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Microhabitat use by fishes in the middle course of the River Gambia in the Niokolo Koba National Park, Senegal: a unique example of an undisturbed West African assemblage

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Snorkelling surveys using a point abundance method revealed high levels of microhabitat differentiation among 14 fish species from a high-visibility site in the middle reaches of the Gambia River. Habitat segregation was most strongly related to the position in the water column, flow velocity, substratum composition and presence of submerged wood.

Key words: Alestidae; Cichlidae; Cyprinidae; fish-habitat association; resource partitioning; Soudanian River.

Environmental factors and habitat settings can affect fish distribution at multiple scales, ranging from a biogeographical perspective to species-specific microhabitat use within local communities. While at large geographical scales an understanding of the structure of tropical freshwater fish communities is emerging (Roberts, 1975; Lowe-McConnell, 1987; Hugueny & Lévêque, 1994), there is a notable gap in the understanding of how tropical river fish communities are structured at a local scale (Lévêque, 1995; Herder & Freyhof, 2006). Knowledge about the freshwater fish fauna of West Africa mirrors these general trends in tropical fish ecology. Fishes in West African rivers have been subject of considerable research in relation to projects on river blindness eradication (Lévêque *et al.*, 2003), and data are available on biogeographical patterns (Paugy *et al.*, 2003). At the mesohabitat scale, information is more limited for West African assemblages. In a study of fish-habitat associations in a coastal river in Ivory Coast, however, Kouamélan *et al.* (2003) found fish distributions were strongly influenced by pollution and a dam, while Kamdem Toham & Teugels (1997) reported high mesohabitat (pools, riffles and raceways)

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segregation among species along gradients of several physical factors in relatively undisturbed, forested streams in southern Cameroon.

The fact that most fish species in West Africa have a relatively wide distribution (in comparison with other tropical regions) and the existence of a large amount of precise and long-term data on West African riverine fish distribution provides a very useful system for detecting changes in fish faunal structure in response to anthropogenic perturbations. Nevertheless, there are no studies that relate habitat use of freshwater fishes at the lowest scale of resolution (microhabitat associations), and there is a requirement for reference data on habitat use of fishes in an undisturbed habitat.

The present study investigated fish-habitat associations at a microhabitat scale in the middle reaches of the River Gambia, Senegal, West Africa. The River Gambia is a typical large West African river of Nilo-Soudanian type and is unique due to a lack of any substantial habitat alterations (*i.e.* dam construction, bank modification and severe water quality decline) (Simier *et al.*, 2006). The study area was located in the Niokolo Koba National Park in south-east Senegal where there is no human settlement along a stretch of *c.* 200 km. The river is not subjected to fishing pressure and is not affected by human-related water pollution. The aim of the study was to compare microhabitat use of riverine species of the local fish fauna and, given the fact that fish fauna in Nilo-Soudanian region is similar across river drainages, to provide reference data for further studies to examine anthropogenic effects on fish habitat use. Specifically, the study related environmental and habitat variables to the occurrence of particular species using underwater observation of fish presence and position in the water column. Additionally, the study was intended to evaluate the utility of underwater observation for small-scale investigation of fish-habitat associations in tropical rivers.

Most studies related to microhabitat use employ point abundance sampling by electrofishing (Copp & Peňáz, 1988); however, the use of electrofishing equipment is problematic under conditions with extremely low water conductivity (Glowacki & Penczak, 2005), which is typical of West African rivers. Another useful method is direct underwater observation (Orell & Erkinaro, 2007), although its use in many tropical waters (including West African rivers) is limited due to low water transparency. The present study capitalizes on the fact that the study stretch was *c.* 90 km downstream of the nearest human settlement, and water visibility exceeded 150 cm. This decreased the probability of waterborne parasitic diseases and permitted direct observations. Direct observation has the advantage of minimizing interaction with the fishes. The limitation in this study is that direct observation was not used at night and therefore may have under-represented night-active species.

The study was undertaken at Badoye (12°55′ N; 13°09′ W; 41 m a.s.l. at the lowest water level) in the middle reaches of the River Gambia, where the river flows through Niokolo Koba National Park. The region has vegetation characteristic of the transition from savannah to woodland, and the river is fringed by a gallery forest. The river is 100–250 m wide, with locally variable flow velocity. During the rainy season (late May to September), the river frequently floods adjacent oxbow lakes and forms small temporary pools. During the dry season (October to mid May), the water level in the river channel gradually decreases, forming large pools connected to shallow, rapidly flowing riffles running through large areas of exposed river bottom. In some sections a deep pool is preceded by relatively long rapids (100–400 m) with shallow water and abundant algal mats. Water visibility is low (<0·3 m) throughout the year, except for areas below rapids where water visibility may exceptionally reach up to 2 m.

The study stretch was the start of a large deep pool situated immediately below rapids with algal mats, where water visibility exceeded 1·5 m; and, at the end of the dry season, the width of the river was 192 m. Water temperature ranged from 24·9 to 31·3° C and dissolved oxygen from 3·6 to 7·8 mg.l^{-1}; pH was 6·8, and conductivity 44 $\mu\text{S.cm}^{-1}$. Sampling was conducted in mid March 2007 between 1000 and 1700 hours local time (sunrise 0700 and sunset 1900 hours). A total of 71 focal samples was taken. Each sampling point was chosen haphazardly within an 8 m wide zone (across the entire 192 m wide river stretch) below the downstream edge of the rapids. In the rapids themselves the water level was too low (0·1–0·2 m) to permit recording, while at the downstream end water depth increased abruptly, which also hindered accurate data collection. The sampling point consisted of one 750 × 750 mm area in front of the observer. The edge of the sampling area was bordered by a line drawn 45° left and 45° right from the axis of the snorkeller.

A snorkeller viewed each point for the presence of fishes. If fishes were present, the snorkeller noted their species, size and maturation class (juvenile, subadult and adult), number of individuals in each class and their position in the water column (surface, middle layer, bottom layer and in contact with substratum), and habitat data were collected. Water temperature (mean ± S.E. 29·0 ± 0·3° C) and dissolved oxygen (5·4 ± 0·1 mg.l^{-1}) were measured using an electronic probe (Greisinger GMH 3610, Regenstauf, Germany) positioned at the exact point at which fishes were located. Water depth (measured to the nearest 10 mm; mean 490 ± 30 mm, range 180–920 mm), occurrence (present or absent) of wood (present at 10% of sampled points) and leaves (4%), and distance from the nearest shore (to the nearest m) were also recorded. Flow velocity was measured indirectly as a categorical variable (Copp, 1992) from no flow (flow 0; 55% of points), weak directional water movement (flow 1; 20%), slow (flow 2; 11%), moderate (flow 3; 11%) and strong flow (flow 4; 3%). Note that for most analyses, flow 2, flow 3 and flow 4 were pooled. The substratum was grouped into five classes; mud (65%), sand (39%), gravel (5–20 mm; 38%), stones (20–250 mm; 73%) and boulders (>250 mm; 44%) (Copp, 1992). Most points comprised multiple substratum types and at each point, the relative proportion of each class was estimated. Substratum heterogeneity at sampling points was high (one substratum class 7%, two classes at 38%, three classes at 44% and four classes at 11% of sampled points). Fishes and habitat data were recorded underwater on a PVC plate. Data collection at each point took between 3 and 5 min, but only fishes present at time when the point was approached were recorded. Water temperature data were corrected to account for a linear increase in water temperature over the course of the day. For data analysis regression residuals were used, after fitting a linear regression through water temperature from morning until the end of the study ($y = 24{\cdot}1 + 0{\cdot}17x$; $r^2 = 0{\cdot}974$).

Species identification was based on Paugy *et al.* (2003); fish identification skills were acquired during 4 years of studies in the area, including a pilot study using snorkelling. The possibility cannot be entirely excluded that some large-bodied individuals were disturbed by the presence of the snorkeller in the water before the sampling point was approached and escaped before they were recorded. Several fish >500 mm standard length (L_S), including large predatory *Hydrocynus brevis* (Günther, 1864) (Alestidae) not recorded during data collection, however, were encountered by the snorkeller during pilot studies and in the present study during movements between sampling points (Reichard *et al.*, 2004; Orell & Erkinaro, 2007).

To compare the tendency of species to occur in shoals, an index of dispersion (I_D) was calculated as the variance divided by mean for each species (Copp, 1992; Herder & Freyhof, 2006). The higher the value of I_D, the higher tendency to occur in shoals is exhibited in a given species. Canonical correspondence analysis (CCA) using the CANOCO software (ter Braak & Šmilauer, 1997) was used to investigate habitat use. CCA is an ordination technique that relates community composition and its variation to variation in environmental variables.

Univariate analyses were used in addition to CCA to test for significant associations between each habitat variable and species. For continuously measured variables (water depth, dissolved oxygen and water temperature) regression analysis was performed using the R 2·4.0 statistical package (R Development Core Team, 2006). The species distribution followed a Poisson (for common species) or negative binomial (for rare species or species that occurred in large shoals) distributions. When the dispersion factor of a Poisson distribution did not equal 1, a quasi-Poisson distribution was substituted in the model. Spearman rank correlations (substratum heterogeneity and distance from the bank) were calculated for ordinal variables, and *G*-tests (flow velocity, presence of wood and substratum) were used for categorical variables. For *G*-test analyses, only the six most abundant species could be tested due to test requirements of expected values (low sample size for other species). Although flow velocity can be considered as a continuous variable, the *G*-test for categorical data was used to enable a distinction to be made between species that preferred areas with moderate flow, but avoid no flow and high flow velocity areas. To meet the assumptions of the *G*-test in this analysis, water velocity classes flow 2, flow 3 and flow 4 were pooled as a single 'high flow' class and tested against 'no flow' and 'weak flow' classes. Although data for all species were collected as three size and maturation classes, they were pooled in all analyses, except for *Raiamas senegalensis* (Steindachner, 1870) in the CCA. Generally, juvenile fishes were rarely encountered, and subadult and adult fishes had consistent habitat associations.

A total of 429 individual fishes belonging to 14 species and six families were recorded (Table I). The most abundant species was *Rhabdalestes septentrionalis* (Boulenger, 1911) whose distribution was highly aggregated (Table I). The highest proportion of sampled points was occupied by *R. senegalensis* (n = 25; 35%) and *Hemichromis bimaculatus* Gill, 1862 (n = 21; 30%). CCA revealed habitat segregation among fish species with regard to flow velocity, substratum composition, presence of submerged wood and depth of water. Water temperature

TABLE I. List of species recorded at sampling points. Their code used in figures, range of standard length (L_S) estimated during snorkelling surveys, maximum L_S reported for given species (Paugy *et al.*, 2003), number of fish recorded during the study (n) and index of dispersion (I_D; variance mean^{-1}). Significant associations ($P < 0{\cdot}05$) with continuous and ordinal habitat variables detected by regression analyses [water depth (depth), water temperature (temp) and dissolved oxygen (oxygen)] and Spearman rank correlation [substrate heterogeneity (SubHet) and distance from the nearest shore (distance)] are shown. The significant fish-habitat associations with categorical variables [flow velocity (no flow, weak flow and high flow), sand substratum (sand), gravel substratum (gravel) and presence of wood (wood)] revealed by *G*-tests are also presented. The *G*-test requirements were met only in six species and therefore categorical habitat variables were not tested in the remaining species (NA, not applicable). Positive (+) or negative (–) associations are indicated, along with details on statistical analysis (footnotes)

						Habitat associations	
Species	Code	L_S range (mm)	L_S maximum (mm)	*n* fish	I_D	Continuous and ordinal variables	Categorical variables
Poeciliidae (Cyprinodontiformes)							
Aplocheilichthys normani (Ahl, 1928)	PoNo	10–30	40	31	11·0	(–) depth*	NA
Alestidae (Characiformes)							
Brycinus nurse (Rüppell, 1832)	BrNu	70–150	220	45	6·1		
Rhabdalestes septentrionalis (Boulenger, 1911)	RhSe	30–50	50	156	25·4	(+) temp*; (+) SubHet‡	(+) weak flow$^{\|}$; (+) sand¶; (+) gravel¶
Distichodontidae (Characiformes)							
Nannocharax ansorgii Boulenger, 1911	NaAn	20–40	40	15	3·0	(+) depth*; (+) SubHet‡	NA
Cichlidae (Perciformes)							
Tylochromis intermedius (Boulenger, 1916)	TyIn	40–150	230	9	3·4		NA
Tilapia guineensis (Günther, 1862)	TiGu	30–70	280	22	4·0	(–) depth*; (+) oxygen*	
Hemichromis bimaculatus Gill, 1862	HeBi	30–60	90	34	1·7	(–) temp†;(+) distance‡	(+) wood§

Table I. Continued

Species	Code	L_S range (mm)	L_S maximum (mm)	*n* fish	I_D	Habitat associations: Continuous and ordinal variables	Habitat associations: Categorical variables
Hemichromis fasciatus Peters, 1857	HeFa	30–150	200	18	1·4		(+) weak flow‖
Cyprinidae (Cypriniformes)							
Raiamas senegalensis (Steindachner, 1870)	RaSe	20–170	250	62	3·3	(–) depth*	(+) high flow‖
Barbus niokoloensis Daget, 1959	BaNi	30–40	50	4	1·0	(+) SubHet‡	NA
Labeo coubie Rüppell, 1832	LaCo	100–450	750	12	2·9	(+) oxygen*	NA
Labeo parvus Boulenger, 1902	LaPa	60–180	350	13	2·4		NA
Labeo senegalensis Valenciennes, 1842	LaSe	350–450	550	4	4·0		NA
Polypteridae (Polypteriformes)							
Polypterus bichir Lacepéde, 1803	PoBi	500	740	1	1·0		NA

*negative binomial distribution, d.f. = 69.

†quasi-Poisson distribution, d.f. = 69.

‡Spearman rank correlation, $n = 71$.

§*G*-test, d.f. = 1.

‖*G*-test, d.f = 2.

¶*G*-test, d.f. = 4.

and dissolved oxygen had a negligible effect overall on fish distribution (Fig. 1). The first two axes in CCA accounted for 30·2 and 25·0% of variability in species-habitat data (cumulative 55·2%). For the first four axes eigenvalues were 0·518, 0·428, 0·264 and 0·171.

CCA distinguished clusters of species that have similar habitat associations. The results of univariate analyses generally supported the CCA. *Nannocharax ansorgii* Boulenger, 1911, *Barbus niokoloensis* Daget, 1959, *Hemichromis fasciatus* Peters, 1857, and *R. septentrionalis* inhabited deeper parts of the study stretch that were further from the shore, had weak (but non-zero) flow velocity and a heterogeneous substratum with high representation of sand (Fig. 1). While *R. septentrionalis* occupied space in the upper layer of the water column where water was warmer (Fig. 2 and Table I), *N. ansorgii*, *B. niokoloensis* and *H. fasciatus* were found at lower levels, though rarely directly in contact with the substratum (Fig. 2). *Aplocheilichthys normani* (Ahl, 1928), *R. senegalensis* and *Tilapia guineensis* (Günther, 1862) showed a negative association with water depth suggesting preference for shallow habitats (Fig. 1 and Table I). Two *Labeo* species, *Labeo parvus* Boulenger, 1902 and *Labeo coubie* Rüppell, 1832, were bottom-dwelling, while *Labeo senegalensis* Valenciennes, 1842, were not (Fig. 2). *Aplocheilichthys normanii* occurred exclusively in the uppermost layer below the water surface near shore with no flow (Figs 1 and 2). *Raiamas senegalensis* and *Brycinus nurse* (Rüppell, 1832) used the middle part of the water column at points where water was flowing (Fig. 2 and Table I). *Hemichromis bimaculatus* was found at points with wood and farther from the shore (Table I). The positive association of *H. bimaculatus* with submerged wood is probably related to the use of space near and below branches as the centre

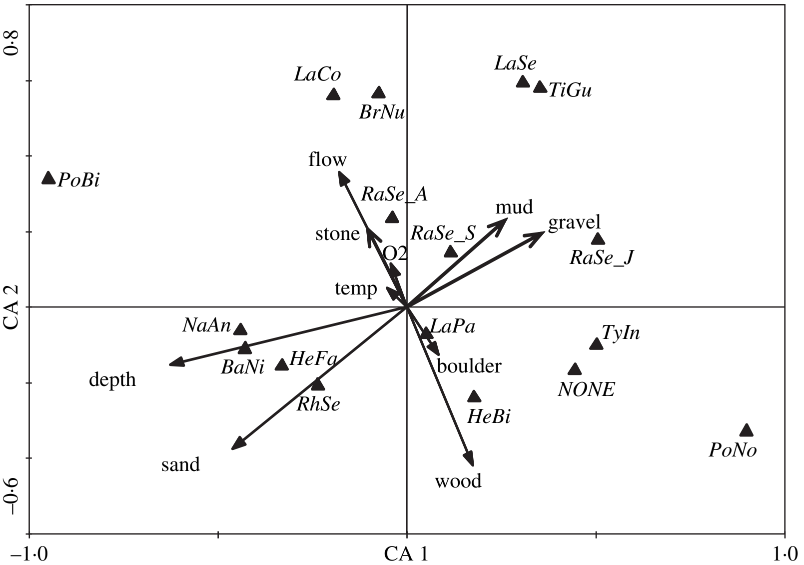

FIG. 1. Bivariate plot of canonical correspondence analysis showing position of species (▲) and habitat variables (⟶) along the first two canonical axes (see Table I for code of species names). The code NONE refers to sampled points where no fishes were recorded.

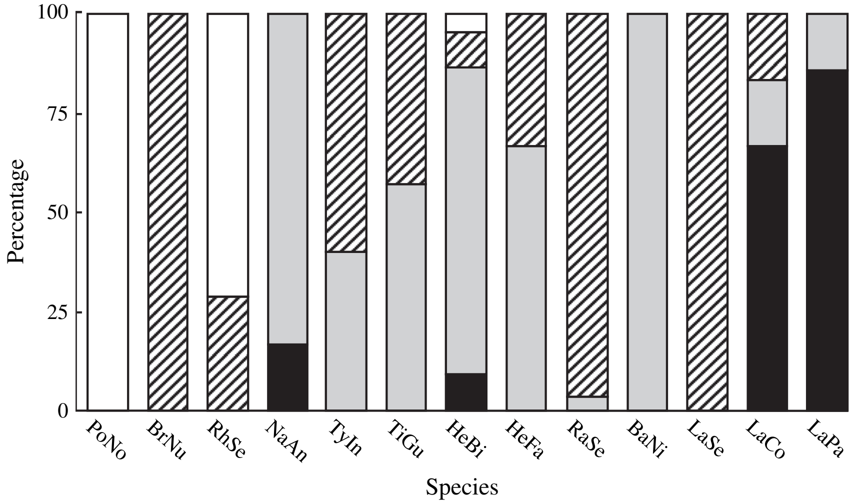

FIG. 2. Water column use by the 13 species (see Table I for code of species names) of freshwater fishes recorded during snorkelling surveys at Badoye, River Gambia, Senegal (□, surface; ▨, middle layer; ▒, lower layer; ■), on substratum.

of a territory, spawning substratum and shelter for juveniles. *Rhabdalestes septentrionalis*, *B. nurse* and *A. normani* were found in shoals, typically with six to 10 individuals per shoal in *B. nurse* (though they were also sometimes solitary) and *A. normani*, and a higher number in *R. septentrionalis*. *Hemichromis* spp. and *B. niokoloensis* were often found alone and *H. bimaculatus* frequently occurred in pairs when guarding young.

In addition to interspecific comparisons, a within-species analysis was performed for *R. senegalensis*, a cyprinid species with a protracted reproductive season (Tedesco & Hugueny, 2006), which enabled changes in habitat use across maturation stages of particular species to be tested. The principal variable that affected the habitat use of *R. senegalensis* maturation stages was the flow velocity. All maturation stages preferred areas with non-zero flow velocity, though the flow strength was positively related to maturation stage (Fig. 1).

In conclusion, the fish-habitat associations recorded in the present study varied enormously across species. An example comes from two species with comparable body size (30 mm L_S). While *A. normani* inhabited shallow marginal areas with no flow where it occurred near the water surface, *N. ansorgii*, at the other end of the habitat continuum, preferred deeper parts of the water column farther from the shore where the substratum heterogeneity was high. While this could be deduced from their morphology and diet specialization (*e.g.* position of the mouth), their respective preferences need to be confirmed by direct observation. Indeed, in *L. senegalensis*, whose body shape strongly suggests a demersal habit, no contact with the river bed was observed. While this result must be taken with caution, since the data were from a small stretch of the river, within a short time period and on small numbers of individuals, it suggests that direct observation is necessary to confirm assumed ecological characteristics. Obviously, more data are needed to substantiate this specific observation, since individuals travelling from one location to another may have been recorded. Habitat use of other species was generally congruent with their morphological adaptations and commonly accepted food habits (Lévêque, 1995).

There are other fish species inhabiting this section of the River Gambia, although they were not recorded in the survey, which was restricted to a single locality. Using beach seines and gillnets, a total of 61 species of freshwater fishes were collected in the floodplain of the River Gambia within the boundary of the Niokolo Koba National Park. Among them, 36 species were recorded in the main river channel (Reichard, 2006), but many are associated with particular mesohabitats, are nocturnal, or are rare (Daget, 1961; pers. obs.). The mesohabitat use and connectivity among habitats within the floodplain is a subject of an ongoing long-term study that uses quantitative sampling of fish communities at numerous locations among multiple years and seasons. Insights into fish-habitat associations at the small scales that emerged in the present study should facilitate interpretation of patterns found at a larger scale. In addition, data on habitat use of species from an undisturbed habitat may present a useful reference point for evaluating impacts of anthropogenic perturbations, particularly since many of the Nilo-Soudanian species in the present study are distributed over a large geographical area (Paugy *et al.*, 2003; Moritz & Linsenmair, 2005).

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