

RELATIONS OF PHYSICAL HABITAT TO FISH ASSEMBLAGES IN STREAMS OF WESTERN GHATS, INDIA

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Abstract. The present study, the influence of habitat structure on fish assemblages were assessed in fifteen selected streams of Western Ghats, India. Each stream 100m reach was quantified for depth, flow, velocity, fish cover, percentage of pool and riffle and fish density. Highest mean velocity (0.4 m/sec.) was recorded in Thalana stream and deeper habitats were found in Kallar stream. High species diversity was found in Achankoil stream ($H' = 1.15$) and low species diversity was recorded in Hanumannadhi stream ($H' = 0.71$). The physical habitat structure (depth, current and substrate) and cover complex were evaluated by using Evenness index (H'/H'_{max}). High diverse of physical habitat complex were encountered in Gugalthurai stream ($E = 2.8$) and high value of cover complex was encountered in Sirkuli stream. Regression analysis showed that there was a significant correlation between habitat variables and fish abundance in all the sites and the cover complex values is not significantly correlated with abundance.

Key words: *fish assemblage, stream habitats, Western Ghats, India*

Introduction

Conservation of biodiversity requires an understanding of the processes involved in the structure and function of biotic communities. Western Ghats region of India is identified as one of the “hot spots” for biodiversity (Myers, 1990) and it is an important watershed of the Peninsular India. Water of mountain streams to lakes may look homogeneous but actually they are separated by variety of environmental factors such as temperature, depth, current and substrates into a great variety of habitats. The fauna of this habitat is known to have a very high degree of endemism. Although, the quality of habitat and variety of species have declined as a result of major changes in landscapes by human activities (Armantrout, 1995).

Resource management requires a better understanding of the condition of fish communities, their habitat requirements and the factors influencing them. In stream ecosystems, the diversity and community structure are influenced by water current, depth, substrates, nutrients and riparian cover, which determine the success or failure of community within the spatial distribution limits (Ricklefs, 1987). The influence of habitat structure and complexity on fish assemblage structure has been tested mostly in North American streams (Angermeier and Karr 1984; Capone and Kushlan, 1991; Fausch and Bestgen, 1997; Gorman and Karr, 1978; Guisan and Zimmermann, 2000; Horig and Fausch, 2002; Oakes et. al., 2005; Schlosser, 1982, 1985, 1987) and

Australian streams (Bishop and Forbes, 1991; Pusey et al., 1993, 1995). Most of the information on fish habitat structure and assemblages are available from temperate streams and very meager information is available in Indian streams (Arunachalam et al., 1997; Arunachalam, 2000; Arunachalam et al., 2005). Hence, the present study addresses the influence of habitat structure on fish assemblage in fifteen different streams of Western Ghats.

Review of literature

Habitat structure has been identified as a major determinant in distribution and abundance of fishes from earlier time (Shelford, 1911). Later the zonation concept was developed by Huet (1954) where he explained the fish community in longitudinal succession with environmental characteristics. The environmental variation may have a significant impact on both assemblage structure and resource availability. Angermeier and Schlosser (1989) have examined the relative importance of habitat area, habitat volume, habitat heterogeneity and number of individuals as determinant of the species richness in a habitat patch. The influences of riparian vegetation (Cummins et al., 1989; Grefory et al., 1991; Ross, 1986), benthic organic matter (Cummins, 1974; Naiman and Sedell, 1979; Newbold et al., 1981a, b) in functional organization in stream community have been documented. Horwitz (1978) has proposed the stream order concept where the spatial heterogeneity associated with upstream versus downstream. The number of species increases in parallel with the stream order, which is attributable to an increase in habitat diversity and stability. Further more Vannote et al. (1980) have proposed the River Continuum Concept to explain the downhill movement of nutrients and organic matter from the riparian zone to the stream. With increase in stream order for each type of stream, the pressure on abiotic factors gradually decreases as spatial heterogeneity and stability improve. Moreover, human impact had now become a factor which modifies the spatial structure of fish community, for example marked changes in flow regime and the water quality (Bovee, 1982). The baseline study on the assemblage structure of fishes in south Indian streams was addressed by Arunachalam (2000) and similar work on Sri Lankan streams also available (De Silva et al., 1980; Kortmulder, 1987; Kortmulder et al., 1990).

Study Area

Western Ghats is a chain of hills of 1600 km in length running parallel to west-coast of Peninsular India (between 8° and 21° N latitudes) from the mouth of river Tapti in Gujarat to Kanyakumari in Tamil Nadu. The four major rivers flowing in the east are Godavari, Krishna, Cauvery and Tamiraparani, while the river Bharathapuzha, Periyar and Chaliyar in Kerala flow towards the west. There are number of numerous quick flowing streams and rivers arising on the western slope discharging into the Arabian Sea. In the present study fifteen streams covering major river basins representing from Tamil Nadu, Kerala and Karnataka states are selected. Summary of the study streams and their general features are given in *Table 1*.

Table 1. Summary of study sites general features in the Western Ghats, India.

Sites	River basin East/West flowing	Latitude/ longitude	Altitude (m)	Stream order	Stream gradient (%)	Air temp (°C)	Mean width (m)
S1-Samikuchi	Chittar - II West flowing	8° 25' N 77° 25' E	500	3	7	28	45.6
S2-Thalayana	Manimuthar East flowing	8° 35' N 77° 25' E	300	3	7	32	25.6
S3-Karaiyar	Tamiraparani East flowing	8° 40' N 77° 20' E	300	3	7	30	13.8
S4-Hanumannadhi	Chittar East flowing	9° 05' N 77° 20' E	200	3	2	30	37.4
S5-Gugalthurai	Cauveri East flowing	11° 40' N 76° 45' E	600	3	6	30	11.5
S6-Kallar	Vamanapuram West flowing	8° 45' N 77° 15' E	800	3	7	28	22
S7-Achankoil	Achankoil West flowing	9° 10' N 76° 50' E	600	4	4	27	20
S8-Panniyar	Periyar West flowing	9° 45' N 77° 15' E	912	3	6	28	14
S9-Thalipuzha	Cauvery East flowing	11° 30' N 76° 15' E	750	3	3	31	9.1
S10-Bavalipuzha	Cauvery East flowing	11° 55' N 76° 45' E	1350	3	4	31	20
S11-Ekachi	Cauvery East flowing	12° 45' N 75° 45' E	700	3	4	26	21
S12- Kigga	Thunga East flowing	13° 20' N 75° 15' E	900	3	8	20	9.5
S13-Thunga	Thungabadhra East flowing	13° 45' N 76° 20' E	600	5	1	26	80
S14-Sirkuli	Aghanasini West flowing	14° 30' N 74° 45' E	900	3	4	34	55
S15-Ganeshpal	Bedti river West flowing	14° 15' N 74° 45' E	700	4	3	29	75

Materials and methods

Quantification of habitat characteristics and habitat inventory were followed by the methods described in Arunachalam (2000). Inventory was carried out at a fixed point, which is designed as a reference point. Each stream a 100 m reach was quantified for depth, flow and substrate characteristics. Number of transects usually 5-10 were taken across the stream channel, the depth, water velocity and dominant substrates were measured or estimated at 0.5 or 1 m intervals across the transects. Water velocity was recorded with a digital electronic Pigmy water current meter (Model: Propeller type no. Lynx pp. 001). The depth measurement were used to determine the proportion of the habitat within six depth categories (D1–6) corresponding to the 0-10, 11-30, 31-60, 61-100, 101-150 and >150cm, respectively. Water velocity was grouped into four categories (F1-4): zero, low, moderate and fast corresponding to 0-0.15, 0.16-0.30, 0.31-0.60 and >0.60m sec⁻¹ respectively. Substrate was classified as Bedrock (>512mm diameter), boulder (128-512mm), cobble (64-128), gravel (16-64mm), sand (1-16) and leaf litters. Fish cover was classified into seven categories: No cover, Small boulder undercut, Boulder undercut, Submerged log, Overhanging vegetation, Bedrock undercut

and Root undercut. The number of unique configuration of each category and their frequencies of occurrence were used to compute Evenness index (H'/H'_{\max}) for each parameters. These index values for depth, current and substrate were summed to give overall measures of physical habitat complexity with a maximum value of three. A total habitat complexity index (Physical + cover) was then estimated by summation of the physical and cover components (Pusey et al., 1995). Area (length x mean width of the channel), Volume (area x mean depth) and % of Pool-riffle habitat in 100m reach of each site were estimated based on Angermeier and Schlosser (1986). Riparian cover in the site was estimated using spherical Densimeter (model: C).

Fish sampling was performed in individual habitats using mono-filamentous gill nets (mesh size 8 to 25 mm), cast net and dragnets. Based on the fish catch and underwater observation, species richness (S) and fish abundance data were generated for each site Pusey et al. (1995) Relationship among number of individuals, habitat areas, habitat volume, % of pool and riffle, % of riparian cover and habitat complexity were examined using linear regression (Angermeier and Schlosser, 1986). Except habitat complexity all other data were \log_{10} – transformed in the analysis in order to minimize effects of non-normality.

Results

Structural characteristics such as mean channel width, mean depth and mean flow were generally varied among the study streams. *Table 2* shows the major structural features of the study sites. Deeper habitats were found in Kallar stream (mean depth 98.6 cm). Mean stream width was varied from 9.1 to 80 m among study stream. Highest mean velocity (0.4 m/sec.) was recorded in Thalayanai stream of Tamilnadu region. *Table 3* shows the major physical habitat variables and the biotic variables. Among the fifteen streams, the high species diversity was found in Achankoil stream ($H' = 1.15$), next to that the Kallar stream ($H' = 1.14$) had greatest species diversity and low species diversity was recorded in Hanumannadhi stream ($H' = 0.71$). Physical habitat complexity index (Physical + cover) ranged from 2.22 to 2.83. Highest habitat complexity was recorded in Gugalthurai stream whereas in Sirkuli stream the cover complexity was high (*Fig. 1*). Habitat volume was high in Thalaiyanai stream, which inhabits greater density of fishes (595 in 100 m reach).

Table 4 shows the result of regression analysis between habitat characteristics and fish abundance. There was a positive correlation between habitat characteristics and fish abundance in all the sites and the results were highly significant ($p > 0.01$) (Habitat volume $r^2 = 0.53$; Habitat area $r^2 = 0.66$; Physical habitat complex $r^2 = 0.76$), whereas in the cover complex values is not significantly correlated with abundance. Regression analysis also showed that habitat complexity, habitat volume, habitat area, instream cover and percentage of pools-riffles had some capability of predicting fish abundance.

Table 2. Structural characteristics of study streams of Western Ghats, India.

Sites	S1	S2	S3	S4	S5	S6	S7
Mean width (m)	45.6	25.6	13.8	37.4	11.5	22	20
Mean depth (cm)	53.2	84.3	51.8	23.3	53.5	98.6	34.8
Depth (%)							
Depth 1	13.0	4.7	6.9	4.3	0	6	2
Depth 2	30.4	9.5	37.9	56.6	31.8	15	23
Depth 3	19.6	26.5	20.7	34.8	27.3	30	42.7
Depth 4	29.6	31.0	20.7	4.3	31.8	24.5	26
Depth 5	7.4	14.3	10.3	0	9.0	20.5	0
Depth 6	0	14.3	3.5	0	0	4	6.3
Mean flow (V = m/sec)	0.23	0.4	0.27	0.17	0.19	0.28	0.32
Flow (%)							
Stagnant	37.5	25	0	55.5	46.0	15	33
Slow	25.0	0	80	44.5	23.3	42.2	15.5
Moderate	37.5	50	20	0	30.7	25	36.5
Turbulent	0	25	0	0	0	17.5	15
Substrates (%)							
Bedrock	57.5	30.8	11.2	26.5	14	9.5	9
Boulder	18.2	40.0	33.7	18.6	24	12.5	12
Cobble	12.3	12.4	15.0	26.5	30	22.0	22
Gravel	3.0	10.0	3.8	0	8	21.5	21
Sand	7.5	4.8	32.5	28.4	17	26.5	28
Leaf litter	1.5	2.0	3.8	0	7	8.0	8
Fish covers (%)							
No cover	0	0	10	10	0	0	15
Small boulder undercut	31	18	22	22	13	37	0
Boulder undercut	28	24	17	17	30	30	0
Submerged log	7	6	6	6	0	0	15
Overhanging vegetation	3	13	17	17	18	15	46
Bedrock undercut	31	24	24	0	30	12	0
Root undercut	0	15	15	17	9	6	24

Sites	S8	S9	S10	S11	S12	S13	S14	S15
Mean width (m)	14	9.1	20	21	9.5	80	55	75
Mean depth (cm)	10	38.9	69.0	36.3	54.3	84.7	52.9	62.5
Depth (%)								
Depth 1	10	3	0	0	0	0	17.2	0
Depth 2	33	39.4	11.1	35	21.4	21.1	38.0	18.2
Depth 3	37	36.4	28.9	65	46.4	26.3	13.8	27.2
Depth 4	20	21.2	51.1	0	28.6	26.3	17.2	36.4
Depth 5	0	0	8.9	0	3.6	7.9	3.5	18.2
Depth 6	0	0	0	0	0	18.4	10.3	0
Mean flow (V = m/sec)	0.3	0.20	0.14	0.2	0.3	0.27	0.27	0.06
Flow (%)								
Stagnant	70	50	60	46.2	50.0	11.1	38.5	90
Slow	20	33.3	10	23.0	16.7	44.4	23.0	10
Moderate	0	16.7	30	30.8	33.3	44.4	30.8	0
Turbulent	0	0	0	0	0	0	7.7	0
Substrates (%)								
Bedrock	23	8	47	35	70.8	10	19.5	60
Boulder	20	42	29.4	13.3	10.8	-	9.7	20
Cobble	14	6	2.0	21	6.6	-	25.3	-
Gravel	12	3	1.9	9	1.4	10	13.4	10
Sand	20	31	14.7	16.8	6.6	80	17.9	10
Leaf litter	11	10	5.0	4.9	3.8	-	14.2	-
Fish covers (%)								
No cover	0	18	10	30	0	67	13	25
Small boulder undercut	40	27	20	26	23	0	17	10
Boulder undercut	12	27	40	17	12	22	13	25
Submerged log	0	0	0	0	0	0	0	0
Overhanging vegetation	20	14	10	9	32	0	13	0
Bedrock undercut	16	9	10	9	12	11	22	35
Root undercut	12	5	10	17	5	0	22	5

Table 3. Physical habitat variables and biotic variables in the study streams of Western Ghats, India.

Streams	Species richness (S)	Species diversity (H')	Habitat		In-stream cover (%)	Pool, riffles (%)	Habitat complexity		Fish density (Nos.)
			area (m ²)	volume (m ³)			Physical	Cover	
Samikuchi	12	1.03	953	306.73	50	71	2.655	0.854	354
Thalayanai	18	1.11	1103	628	80	63	2.664	0.956	595
Karaiyar	10	0.94	884	326.62	75	80	2.433	0.962	278
Hanumannadhi	6	0.71	589	206.4	20	60	2.675	0.961	239
Gugalthurai	15	1.08	912	428.23	60	65	2.833	0.94	407
Kallar	17	1.14	924	265.5	75	63	2.788	0.893	521
Achankoil	17	1.15	964	288.54	80	69	2.696	0.915	568
Panniyar	10	0.90	597.8	225.34	70	53	2.671	0.926	249
Thalipuzha	9	0.88	764.1	367.63	25	65	2.564	0.925	239
Bavalipuzha	15	1.08	842	267.69	65	63	2.381	0.898	296
Ekachi	11	1.01	659	233.5	65	79	2.805	0.946	306
Kigga	11	0.97	399	147.11	85	65	2.335	0.899	246
Thunga	16	1.16	896	525.8	40	65	2.419	0.768	398
Sirkuli	11	0.95	1115	388.47	65	71	2.78	0.984	307
Ganeshpal	9	0.91	755	327.42	30	66	2.222	0.895	281

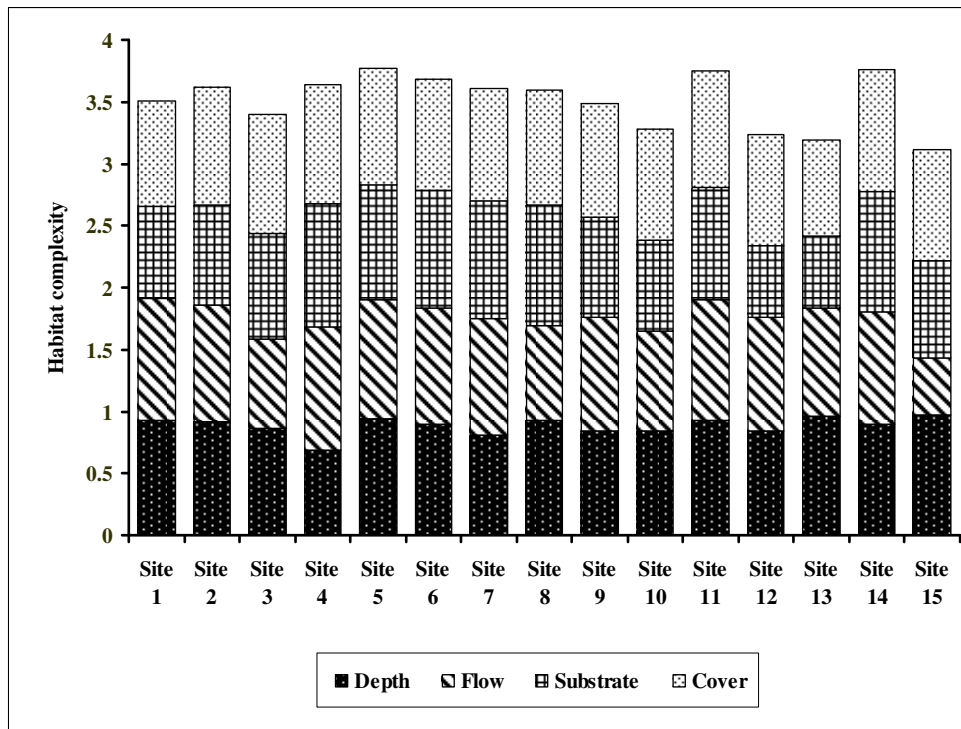


Figure 1. Habitat complexity index of fifteen streams of Western Ghats, India.

Table 4. Regression of fish abundance vs. habitat area, habitat volume, instream cover, percentage of pool-riffle and habitat complexity.

Variables	Intercept B	Slope A	r ²
Habitat area	0.58	1.45	0.66*
Habitat volume	0.62	0.91	0.53*
Instream cover	0.66	0.08	0.45
% of pools-riffles	0.21	1.31	0.56*
Physical Habitat complex	1.11	-1.23	0.76*
Cover complex	0.16	2.90	0.32

*P<0.01

Discussion

The physical habitat (depth, current and substratum) forms the 'structure' within which an organism makes its home. This habitat structure determines the abundance and diversity of organism (Baretto and Uieda, 1998; Hubert and Rahel, 1989; Hynes, 1970; Pusey et al., 1993; Schlosser, 1982). The basic pattern of increasing species richness and low replacement are consistent with the hypothesis based on habitat diversity (Horwitz, 1978). Importance of habitat structure has been identified as the primary basis on which many biological communities are organized (Schoener, 1974) and several studies have supported this generalization for fish communities (Aadland, 1993; Angermeier and Karr, 1984; Angermeier and Schlosser, 1986; Bain et al., 1988; Evans and Noble, 1979, Jackson et al., 2001, Lohr and Fausch, 1997, Matthews et al., 1994, Pusey et al., 1995; Romanuk et al., 2006; Schlosser and Toth, 1984; Schlosser, 1982; Tallman and Gee, 1982). The organization of fish assemblages in the present study also follows the uniform pattern reported from other regions. Also Williams (1964) emphasized that in larger surface areas there will be many habitats and the fauna will increase when the surface area increases. In the present study significant correlation between fish species abundance and habitat area supports the hypothesis. However, in aquatic environment, the third spatial dimension (i.e., depth) can be included in habitat patch (Angermeier and Schlosser, 1986). The volume predicted fish abundance more than habitat area, thereby suggesting that the area and depth of stream habitat also influence distribution of stream fishes (Angermeier and Schlosser, 1986, Harvey and Stewart, 1991; Pusey et al., 1995). The influence of depth on fish abundance in the present study also falls in line with the earlier findings.

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REFERENCES

- [1] Aadland, L.P. (1993): Stream habitat types: Their fish assemblages and relationship to flow. – *North American Journal of Fisheries Management* 13: 790-806.
- [2] Angermeier, P.L., Karr, J.R. (1984): Relationships between woody debris and fish habitat in a small warm water stream. – *Trans American Fisheries Society* 113: 716-726.
- [3] Angermeier, P.L., Schlosser, I.J. (1989): Species area relationship for stream fishes. – *Ecology* 70: 1450-1462.
- [4] Armantrout, N.B. (1995): Condition of the world's aquatic habitats. – Oxford IBH Publishers, New Delhi.
- [5] Arunachalam, M., Madhusoodanan, K., Nair, C., Vijverberg, J., Kortmulder, K. (1997): Food and habitat partitioning among fishes in stream pools of south Indian river. – *International Journal of Ecology and Environmental Sciences* 23: 271-395.
- [6] Arunachalam, M. (2000): Assemblage structure of stream fishes in the Western Ghats (India). – *Hydrobiologia* 430: 1-31.
- [7] Arunachalam, M., Sivakumar, P., Muralitharan, M. (2005): Habitat evaluation of pristine headwater streams of Western Ghat mountain ranges, Peninsular India. – In: Johal, M.S. (ed.) *New trends in Fishery Development in India*, Punjab University, India, pp. 253-286.
- [8] Bain, M.B., Finn, J.T., Booke, H.E. (1988): Stream flow regulation and Fish community structure. – *Ecology* 69: 382-392.
- [9] Baretto, M.G., Uieda, V. S. (1998): Influence of the abiotic factors on the ichthyofauna composition in different order stretches of Capivara River, Sao Paulo State, Brazil. – *Verh. International Limnology* 26: 2180-2183.
- [10] Bishop, K.A., Forbes, M.A. (1991): The freshwater fishes of northern Australia. – In: Haynes, C.D., Ridpath, M.G., Williams, M.C. (eds.), *Monsonal Australia: Landscape, Ecology and Men in the Northern Lowlands*, Rotterdam, pp. 79-108.
- [11] Bovee, K.D. (1982): A guide to stream habitat analysis using the Inflow Incremental Methodology. – U. S. Fish and Wildlife Service, FWS/OBS 82/26.
- [12] Capone, T.A., Kushlan, J.A. (1991): Fish community structure in dry season stream pools. – *Ecology* 72: 983-992.
- [13] Cummins, K.W. (1974): Structure and function of stream ecosystems. – *Bio Science* 24: 631-641.
- [14] Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B., Taliaferro, W.B. (1989): Shadders and Riparian Vegetation: Leaf litter that falls into the streams influences communities of stream invertebrates. – *Bio Science* 39(1): 27-30.
- [15] De Silva, S.S., Cumarantunga, P.R.T., De Silva, C.D. (1980): Food, feeding ecology and morphological features associated with feeding of four co-occurring cyprinids. – *Netherland Journal of Zoology* 30: 54-73.
- [16] Evans, J.W., Noble, R.L. (1979): The longitudinal distribution of fishes in an east Texas stream. – *American Middle Naturalist* 101: 333-343.
- [17] Fausch, K.D., Bestgen, K.R. (1997): Ecology of fishes indigenous to the central and southwestern Great Plains. – In: Knopf, F.L., Samson, F.B. (eds.), *Ecology and conservation of Great Plains vertebrates*. - Springer-Verlag, New York, pp. 131-166.
- [18] Gorman, O.T., Karr, J.R. (1978): Habitat structure and stream fish community. – *Ecology* 59: 507-515.
- [19] Grefory, S.V., Swanson, F.D.J., Mckee, W.A., Cummins, K.W. (1991): An ecosystem perspective of riparian zones. – *BioScience* 41: 540-549.
- [20] Guisan, A., Zimmermann, N.E. (2000): Predictive habitat distribution models in ecology. – *Ecological Modeling* 135: 147-186.
- [21] Harvey, B.C., Stewart, A.J. (1991): Fish size and habitat depth relationship in headwater streams. – *Oecologia* 87: 29-36.
- [22] Horig, K.B., Fausch, K.D. (2002): Minimum habitat requirements for establishing translocated cutthroat populations. – *Ecological Applications* 12: 535-551.

- [23] Horwitz, R. J. (1978): Temporal variability patterns and the distributional patterns of stream fishes. – *Ecological Monograph* 48: 307-321.
- [24] Hubert, W.A., Rahel, F.J. (1989). Relations of physical habitat to abundance of four nongame fishes in high – plains streams: a test of Habitat Suitability Index models. – *North American Journal of Fisheries Management* 9: 332-340.
- [25] Huet, M. (1954): Biologie Profiles en long et en travers des *Caux courantes*. – *Bull. Franc. Piscicul* 27: 41-53.
- [26] Hynes, H.B.N. (1970): *The ecology of Running Waters*. – Liverpool University Press, Liverpool.
- [27] Jackson, D.A., Peres-Neto, P.R., Olden, J.D. (2001): What controls who is where in freshwater fish communities – the roles of biotic, abiotic and spatial factors. – *Canadian Journal of Fish and Aquatic Sciences* 58: 157-180.
- [28] Kortmulder, K. (1987): Ecology and behaviour in tropical freshwater Fish communities. – *Arch. Hydrobiol. Beik. Ergebn. Limnol.* 28: 503-513.
- [29] Kortmoulder, K., Padmanathan, K.C., De Silva, S.S. (1990): Patterns of distribution and endemism in some cyprinid fishes as determined by the geomorphology of south – west Srilanka and south Kerala. – *Ichthological Exploration of Freshwater* 1: 97-112.
- [30] Lohr, S.C., Fausch, K.D. (1997): Multiscale analysis of natural variability in stream fish assemblages of a Western Great Plains watershed. – *Copeia* 1997: 706-724.
- [31] Matthews, W.J., Harvey, B.C., Power, M.E. (1994): Spatial and temporal pattern in the fish assemblages of individual pools in a mid Western stream (U. S. A.). – *Environmental Biology of Fishes* 39: 381-397.
- [32] Myers, N. (1990): The biodiversity challenge: expended “hot spots” analysis. – *Environmentalist* 10: 243-256.
- [33] Naiman, R.J., Sedell, J.R. (1979): Benthic organic matter as a function of stream size in Oregon. – *Archiv. Fur. Hydrobio.* 87: 404-422.
- [34] Newbold, J.D., Elwood, J.W., O’Neill, R.V. (1981a): Measuring nutrient spiraling in streams. – *Journal of fisheries Aquatic Sciences* 37: 834-847.
- [35] Newbold, J.D., Elwood, J.W., O’Neill, R.V. (1981b): Measuring nutrient spiraling in streams. – *Canadian Journal fisheries Aquatic Sciences* 38: 860-863.
- [36] Oakes, R.M., Gido, K.B., Falke, J.A., Olden, J.D., Brock, B.L. (2005): Modeling of stream fishes in the Grate Plains, USA. – *Ecology of Freshwater Fish* 14: 361-374.
- [37] Pusey, B.J., Arthington, A.H., Read, M.G. (1993): Spatial and temporal variation in fish assemblage structure in the Mary River, southeastern Queensland: the influence of habitat structure. – *Environmental Biology of Fishes* 37: 355-380.
- [38] Pusey, B.J., Arthington, A.H., Read, M.G. (1995): Species richness and spatial variation in fish assemblage structure in two rivers of the Wet Tropics of northern Queensland, Australia. – *Environmental Biology of Fishes* 42: 181-199.
- [39] Ricklefs, R.E. (1987): Community diversity: relative roles of local and regional processes. – *Science* 235: 167-171.
- [40] Romanuk, T.N., Jackson, L.J., Post, J.R. McCauley, E., Martinez, N.D. (2006): The structure of food webs along river networks. – *Ecography* 29: 3-10.
- [41] Ross, S.T. (1986): Resource portioning in fish assemblages: a review of field studies. – *Copeia*, pp. 352-388.
- [42] Schlosser, I.J., Toth, L.A. (1984): Niche relationships and population ecology of rainbow (*Etheostoma Caeruleum*) and fantail (*E. flabellare*) darters in temporally variable environment. – *Oikos* 42: 229-238.
- [43] Schlosser, I.J. (1982): Fish Community structure and function along two habitat gradients in a headwater stream. – *Ecology Monograph* 52: 395-414.
- [44] Schlosser, I.J. (1985): Flow regime, juvenile abundance and the assemblage structure of stream fishes. – *Ecology* 66: 1484-1490.
- [45] Schlosser, I.J. (1987): The role of predation in age and size related habitat use by stream fishes. – *Ecology* 68: 651-659.

- [46] Schoener, T.W. (1974): Resource partitioning in ecological communities. – *Science* 185: 27-39.
- [47] Shelford, V.E. (1911): Ecological succession: stream fishes and the method of physiographic analysis. – *Biological Bulletin* 21: 9-35.
- [48] Tallman, R.F., Gee, J.H. (1982): Interspecific resource partitioning in a headwater stream fish, the pearl dace *Semotilus margarita* (cyprinidae). – *Environmental Biology of Fishes* 7: 243-249.
- [49] Vannote, R.L., Minshall, G.W., Cummins, K.W., Sebell, J.R., Cushing, C.E. (1980): The river continuum concept. – *Canadian Journal Fisheries Aquatic Sciences* 37: 130-137.
- [50] Williams, C.B. (1964): Patterns in the balance of nature and related problems in quantitative ecology. – Academic Press, New York.