BIOTROPICA 0(0): 1–10 2011
10.1111/j.1744-7429.2011.00840.x

Hydrologic Connectivity Affects Fish Assemblage Structure, Diversity, and Ecological Traits in the Unregulated Gambia River, West Africa

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ABSTRACT

The Gambia River of West Africa is a large unobstructed river, characterized by a natural flow regime and lateral connectivity across its floodplain. Construction of a major dam, however, is planned. We compared patterns of fish diversity, habitat use, assemblage structure, and the distribution of trophic position and body morphology in riverine and floodplain habitats in Niokolo Koba National Park, located downstream of the planned dam site. A total of 49 fish species were captured, revealing a lognormal distribution as expected for species-rich assemblages. Fish species exhibited a range of habitat use patterns, from generalist to highly habitat-specific, and appeared to migrate laterally among habitats between seasons. Species richness was homogenous among habitats in the wet season yet appeared to increase with isolation from the main river in the dry season. Fish assemblage structure was best explained by the interaction between habitat type and season, underlining the importance of the natural flow regime and lateral connectivity among floodplain habitats. The abundance of fishes having elongate bodies increased with isolation from the main channel in the wet season only. The distribution of fishes having compressed cross-sectional morphology decreased with isolation from the main channel in the dry season only. These patterns of trait distribution support the conclusion that variation in hydrologic connectivity structures the fish assemblage. Our results suggest that altered flow regimes and loss of floodplain habitats after damming could lead to both decreased taxonomic and functional diversity of the fish assemblage.

Abstract in French is available in the online version of this article.

Key words: fish assemblage; functional morphology; large tropical rivers; lateral migration; multivariate analysis; pre-impoundment; reference condition; trophic position.

BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Maintaining connected, off-channel habitats and natural flow regimes is important for the reproduction, growth, and survival of floodplain biota. The seasonal inundation of off-channel habitats (Ward & Stanford 1995a) and naturally dynamic flow regimes (Junk *et al.* 1989, Poff *et al.* 1997) are crucial for maintaining ecological integrity of river systems (Robinson *et al.* 2002). These principles have also been established for West African river systems (Lévêque 1995, Tedesco *et al.* 2004), but many questions regarding the seasonal habitat use, functional mechanisms, and potential alterations in fish assemblages caused by anthropogenic changes remain unaddressed. Ward and Stanford's (1995a) description of an ecologically intact river-floodplain system includes a diversity of water body types with varying connectivity to the main channel, forming a mosaic of habitat patches across the floodplain. The seasonal connectivity among these habitats is hypothesized to support a likewise diverse fish assemblage, yet much of this fish diversity is still in the process of being understood in tropical river systems, including West Africa.

Examples of the influence of hydrologic connectivity on fish assemblages come from diverse aquatic ecosystems and regions of the world (McConnell & Lowe-McConnell 1987), yet all reveal similar patterns. In the rainy or wet season, environmental conditions such as salinity and dissolved oxygen (de Macedo-Soares *et al.* 2010) and food resources (Agostinho & Zalewski 1995, Roach *et al.* 2009a) tend to be homogenous, and subsequent drying of off-channel habitats and decreased hydrologic connectivity serve to intensify environmental factors (Thomaz *et al.* 2006). These seasonal changes often yield differentiated fish assemblages (Petry *et al.* 2003) and distribution of fish having diverse ecological traits (Sheaves *et al.* 2007) among habitats in the dry season. More generally, intact seasonal flood pulses and hydrologically connected habitats host riverine fauna with complex life cycles and evolved morphologies, physiologies, and behaviors (Robinson *et al.* 2002); these patterns can be drastically altered by anthropogenic change (Tejerina-Garro *et al.* 2006). Clearly, hydrological connectivity and seasonal flood patterns are integral drivers of fish assemblages; these patterns are likely to be severely disrupted after the installation of large dams (Bergkamp *et al.* 2000).

The Gambia River of West Africa is scheduled to be dammed at Sambangalou, upstream of Niokolo Koba National Park at the Senegal-Guinea border (DeGeorges & Reilly 2007). Ecological literature suggests that many riverine fishes will experience substantial population declines subsequent to the dam's installation along with the detriment of other flora and fauna that are dependent on intact river floodplains and natural flow regimes (Robinson *et al.* 2002, Lucas 2008). Five decades ago, the Gambia River's middle section including the National Park was described as lined with gallery forest and having floodplain water bodies extending into adjacent woodlands and grasslands, all of this supporting a diverse fish assemblage (Daget 1960). At the time our field study was conducted, this natural condition of the

Received 20 November 2010; revision accepted 2 September 2011.

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river habitat remained relatively unchanged. At least since the 1990s, however, media reports implicate local villagers in tree cutting and crop planting around the park's perimeter, with negative effects on park wildlife (Katz Miller 1990). These ongoing and impending transformations represent the loss of a chance to study one of the few remaining undisturbed rivers in the world.

The present study seeks a general understanding of the relationship among tropical floodplain fishes and habitats with varying degrees of hydrologic connectivity with the main river channel, in addition to providing baseline information on the fish assemblage in a relatively unperturbed state of the middle course of the Gambia River. Similar descriptions of Gambia River fishes were recently conducted on the river's lower reaches (Louca *et al.* 2009a) and its estuary (Albaret *et al.* 2004, Simier *et al.* 2006); whereas fish assemblages in the river's middle stretch, including Niokolo Koba National Park, are more likely to be directly affected by the dam because of its close proximity and have not received the same attention. The specific objectives of the study were to: (1) document the occurrence and relative abundance of fish species of the Gambia River in and near Niokolo Koba National Park; (2) describe the seasonal composition of the fish assemblage among habitats with varying degrees of hydrologic connectivity; and (3) describe the distribution of certain fish traits such as body morphology and trophic position (Table S1) among habitats and seasons, which in recent literature have been shown to be reliant upon seasonality and hydraulic connectivity (Dudgeon 2000, Roach *et al.* 2009b).

METHODS

STUDY SITE.—The study was undertaken in the floodplain of the middle reaches of the River Gambia, Senegal, West Africa (Fig. 1). The Gambia is a typical large river of Nilo-Sudanian type, sourcing in the Fouta Djalon mountain range in Guinea and flowing through Senegal and Gambia. It is 1120 km long with a catchment area of 77,000 km^2 (Paugy *et al.* 1994). The Gambia is unique among large West African rivers because of a lack of substantially altered habitat and river flow (Simier *et al.* 2006), although there are plans to install a large dam at Sambangalou (DeGeorges & Reilly 2007). Mean annual discharge at the gauging station in Kedougou fluctuated between 40 and 120 m^2/s (year sum of 1×10^9 to 3.5×10^9 m^2) in the years 1970–2000 (CSE 2005). A single rainy season occurs from June to September (DPN 2007), leading to the highest river discharge in late August and September (Fig. 2) when the river inundates a large floodplain composed of oxbow lakes, temporary water bodies and connecting channels, a configuration similar to the laterally connected riverine ecosystem described by Ward and Stanford (1995a) (Fig. S1).

Our study area was situated in Niokolo Koba National Park (founded in 1954) in southeast Senegal, one of the largest (9130 km^2) national parks in West Africa, and its immediate proximity. The region has vegetation characteristics of the savannah-woodland transition, and the rivers are fringed by gallery forest. Whereas the Gambia River has a long history of human settlement in its lower reaches (Webb 1992), the section in our study (channel width 100–250 m) bisects the park with a stretch of approximately 200 km with no significant human impacts. The stretch is not subjected to fishing pressure and there is no human-related water pollution. Within the park, major tributaries are the Niokolo (channel width 6–25 m at our sampling sites) and the Nieriko (2–16 m width) from the north and the Koulountou (15–30 m width) from the south. Oxbow lakes and seasonal floodplain pools are located in the proximity of the Gambia River (< 5 km from the main channel) and connected to the main river during the highest discharge. During the dry season (October to mid-May), the water level in the river channel gradually decreases (Fig. 2). This is mirrored by a gradual desiccation of floodplain habitats lagging behind discharge decrease in the main channel. A complete desiccation of larger temporary streams and pools occurs in late December and desiccation of some oxbow lakes may appear in some years between March and May. Conductivity, pH, and water temperature were measured at several locations on-site during fish sampling. Their overall among-site variability was negligible compared to the lower Gambia (Louca *et al.* 2009a), though exact values varied somewhat by habitat and season (Table 1).

FISH SAMPLING AND TRAIT INFORMATION.—Quantitative fish sampling was conducted during daylight hours using a seine (7 × 1 m, mesh size 4 mm) operated by two people. Each haul covered an approximate area of 21 m^2. Typically, three seine hauls were completed at each site (henceforth referred to as a single sample), although only one or two seine hauls were completed if the habitat size did not permit more hauls to be taken (*e.g.,* in small temporary water bodies). Sampling was conducted at five habitat types with decreasing connectivity to the main channel (Fig. 1): (1) the main river channel itself (four locations yielding 22 samples over 4 yr) in both wet and dry seasons; (2) tributaries (five locations positioned on four tributary rivers, yielding 22 samples) in both wet and dry seasons; (3) oxbow lakes (four lakes, 15 samples) in both dry and wet seasons; (4) temporary water bodies (five sites comprising three pools and two streams, 15 samples) only during the wet season because those sites contained no water during the dry season; and (5) spring areas (three sites, five samples) only during the dry season because of impassable roads during the wet period. In the main river, tributaries, and large oxbows, one location sometimes provided several independent samples collected from different microhabitats (*e.g.,* steep vs. shallow banks, eroded banks vs. sandy beaches, river pools vs. flowing sections) from within a 1 km perimeter.

Although seining was likely to be somewhat less efficient in the main river sites than in other habitats such as small tributary streams or spring pools, it was more appropriate to employ the same sampling gear than to use different methods with widely ranging efficiencies in the different habitats. Gill netting and angling were occasionally employed, but fish species caught using those methods were very rare and not considered in statistical analyses.

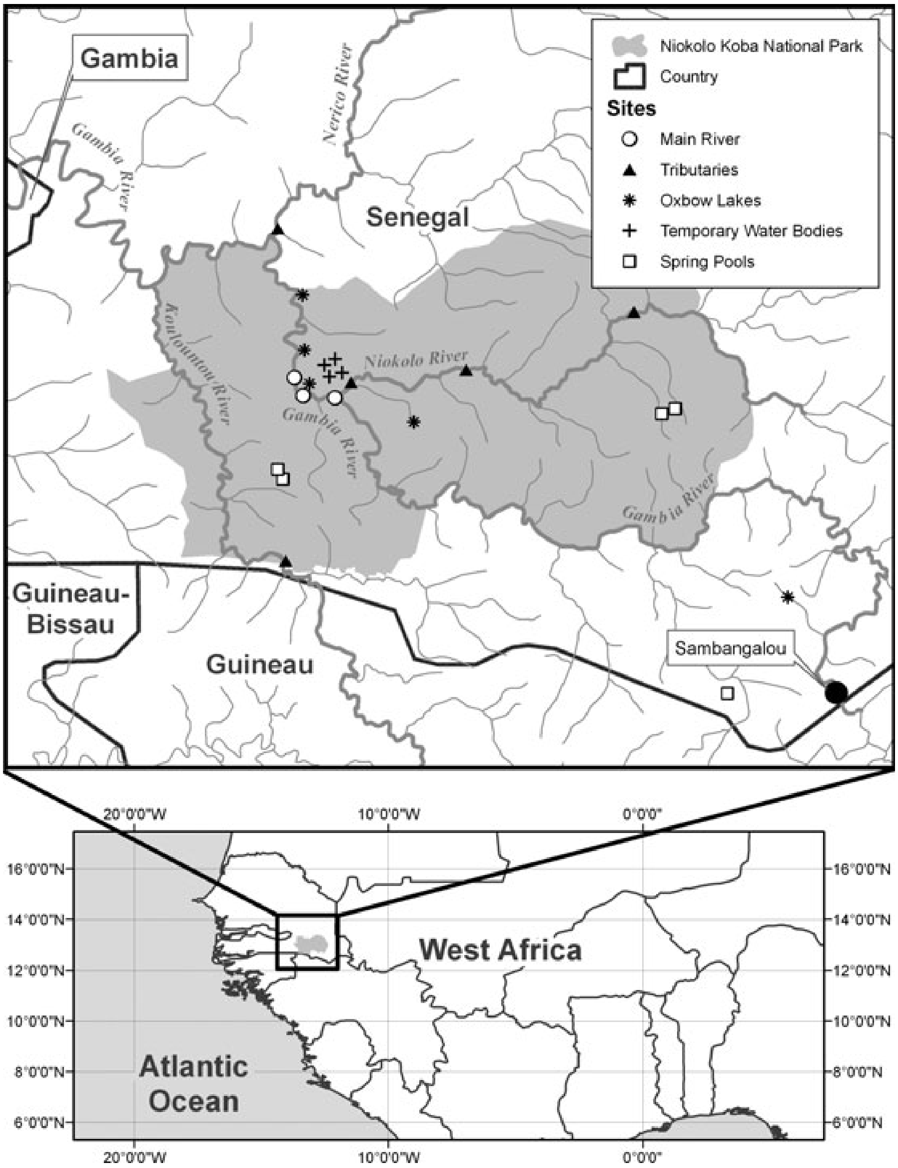

FIGURE 1. Middle course of the Gambia River including major tributaries and country boundaries. Individual symbols indicate sampling sites by habitat: main river (○), tributaries (▲), oxbow lakes (*), temporary water bodies (+), and spring areas (□). Note that one symbol may represent several nearby sampling sites.

Fish captured in the seine were collected and preserved in eight percent formaldehyde for later identification, with the exception of large and easily distinguishable fish that were identified immediately on the bank and released. Preserved fish were identified in the field station 1–20 d after capture according to established regional guides (Lévêque & Paugy 1994, Paugy *et al.* 2003) and our own field key and comparative material.

Sources of trophic position and morphology (Table S1) included the online FishBase life-history tool (Froese & Pauly 2000) and published data (Blache 1964, Moreau *et al.* 1995, Paugy 2003, Lamboj 2004, Lévêque 2006, Tedesco & Hugueny 2006). Missing entries for some species were additionally completed from our own designations of morphology.

DATA ANALYSIS.—Catch per unit effort (CPUE) for each fish species was calculated as the number of individuals captured per seine haul for each sampling event and averaged by season and habitat. We then reported Shannon diversity (H') and species richness using the bias-corrected Chao estimator (Chao 1987, Colwell & Coddington 1994). The biased-corrected Chao statistic and upper confidence interval could not be estimated for dry season oxbows because of the erratic occurrence of some species; we therefore computed the classic Chao estimate in this case. To describe fish assemblage structure among seasons and habitats, we computed a multivariate ordination with nonmetric multidimensional scaling (NMS), a nonparametric procedure that produces axis scores based on ranked distances (Kruskal 1964, Mather 1976). We calculated a two-dimensional solution in NMS

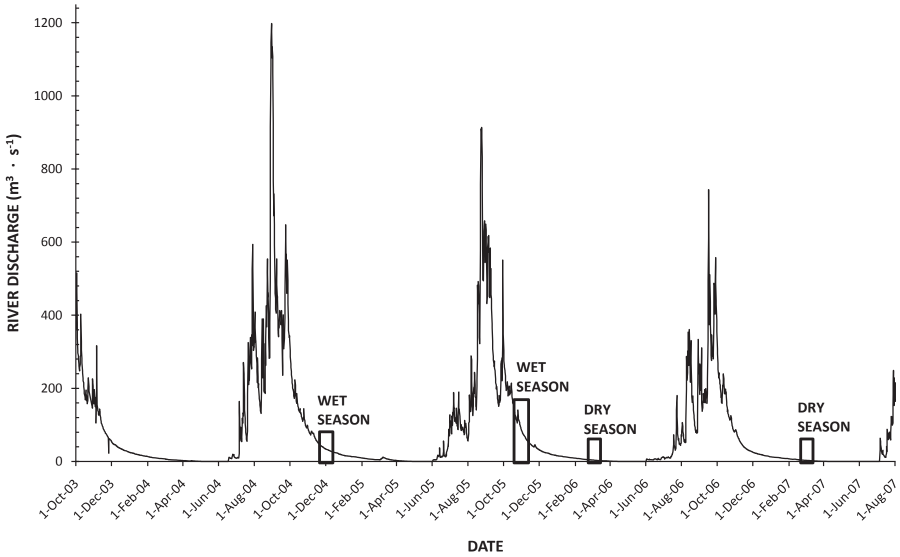

FIGURE 2. River discharge in the middle Gambia River from 2003 to 2007, indicating the periods of fish sampling (boxes). Years 2004–05 were sampled in the wet season subsequent to peak flows with high water level in the floodplain; years 2006–07 were sampled in the dry season at baseline flows.

TABLE 1. *Water quality by habitat and season, through all years of the study. Temperature, pH, and conductivity are reported as mean ± SD.*

Season	Mesohabitat	Number of measurements (*N*)	Temperature (°C)	pH	Conductivity (mS/cm)
Wet	Main river	1	28.40	7.54	40.00
	Tributaries	2	26.5 ± 0.44	6.51 ± 0.48	45.5 ± 3.5
	Oxbows	1	32.10	6.59	42.00
	Temporary	4	24.5 ± 0.63	6.65 ± 0.09	56.2 ± 8.77
Dry	Main river	14	28.6 ± 0.41	7.11 ± 0.12	48.6 ± 4.46
	Tributaries	16	29.4 ± 0.82	7.04 ± 0.29	57.4 ± 4.93
	Oxbows	7	29.5 ± 1.37	6.93 ± 0.41	69.2 ± 29.0
	Spring pools	5	22.9 ± 2.47	5.69 ± 0.37	34.8 ± 12.4

using Sørensen distance and 250 runs of real data allowing up to 500 iterations to evaluate stability. To evaluate the probability ($\alpha = 0.05$) that ordination axes explained more variation than expected by chance, 250 Monte Carlo runs were compared against runs of the real data. To dampen the effects of highly abundant species and allow less-common species to determine metrics of fish assemblage structure, we performed relativization by species maximum. Weighted averaging scores were then computed to evaluate the relative influence of each fish species on assemblage structure. One sample event in temporary water bodies (wet season 2005) was disregarded as a multivariate outlier because of high variance (> 2 standard deviations from the mean, Sorensen's distance).

To determine whether multivariate fish assemblage structure was associated with habitats, seasons, or year of sampling, we conducted multi-response permutation procedures (MRPP) (Mielke 1984, Mielke & Berry 2001). MRPP is a nonparametric, multivariate analog to analysis of variance (ANOVA) but without strict distributional assumptions and allowing for an unbalanced study design such as ours. Our response variables were the multivariate abundances of fish species, and the predictor variables were the following categorical groups, with a separate test conducted for each: year, season (wet vs. dry), habitat, and season by habitat. Because the 2005 wet season and 2006 dry season fell into the same annual discharge cycle and therefore the distribution of fishes among years was likely non-independent, we conducted two separate tests for a yearly effect: wet seasons 2004 vs. 2005 and dry seasons 2006 vs. 2007. For compatibility with the previously described NMS analysis, we used the same data structure and analysis options: relativization by species totals, Sørensen distance, and rank-transformation of the distance matrix.

To evaluate patterns in the distribution of trophic position and body morphology, we calculated the abundance of each trait by multiplying the matrix of fish abundance per sample event by a matrix of fish traits for species (*as per* Legendre *et al.* 1997). These data were log(x + 1) transformed to account for large differences in abundance, and evaluations of trait distributions by season and habitat were made based on visual inspection of boxplots. Because our evaluation of fish traits was conducted in an exploratory, *post hoc* fashion, we did not conduct formal tests of significance.

Metrics of fish assemblage diversity, NMS, and MRPP were performed using PC-ORD v.6.03 (McCune & Mefford 2011), software specifically designed for analyses of ecological data.

RESULTS

Fish occurrence and diversity.—A total of 49 fish species were caught via beach seining and considered in statistical analyses (Table S2). Individuals from an additional 14 species were caught rarely using other methods (gill nets and angling) and therefore not considered in statistical analyses. Like most species-rich biotic assemblages, fishes of the middle Gambia River followed a log-normal distribution and consisted of a few common and many rare species. Relative abundance of individuals varied widely, with catch per unit effort (CPUE) ranging from 115 (*Barbus leonensis* in dry season oxbows) to 0.01 (*Polypterus bichir* in dry season main river) individuals/seine haul. The specificity of fish to habitats and seasons also varied widely, with some fish such as *Barbus macrops, Barbus pobeguini,* and *Rhabdalestes septentrionalis* occurring generally among all habitats and seasons; whereas other fish were highly specific to certain habitats and/or seasons, such as *Brienomyrus brachyistius* which only occurred in spring pools, or *Ctenopoma petherici* which was present only in temporary floodplain pools in the wet season and tributaries and oxbow lakes in the dry season (Table S3).

In the wet season, Shannon diversity and species richness showed no apparent relationship with degree of hydrologic connectivity (Table 2), whereas in the dry season estimates of species richness appeared to increase along with isolation from the main channel with the exception of spring pools, which exhibited the lowest species richness (for many cases, however, variation of richness estimates was quite high in the dry season) (Fig. 3). Species richness tended to increase from wet season to dry in the main river, tributaries, and oxbows; whereas temporary water bodies harbored much of the fish diversity in the wet season.

Fish assemblage structure among seasons and habitats.—The fish assemblage formed a strong gradient based on the multivariate distribution of species. Ordination using NMS yielded a 2-axis solution that was highly significant (*P-value* = 0.02) with moderately good fit (final stress = 20.0) and low instability ($< 1.0\ e^{-5}$) after 83 iterations for the final solution. Calculations of weighted averaging (*WA*) scores revealed that the influence of fish species on the ordination varied widely (Table S2), ranging from *Gymnarchus niloticus* as the strongest (*WA* = –4.03) and *Labeo coubie* as the weakest (*WA* = 0.09) influence on fish assemblage structure.

Fish assemblage structure varied slightly according to years, seasons, and habitats, but most strongly according to the interaction among season and habitat, with that grouping being highly significant (*P-value* $< 1.0\ e^{-8}$) and having the largest effect size (*A-statistic* = 0.40) according to MRPP (Table 3). Visual representation of ordinations grouped by season and habitat revealed that in the wet season (Fig. 4A), the fish assemblage in the main river and tributaries were similar as expected, whereas oxbow lakes and temporary water bodies formed distinct assemblages. In the dry season (Fig. 4B), the main river and tributaries were relatively distinct from one another as compared to the wet season, whereas tributary and oxbow assemblages became similar to one another. Also in the dry season, spring pools formed an assemblage distinct from that of hydrologically connected main river and tributary habitats.

Distribution of fish traits.—Visual inspection of patterns in selected fish traits revealed distinct trends among seasons and habitats. The abundance of fishes occupying the top trophic position appeared to increase along with isolation from the main river in the wet season, yet no association was noted in the dry season (Fig. 5A). Similarly, and likely because of correlation among traits (see Discussion), the abundance of fishes having elongate body shape increased with habitat isolation in the wet season, with no association in the dry season (Fig. 5B). Conversely, the abundance of fishes having a compressed cross-section appeared relatively

TABLE 2. *Fish assemblage characteristics by season and habitat in the middle course of the Gambia River. Shannon diversity (H') is reported as mean ± one standard error. Biased-corrected Chao2 estimates of maximum species richness (S_{max}) are shown in addition to the upper 95% confidence interval (with the exception of wet season oxbows, for which classic Chao2 estimator was used; because it is not comparable to other estimates, we do not report the upper bound in this instance).*

Season	Mesohabitat	Sampling events	Shannon diversity (*H'*)	S_{max} (Chao2)	Upper 95% CI for S_{max}
Wet	Main river	13	1.37 ± 0.12	20.92	23.97
	Tributaries	4	1.76 ± 0.33	24.75	28.75
	Oxbows	8	1.30 ± 0.19	15.13*	N/A
	Temp. water bodies	15	1.05 ± 0.13	27.36	35.48
Dry	Main river	19	1.03 ± 0.10	29.95	49.35
	Tributaries	18	1.61 ± 0.11	36.41	54.39
	Oxbows	7	1.39 ± 0.20	46.50	75.83
	Spring pools	5	0.77 ± 0.20	15.00	23.92

*For wet season oxbows, the classic form of Chao estimate used to calculate species richness.

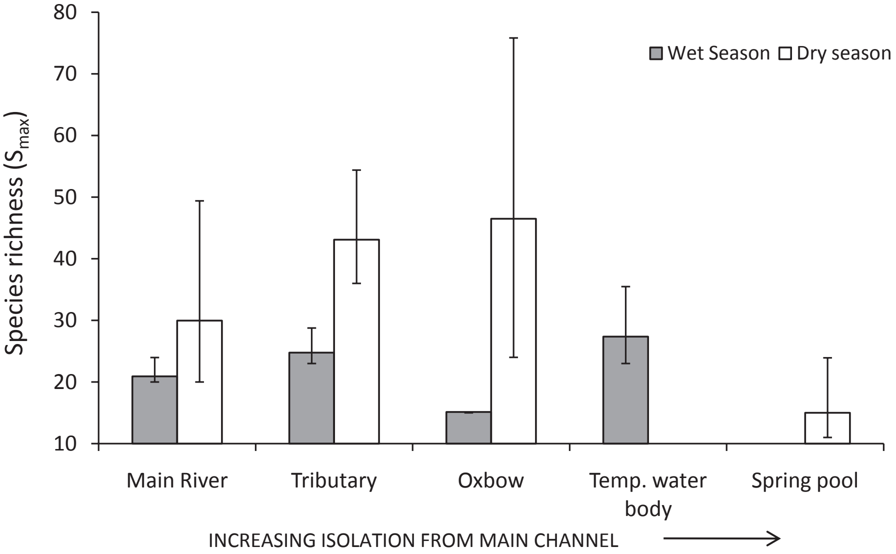

FIGURE 3. Species richness (S_{max} from Chao2 estimate) of habitats with increasing hydrologic isolation from the main channel. Temporary water bodies do not exist in the dry season; whereas spring pools were innaccessible in the wet season. Upper error bars represent 95% confidence interval for upper bound Chao2 estimate of species richness (upper confidince interval was not computed for oxbows in the wet season); lower error bars represent actual number of species observed.

TABLE 3. *Multi-response permutation procedure (MRPP) results for differences in the distribution of fish assemblage structure among seasons, habitats, season-habitat interaction, and years for fishes in the middle course of the Gambia River. Wet season sampling occurred in 2004 and 2005 whereas dry season sampling occurred in 2006 and 2007. Chance-corrected within-group agreement (A) is a measure of effect size for each test, whereas* P-*values represent the likelihood that observed differences are due to chance.*

Season (*N* = sample size)	Factor (No. levels)	Chance-corrected within-group agreement (*A*)	*P*-value
Wet (*N* = 39)	Year (2)	0.04	0.04
Dry (*N* = 49)	Year (2)	0.03	0.03
Both (*N* = 88)	Season (2)	0.09	$< 1.0\ e^{-8}$
	Habitat (5)	0.28	$< 1.0\ e^{-8}$
	Season × habitat (8)	0.40	$< 1.0\ e^{-8}$

uniform in the wet season, yet in the dry season sharply decreased with habitat isolation (Fig. 5C).

DISCUSSION

The World Commission on Dams (WCD) (Bergkamp *et al.* 2000) synthesized effects of large dams on downstream riverine ecosystems. Considering the immediate impacts of hydrology and river geomorphology alone, consequences to the Gambia River at Niokolo Koba National Park are likely to include changes in intensity, timing, and frequency of downstream flow; leading to reduced flow variability, reduced frequency and extent of overbank flow, reduced ground water recharge to riparian areas, and decreased total runoff via irrigation and/or evaporation from the reservoir. Most importantly for floodplain habitats, reduced sediment transport below dams can lead to lowering of the river bed and channel incision, which further severs floodplains from their main channel because a higher water level is required for overbank flow. Reduced sediment transport also leads to reduced creation of new floodplains, leading to a further loss of habitat diversity. Direct and indirect impacts on fish downstream of reservoirs include loss of the flood signal triggering fish migration, reduced fitness for fish adapted to high flow variability, a general reduction in habitat area (especially in floodplains), and increased risk of fish predation in water bodies cut off from the main channel. These and additional alterations to thermal regime, water chemistry, and nutrient loading typically lead to the loss of fish species—in their survey of the effects of dams in 66 global rivers, WCD reports that fish diversity declined in 73 percent of the cases (Bergkamp *et al.* 2000).

The findings of our study demonstrate that the middle course of the Gambia River, an ecosystem exhibiting dynamic temporal and spatial patterns of discharge and lateral floodplain connections, supports a fish assemblage that is taxonomically and functionally diverse. Connections among fluvial and floodplain habitats theoretically allow fish to successfully complete requirements of their ontogenetic stages and seasonal shifts in habitat use (Schlosser & Angermeier 1995, Louca *et al.* 2009b). Our findings demonstrated that seasonal habitat use of fishes varied greatly, indicating a high degree of behavioral diversity.

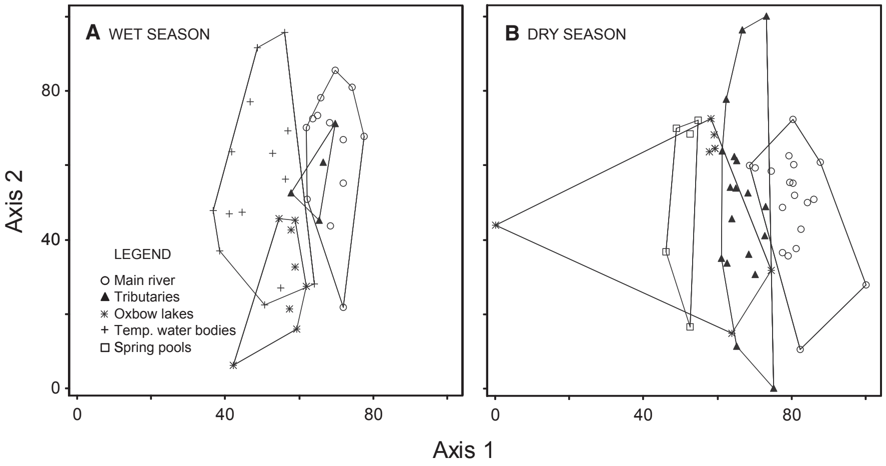

FIGURE 4. Nonmetric multidimensional scaling (NMS) results for (A) wet season and (B) dry season sampling in the middle course of the Gambia River. Axes are composed of fish species loadings and are expressed as percent minimum (0) to maximum (100) of axes scores. Points represent individual sample events, with those close together having similar fish assemblages and those far apart having different fish assemblages.

We found that fishes were associated with distinct patterns in habitat use by season, exemplified by a few characteristic species (Table S3). Habitat generalists such as *Barbus macrops, Barbus pobeguini,* and *Rhabdalestes septentrionalis* were found in all habitats and seasons, and therefore may be at least risk from potential changes from damming. However, several fish species exhibited strong associations with in- and off-channel habitats whereas others, based on their seasonal distributions among habitats, appeared to migrate laterally. This clearly underscores the importance of maintaining a diversity of riverine components and a natural flow regime. For example, *Brienomyrus brachyistius* occurred only in spring pools, whereas *Ctenopoma petherici* was present only temporary floodplain pools in the wet season and in tributaries oxbow lakes in the dry season, and was therefore likely migrating laterally across habitats through seasons to meet seasonal demands of feeding and reproduction. It would stand to reason that changes to the flow regime and loss of laterally connected, floodplain habitat would be detrimental to these and other floodplain specialists (Ward & Stanford 1995b, Espírito-Santo *et al.* 2009).

Fish species richness appeared to increase with hydrologic isolation from main channel in the dry season (with the exception of spring pools) but was homogenous in the wet season (Fig. 3), a pattern corroborated by several studies in tropical floodplain rivers. Thomaz *et al.* (2006) conducted a meta-analysis of river systems in North America, South America, and Europe and concluded that habitat characteristics likely to affect fish assemblages were homogenous in the wet season and differentiated in the dry season. Likewise in the Fitzroy River basin, Australia, fish habitat and fish assemblages differ according to degree of hydrologic connectivity, especially in terms of the proportion of marine-spawned versus freshwater-spawned fish species in pools (Sheaves *et al.* 2007). The Brazilian Paraná River fish assemblage and environmental conditions are similarly affected by degree of hydrologic connectivity (Petry *et al.* 2003). In coastal lagoons of Brazil, environmental factors such as salinity and dissolved oxygen and the associated fish assemblages are homogenous in the wet season, yet environmental characteristics become differentiated among habitats and more influential on the fish assemblage in the dry season (de Macedo-Soares *et al.* 2010). Contrary to our study, fish species richness and native species abundance in the Loire River in France were shown to increase with hydrologic connectivity of habitats across the floodplain (Lasne *et al.* 2007). In the Loire River, however, exotic species were present and dominated isolated habitats; a factor not likely to affect fish assemblage structure in the Gambia River.

Whereas shifts in the fish assemblage in the tidally influenced lower reaches of the Gambia River were attributed to physio-chemical variables (especially pH) (Louca *et al.* 2009a), the range of physio-chemical variables in our study was markedly narrower (Table 1). In the case of our study, seasonal inundation and desiccation of riverine and floodplain habitats appeared to drive shifts in the fish assemblage. We found that the largest and most statistically significant difference in the multivariate composition of the fish assemblage was explained by the interaction between season and habitats (Table 3; Fig. 4). Because we also tested against year of sampling, this result signified that presumably stochastic inter-annual variation was minor compared to that of more deterministic processes influencing the fish assemblages in floodplain habitats. In floodplains of the Orinoco River of Venezuela and Colombia, deterministic processes influenced the development of fish assemblage structure as habitats became seasonally isolated (Lewis *et al.* 2000). Our finding that the season-habitat interactions described most of the variation in fish assemblage indicates that deterministic processes involving habitat and the annual flow regime are likely to be strong drivers of fish assemblage structure.

We noted distinct patterns of ecological and morphological trait distributions among seasons and habitats. The abundance of predators increased with habitat isolation in the wet season, yet no pattern was noted in the dry season (Fig. 5A). Likewise,

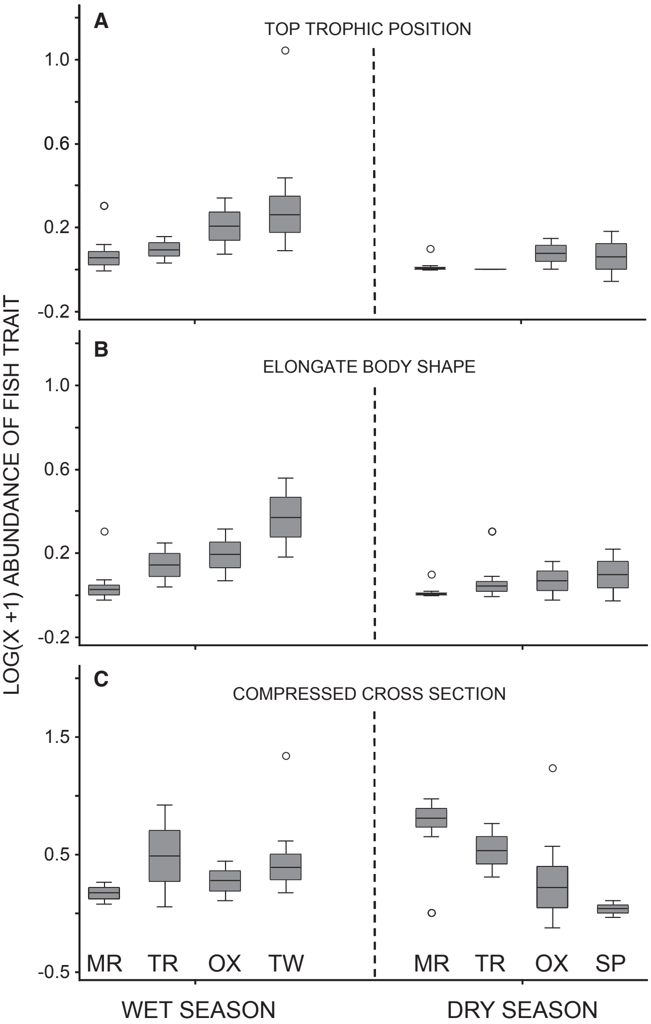

FIGURE 5. Box and whisker plots of log(x + 1) abundance of fish traits (A) top trophic position; (B) elongate body shape; and (C) compressed cross-section by season and habitat in the middle course Gambia River. Habitats are categorized by main river (MR), tributary (TR), oxbow lake (OX), temporary water body (TW), and spring pools (SP). Box heights are plus and minus one standard error from the mean (horizontal line), whiskers show plus and minus two standard errors, and open circles represent outliers > 2 standard errors from the mean.

Roach *et al.* (2009b) discovered via diet and isotope analyses in the Mississippi River that trophic position of the fish assemblage was higher in spring yet contrary to our study, was lower in backwater habitats. In the Orinoco River basin in Venezuela, Roach *et al.* (2009a) reported that hydrologic connectivity did not affect trophic position as determined from isotope analysis, likely because of an extended annual flood providing basal food resources for fish from sestonic and allochthonous sources throughout much of the year. Conversely, the annual hydrograph of the middle Gambia River is characterized by distinct peaks followed by prolonged periods of drying (Fig. 2), which is likely to generate distinct environmental conditions and fish assemblage structure with habitat desiccation.

Dudgeon (2000) described a continuum of fish morphologies across a lateral transect of floodplain to upland habitats in tropical Asian floodplain rivers—with morphologically streamlined fishes occupying the main channel, laterally compressed fishes occupying near-channel backwater and fringe habitats, and laterally compressed or elongated fishes occupying floodplain water bodies and fringes of the river channel. In our study, we confirmed the higher abundance of elongated morphology in temporary, floodplain water bodies but during the wet season only (Fig. 5B). However, elongated body shape is likely correlated with trophic feeding position (Table S1), causing difficulties in assigning a mechanism for habitat use to either characteristic. A more instructive example of body morphology was compressed cross-sectional body shape. Whereas Dudgeon (2000) observed that laterally compressed fish were more common in backwater and fringe habitats, we observed that compressed morphologies became less abundant with isolation from the main river channel in the dry season (Fig. 5C). This pattern was absent in the Gambia River in the wet season, indicating that desiccation and subsequent changes in physiochemical or biotic factors likely determined the traits suited to the particular environments.

The opposing findings of Dudgeon (2000) and our study are perhaps explained by the diverse microhabitats existing in the main river channel of the Gambia and its tributaries, allowing the persistence of varied morphologies in all seasons. In the same section of the Gambia River, Reichard (2008) observed 14 fish species in the dry season via snorkeling, each displaying microhabitat segregation based on position in the water column, flow velocity, and other factors that would constrain the adaptive morphology of fishes (Matthews 1998). Alternatively, a departure from Dudgeon's (2000) conceptualization could simply be caused by one or a few fish species with compressed morphologies, such as *Pollimyrus isidori*, having extremely high CPUE in the main river during the dry season (Table S3). Regardless of the differences among studies, the findings suggest that the expected homogenization of habitats from river damming (Bergkamp *et al.* 2000) could lead to decreased specialization of the fish assemblage, thus diminishing not only taxonomic diversity but what Gould (1991) described as 'disparity', or the functional diversity of biota.

In summary, a diversity of habitats and seasonal patterns of inundation supported a likewise taxonomically and functionally diverse fish assemblage in the middle course of the Gambia River. Future damming and other related human modifications may decrease seasonal discharge and habitat diversity, which in turn will likely decrease fish species richness, species diversity, and functional disparity. More understanding of reference, tropical river ecosystems like the middle course of the Gambia River is crucial for the conservation of fish assemblages. We suggest that further elucidation of seasonal habitat use of intact riverine floodplain systems will be valuable future research contributing to fish conservation, especially with planned global increase in dam building (Bergkamp *et al.* 2000). In particular, further insights into how seasonal heterogeneity in off-channel habitats affects the distribution of ecological traits seems a promising approach because of its generality across taxonomic groups, river systems, and even continents (McGill *et al.* 2006).

ACKNOWLEDGMENTS

We thank Radim Blažek and Barbora Bímová for field assistance, and Dr. Jacques André Ndione and Mr. Gora Ndiaye for providing river discharge data. Dr. Frederieke Kroon and two anonymous reviewers provided invaluable suggestions to improve the manuscript. Dr. Peter Galbreath and Mr. Paul Pradeau translated the abstract into French. Ms. Denise Kelsey provided the study area map. The study was supported by a grant from GAAV (IAA6093404). Data analysis and manuscript preparation were supported by the J.W. Fulbright Commission.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Fish species caught by seining and their feeding ecology/body morphology in the Gambia River at and near Niokolo Koba National Park, Senegal, 2004–*2007.

TABLE S2. *Weighted averaging scores from nonmetric multidimensional scaling axis by fish species, habitat type, and season.*

TABLE S3. *Catch per unit effort for each fish species by season and habitat type.*

FIGURE S1. Detail of Gambia and Niokolo River confluence area.

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