedti, our findings for Sharavati and Kali were contrasting. Recent modifications of natural stream habitats due to construction of reservoirs and dams as well as industrial pollution on Sharavati and Kali are likely causes for this.

The increase in species richness resulted more from a longitudinal downstream addition of species rather than any sizable reduction or loss of species. In fact, a large number of species found upstream were also found to occur in the downstream sites. Many of the species additions were found to be estuarine or brackish-water species also occurring in freshwater systems. Longitudinal gradients in guild structure were also observed in these rivers, with most herbivores occupying the upper reaches and most piscivores being found downstream. Other groups like omnivores and carnivores, though present all along the gradient, increased downstream while algivores reduced in proportion. However, more detailed studies on the feeding habits and preferences of these species are required for a better understanding of patterns in feeding guilds.

Nine environmental variables were used for the multivariate ordination analysis, out of which four variables (depth, altitude, pebble substratum type and % canopy cover) contributed to more than half (47%) of the total variance explained by the variables (80%). Out of these, altitude was found to be the most important variable (variance explained = 20%) in explaining the distribution of species, while depth, substratum types pebble, rock, sand, pH and % canopy cover also contributed substantially. The second most important variable observed in our study was depth (variance explained = 10%). This was also found to have a significant positive relation with species richness. Studies conducted in other tropical areas (Kamdem Toham & Teugels, 1998) report catchment area as the most important variable, reflecting similar gradients in other physical variables like depth, width and distance from source. Angermeier & Karr (1983, in Panama) and Hugueny (1990, in West Africa) found a significant relationship between species richness and width as well as an increasing gradient of depth.

The substratum type (pebble, rock and sand) was also found to be a major environmental parameter explaining the distribution of species in the sampling sites. Diversity of substratum types did not substantially increase downstream. However, species preferences for certain substrates can be observed from this study. For example, upstream sites with more rocks and gravel were associated with species like *Lepidocephalus thermalis*, *Mystus malabaricus* and *Osteocheilus nashii* while sites with more sandy and silty substrata at downstream sites were associated with *Periophthalmus* spp., *Glossogobius giuris*, etc. The % canopy cover variable is also observed to be an important parameter. Species like *Puntius ticto*, *Puntius bimaculatus*, *Mastacembelus armatus* and *Aplocheilus lineatus* were most often associated with a maximal canopy cover, while species like *Salmostoma boopis*, *Puntius filamentosus*, *P. jerdoni*, *Glossogobius giuris* frequently occurred in more open water and low canopy conditions. The functional role of overhanging vegetation in determining the temperature and hydrological regime and also as a source of organic nutrients (through fallen leaves and litter) has already been documented (Lowe-McConnell, 1975). These interesting associations deserve more detailed investigations.

The relation of sites to species can be understood by overlaying the species CCA plot (Fig. 3(a)) with the sites plot (Fig. 3(b)). The clusters with higher scores on the first axis are the downstream sites on all the four rivers, while upstream sites are clustered together with negative values for the first axis. Downstream sites are characterized by greater width and depth parameters and sandy substratum. Upstream sites have a predominance of rocks and pebbles as well as greater % canopy cover. It is interesting to note that site 16 (Dandeli, situated on Kali and the most polluted site of all) is located as an outlier (not shown in the graph as it lies far above the other clusters). This site is located just about a kilometer downstream of local mills and is subjected to pollution from the effluents discharged. Species composition at this site is restricted to extremely tolerant species like *Parambassis dayii* and introduced larvivorous species like *Aphanius dispar*.

The rivers of the WG, which were until recently undisturbed, are now facing the consequences of our ever increasing demands; one of the main reasons for their exploitation is the harnessing of energy as hydroelectric power. In particular, rivers like Kali and Sharavati have been subjected to deforestation and habitat alterations to such an extent that their effect on aquatic communities is evident. Fish based indices like the Index of Biotic Integrity (Karr, 1981), successfully applied for assessment of aquatic habitats in many other regions, can be used to assess anthropogenic impacts as well as for conservation prioritization (Bhat, 2002). An understanding of the mechanisms determining the spatial segregation of species is of great importance in the conservation and management of aquatic resources. The present study is a step in this direction and hopes to provide a basis for conservation and management strategies.

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Appendix 1. Study locations with latitude, longitude, altitude, canopy cover, dominant substrate types etc.

S. no.	Sampling site (code)	River	Canopy	Altitude (m)	Latitude	Longitude	Substrate types
1	Allanki (1)	Sharavati	1	30	14° 14′ 584	74° 34′ 177	S
2	Gersoppa bate (2)	Sharavati	2	40	14° 14′ 272	74° 38′ 986	S
3	Gersoppa nursery (3)	Sharavati	2	40	14° 14′ 571	74° 40′ 121	S
4	Jog falls (4)	Sharavati	3	496	14° 13′ 882	74° 49′ 112	R
5	Joginmatha (6)	Sharavati	2	476	14° 13′ 882	74° 49′ 394	S, R
6	Chaina Gate (5)	Sharavati	1	374	14° 11′ 578	74° 49′ 660	R
7	Kirtigadde (24)	Aghanashini	3	28	14° 25′ 778	74° 36′ 109	S, P
8	Hulidevarakodlu (23)	Aghanashini	3	38	14° 26′ 540	74° 38′ 489	S, P
9	Bilgi Bridge (7)	Aghanashini	5	630	14° 21′ 542	74° 47′ 432	S, P, R
10	Tattikai (8)	Aghanashini	5	500	14° 30′ 417	74° 45′ 465	S, P, R
11	Manihole (9)	Aghanishini	4	603	14° 26′ 083	74° 47′ 341	S, P, R
12	Balur (10)	Aghanashini	4	633	14° 28′ 861	74°48′ 584	S, P, R
13	Hoskambi (22)	Bedti	3	20	14° 40′ 798	74°29′ 380	S, P
14	Ramanguli (21)	Bedti	3	60	14° 47′ 798	74° 36′ 504	S, P
15	Pattnahole (11)	Bedti	4	472	14° 42′ 959	74° 42′ 275	S, P, R
16	Manchikeri (13)	Bedti	3	422	14° 53′ 467	74° 47′ 178	R
17	Kumbri (14)	Bedti	4	428	14° 54′ 751	74° 48′ 228	P, R
18	Ganeshpal (12)	Bedti	3	395	14° 46′ 993	74° 45′ 551	P, R
19	Kadra (20)	Kali	1	20	14° 54′ 404	74° 19′ 353	S
20	Nujji (19)	Kali	5	560	15° 06′ 107	74° 22′ 886	S, P, R
21	Ganeshgudi (18)	Kali	3	80	15° 16′ 627	74°32′ 157	S, R
22	Maulangi (17)	Kali	2	460	15° 15′ 371	74° 35′ 536	S, P, R
23	Dandeli (16)	Kali	3	440	15° 14′ 725	74° 38′ 204	S, R
24	B.P. Damsite (15)	Kali	2	427	15° 09′ 991	74° 42′ 611	S, R

S = sandy-silty; P = pebble-gravel; R = rocky. Canopy categories: 1 = 0–20%; 2 = 20–40%; 3 = 40–60%; 4 = 60–80%; 5 = 80–100% canopy cover.

Appendix 2. Species names, codes and family names of the dominant species collected from the Uttara Kannada region.

Code	Family
Cyprinidae	
Gd	*Gonoproktopterus dubius (Day)*
Gk	*Gonoproktopterus kolus (Sykes)*
Lk	*Labeo kawrus (Sykes)*
Lp	*Labeo spp (potail?) (Sykes)*
Lpr	*Labeo porcellus (Heckel)*
Ob	*Osteobrama bakeri (Heckel)*
On	*Osteocheilus nashii (Day)*
Pa	*Puntius amphibius (Valenciennes)*
Pb	*Puntius bimaculatus (Bleeker)*
Pc	*Puntius conchonius (Hamilton-Buchanan)*
Pf	*Puntius fasciatus (fasciatus)*
Pfi	*Puntius filamentosus (Valenciennes)*
Pj	*Puntius jerdoni (Day)*
Pn	*Puntius narayani (Hora)*
Ps	*Puntius sahyadrensis (Silas)*
Pss	*Puntius sarana sarana (Hamilton-Buchanan)*
Pso	*Puntius sophore (Hamilton-Buchanan)*
Pt	*Puntius ticto (Hamilton-Buchanan)*
Pv	*Puntius vittatus (Day)*
Tk	*Tor khudree (Sykes)*
Sb	*Salmostoma boopis (Day)*
Br	*Brachydanio rerio (Hamilton-Buchanan)*
Da	*Danio aequipinnatus (McClelland)*
Ed	*Esomus danricus (Hamilton-Buchanan)*
Rd	*Rasbora daniconius (Hamilton-Buchanan)*
Gg	*Garra gotyla stenorhynchus (Jerdon)*
Balitoridae	
Ba	*Bhavania australis (Jerdon)*
Na	*Nemacheilus anguilla (Annandale)*
Nd	*Nemacheilus denisoni (Day)*
Nb	*Nemacheilus botia (Hamilton-Buchanan)*
Np	*Nemacheilus pulchellus (Day)*
Nr	*Nemacheilus rupelli (Sykes)*
Ns	*Nemacheilus striatus (Day)*
Lt	*Lepidocephalus thermalis (Valenciennes)*
Bagridae	
Mc	*Mystus cavacius (Hamilton-Buchanan)*
Mm	*Mystus malabaricus (Jerdon)*
Hb	*Horabagrus brachysoma (Gunther)*
Siluridae	
Sw	*Silurus wynaadensis (Day)*
Ga	*Glyptothorax annandalei (Hora)*
Omb	*Ompok bimaculatus (Bloch)*

Appendix 2. (Continued)

Code	Family
Belonidae	
Xc	*Xenontodon cancila (Hamilton-Buchanan)*
Aplocheilidae	
Al	*Aplocheilus lineatus (Valenciennes)*
Peocilidae	
Ad	*Aphanius dispar (Ruppell)*
Syngnathidae	
Ic	*Ichthyocamus carce (Hamilton-Buchanan)*
Mastecembelidae	
Ma	*Mastacembelus armatus (Lacepede)*
Chandidae	
Cn	*Chanda nama (Hamilton-Buchanan)*
Path	*Parambassis thomasii (Day)*
Pad	*Parambassis dayii (Bleeker)*
Gobidae	
Glg	*Glossogobius giuris (Hamilton-Buchanan)*
Pew	*Periophthalmus weberi (Eggert)*
Pek	*Periophthalmus koelreuteri (Pallas)*
Nandidae	
Nan	*Nandus nandus (Hamilton-Buchanan)*
Cichlidae	
Esur	*Etroplus suratensis*
Orm	*Oreochromis mossambica (Peters)*
Megalopidae	
Mcyp	*Megalops cyprinoides (Lacepede)*
Teraodontidae	
Tt	*Tetrodon travancoricus (Hora and Nair)*
Eleotridae	
Ecan	*Eleotris canarensis (Bloch and Schneider)*
Gerridae	
Gers	*Gerres setifer (Hamilton-Buchanan)*
Hemiramphidae	
Hyl	*Hyporhampus limbatus (Valenciennes)*