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Fish diversity in the Niokolo Koba National Park, middle Gambia River basin, Senegal

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Sampling over five years (2004–2008) in Niokolo Koba National Park yielded 62 fish species from 22 families. Data are compared with records from the 1950s, yielding a conservative estimate of 73 fish species occurring in the park. Only native species are found. We compare species richness in five major habitat types (main river, tributaries, large oxbow lakes, temporary water bodies and spring pools) and thoroughly discuss putative differences observed in the fish community between the 1950s and 2000s.

Introduction

The River Gambia is unique in being the last major river in West Africa with a natural hydrological regime (WWF, 2006). The river flows through Guinea, Senegal and The Gambia. The large adjacent floodplains in the lower half of the river are seasonally inundated by floodwater (Lesack, 1986). There have been several plans to dam the river for generating hydropower, controlling floods, barraging salinity and tidewater and enabling irrigation-supported agriculture in adjacent areas at various locations along the river stretch, though none of these have obtained final approval (Mathes & Gilbert, 1985; Webb, 1992). The most recent plan for a hydroelectric power plant and dam on the River Gambia suggests damming the river at Sambangalou, on the Senegal-Guinea border (DeGeorges & Reilly, 2007), with expected effects on the hydrology of the river having wide ecological consequences along the entire stretch of the River Gambia (Louca et al., 2008).

The fish fauna of the River Gambia consists mainly of Nilo-Sudanian species, with Guinean species present in the upper part of the river (Johnels, 1954; Daget, 1960; Lévêque et al., 1991; see Figure 1 for distinction between the upper, middle and lower reaches of the river). Additionally, the lower part of the river has a long, brackish ecotone zone (250 km), affected by tidal water fluctuations and inhabited by many estuarine and marine species (Albaret et al., 2004). One hundred and eight fish species have been reported from along the whole course of the river, though none are endemic (Lévêque et al., 1991; Paugy et al., 2003). Several recent studies have described the

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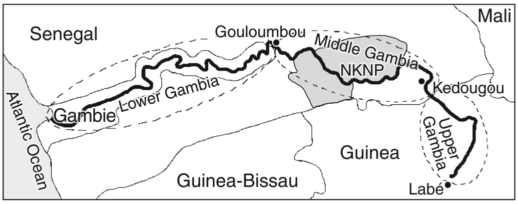

Fig. 1. River Gambia with gauging stations (Kédougou, Gouloumbou) and delimitation of the upper, middle and lower reaches.

fish communities of the lower and estuarine parts of the River Gambia and its floodplains (e.g. Darboe, 2002; Albaret et al., 2004; Guillard et al., 2004; Vidy et al., 2004; Ecoutin et al., 2005; Simier et al., 2006; Louca et al., 2008). This is in sharp contrast to the sparse information available on the fish assemblages of the middle reach of the river, which was last intensively studied more than 50 years ago (Daget, 1960; Daget, 1961). During wet and dry seasons between 1955 and 1959, a total of 59 species were collected at various habitats (main river, tributaries, oxbow lakes and small pools) in the Niokolo Koba National Park, yielding 3 species new to science (Daget, 1959, 1961).

Here, we present data on fish species richness and community composition from various aquatic habitats within the main stretch and floodplain of the middle reach of the River Gambia. The study was conducted over five years (2004–2008) as part of a project to catalogue vertebrate diversity in the Niokolo Koba National Park (NKNP). We compare our estimates with reports by Daget (1960, 1961) and discuss observed differences in the fish community following 50 years of existence of the national park. Our study can also be used as a reference for any future assessment of the effects of river damming on the fish community.

Material and methods

Study area. The study was undertaken on the River Gambia and its floodplain within the NKNP and its surroundings, in Senegal, West Africa. The River Gambia has its source on the Fouta Djallon plateau in Guinea and flows into the Atlantic Ocean. It is approximately 1270 km long and has a catchment area of 78 000 km^2 (Paugy et al., 1994). The last 500 km of the river only has a 1 m altitudinal difference and hence tidal effects can be observed along the entire lower reach of the river (Webb, 1992). The middle reach (480 km long) lies entirely within the political borders of Senegal (delimited by the town of Kédougou at the upstream point, 40 km downstream of the

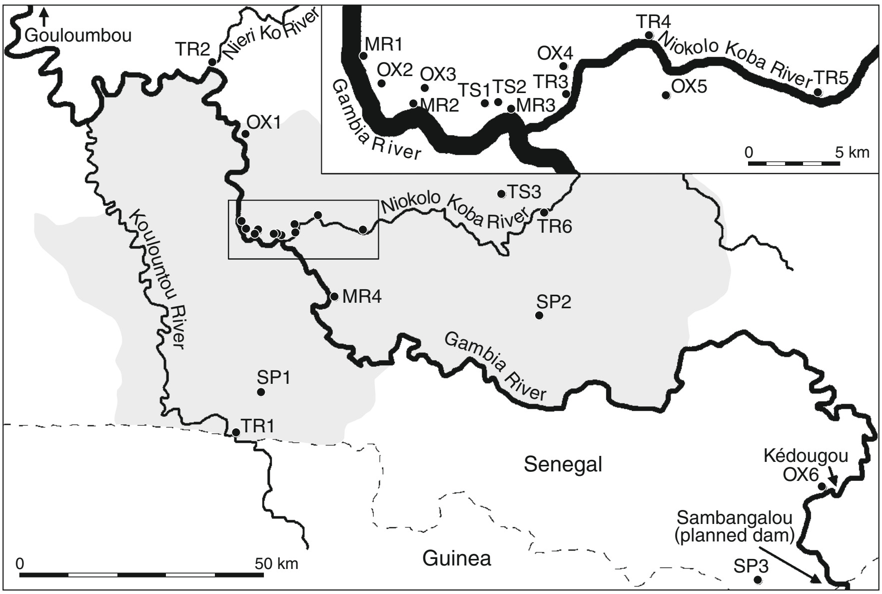

Fig. 2. Niokolo Koba National Park with sampling sites, Sambangalou projected dam and Gouloumbou and Kédougou gauging stations.

planned dam at Sambangalou), and the upper reach (290 km long) is separated from the middle reach by a series of rapids (Daget, 1960) (Fig. 1). An extensive floodplain is associated with the river along its lower 670 km (Louca et al., 2008), of which the uppermost part spans most of the NKNP. The most important tributaries are the Sandougou, the Koulountou, the Nieri Ko and the Niokolo Koba; the last three flowing through the NKNP (Fig. 2). The River Gambia is unique in not having been affected by environmental changes associated with landscape modification and with human disturbance (Lesack, 1986).

Most of the middle reach of the River Gambia (almost 300 km) was included into the NKNP when it was established in 1954. The NKNP, which covers an area of 9130 km^2, is the largest Biosphere Reserve in West Africa and is a UNESCO Endangered World Heritage site. There are no permanent settlements within the NKNP and fishing is limited to local poaching in marginal areas, with no commercial or large-scale fishing at present or in the past. The reserve is dominated by woodland savannah and semi-arid Soudanese forest, with significant areas of gallery forest and seasonal wetlands (Hejcmanová-Nežerková & Hejcman, 2006).

The flow regime of the river is natural, with a peak discharge in September of 350–1200 $m^3 \cdot s^{-1}$ recorded (between 1970 and 2007) at the Kédougou gauging station (Fig. 1; 800–1200 $m^3 \cdot s^{-1}$ during our study period) and an annual minimum discharge of below 0.5 $m \cdot s^{-1}$ (complete stretch desiccation often recorded at the gauging station) from May to June. The discharge at Gouloumbou (located on the Senegal-Gambia border and forming the boundary between the lower and middle reaches of the river; Fig. 1) fluctuates between 4.5 $m^3 \cdot s^{-1}$ and 1500 $m^3 \cdot s^{-1}$ (Simier et al., 2006). Although no quantitative data from the NKNP are available, the discharge along the study stretch is comparable to that at the Gouloumbou gauging station (Lesack et al., 1984) and, while the main river stretch never desiccates, it may become disconnected and form isolated pools during periods of lowest flow. Floodplain habitats are seasonally inundated; however, temporal streams and pools disappear annually (typically from December to January). Oxbow lakes are connected to the main river during peak discharge but remain isolated for most of the year, and may desiccate completely depending on the intensity and length of the rainy season (White et al., 2012).

Sampling. Five collecting trips were undertaken in the NKNP between 2004 and 2008, with a total of 22 localities sampled (Fig. 2; Table 1). Collections in 2004 and 2005 were completed soon after the end of the rainy season in October and November (high water level, temporary habitats present). The collections in 2006–2008 took place at the end of the dry season in March and April. Sampling during wet and dry seasons was required for associated ecological studies (Reichard, 2008; White et al., 2012). Water temperature at the study sites varied from 23 to 32 °C, pH from 5.7 to 7.5 and conductivity from 35 to 70 $\mu S \cdot m^{-1}$ (White et al., 2012). Variation in these parameters was negligible, especially compared to very high fluctuations in the lower stretch of the Gambia (Louca et al., 2008). We defined five general habitat types, to which we refer throughout the paper: main river channel (River Gambia; coded MR in the Fig. 2 and Tables 1–2), tributaries (the Nieri Ko, the Koulountou and the Niokolo Koba; coded TR), oxbow lakes subject to occasional desiccation, but typically with an open water surface and dense littoral vegetation (coded OX), temporal streams and pools undergoing regular annual desiccation (coded TS), and non-desiccating spring pools, typically at relatively higher altitudes (coded SP).

Sampling was mainly conducted using seine and gill nets, with some data also obtained from angling using rod and line. Our initial trials included electrofishing (portable battery electrofishing backpack), cast nets, dip nets and fyke nets; however, we found these methods ineffective. Wherever possible, we used a seine (length 7 m, height 1 m, mesh size 4 mm) in combination with a set of gill nets (length 30 to 50 m, mesh size 18, 28, 38, 40 and 50 mm). While the seine was less effective in capturing large and nocturnal fishes, the use of gill nets was limited by the high abundance of Nile crocodiles and hippopotamuses in the large habitats suitable for this method. Additional data were obtained, therefore, by using rod and line at dusk and at night.

After capture, fish were determined to species according to Paugy et al. (2003). Fish were either released at the capture site after determination or anaesthetised in clove oil and fixed in 4 % formaldehyde for later determination. Photographs of live representative specimens of all the species were taken and a collection of preserved specimens is deposited at the Institute of Vertebrate Biology, Academy of Sciences, Brno, Czech Republic.

Data analysis. Only presence/absence data are presented in this study due to the uneven sampling effort among habitats and sampling sites, and the differing effectiveness of our sampling gear/methods in capturing various species. Numerical estimates would clearly overestimate shoaling and nearshore species and underestimate benthic and nocturnal species. We report the number of sites (22 in total) where each species was present and list particular sites. We further give details on the sampling method that yielded particular species and overall frequency of occurrence for a total of 51 sampling occasions (sites sampled across several years included as separate sampling occasions). Quantitative data on fish abundance were collected from 2004 to 2007. In 2008, we only targeted new species records and overall numerical abundance in samples was only estimated visually, after which most fish were released. Between 2004 and 2007, we collected 13408 fish by seine, 845 fish in gill nets and 230 fish using rod and line. Samples from 2008 increased the total number of fish collected to approximately 15000 individuals using seine, 1000 individuals from gill nets and 380 individuals from angling.

Results

We collected a total of 62 fish species, belonging to 22 families and 9 orders, from 20 sites in the NKNP and from two sites close to the park. The most common species were *'Barbus' macrops*, *Rhabdalestes septentrionalis*, *Hemichromis fasciatus* and *Tilapia guineensis*, captured at 15 (68 %) of the 22 sites. In contrast, *Brienomyrus brachyistus*, *Brycinus longipinnis*, *'Barbus' salessei*, *Heterobranchus bidorsalis*, *Malapterurus occidentalis*, *Synodontis clarias* and *Scriptaphyosemion geryi* were only collected at a single site. Pooling all samples together (total of 51 samples), *'Barbus' macrops* and *Brycinus nurse* were the most frequent species (found in 75 % of samples), followed by *Rhabdalestes septentrionalis* (71 %) and *Tilapia guineensis* (67 %) (Table 2). *Brienomyrus brachyistus*, *'Barbus' salessei*, *Heterobranchus bidorsalis* and *Synodontis clarias* were only recorded during one sampling occasion (<2 %), with only a single specimen of *H. bidorsalis* caught on that occasion (Table 2).

We found that seine was the most effective sampling method, followed by gill netting and rod and line; however, a combination of all three methods proved useful in obtaining highest species richness as all were complementary. Seine was effective in capturing most of the recorded species (54 of 62), with 17 species captured only by seine. Gill netting provided 40 species, with 3 species *(Polypterus senegalus*, *Distichodus rostratus* and *Synodontis clarias)* collected exclusively by this method. Angling catches yielded 27 species, with two species *(Malapterurus occidentalis* and *Heterobranchus bidorsalis)* captured by rod and line exclusively. A total of 19 species were collected by all three sampling methods (Table 2).

Highest species richness was recorded at Simenti, on the River Gambia's main course, and at Passage Koba on the River Niokolo Koba, a tributary of the River Gambia (41 species at each site). Conversely, only a single species was found in the Mare de Woeni oxbow lake (late stage of desiccation) and in a small temporal stream (site TS3) on the NKNP's periphery (Table 1).

Discussion

Published summaries of fish species richness in the Gambia River Basin give a total of 84 species (Lévêque, 2006), 89 species (Hugueny, 1989), 91 (including estuarine) species (Lévêque et al., 1991), 95 (including 18 estuarine) species (Daget, 1961) or 108 (including 25 estuarine) species (Paugy et al., 2003).

For the middle reach of the Gambia Basin, Daget (1961) reported the occurrence of 59 fish species within the area of the NKNP, collected during several expeditions between 1955 and 1959. This is comparable to our results of 62 fish species from the same area 50 years later. The species list overlap, however, is far from complete. Our samples included 22 species not reported by Daget (1961) and, in contrast, Daget (1961) mentioned 19 species not observed in the present study. There are several reasons for this inconsistency. First, in accordance with recent literature (Lévêque et al., 1991; Darboe, 2002; Paugy et al., 2003; Albaret et al., 2004; Louca et al., 2008), it is likely that 4 species *('Barbus' ablabes*, *Chrysichthys walkeri*, *Schilbe mystus*, *Scriptaphyosemion roloffi)* were misidentified by Daget (1961) and are as *'Barbus' macrops*, *Chrysichthys maurus*, *Schilbe intermedius*, and *Scriptaphyosemion geryi*, respectively, in our samples. Second, *Malapterurus electricus* was recently recognised as a group of species (Norris, 2002), with *Malapterurus occiden-*

talis actually inhabiting the middle Gambia. Third, *Tylochromis jentinki* and *Ctenopoma kingsleyae*, reported by Daget (1961) from the NKNP, are almost certainly identical to *Tylochromis intermedius* and *Ctenopoma petherici* present in our samples. *Ctenopoma petherici* and *C. kingsleyae* are difficult to separate morphologically, but current distributional data support our identification that only *C. petherici* occurs in the NKNP (Norris & Douglas, 1992); our determination was confirmed by S. Norris (pers. comm.). Distinction between *T. jentinki* and *T. intermedius* relies on a relative comparison between a set of individuals (mouth more or less horizontal vs. inclined at an angle of 15–20°, and lip thickness) and both species apparently co-occur in the Gambia Basin (Paugy et al., 2003). While our determination suggested that we recorded *T. intermedius*, it is possible that either both species co-occur in the NKNP or, more conservatively, that there is a single species of *Tylochromis* that has been incorrectly determined by us or Daget (1961). We note that these inconsistencies can be settled by direct examination of Daget's material deposited in Muséum National d'Histoire Naturelle, Paris, though it was not possible for the purpose of the current study.

Taking these circumstances into account, this gives a distinction of 12 species recorded by Daget (1961) but not represented in our samples and 15 species recorded by us but not by Daget (1961), and a total of 47 species shared between collections from the 1950s and 2000s. For the 11 species reported exclusively by Daget (1961), three species (*Nannaethiops unitaeniatus*, *Clarias macromystax* and *Kribia nana*) are likely the result of mistaken determination of *Neolebias unifasciatus*, *Clarias buettikoferi* and *Kribia kribensis*, respectively, as reflected in both recent compendia on West Af-

Table 1. Name, code, coordinates and altitude of each sampling site in Niokolo Koba National Park, years of sampling, total species richness (richness) and sampling methods used (S, seine; G, gill net; A, rod and line).

sampling site	code	coordinates		altitude	sampling year	richness	method
River Gambia, Gué de Damantan	MR1	13°02.712' N	13°19.266' W	15	2005, 2006, 2007, 2008	35	S,G,A
River Gambia, Simenti	MR2	13°01.395' N	13°17.350' W	16	2004, 2005, 2006, 2007, 2008	41	S,G,A
River Gambia, Camp du Lion	MR3	13°01.493' N	13°14.491' W	16	2004, 2005, 2006, 2007, 2008	26	S,G,A
River Gambia, Badoye	MR4	12°55.066' N	13°08.837' W	20	2006,2007	19	S,G
River Koulountou, Gué de Sambailo	TR1	12°39.478' N	13°19.852' W	30	2006, 2007	23	S,G
River Nieri Ko, Wassadougou	TR2	13°21.429' N	13°21.340' W	19	2005, 2007	23	S
River Niokolo Koba, Pont Suspendu	TR3	13°01.522' N	13°13.220' W	24	2008	17	S
River Niokolo Koba, Passage Koba	TR4	13°03.928' N	13°10.144' W	28	2004, 2005, 2006, 2007, 2008	41	S
River Niokolo Koba, Lengekountou	TR5	13°01.938' N	13°04.898' W	30	2006, 2007	21	S,G
River Niokolo Koba, Post Niokolo	TR6	13°04.395' N	12°43.232' W	62	2005, 2006	19	S,G
Mare de Wouring Oxbow	OX1	13°13.229' N	13°18.199' W	16	2007, 2008	31	S,G
Mare de Kountadala Oxbow	OX2	13°01.964' N	13°18.605' W	20	2004, 2006	6	S
Mare de Simenti Oxbow	OX3	13°01.790' N	13°17.608' W	21	2004, 2005, 2006, 2008	38	S,G,A
Mare de Woeni Oxbow	OX4	13°01.827' N	13°13.006' W	23	2008	1	S
Mare de Sitandi Oxbow	OX5	13°02.843' N	13°09.914' W	25	2006, 2007	2	S
Mare de Fadiga Oxbow	OX6	12°33.171' N	12°12.086' W	109	2007	6	S
Temporary stream near Simenti	TS1	13°01.652' N	13°15.482' W	27	2004, 2005	24	S
Temporary stream near Camp du Lion	TS2	13°01.692' N	13°14.858' W	26	2004, 2005	13	S
Temporary stream near Post Niokolo	TS3	13°06.967' N	12°47.628' W	71	2005	1	S
Spring pool, Dalaba	SP1	12°44.954' N	13°16.562' W	70	2006, 2007	7	S
Spring pool, Assirik	SP2	12°52.786' N	12°50.879' W	77	2006, 2007	10	S
Spring pool, Dindefello	SP3	12°21.034' N	12°19.243' W	426	2007	3	S

Table 2. Fish species recorded in and around Niokolo Koba National Park, with presence (+) or absence (–) in our samples [OS] and those reported in Daget (1961) [Dag], Lévêque et al. (1991) [Lev], and Paugy et al. (2003) [Pau]. For species recorded in our samples, sites where a given species was recorded (sites of observation), number of sites where it was recorded (N sites, from a total of 22), sampling method by which it was captured (method; see Table 1) and frequency of occurrence (% freq, from a total of 51 samplings across years). Species not recorded in middle reach of Gambia by Daget (1961), but cited as present in lower (LR) or upper reaches (UR) and species reported under a different name (DN) also included.

family / species	OS	Dag	Lev	Pau	sites of observation	N sites	method	% freq
Protopteridae								
Protopterus annectens (Owen, 1839)	–	+	+	+	–	–	–	–
Polypteridae								
Polypterus bichir Lacepède, 1803	+	+	+	+	MR1-4, TR1,4, OX1	7	S, G, A	17.65
Polypterus senegalus Cuvier, 1829	+	+	+	+	OX1,3	2	G	7.84
Clupeidae								
Pelonulla leonensis Boulenger, 1916	+	+	+	+	MR1-3, TR3-5, OX1	7	S	25.49
Osteoglossidae								
Heterotis niloticus (Cuvier, 1829)	+	+	+	+	TR4, OX1-3	4	S, G	11.76
Notopteridae								
Papyrocranus afer (Günther, 1868)	+	LR	+	+	MR1,2, TR4, OX3	4	S, G, A	11.76
Mormyridae								
Brienomyrus brachyistus (Gill, 1862)	+	+	+	+	SP2	1	S	1.96
Brienomyrus niger (Günther, 1866)	+	+	+	+	OX2,3	2	S, G	3.92
Marcusenius senegalensis (Steindachner, 1870)	+	+	+	+	OX3, TS1,2, SP1	4	S, G	9.80
Mormyrops anquilloides (Linnaeus, 1758)	+	+	+	+	MR2, OX3	2	G, A	7.84
Mormyrus hasselquistii Valenciennes, 1847	+	+	+	–	MR1,2	2	G, A	3.92
Mormyrus rume Valenciennes, 1847	+	LR	+	+	MR2, OX3	2	G, A	3.92
Petrocephalus bovei (Valenciennes, 1847)	+	LR	+	+	TR2,4, OX3, TS1,2	5	S, G	13.73
Pollimyrus isidori (Valenciennes, 1847)	+	+	+	+	TR1,4	2	S	5.88
Gymnarchidae								
Gymnarchus niloticus Cuvier, 1829	+	+	+	+	MR2, OX2,3	3	S, G, A	7.84
Hepsetidae								
Hepsetus odoe (Bloch, 1794)	+	+	+	+	MR1, TR1,4,6, OX1,3, TS1	7	S, G	21.57
Characidae								
Alestes baremoze (Joannis, 1835)	+	+	+	+	MR1-3, TR1,2,4, OX1,3	8	S, G, A	31.37
Brycinus leuciscus (Günther, 1867)	+	+	+	+	MR1-3, TR1-6, OX1,3, TS1	12	S, G, A	58.82
Brycinus longipinnis (Günther, 1864)	+	–	+	+	TR1	1	S	3.92
Brycinus nurse (Rüppell, 1832)	+	+	+	+	MR1-4, TR1-6, OX1,3,6, TS1	14	S, G, A	74.51
Hydrocynus brevis (Günther, 1864)	+	+	+	+	MR1-4, TR2-4, OX1,3, TS2	10	S, G, A	29.41
Rhabdalestes septentrionalis (Boulenger, 1911)	+	+	+	+	MR1-4, TR1-6, OX1,3, TS1,2, SP2	15	S, G, A	70.59
Distichodontidae								
Nannaethiops unitaeniatus Günther, 1872	–	+	–	–	–	–	–	–
Nannocharax ansorgii Boulenger, 1911	+	+	+	+	MR1-4, TR1,2,4,5, TS1	9	S	31.37
Neolebias unifasciatus Steindachner, 1894	–	–	+	+	–	–	–	–
Paradistichodus dimidiatus (Pellegrin, 1904)	+	+	+	+	MR1-3, TR1-6, OX1,3, TS1,2	13	S	49.02
Citharidae								
Citharinus citharus (Geoffroy Saint-Hilaire, 1809)	+	+	+	+	MR1-3, TR2-4,6, OX1,3	9	S, G	27.45
Distichodus rostratus Günther, 1864	+	LR	+	+	MR1, OX1,3	3	G	7.84
Cyprinidae								
'Barbus' ablabes (Bleeker, 1863)	–	+	–	–	–	–	–	–
'Barbus' baudoni Boulenger, 1918	+	LR	+	+	MR1-3, TR1-5, OX1,3,4, TS1	12	S	39.22
'Barbus' leonensis Boulenger, 1915	+	+	+	+	MR2, TR4-6, OX1-3, TS1,2, SP1	10	S	29.41
'Barbus' macrops Boulenger, 1911	+	–	+	+	MR1-3, TR1-6, OX1,3,6, TS1, SP1,2	15	S, A	74.51

Table 2. (continued).

family / species	OS	Dag	Lev	Pau	sites of observation	N sites	meth-od	% freq
'Barbus' niokoloensis Daget, 1959	+	+	+	+	MR1-4, TR1-6, TS1	11	S, A	50.98
'Barbus' pobeguini Pellegrin, 1911	+	+	+	+	MR1-3, TR2,4-6, OX3, TS1-3, SP2	12	S	54.90
'Barbus' salessei Pellegrin, 1908	+	UR	+	+	SP3	1	S	1.96
'Barbus' sublineatus Daget, 1954	–	+	+	+	–	–	–	–
Labeo coubie Rüppell, 1832	+	+	+	+	MR1-4, TR1,4-6, OX1,3	10	S, G	33.33
Labeo parvus Boulenger, 1902	+	+	+	+	MR2-4, TR2,4, OX1, TS1	7	S, G	19.61
Labeo senegalensis Valenciennes, 1842	+	+	+	+	MR1-4, TR2,4,6, OX1,3	9	S, G	29.41
Raiamas senegalensis (Steindachner, 1870)	+	+	+	+	MR1-4, TR1,3-5, OX1	9	S, G, A	43.14
Bagridae								
Auchenoglanis occidentalis (Valenciennes, 1840)	+	+	+	+	MR1,3,4, TR4-6, OX1,3	8	S, G, A	21.57
Claroteidae								
Chrysichthys johnelsi Daget, 1959	–	+	+	+	–	–	–	–
Chrysichthys maurus (Valenciennes, 1840)	+	–	+	+	MR1,2, TR3,4	4	S, A	11.76
Chrysichthys walkeri Günther, 1899	–	+	–	–	–	–	–	–
Schilbeidae								
Parailia spiniserrata Svensson, 1933	–	+	+	+	–	–	–	–
Schilbe intermedius Rüppell, 1832	+	–	–	+	TR2,4,5, OX1,3, TS1,2	7	S, G	23.53
Schilbe mystus (Linnaeus, 1758)	–	+	+	–	–	–	–	–
Amphilidae								
Amphilius rheophilus Daget, 1959	–	+	+	+	–	–	–	–
Clariidae								
Clarias anguillaris (Burchell, 1822)	+	+	+	+	MR1,2, OX1-3,5,6, TS1,2, SP1,2	11	S, G, A	25.49
Clarias buettikoferi Steindachner, 1894	–	–	+	+	–	–	–	–
Clarias macromystax Günther, 1864	–	+	–	–	–	–	–	–
Heterobranchus bidorsalis Geoffroy Saint-Hilaire, 1809	+	–	+	+	MR2	1	A	1.96
Heterobranchus longifilis Valenciennes, 1840	+	+	+	+	MR2-4, OX5	4	S, G, A	7.84
Malapteruridae								
Malapterurus electricus (Gmelin, 1789)	–	+	+	–	–	–	–	–
Malapterurus occidentalis Norris, 2002	+	–	–	+	MR2	1	A	5.88
Mochokidae								
Synodontis annectens Boulenger, 1911	–	+	+	+	–	–	–	–
Synodontis batensoda Rüppell, 1832	+	LR	+	+	TR4, OX1,3, TS1,2	5	S, G	15.68
Synodontis clarias (Linnaeus, 1758)	+	+	+	+	OX1	1	G	1.96
Synodontis membranaceus (Geoffroy Saint-Hilaire, 1809)	+	LR	+	+	TR4,6, OX3	3	S, G	5.88
Synodontis nigrita Valenciennes, 1840	+	LR	+	+	MR2, TR2-4,6, OX1,3, TS1	8	S, G, A	17.65
Synodontis ocellifer Boulenger, 1900	+	+	+	+	MR1,2, TR4, OX3	4	S, G, A	15.69
Synodontis schall (Bloch & Schneider, 1801)	+	+	+	+	MR1,2, TR4	3	S, G, A	9.80
Syngnathidae								
Enneacampus ansorgii (Boulenger, 1910)	+	LR	–	+	MR1,2, TR1	3	S	9.80
Aplocheilidae								
Epiplatys bifasciatus (Steindachner, 1881)	+	+	+	+	TR1,2,4,5, SP1,2	6	S	17.65
Epiplatys spilargyreius (Duméril, 1861)	–	+	+	+	–	–	–	–
Micropanchax pfaffi (Daget, 1954)	–	+	+	+	–	–	–	–
Nothobranchius kiyawensis Ahl, 1928	+	LR	+	+	TS1,2	2	S	3.92
Poropanchax normani (Ahl, 1928)	+	+	+	+	MR1-4, TR1,2,4-6, SP3	10	S	29.41
Scriptaphyosemion geryi (Lambert, 1958)	+	DN	+	+	SP2	1	S	3.92
Channidae								
Parachanna obscura (Günther, 1861)	–	+	+	+	–	–	–	–
Cichlidae								
Hemichromis bimaculatus Gill, 1862	+	+	+	+	MR1,3,4, TR1,4-6, OX3,6, TS1, SP2	11	S	29.41

Table 2. (continued).

family / species	OS	Dag	Lev	Pau	sites of observation	N sites	meth-od	% freq
Hemichromis fasciatus Peters, 1857	+	+	+	+	MR1-4, TR1-6, OX1,3,6, TS1, SP1	15	S, G, A	50.98
Oreochromis niloticus (Linnaeus, 1758)	+	+	–	+	MR2, TR4, OX1,3, TS1	5	S, G, A	17.65
Sarotherodon galilaeus (Linnaeus, 1758)	+	+	+	+	MR1-4, TR1-4, OX1,3	10	S, G, A	33.33
Tilapia guineensis (Günther, 1862)	+	–	+	+	MR1-4, TR1-6, OX1-3, TS1,2	15	S, G, A	66.67
Tilapia zillii (Gervais, 1848)	+	+	+	–	MR1,2,4, OX3, SP2	5	S, G	9.80
Tylochromis intermedius (Boulenger, 1916)	+	–	+	+	MR1-4	4	S, G	11.76
Tylochromis jentinki (Steindachner, 1894)	–	+	+	+	–	–	–	–
Gobiidae								
Porogobius schlegelii (Günther, 1861)	+	LR	–	+	MR1,2, TR3-5	5	S	9.80
Eleotrididae								
Kribia kribensis (Boulenger, 1907)	–	DN	+	+	–	–	–	–
Anabantidae								
Ctenopoma kingsleyae Günther, 1896	–	+	+	+	–	–	–	–
Ctenopoma petherici Günther, 1864	+	–	+	+	TR1,2,4, OX1,3,6, TS1,2, SP1-3	11	S, G	25.49

rican fish species (Lévêque et al., 1991; Paugy et al., 2003; see Table 2) and, therefore, we discuss these species further using their correct identification. Three large species *(Protopterus annectens*, *Parachanna obscura*, *Clarias buettikoferi)* have possibly been missed in our sampling, as their numerical abundance is probably low. Further, *Chrysichthys johnelsi* and *Amphilius rheophilus* inhabit sections with rapid flow and *Synodontis annectens* is a nocturnal species; for them, our sampling was ineffective. *Neolebias unifasciatus*, *Parailia spiniserrata* and *Kribia kribensis* are also stream fishes for which our sampling may have been ineffective, particularly further from the shore. We failed to record two other species *(Micropanchax pfaffi*, *Epiplatys spilargyreius)*. These fish are small cyprinodontiform species inhabiting stream and lake margins (Paugy et al., 2003), habitats for which our sampling by seine was most effective, as also confirmed by abundant catches of related cyprinodontiforms in permanent water bodies (main river channel, tributaries and spring pools; Table 2). It is possible that they occur in the NKNP, but at sites that we did not sample. Finally, *'Barbus' sublineatus*, reported by Daget (1961), has a general coloration identical to that of *'Barbus' baudoni* recorded by us. There is a clear distinction between the two species, however, in the length of both pairs of barbels, and Daget (1961) lists *'B.' baudoni* as a species characteristic for the lower reach of the River Gambia. We paid particular attention to the distinction of all small *'Barbus'* species and are confident that our identification is in accordance with Paugy et al. (2003).

The most important disparate identification between our study and that of Daget (1961) is in the identity of the commonest *Tilapia* species. We determined this species (present in 68 % of sampled sites; one of the most abundant species in the NKNP) as *Tilapia guineensis*, while Daget (1961) reports *Tilapia melanopleura* Duméril, 1859 (currently a junior synonym of *Tilapia zillii*, though considered a distinct species in Daget (1961)) as the only *Tilapia* (sensu stricto) species from the NKNP. We collected *T. zillii* at several sites, including the main river, a large oxbow lake and a spring pool (Table 2), but its abundance was low compared to *T. guineensis*. Daget (1961) did not mention *T. guineensis* to occur in the Gambia Basin at all but clearly distinguished *T. melanopleura* as distinct from *T. zillii* (from the Niger). In contrast, Albaret et al. (2004), Vidy et al. (2004), Louca et al. (2008) and Louca et al. (2010) report *T. guineensis* to be a widespread species in the lower Gambia. Hence, we believe that *T. zillii* reported by Daget (1961) may actually be a mixture of both species, which are difficult to separate, especially as juveniles. It is therefore possible that *T. guineensis* was already present in NKNP habitats in the 1950s and it does not represent a case of recent range expansion.

A further 14 species recorded uniquely by us were rare *(Papyrocranus afer*, *Heterobranchus bidorsalis*, *Enneacampus ansorgii)* or nocturnal mormyrids *(Mormyrus rume*, *Petrocephalus bovei)* and mochokids (*Synodontis batensoda*, *Synodontis membranaceus*, *Synodontis nigrita*). *Nothobranchius kiyawensis* is an annual killifish that only inhabits temporary pools formed during the rainy season and survives most of the year in the form of eggs buried in dry sediment. Notably, we collected *N. kiyawensis* only in 2005, despite the 2004 collection being conducted in the same season, including the same sampling sites as in 2005, and being similarly exhaustive. This suggests that *N. kiyawensis* abundance may fluctuate greatly between years. *Brycinus longipinnis* is a species characteristic for the Guinean rather than Soudanian region and we only recorded it in a southern tributary of the Gambia (the River Koulountou, a Guinean tributary), where the species was abundant. Daget (1961) did not sample the Koulountou and hence could not have recorded its presence within the NKNP. Similarly, *'Barbus' salessei* is a Guinean species that we recorded outside the boundary of the NKNP, in a stream at high altitude near the Guinean border (Fig. 2). *'Barbus' salessei* was a common species at this site and, indeed, Daget (1961) listed this species as typical for the upper reaches of the Gambia Basin. *Distichodus rostratus* is a large species of which we only collected 12 individuals in gill nets placed across two oxbow lakes and one main river site. Finally, a gobiid, *Porogobius schlegelii*, was found in the main river and in one tributary, though in small numbers. Daget (1961) actually reports 11 of these 14 species as being present in the lower reaches of the Gambia River Basin (Table 2). The last of these species (*Heterobranchus bidorsalis*) is certainly a new record for the NKNP, though it has been reported from the Gambia Basin in recent compendia on West African fishes (Lévêque et al., 1991; Paugy et al., 2003) and its occurrence in the middle Gambia is not unexpected. In conclusion, therefore, we consider most differences in species lists reported by us and by Daget (1960, 1961) as representing a sampling (presence or absence of rare species) and taxonomic (misidentification, recognition of new species) artefacts rather than a consequence of species turnover.

A final comprehensive list of fishes reliably recorded in the NKNP (taken as a representative set of middle Gambia Basin habitats) includes 73 species as a conservative figure. This estimate excludes *'Barbus' salessei* (from the upper Gambia Basin) and *Ctenopoma kingslaye* (a likely misidentification), and treats *Tylochromis intermedius* and *T. jentinki* as a single species. As such, only native species are presently found in the middle Gambia Basin. It is also notable that the River Gambia is unique in the absence of the Nile perch *Lates niloticus*, a large predatory species found in all other West African basins (Paugy et al., 2003).

Highest species richness was observed in the main river (41 species at Simenti, 45 species in total), followed by large, typically permanent, oxbow lakes (38 species in Mare de Simenti, 31 species at Mare de Wouring, 44 species in total for all 6 oxbow lakes combined), and tributaries (41 species at Passage Koba on the River Niokolo Koba, 43 species in total). There are likely to be objective differences between sites and habitat types that are mirrored in the species richness estimates presented in Table 1. Sampling intensity, however, is certainly responsible for part of the between-site variation, sites with the highest estimated species richness being investigated more intensively, across all years, and with the widest variety of sampling methods.

Marked differences were observed in species richness among oxbow lakes (Table 1), differences being related to the degree of lake desiccation, with oxbows at a later stage only being inhabited by species adapted to low oxygen conditions (e. g. *Heterotis niloticus*, *Gymnarchus niloticus*, *Ctenopoma petherici*, *Clarias anguillaris*, *Heterobranchus* spp.). There appears to have been a recent shift to almost annual desiccation of many large oxbow lakes that previously supported relatively species rich fish communities. This is probably due to the high abundance of scrub resulting from the highly invasive, non-native giant sensitive plant *Mimosa pigra*, a wetland species from the Neotropics. In the absence of elephants (eliminated by poaching), it is not consumed by local herbivores, resulting in an increased surface evaporation rate and the obstruction of large parts of the water surface.

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