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Patterns of microhabitat use among fourteen abundant fishes of the lower Ntem River Basin (Cameroon)

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Abstract

A study of microhabitat use by fourteen abundant fish species was undertaken in the lower Ntem River Basin in Cameroon (Africa). Seventy-one microhabitats including pools, raceways and riffles were studied twice during the 1994 and 1995 dry season. Results obtained by Canonical Correspondence Analysis (CCA) showed a good niche separation along the ordination axes I ($\lambda_1 = 0.37$) and II ($\lambda_2 = 0.20$). Microhabitat selection by these species reflects response to several physical factors including width, depth, current velocity and substrate type. However, a substantial part of the variation in species segregation was explained by both instream (% leaves, woods and roots, and aquatic plants) and bankside (% mean canopy closure) cover. A striking pattern encountered during this study was the frequent size-related variation in habitat use displayed by many species. For example, smaller individuals of *Brycinus longipinnis*, *Barbus camptacanthus*, *Distichodus notospilus*, and *D. hypostomatus*, occurred more often in faster flowing waters than did their larger conspecifics. The association displayed by CCA was high (0.957 and 0.938, respectively for the first and second axis), and Monte Carlo test (99 permutations) revealed that these associations were significantly different from random ($p = 0.01$). The implications of these results for habitat management are discussed.

Keywords: Habitat selection, niches, freshwater fishes, Canonical correspondence analysis, management, Africa.

Sélection du microhabitat par 14 espèces abondantes du bassin inférieur du Ntem au Cameroun.

Résumé

Une étude de la ségrégation spatiale dans les microhabitats de quatorze espèces abondantes a été entreprise dans le cours inférieur du bassin du Ntem au Cameroun (Afrique) pendant les saisons sèches de 1994 et de 1995. Soixante-et-onze microhabitats comprenant des mouilles, des plats et des radiers ont été étudiés. Les résultats obtenus par une Analyse Canonique de Correspondance (ACC) montrent une bonne séparation des niches spatiales des espèces le long des axes d'ordination I ($\lambda_1 = 0,37$) et II ($\lambda_2 = 0,20$). La sélection du microhabitat par les espèces dépend des facteurs physiques tels que: la largeur, la profondeur, la vitesse du courant et le type du substrat. Cependant une part importante de la variation est expliquée par la présence d'un couvert végétal sur le substrat (% de feuilles, bois morts, racines d'arbres et plantes aquatiques) et au-dessus du microhabitat (% de fermeture de la canopée). Fait remarquable, plusieurs espèces notamment, *Brycinus longipinnis*, *Barbus camptacanthus*, *Distichodus notospilus*, et *D. hypostomatus* montrent une sélection de l'habitat liée à la taille des individus. Les différentes associations révélées par l'ACC montrent une corrélation espèce-habitat élevée (0,957 et 0,938, respectivement pour les axes 1 et 2). La significativité de ces associations est testée à l'aide d'un test de Monte Carlo (avec 99 permutations) et montre qu'elles ne

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sont pas dues au hasard ($p = 0{,}01$), mais bien à l'action des variables de l'habitat. Les implications de ces résultats pour une gestion et une prédiction des travaux qui induisent des modifications physiques des rivières sont discutées.

Mots-clés: Sélection de l'habitat, poissons d'eaux douces, Analyse Canonique de Correspondance, gestion, Afrique.

INTRODUCTION

Knowledge of habitat requirements of fishes is an essential component of water quality management (Karr, 1986). Habitat partitioning is hypothesized to be of primary importance in the coexistence of species in terrestrial (Schoener, 1974) as well as in aquatic systems (Ross, 1977; Gorman and Karr, 1978; Baker and Ross, 1981; Schlosser, 1982; Greenberg, 1991), with differences in food utilization being viewed as a result of difference in space utilization (Keast, 1966; Mendelson, 1975). However, a conflicting view has been proposed by Ross (1986) for whom food partitioning is more important than habitat separation. Despite this difference and opposite to the stochastic hypothesis (Grossman *et al.*, 1985), both views highlight the role played by deterministic processes such as competition, predation, physical factors, flow regime, etc., in the organization of fish communities.

General studies on feeding behaviour are relatively common for some African freshwater fishes (*see* Lauzanne, 1988; Paugy, 1994; Kouamelan *et al.*, 1997), but a multivariate approach of fish-habitat studies is very uncommon. The study of Pouilly (1993) is the only comprehensive approach that has so far been undertaken. Although some general observations can be found in some studies (*see* Roberts and Stewart, 1976; De Merona *et al.*, 1979; Welcomme and De Merona, 1988), the relationships between natural habitat and its associated fish fauna have not been quantified in such a way that they could lead to practical applications in fisheries management.

To better understand the fish-habitat relationships, a study of microhabitat use by fourteen of the most abundant fish species of the lower Ntem River Basin was undertaken as part of an overall programme on the biology and conservation of the fishes of this basin. This paper therefore (1) identifies the variables characterizing the main habitat types (2) describes the microhabitat partitioning among the fish assemblages and (3) indicates the life stages associated with the major habitat types.

MATERIAL AND METHODS

Study sites

The study was conducted in 8 small streams of the lower Ntem River Basin (*see* Fig. 1). These streams are characterized by brown, though relatively transparent (water transparency goes as far as depth), acidic water ($4.4 \leq \text{pH} \leq 6.4$); dissolved oxygen is low [$2.5 \leq O_2$ mg.l^{-1} ≤ 4.6], as is the conductivity [$21.1 \leq$ cond. µS.cm^{-1} ≤ 31.2]. Water temperature is between 20 and 26 °C (mean = 23.5 °C). The substrate consists mainly of physical (in increasing size, from clay-mud to large rocks) and biotic (leaves, woods and roots, and aquatic plants) structures. The study area is located within the coastal plain which borders the Gulf of Guinea. It is below 300 m above sea level and usually much less. Rainfall is abundant (always more than 2 m per year), the humidity of the atmosphere is always high and the mean annual temperature ranges between 25 ° and 27 °C. These conditions favour the development of shaded , luxuriant forest called Atlantic or Cesalpiniacae forest.

Sampling

The streams were sampled during the dry season, which extends from mid-December to mid-March. During this period, almost all the streams exhibited a reduced flow, and habitat patches could be easily identified. They included pools and riffles as predominant habitat types. Besides these, shallower stretches of raceways and backwaters were also present, but only pools, riffles and raceways were sampled. The two former were more frequently sampled than the latter. Sixteen pools, 12 riffles and 3 raceways were sampled in 1994, whereas 14 pools, 20 riffles and 6 raceways were sampled in 1995. In total, 71 microhabitats were studied (Table 1). They were assessed on a series of transects following methods described by Angermeier and Karr (1983). Distance between transects ranged from 1 to 3 m and distance between sampling points from 0.5 to 1 m. Depth, substrate, current velocity and cover availability were measured at each sampling point, while canopy closure and height were evaluated at the center of each transect.

Fish sampling was done using a backpack electrofisher from Smith Root Inc. (Model 12 Pow, battery powered) which is highly efficient in these low-conductivity waters. Each microhabitat was sampled using

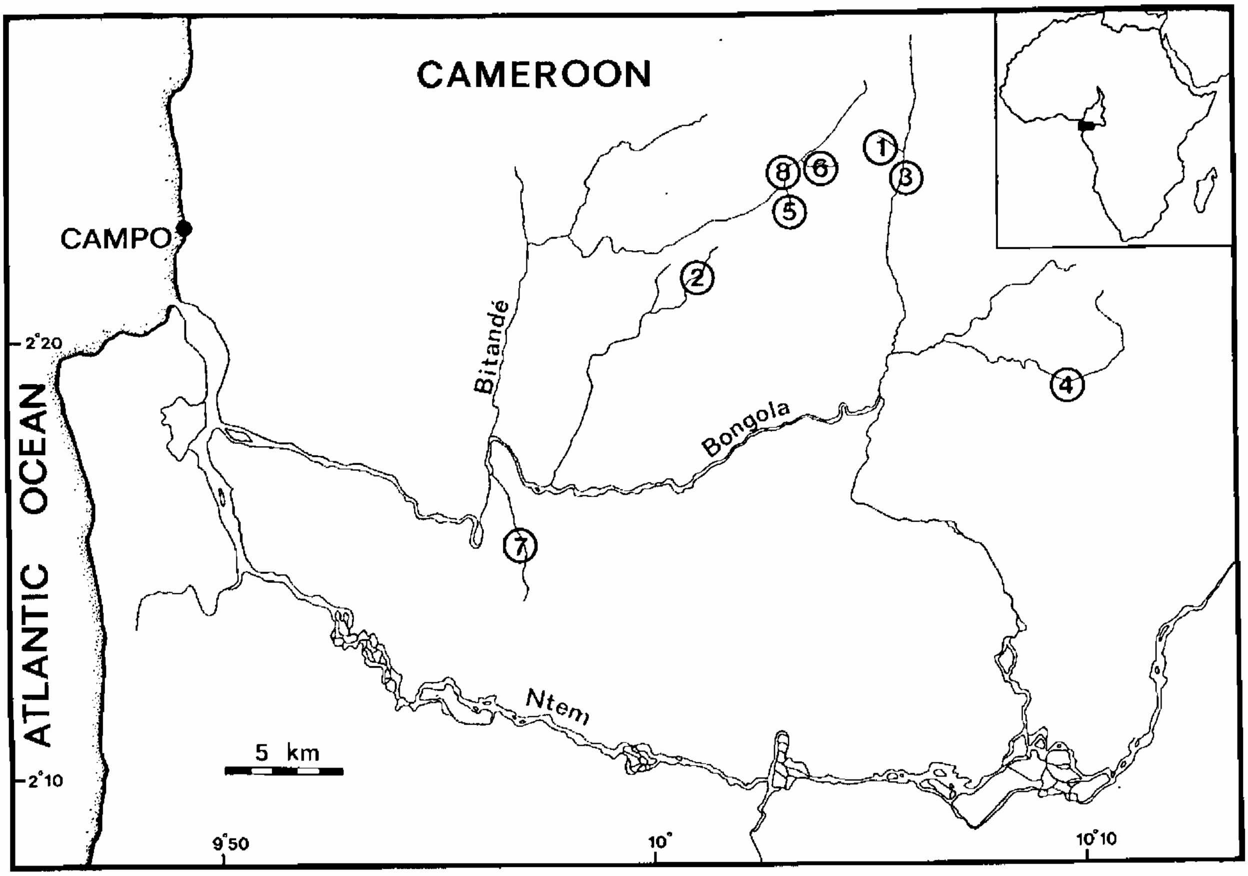

Figure 1. – Map of the study area in the lower Ntem River Basin indicating the sampled streams.

three passes of electrofishing following the procedure described in Kamdem Toham and Teugels (in press): capture efficiency varies with species, size of fish, visibility and flow conditions and habitat structure. After five passes, capture rates declined to zero. New species were not added after three passes and approximately 80-90 % of the individuals were captured. Due to the abundant cover, some fish probably escaped from sampling. However, because of the small size of the stream and the repetitive electrofishing, it is unlikely that a large number of fish could escape.

Data analysis

Canonical Correspondence Analysis (CCA) was used to evaluate fish-habitat relationships, and to identify habitat variables contributing to spatial segregation. In CCA the ordination of the main matrix (the species data, by reciprocal averaging), is constrained by a multiple regression on variables included in the second matrix (habitat variables). CCA excels at representing community data where species response to environmental variables show a unimodal curve (Jongman *et al.*, 1987). This is based in the assumption that all species occur in a characteristic, limited range of habitats, and within their range, they tend to be most abundant around their particular environmental optimum (Ter Braak and Verdonschot, 1995). Thus, CCA leads to an ordination diagram that expresses the main relations between the species and each of the environmental variables (Jongman *et al.*, 1987). The position of the species center (the weighted averages of the species) along the ordination axes represents their optima, thereby being appropriate for the goals defined for this study.

Monte Carlo permutation tests (99 permutations) were used to statistically test under null model (random distribution of species in the habitat), the significance of the association displayed by CCA. The tests are carried out by randomly linking the habitat variables to the species data, which results in a "random data set". For each random data set, CANOCO calculates one or two test statistics, namely the first eigenvalue and/or the sum of all eigenvalues. If the test statistic for the data is larger than any of the 99 permutations, than the test is significant, and one can assume that the observed association is well explained by the habitat variables.

By looking at the signs and relative magnitudes of the intraset correlations, we infer the relative importance of each habitat variable for predicting spatial segregation, and hence the nature of species-environment correlation. The intraset correlations are the correlation coefficients between the habitat variables and the ordination axes. The species-environment correlation is a measure of the association between species and environment (habitat variables). The importance of the association is well expressed by the eigenvalue (λ), which is a measure of the maximum niche separation along the ordination axis (Ter Braak and Verdonschot, 1995).

Prior to ordination, ln (x + 1) or ArcSin $\sqrt{x}$ transformations were used where appropriate.

Five species were separated into size-classes for analysis, viz.: *Brycinus longipinnis, Barbus camptacanthus, Distichodus notospilus, D. hypostomatus,* and *Chromidotilapia batesii.* Their size-classes are given in Table 2. They were distinguished by correlating the standard length range of the species captured with the different microhabitats.

The analysis was performed on the standardized abundance (fish/m^2) and habitat-specific variables (given in Table 1) matrix using the computer program CANOCO (Ter Braak, 1991). For graphs the STATISTICA package (Statsoft, version 5.0) was used.

RESULTS

Thirty-four species were collected from the habitats (Tables 1, 2). Fourteen of them representing at least 5 % of the catches in each of the microhabitats were further considered for comparisons. The fourteen species represented 2 860 individuals and comprise 7 families and 11 genera.

Species-habitat relationships

Results of a CCA offer a clearer insight into the important variables structuring habitat use by fishes. Among the ordination axes extracted from the analysis, only the first and second showed a maximum niche species separation (with respectively $\lambda_1 = 0.37$, and $\lambda_2 = 0.20$), therefore our interpretation will be limited to these two axes. The first CCA axis mainly reflects the longitudinal gradient. Width, depth, and % boulders were positively correlated with the first axis, whereas % canopy closure, % leaves and woods, and aquatic plants were negatively correlated (Table 3, Fig. 2). Consequently, large site scores indicate deeper habitats with more coarse substrate, an open canopy and less abundant leaves. Conversely, large negative scores indicate shallower habitats with less coarse substrate (gravel or sand), a more closed canopy and abundant leaves.

The second CCA axis mainly reflects the flow gradient (Table 3, Fig. 2). The variables strongly correlated with this axis include depth and current velocity. The first one was negatively correlated, while the second one was positively correlated. Therefore, along the second axis, large positive scores represented habitats with swifter velocity and shallower depth: they correspond to riffles, which are located in the upper part of the graph. Large negative scores represent deeper habitats with slow velocity: they correspond to pool habitats and they are located in the lower part of the graph (Fig. 2). In between are the raceway habitats: they formed a fairly tight cluster in the middle left part of the graph (Fig. 2), suggesting as shown by sites scores, a moderate depth and current velocity, and a more fine substrate for this habitat category.

Species scores (the weighted averages) on both axes were used to relate each species to its habitat preferendum. *Aphyosemion lugens* and *A. ahli* were associated with shallower riffles of moderate velocity, a lower canopy height and a maximal canopy closure, abundant leaves and aquatic plants, and gravel as substrate type (Fig. 2). In contrast, *Epiplatys sexfasciatus* and *Brienomyrus kingsleyae* made wide use of a range of velocity, as they are found in each habitat type. Their position near the origin indicated that the habitat condition described in this study has a neglected effect in their distribution. However, the weighted averages of *B. kingsleyae* suggest that this species prefers habitats with at least slow flowing water.

The three spiny eel species (Mastacembelidae) exhibited marked differences in habitat use (Fig. 2). *Aethiomastacembelus sclateri*, which is often found syntopically with *Caecomastacembelus cryptacanthus*, prefers habitats of very swift velocity and rocky substrate with a more open, higher canopy. In contrast, the latter prefers habitats of moderate depth and slow velocity, abundant leaves and a sandy substrate. *Caecomastacembelus marmoratus*, which does not occur in the same river as the other two species, seems to use all types of habitats, but with an apparent preference for shallower habitats (than *C. cryptacanthus*).

Among the Cyprinidae, the main difference in habitat utilization between *Raiamas buchholzi* and *Opsaridium ubangense* is related to the current velocity (Fig. 2). The first species prefers deeper areas of slow velocity, while the second prefers areas of swifter velocity.

The species-environment correlations for the association displayed was 0.957 and 0.938 (respectively for the first and second axis), and Monte Carlo test was significantly different from random, indicating therefore that variation in species segregation was well explained by the measured habitat variables.

Size-related differences in microhabitat use (Fig. 2)

The CCA also revealed that significant size-related differences in microhabitat utilization were frequent. Small-sized and adult individuals of *Brycinus longipinnis* and *Barbus camptacanthus* were more specialized in their habitat use, being respectively associated with moderate depth and swifter velocity habitat, and

Table 1. – Physical characteristics of each sampled habitat in the lower Ntem River Basin. All the variables listed are quantitative, except aquatic plant which is expressed in presence-absence data. $r_{\alpha}rv_{\beta}$ or $P_{\alpha}rv_{\beta}$ or $ra_{\alpha}\,v_{\beta}$ mean respectively riffle$_{\alpha}$ of river$_{\beta}$, pool$_{\alpha}$ of river$_{\beta}$, and raceway$_{\alpha}$ of river$_{\beta}$. Abbreviations are as follows: Mic (microhabitat unit); Wth (width); Avd (average depth); Mad (maximum depth); Cur (mean current velocity); %sa (% sand); % SGP (% mixed sand-gravel and pebble); % Gra (% gravel); % Ple (% pebble); % Mu (% mud); % Bou (% boulder); % Lr (% large rocks); % Cl-m (% mixed clay-mud); AqP (aquatic plant); % Lw (% leaves, roots, dead woods); Cah (canopy heigth); % Cac (% canopy closure).

Code	Mic	Wth (m)	Avd (m)	Mad (m)	Cur (m/s)	% sa	% SGP	% Gra	% Ple	% Mu	% Bou	% Lr	% Cl-m	AqP	% Lw	Cah (m)	% Cac
1	r1rv1	0.8	0	0	0.2	9.1	54.5	36.4	0	0	0	0	0	1	72.7	14.2	95
2	r2rv1	0.7	0	0.1	0.2	15	45	40	0	0	0	0	0	1	55	13.4	100
3	r3rv1	0.7	0	0	0.1	10	90	0	0	0	0	0	0	1	30	7.3	66
4	r4rv1	0.7	0	0.1	0.1	20	80	0	0	0	0	0	0	1	80	5.4	75
5	r5rv1	0.9	0	0.1	0.2	13.4	56.1	30.1	0.2	0.1	0.2	0	0	1	75	14.5	86.5
6	r6rv1	0.8	0	0.1	0.2	4.4	26.1	69.6	0	0	0	0	0	1	0	10.3	30
7	p1rv1	1.3	0.1	0.1	0	56.3	43.8	0	0	0	0	0	0	1	80	6.3	98
8	p2rv1	1	0.1	0.1	0	25	62.5	12.5	0	0	0	0	0	1	68.8	4.8	95
9	p3rv1	1.5	0.1	0.2	0	22.8	50	27.1	0.1	0	0	0	0	1	78.5	9	100
10	p4rv1	1	0.1	0.2	0	33.3	66.7	0	0	0	0	0	0	1	83.3	43.3	1.4
11	p5rv1	1.7	0.1	0.3	0	87.5	12.5	0	0	0	0	0	0	0	93.7	10	85
12	p6rv1	1.5	0.1	0.2	0	7.3	4.3	78.2	0	0	4.1	0	6.1	1	100	10	90
13	r1rv2	1.6	0.1	0.2	0.2	17.2	17.2	62.1	0	0	0	0	3.4	1	58.6	6.5	86.9
14	r2rv2	1.7	0.1	0.2	0.3	29.5	6.8	47.2	5.2	0	9.1	2.3	0	1	31.8	10.2	90.9
15	r3rv2	2.1	0	0.1	0.2	52.6	0	47.4	0	0	0	0	0	1	44.7	3.9	94.4
16	p1rv2	1.8	0.2	0.3	0.1	40	16.7	43.3	0	0	0	0	0	1	56.7	12.1	80.7
17	p2rv2	2.9	0.1	0.5	0.1	37.8	20	11.1	13.4	0	11.1	6.7	0	1	28.9	8.1	96.4
18	p3rv2	2.6	0.2	0.3	0	43.4	18.9	5.6	1.9	30.3	0	0	0	1	56.6	5.6	86.4
19	r1rv3	2.1	0.1	0.2	0.4	18.8	18.8	60.4	0	0	0	0	2.1	1	37.5	11.8	80.9
20	r2rv3	3.5	0.1	0.2	0.2	7.1	3.6	85.7	3.6	0	0	0	0	1	40.5	19.9	76.1
21	r3rv3	1.8	0.1	0.2	0.3	24	44	28	2	0	0	0	2	1	60	13.6	87.8
22	r4rv3	2.3	0.1	0.2	0.1	11.1	5.5	61.1	13.9	0	0	8.3	0	1	80.6	15.6	87.9
23	r5rv3	2	0.1	0.2	0.2	8.3	13.9	75	2.8	0	0	0	0	1	38.9	27.4	99.4
24	ra1rv3	3	0.1	0.2	0.1	20.5	20.5	56.4	2.6	0	0	0	0	1	82.1	5.1	99.3
25	p1rv3	5.4	0.1	0.3	0.1	29.8	22.8	42.1	1.8	0	0	3.5	0	1	28.1	12.6	90
26	p2rv3	3.8	0.1	0.3	0	15.5	10.3	55.2	17.2	0	0	1.7	0	1	81	22	95
27	p3rv3	4.4	0.2	0.4	0	45.5	24.2	25.8	4.5	0	0	0	0	1	62.1	35	60
28	p4rv3	3.7	0.2	0.4	0	23.6	7.3	50.2	4.3	0	0	14.5	0	1	78.2	9.6	75.7
29	r1rv4	1.5	0.1	0.1	0.2	82.8	0	0	0	0	0	0	17.2	0	44.8	14.5	53.8
30	r2rv4	2	0.1	0.2	0.2	100	0	0	0	0	0	0	0	0	36.1	18.1	61.3
31	p1rv4	2.8	0.2	0.5	0	94.6	0	0	0	1.4	0	0	4.1	0	54.1	11.4	67.7
32	p2rv4	2.3	0.1	0.3	0	76.2	11.1	0	0	0	0	0	12.7	1	49.2	11.6	80.5
33	p3rv4	3.8	0.3	0.8	0	95.9	0	0	0	0	0	0	4.1	0	49	12.7	100
34	r1rv5	3.4	0.1	0.2	0.4	6.8	11.9	64.4	15.3	0	1.7	0	0	1	37.3	12.2	85
35	r2rv5	3.9	0.1	0.2	0.3	4	8	60	28	0	0	0	0	1	32	0.5	87.5
36	r3rv5	3.4	0.1	0.2	0.3	6.8	20.3	67.8	3.4	0	1.7	0	0	1	40.7	2.8	83.5
37	r4rv5	3.5	0.1	0.2	0.3	1.6	3.3	82	8.2	0	4.9	0	0	1	36.1	1.4	87.5
38	ra1rv5	2.8	0.1	0.3	0	2.2	0	84.7	8.7	2.2	2.2	0	0	1	39.1	29.4	44.3
39	ra2rv5	2.9	0.1	0.3	0.1	6.3	9.4	62.5	9.4	0	0	0	12.5	1	15.6	2.6	93
40	ra3rv5	3	0.1	0.3	0.1	5	15	45	35	0	0	0	0	0	10	3.2	95
41	p1rv5	3.3	0.2	0.5	0	0	7	79.1	2.3	0	9.3	2.3	0	1	55.8	13	93
42	p2rv5	3.1	0.2	0.5	0.1	17.1	56.1	9.8	7.3	0	7.3	2.4	0	1	65.9	13.9	71

Table 1. – (continued).

Code	Mic	Wth (m)	Avd (m)	Mad (m)	Cur (m/s)	% sa	% SGP	% Gra	% Plc	% Mu	% Bou	% Lr	% Cl-m	AqP	% Lw	Cah (m)	% Cac
43	p3rv5	4.2	0.2	0.3	0	9.7	26.4	31.9	19.4	6.9	4.2	0	1.4	1	51.4	8.1	54
44	p4rv5	4.3	0.2	0.4	0	6.5	7.6	63	7.6	5.4	9.8	0	0	1	55.4	22.6	67.5
45	r1rv6	1.9	0.1	0.2	0.1	0	2.1	79.2	6.3	2.1	10.4	0	0	1	62.5	33	84.8
46	r2rv6	2.3	0	0.1	0.4	14.6	9.8	65.9	7.3	0	2.4	0	0	1	65.9	1.3	84.4
47	r3rv6	1.7	0.1	0.2	0.2	9.3	9.3	30.2	51.2	0	0	0	0	1	34.9	15	70
48	ra1rv6	2.3	0.1	0.3	0	3.5	3.5	56.1	12.3	0	19.3	5.3	0	1	50.9	24.8	99.1
49	p1rv6	2.5	0.3	0.7	0	7.1	8.9	64.3	7.1	0	8.9	1.8	1.8	1	73.2	10.9	84
50	p2rv6	2.5	0.3	0.8	0	19.6	29.4	17.6	15.7	0	9.8	5.9	2	1	74.5	12.5	85.6
51	p3rv6	2.5	0.1	0.3	0	29.4	29.4	23.5	17.6	0	0	0	0	1	88.2	9	100
52	p4rv6	2.4	0.2	0.5	0	18.5	7.4	59.3	0	7.4	3.7	3.7	0	1	92.6	16.6	65
53	p5rv6	3.8	0.2	0.3	0	31.7	19.5	12.7	36.1	0	0	0	0	1	63.4	4	57.5
54	p6rv6	3.5	0.1	0.3	0.1	0	2.6	78.9	18.4	0	0	0	0	1	92.1	31.6	32
55	ra2rv6	2.5	0.1	0.3	0.1	0	0	30	19.3	0	39.3	11.4	0	1	46.4	13	60
56	r1rv7	2.8	0.2	0.3	0.4	4.5	29.5	36.4	6.8	0	0	22.7	0	1	36.4	4.7	84.1
57	ra1rv7	5.9	0.1	0.5	0.1	73.6	0	0	0	25.3	0	0	1.1	1	93.1	3.6	77.9
58	ra2rv7	3.7	0.2	0.4	0.1	81.3	2.1	0	0	14.6	2.1	0	0	1	70.8	2.3	76.3
59	ra3rv7	4.2	0.2	0.3	0.1	44.4	36.1	0	0	16.7	2.8	0	0	1	83.3	2	70.8
60	p1rv7	5.1	0.2	0.5	0	56.7	8.2	0	0	35.1	0	0	0	1	86.6	6.2	79
61	p2rv7	3.8	0.3	0.6	0.1	32.4	20.3	13.5	0	18.9	1.4	13.5	0	1	51.4	6.2	98.8
62	p3rv7	3.9	0.3	0.5	0	23.8	33.3	0	0	40.5	2.4	0	0	1	95.2	9	86
63	r1rv8	5.6	0.1	0.4	0.3	5.7	26.4	6.3	12.1	0	49.4	0	0	0	12.6	29.3	0
64	r2rv8	6.6	0.1	0.3	0.3	6	27.4	6	19	0	41.7	0	0	1	41.7	6.7	99.2
65	r3rv8	4.2	0.1	0.2	0.6	0	0	100	0	0	0	0	0	0	30	25	75
66	r4rv8	7.4	0.1	0.3	0.6	0	0	61.2	38.8	0	0	0	0	1	65.3	9.4	41.3
67	r5rv8	6	0.1	0.5	0.4	0	0	22	9.8	2.4	53.7	12.2	0	1	22	22.5	0
68	r6rv8	6.1	0.1	0.4	0.7	0	16.9	13	15.6	0	39	14.3	1.3	0	1.3	35.7	0
69	r7rv8	8.5	0.2	0.4	0.4	0	4.3	43.5	30.4	0	21.7	0	0	1	18.8	9.5	65
70	p1rv8	8.2	0.5	1.2	0	21.1	21.1	7	16.9	0	23.9	9.9	0	0	47.9	12.5	25
71	p2rv8	8.9	0.5	1.3	0	13.4	16.5	9.3	17.5	0	37.1	6.2	0	0	0	6.9	55.5

deeper habitat with slow velocity. In contrast, the intermediate sized individuals of both species used a wide range of different habitats. This pattern was also encountered for other species, including *Distichodus notospilus* and *D. hypostomatus*. Larger individuals of these species occupied deeper areas, whereas small-sized fish did prefer swift flowing water and shallower areas. Among the Cichlidae, young individuals of *Chromidotilapia batesii* seemed to use all kinds of habitats, but with an apparent selection for moderate depth and velocities, while larger individuals were associated with deeper habitat of slow velocity.

DISCUSSION

Our results demonstrate the influence of the habitat characteristics in species abundance and distribution patterns. Spatial segregation of fishes in the Lower Ntem Basin reflects responses to several physical factors, including: width, depth, current velocity and substrate type, which may vary for different life history stages. These results are in agreement with research carried out in temperate rivers (Gorman, 1987; Grossman *et al.*, 1987) as well as in tropical rivers (Moyle and Senanayake, 1984; Pouilly, 1993).

This study also demonstrates, however, that the habitat variables evoked above do not account for all the variation in the species segregation. The occurrence of some species for instance is positively correlated with both instream (% wood, dead wood and leaves, and aquatic plants) and bankside (% mean canopy closure) cover, viz., *Aphyosemion lugens*, *A. ahli*, *Chromidotilapia batesii*, *Barbus camptacanthus*, *Caecomastacembelus marmoratus*. The importance of instream cover has been stressed for tropical rivers (*see* Lowe-McConnell, 1975; Pouilly, 1993; Pouilly and Souchon, 1995), but its role in the physical, chemical and biological

Table 2. – Fish species collected in the 71 microhabitats, with total number observed (N) and size-classes distinguished for four species in the Lower Ntem River Basin.

Species	Code	N	Size-class (mm)
Mormyridae			
Brienomyrus brachyistius		17	
Brienomyrus kingsleyae	*Bk*	256	
Brienomyrus sphecodes		15	
Isichthys henryi		106	
Petrocephalus simus		68	
Brienomyrus hopkinsi		2	
Characidae			
Brycinus longipinnis	*Byl*		
	Byl1	60	< 45
	Byl2	195	45-70
	Byl3	223	> 70
Distichodontidae			
Distichodus hypostomatus	*Dh*		
	Dh1	70	< 85
	Dh2	52	> 85
Distichodus notospilus	*Dn*		
	Dn1	35	< 70
	Dn2	24	70-80
	Dn3	59	> 80
Cyprinidae			
Barbus camptacanthus	*Bc*		
	Bc1	142	< 70
	Bc2	86	71-85
	Bc3	41	> 85
Barbus guirali		13	
Opsaridium ubangense	*Opu*	94	
Raiamas buchholzi	*Rb*	55	
Claroteidae			
Anaspidoglanis macrostoma		21	
Parauchenoglanis ballayi		25	
Clariidae			
Clarias camerunensis		68	
Clarias longior		27	
Clarias jaensis		7	
Clarias platycephalus		3	
Cyprinodontidae			
Aphyosemion lugens	*Al*	213	
Aphyosemion ahli	*Aa*	80	
Epiplatys sexfasciatus	*Es*	330	
Procatopus nototaenia		208	
Cichlidae			
Chromidotilapia batesii	*Chb*		
	Chb1	181	< 65
	Chb2	79	> 65
Chromidotilapia finleyi		20	
Hemichromis fasciatus		103	
Malapteruridae			
Malapterurus electricus		28	
Gobiidae			
Sicydium crenilabrum		3	
Sicyopterus imitoratus		1	
Eleotridae			
Kribia kribensis		68	
Anabantidae			
Ctenopoma nanum		4	
Mastacembelidae			
Aethiomastacembelus sclateri	*Aes*	298	
Ceacomastacembelus marmoratus	*Cm*	75	
Caecomastacembelus cryptacanthus	*Cc*	155	

Codes are only given for species included in the analysis

Table 3. – Intraset correlation coefficients between habitat variables and CCA axes.

Habitat variables	Axis 1 0.37	Axis 2 0.20
Width	0.798	– 0.237
Mean depth	0.560	– 0.770
Maximum depth	0.666	– 0.657
Mean current velocity	0.356	0.753
Sand	– 0.291	– 0.308
Mixed sand-gravel-pebble	– 0.112	– 0.078
Gravel	– 0.154	0.226
Pebble	0.501	0.021
Mud	– 0.127	– 0.300
Boulders	0.795	0.085
Large rocks	0.451	– 0.161
Clay-mud	– 0.029	– 0.123
Aquatic plant	– 0.617	0.069
Leaves, woods and roots	– 0.628	– 0.087
Mean canopy height	0.155	0.223
Mean canopy closure	– 0.656	– 0.288

processes in streams has been well established for temperate rivers. For example, woody debris are an ubiquitous component of forested streams and are known to influence habitat features such as depth and current (Keller and Swanson, 1979; Angermeier and Karr, 1984) that are important for fishes. They are also known to enhance invertebrate production (Benke *et al.*, 1984), which is a major food for fishes. The frequent fish-woody debris association observed in this area has been generally related to protection from current, food (invertebrate) availability or camouflage from predators. Our results are in some ways consistent with these findings. For example, *Aphyosemion lugens* and *A. ahli* which are known to occur in less swift habitats, were often encountered in riffle habitats in our study. The presence of cover here may probably protect them from current, which agrees well with Amiet's (1987) observations. In contrast, the significant association found between *Caecomastacembelus marmoratus* (a species occurring in all types of habitats) and instream cover may be explained by the fact that this aquatic invertebrate feeder probably found abundant food here. We do recognize, however, that for many species our interpretation can only be descriptive, as without experimental manipulation, it is not

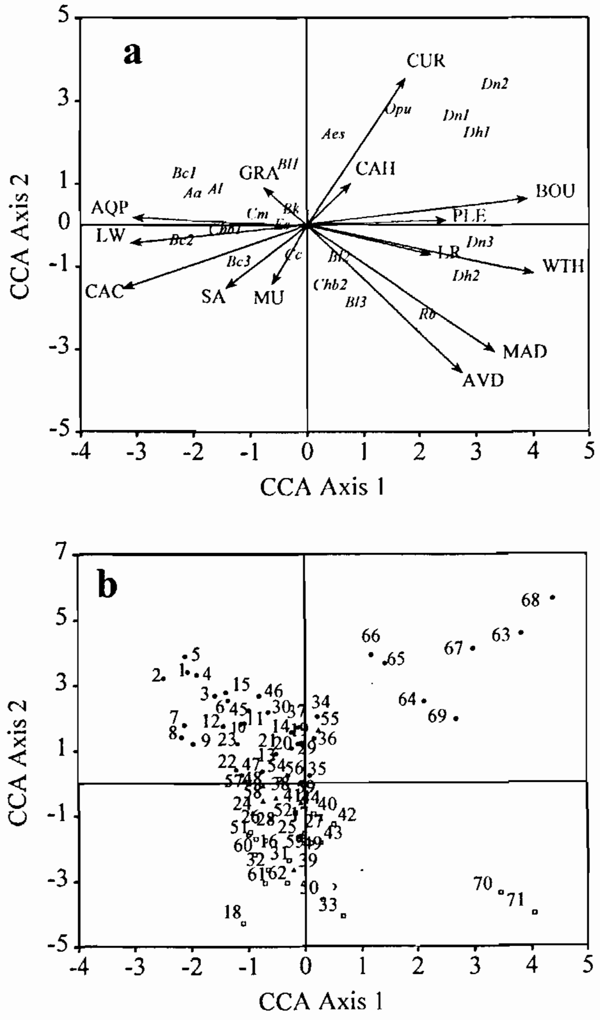

Figure 2. – a) A species-habitat variables biplot of a canonical correspondence analysis (CCA) based on 71 microhabitats. The microhabitat samples are abbreviated as follows: (●) riffles; (%) raceways; and (□) pools. The habitat variables are represented by arrows. Important habitat variables have more longer arrows than less important one. b) Microhabitat scores. The assigned number corresponds to the habitat code given in Table 1. By superimposing (a) and (b) one can infer the habitat conditions associated with each habitat or taxon.

possible to split infinitively the significance of fish-instream cover relation for each species. The importance of outstream cover has been recently discussed in Kamdem Toham and Teugels (in press), and for this reason will not be discussed here.

A more striking pattern encountered during this study was the frequent size-related variation in habitat use displayed by many species. Smaller individuals of *Distichodus notospilus*, *D. hypostomatus*, *Brycinus longipinnis*, *Barbus camptacanthus*, and *Chromidotilapia batesii*, occurred in faster flowing waters than did their larger conspecifics. A similar pattern has been reported for temperate rivers and it has been attributed in part to predation (Power, 1984; Schlosser, 1987) and in part to competition (Glova, 1986; Fausch and White, 1986). With regard to the predation hypothesis, Schlosser (1987) suggested that as a result of the predation by large piscivores and the avoidance of the latter by small fishes, the large fish mainly occur in pool habitats while the small fishes are restricted to shallower and more swifter habitats. Power (1984) hypothesized that large species are excluded from shallower habitats, where their mobility is limited and exposure to terrestrial predators is greater.

In relation to the predation hypothesis, Kamdem Toham and Teugels (in press) studied the diet of potential large piscivorous species, mainly: *Hemichromis fasciatus*, *Opsaridium ubangense*. Although feeding partly on fishes, their diets comprise a substantial proportion of ants (Lapidae and Formicidae), Decapods, Trichoptera, Ephemeroptera, and Chironomidae nymphae, which suggests a more generalized diet (carnivorous) rather than a specialized one (piscivorous). It is probable that predation by large carnivorous species might explain part of the variation in the size-related differences, but here again, without laboratory experiments, it is not possible to go beyond this interpretation and assess the mechanisms maintaining those differences. Regarding Power's (1984) contention, to our knowledge, the only terrestrial predators found within small streams of the Ntem River Basin include a bird (probably a kingfisher) and a snake. An aquatic mammalian predator (*Potamogale velox*) is also present (observed only twice during a two-year study). The real impact of these predators is not known and results obtained by Brosset (1982) in his study on the cyprinodonts of the Ivindo River Basin in Gabon, suggest that predation on fish of small streams is likely to be occasional.

The competition hypothesis evoked above is well known in coldwater streams where aggressive, territorial feeding interactions between salmonids restrict subordinate individuals to energetically less profitable foraging habitats (Fausch and White, 1986; Glova, 1986). Regrettably, the trophic biology of small size-class individuals is poorly understood in many African rivers, thereby precluding any comparison.

Management implications

The understanding of the mechanisms by which spatial segregation of species occurred is of vital importance for water resources management. Increasing pressures on stream resources of many African rivers, such as deforestation, hydropower demand, and the consequences of habitat fragmentation associated with island biogeography theory, underscore the need to develop and apply reliable quantitative methods that evaluate the suitability of aquatic habitats for fishes. Indirect consequences of deforestation on small streams may probably result in the loss of the main habitat through siltation, thereby shifting the size structure of fish, as implicitly demonstrated in our study. Hydropower demand often causes more frequent and much higher changes in velocities. Indirect evidence highlighted by our study, suggests that such flow variations may affect the resilience capacity of fishes, thereby causing serious damage to the resident community. Because a series of habitat patches within a stream is conceptually viewed as an archipelago (*see* Angermeier and Schlosser, 1989), they are also subjected to the problems associated with island biogeography (Mac Arthur and Wilson, 1967; Hugueny, 1989), and especially the impacts and processes resulting from habitat fragmentation (here loss of habitat heterogeneity or habitat loss, etc.). This may ultimately lead to the reduction in species abundance, and thus to species extinction.

One method that has been used to assess the suitability of stream habitat for fishes is the Index of Biotic Integrity (IBI). The IBI is composed of a number of fish community attributes termed metrics. Some of these metrics referred to some key species which may be chosen as suggested by Karr *et al.* (1986) and Hugueny (1989), for their particular habitat requirements or for their economical interest. The multivariate approach used in this study as well as the inferred indirect evidence, provide a direct mean for selection of such metrics.

However, for the patterns observed in this study to be used for conservation designs at large scale, they need to be tested across large geographic area. This is because a species may occupy a wider range of habitats than is evident from a study of a particular drainage. Our study was only interested in how far species make use of the spatial dimension. Further studies must try to assess the effect of trophic and temporal dimensions in the habitat selection by these fishes.

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