Climatic and anthropogenic effects on fish diversity and fish yields in the Central Delta of the Niger River

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Abstract

For last 20 years, the fish communities in the Central Delta of the Niger River have been subjected to: (i) two drought periods in 1973 and 1984, (ii) a dramatic increase of fishing and, (iii) the building of an electric-power dam in 1984. At different levels, these various factors modified the biological cycle of the fish which are adapted to the former hydrological cycles of the Niger and the Bani rivers. The Sahelian drought is responsible for a decrease in both flood duration and of the inundated area of floodplain which varies from 20 000 km^2 to 5 000 km^2. From 1968 to 1989, fish landings declined from 90 000 metric tons to 45 000 metric tons. During the same period, as fish catches fell, yields per hectare increased from 40 kg in 1968 to 120 kg in 1989. This phenomenon is linked to the decrease of the average age of the fish (69% of fish catches are under one year old) in response to the increased fishing mortality and natural mortality which is higher during the drought period. The increase in fish productivity is characterized by a depletion of species such as *Gymnarchus niloticus*, *Polypterus senegalus*, *Gnathonemus niger*, whose reproduction are linked to the floodplains and of species like *Citharinus citharus* and *Clarotes laticeps* which visit frequently flooded areas. Concurrently, families such as the Cichlidae or Clariidae, which are resistant to low oxygen concentration, increase. Species which are under one year old at first reproduction and have several spawning periods per year, are the more abundant in fish communities.

Keywords: Central Delta, Niger River, floodplain, hydrology, fish communities, fishing yields, adaptation.

Modifications climatiques et anthropiques dans le Delta Central du Niger: impacts sur la diversité des poissons et sur la productivité biologique.

Résumé

L'histoire récente des peuplements ichtyologiques du Delta Central du Niger au Mali est marquée, entre autres, par deux périodes de sécheresse survenues en 1973 et 1984, un accroissement important de l'effort de pêche depuis les années 1960 et la construction d'un barrage hydro-électrique mis en service en 1984. A des degrés divers, ces événements sont venus perturber le cycle biologique des poissons qui reposait sur une adaptation des espèces aux cycles hydrologiques des fleuves Niger et Bani. La sécheresse provoque ainsi une réduction des surfaces en eau et une baisse de la durée d'inondation qui divisent par quatre les surfaces moyennes inondées dans l'année. De 1968 à 1989, la diminution des captures est évaluée à 45 000 tonnes passant ainsi de 90 000 à 45 000 tonnes. Dans le même temps, malgré la baisse des prises totales, on observe une augmentation des rendements à l'hectare qui passent de 40 kg en 1968 à 120 kg en 1989. Ce phénomène est à rapprocher de l'abaissement de l'âge moyen des poissons (69 % des individus pêchés ont moins d'un an) dû à une augmentation de la mortalité par pêche et de la mortalité naturelle plus forte en cette période de sécheresse. Cette augmentation de productivité s'accompagne également d'une raréfaction de certaines espèces comme *Gymnarchus niloticus*, *Polypterus senegalus*, *Gnathonemus niger* dont les reproductions sont inféodées aux zones d'inondation et d'espèces comme *Citharinus citharus* et *Clarotes laticeps* qui se distinguent par une fréquentation intensive des plaines d'inondation. Dans le même temps, on assiste à un développement de certaines familles comme les Cichlidés et les Clariidés qui présentent dans les deux cas de fortes résistances à l'anoxie. D'une manière générale, les espèces présentant des âges de première maturité faibles (inférieurs à 1 an) et plusieurs périodes de reproduction dans l'année sont celles qui sont actuellement les mieux représentées dans les peuplements.

Mots-clés : Delta Central du Niger, plaine inondée, hydrologie, communautés de poissons, pêche, rendements, adaptation.

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INTRODUCTION

The numerous environmental changes, especially since World War II, have led scientists to introduce the concept of biodiversity to understand ecosystems structure. The role of biological diversity in ecosystem stability and it's effects on biological productivity are still two major questions for ecologists (Lévêque, 1995). Such an approach implies that the biological system was studied before dramatic changes in the ecosystem occurred. So far very few studies of this type have been realized.

Environmental changes due to human activities and natural climatic variations make the biodiversity concept really interesting and the answers to the industrialization and agro-industry are backward compared to developed countries, the role of biodiversity must be studied because the results might govern the trend of development over the next decades.

The study of the Central Delta of the Niger River in Mali might provide a contribution to this approach. This region has been investigated since 1950 (Blanc *et al.*, 1955; Daget, 1949*a*, 1954, 1973) and in 1989 (Laë, 1991, 1992*a*, 1992*b*; Laë *et al.*, 1994). Between those two periods, hydrology and fishing in the Central Delta were greatly modified due to climatic and human disturbances: there were two drought periods the first around 1973 and another in 1984, as well as the building of dams and a dramatic increase of fishing.

During the drought, discharges in the Niger River and Bani River decreased strongly. Consequently the areas flooded were considerably reduced, as well as the duration of flood. From 1969 to 1986, floodplain areas contracted from 20000 km^2 to 5000 km^2 and the fish production from these areas decreased from 87000 metric tons in 1969-1970 to 37000 metric tons in 1984-1985. The decreased of fish landings is directly linked to the lesser area flooded (Laë, 1992*a*).

In other respects, the Markala dam, built in 1943, and the Selengue dam, built in 1984, contribute to increase the effects of drought by further lowering the already reduced flood flows. The annual loss in total catches due to the two dams was estimated to be 5000 metric tons in 1984 (Laë, 1992*b*). The dams also affect upstream fish production by disrupting longitudinal migrations of fish. However they don't jeopardize species reproduction because the spawning areas are located downstream of Markala dam (Daget, 1949*b*). Electric-power production at Selengue requires large volumes of water and creates better flows during the dry season than those encountered before the sahelian droughts. Consequently, the survival rate of spawners is increased ensuring adequate reproductive success each year (Laë, 1992*b*).

During the last twenty years the fishery deteriorated for three reasons (Laë *et al.*, 1994): (i) the demographic increase at 3% per year led to a doubling in the number of fishermen over 20 years, (ii) the increase in individual fishing efficiency due to new fishing materials and new fishing gears, (iii) the policy of the Malian authorities to insert the fishery into the market economy.

The drought, intensified by the impacts of new dams led to fragmentation or disappearance of habitats usually occupied by numerous fish species. This study evaluates the adaptative strategies of the fish and fish communities of the Central Delta to these various disruptions with emphasis on the role of biodiversity in ecosystem resilience and in influencing yields. The fact that changes in population structure and in certain biological characteristics of the population are induced by several types of stress, including fishing, climate changes and eutrophication makes it difficult to estimate the relative importance of hydrological changes and the increase of fishing activities.

Hydrological pattern and fish communities

The Niger River and his tributary the Bani delimit a floodplain three hundred kilometres long and one hundred kilometres wide (*fig.* 1). The hydrological regime (*fig.* 2*a*) of this internal delta may be divided into four seasons (Brunet-Moret *et al.*, 1986). The flood begins in July and August. Although these months correspond to the local rains 90% of the water in the river comes from Guinea and Ivory Coast. Flooding commences as water spills into the southern delta, upstream of the permanent lakes, and reaches it's maximum in September and October when the whole basin is covered. Draw-down begins in November and December upstream of the lakes, and in March in the northern sectors. The lowest water level is in April and May when floodplain pools dry up and only the Niger and Bani rivers and some lakes retain water. During the same hydrological cycle, flooded areas can vary from 20000 km^2 at the maximum of flood to 3500 km^2 at the end of the low water season (Raimondo, 1975). There is a three months time lag between the onset of the flood (*fig.* 2*b*) in the south (Ke Macina) and in the north (Dire) of the delta during a good hydrological period (1954-1955). This can be reduced to one month when hydrological conditions are poorer (1973-1974) and in the actual drought period, river flows are much reduced as well as the time and extent of flooding.

Hydrological variations lead to changes in the plant communities of the river-floodplain system. For example, there has been strong retrogression of *Eragrostis barteri* in response to the lessened flood intensity. The "bourgou", *Echinocloa stagnina*, has expanded in areas covered by open water in the past, but has been replaced by water lily in some areas formerly occupied by bourgou (Quensière *et al.*, 1994).

The fish communities of the Central Delta include 130 to 140 species (Daget, 1954) which are adapted to the seasonal and inter-annual variations. The concept of habitat within flood rivers is difficult to apply as the same space within the system will be in a constant state of transition from one state to the next

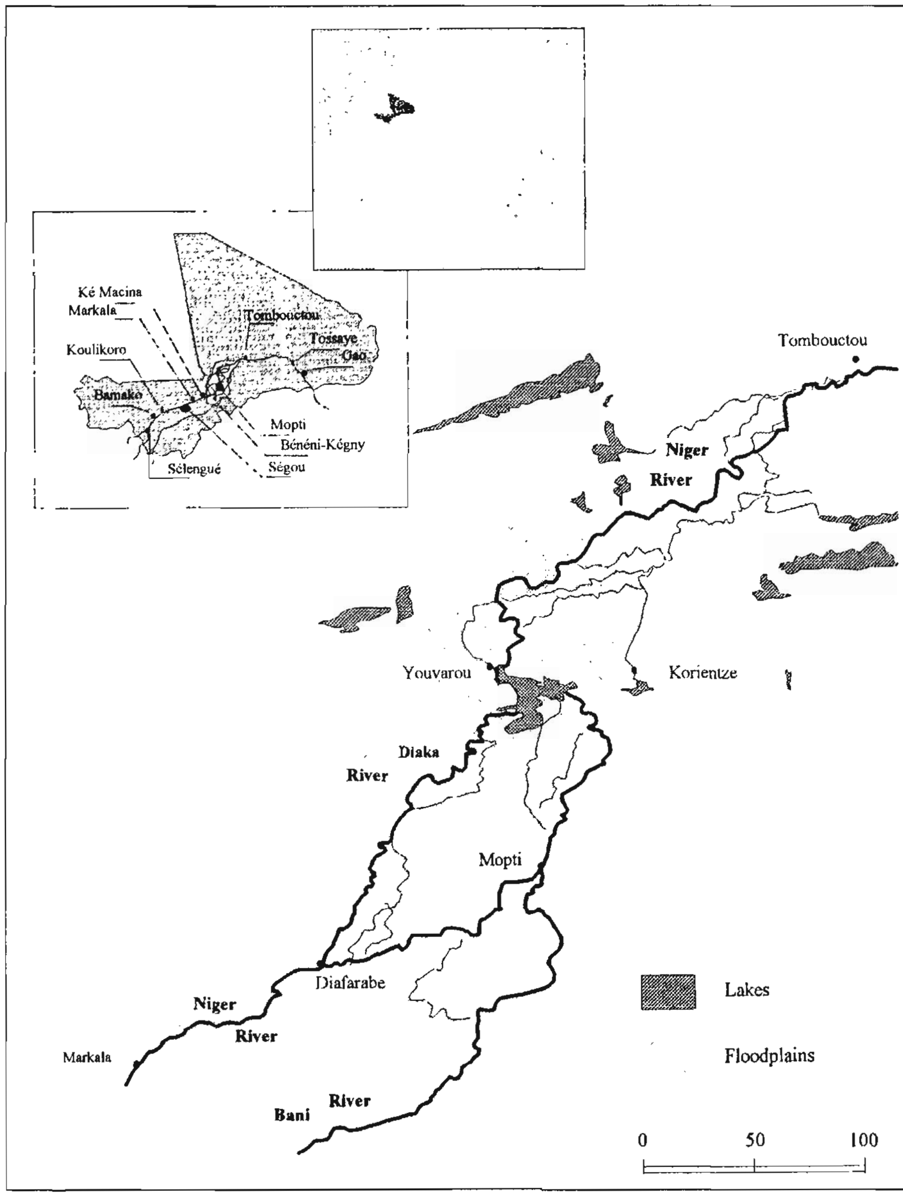

Figure 1. – The Central Delta of the Niger River in Mali.

(Welcomme, 1991). Fish species have to be adapted to these changing conditions particularly with regard to respiration and reproduction. Two major groups of fish can be identified on the basis of their strategies (Quensière, 1994).

The first group includes migratory fishes which exploit environmental variability. These move from lateral areas to the main channel as return migrations of adults and juveniles from the floodplains on the falling flood and in the main channel as longitudinal migrations following the peak flood. These fishes exhibit a high fecundity and a short breeding period that coincides with the earlier part of the flood. Such behaviour helps genetic mixing because spawners concentrate at a limited number of spawning sites. After spawning fish are redistributed over the whole river area. Some species of this group move over short distances (*e.g. Hydrocynus brevis* and *Bagrus bayad*) while other species (*e.g. Alestes baremoze* or *Alestes dentex* or *Brycinus leuciscus*) disperse throughout the delta.

The second group includes opportunistic species which are less mobile and show various behavioral and physiological adaptations that help them to survive in the anoxic environments of the floodplain. Some species have anatomical features such as lungs (*e.g. Protopterus annectens, Polypterus senegalus*), arborescent respiratory organs (*Clarias anguillaris, Heterobranchus bidorsalis*), supra-branchial organs (*Ctenopoma kingslaye*) or highly vascularized intestines (*Heterotis niloticus, Gymnarchus niloticus*). Other species show physiological or behavioral modifi-

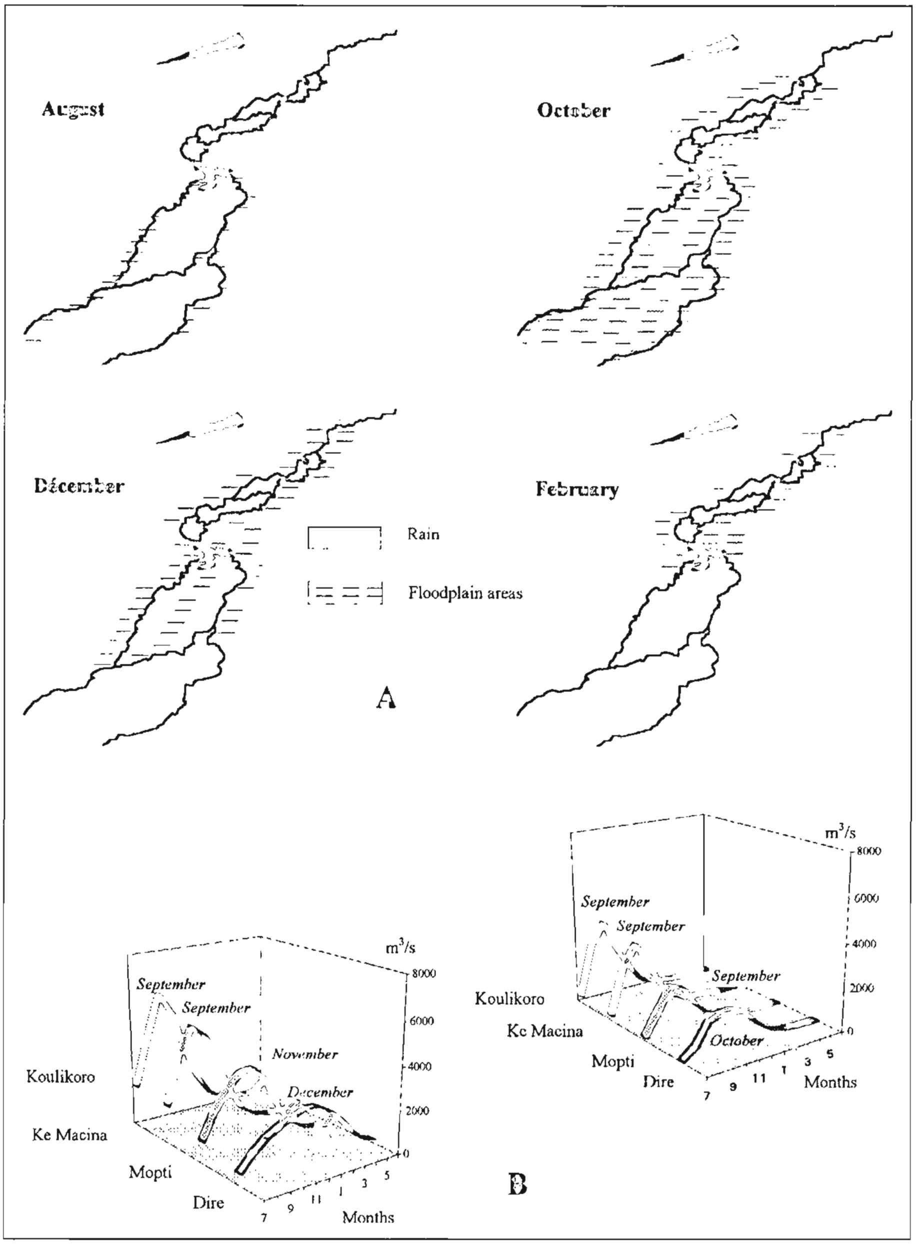

Figure 2. – *a* Seasonal flood of the Central Delta (from R. A. Farrow, 1975). *b* Monthly flow in various places of the delta for one rainy period (1954-1955) and one dry period (1973-1974).

cations including breathing from the water surface-film (Cichlidae, *Hemisynodontis membranaceus*). These species generally have low fecundity but can breed several time a year. Survival of the young is improved by various degrees of parental care ranging from territorial behaviour associated with nest building to mouth brooding.

These two groups are present in other parts of world but Welcomme (1989) pointed out that longitudinal migrations in African rivers rarely attain the proportions of the extensive movements of Asian or South American species. The relative abundance of these two groups depends on the variability of the hydrological pattern in space and in time (Lowe McConnell, 1975).

MATERIAL AND METHODS

Data collection

Data were obtained by sampling small scale fisheries from June 1990 to May 1991. The Study period spanned one hydrological cycle of the Delta which also corresponded to one biological cycle of fishes and the fishery. The methodology selected was based on two stratifications (Laë, 1991 ; Laë *et al.*, 1994*b*) :

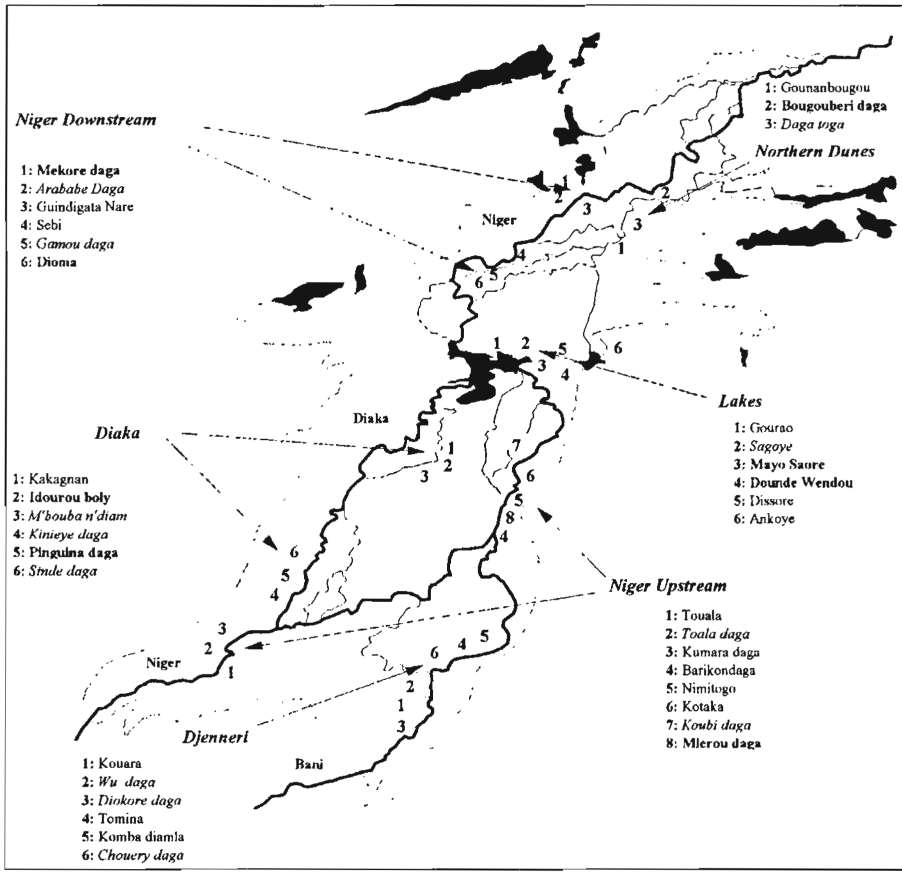

Figure 3. – Location and specifications of villages sampled during the statistical survey (bold characters = temporary camping place, italic characters = permanent camping place, Roman characters = villages).

(i) geographical stratification of the delta into six homogeneous sectors (Niger upstream, Djenneri, Diaka-kotia, lakes, Northern dunes, Niger downstream);

(ii) stratification of the fishery based on the different classes of fishermen (migrant fishermen, sedentary fishermen and fishermen/farmer).

Every sector included six sampling stations (2 villages, 2 permanent camps, 2 temporary camps) which were each sampled over a ten day period per month (*fig.* 3). Capture and fishing effort data were collected independently at every sampling site:

Fishing effort was computed from a daily survey of the activities at most of 20 fishing families in the same village. Six hundred fishing families were investigated each month composed as follow: – migrant fishermen – 37%, settled fishermen – 40% and fishermen/farmers – 23%.

Estimates of catch and biological data were collected from returning fishing canoes sampled at the landing stage with an average of 1 300 surveys being made per month (*table* 1).

Fishing effort data and fish landing data collected by the survey network were extrapolated to the whole delta and to individual populations of fishermen using descriptors of the fishery, such as the number of

Table 1. – Number of canoes sampled at landing sites when coming back fishing.

	June	July	August	September	October	November	December	January	February	March	April	May	Total
Lines	152	333	202	91	141	237	316	328	199	177	105	130	2 411
Pushed nets	73	6	1	0	0	0	0	25	61	86	85	118	455
Sweep nets	323	231	131	122	115	176	208	178	212	309	336	266	2 607
Standing nets	381	300	426	404	469	464	378	371	435	509	429	304	4 870
Drift nets	38	185	231	266	270	178	52	42	38	15	11	10	1 336
Small nets	303	341	379	373	331	177	170	139	142	185	182	130	2 852
Big traps	7	25	1	0	1	0	0	6	14	12	2	3	71
Drawn nets	144	50	89	24	1	22	26	82	78	117	154	89	876

fishermen by professional class or the number of fishing units, which had been estimated during the first statistical surveys made in the delta (Quensière *et al.*, 1988; Morand *et al.*, 1990).

Small scale fisheries in Mali are very dynamic. They involved almost 60 000 fishermen and provided 48 000 metric landed tons of fish in 1990-1991 (Laë *et al.*, 1994*a*). They use very diverse fishing gear to capture a wide range of target species in various biotopes and are adapted to seasonal variations in the ecosystem and the fish communities. Adjustment of the gear to fish abundance is very rapid and catches as well as the nature of the fishery give a good idea of the phase of fish community available to exploitation. The fishing gears with the highest performance relative to catch are standing nets (12 800 tons), small traps (8 900 tons), sweep nets (7 200 tons), draw nets (5 900 tons) and unbaited multihook lines (5 200 tons). Together these form an interesting means of assessing the fishery because they cover the full range of biotopes and fishing activities and express the diversity and the spatial and temporal variability of the fish communities. Sampling the fishery therefore represents a satisfactory alternative to experimental fishing which often uses a limited range of selective gear and which cannot be used in all biotopes.

RESULTS

Seasonal variation of fish catches

There is considerable heterogeneity in fish abundance in the delta in both space and time. There is also a dominant role of the floodplains during the rising flood (*fig.* 4).

The Diaka-Kotia area, whose plains are still widely flooded during rising waters, provides 31% of total annual catches. When flooded these plains are favourable biotopes for the reproduction and growth of various fish species. Wide areas under water help prey species to disperse and offer numerous possibilities for shelter in the surrounding vegetation. Fishing is particularly important in fairways and backwaters during falling waters when the fish are returning to the river and when these features constitute natural systems for fish concentration.

Due to the present drought, the area of the temporarily flooded plains in the Djenneri and Northern dune are greatly reduced. Consequently their contribution to fish production is far less important now at 4.9 and 6.6% of total catches respectively, than in the past.

Permanently flooded areas also contribute significantly to fish landings, especially lakes Debo and Walado which are the only important open water areas remaining during the low-water season when the fish are particularly densely concentrated (28% of catches). The Niger river upstream of the lakes represents a productive area throughout the year (23% of catches), unlike the downstream zone where lack of flooding limits the extent of areas suitable for breeding and growth (7% of catches).

Seasonal variations of specific diversity

Seventy six fish species, out of a total of 140, were observed during the fishing survey. This was due in part to the scarcity of some species and to difficulties with their identification. Detailed taxonomy was not always possible in the field. Only 17 of the 76 species represented 85% of the annual fish landings (*table* 2). Cichlids were the most abundant and contributed 26.6% of the total production, with *Oreochromis niloticus* (10.2%), *Tilapia zillii* (8.3%), *Sarotherodon galilaeus* (6.2%) and *Oreochromis aureus* (1.9%). Clariid catfishes were only represented by *Clarias anguillaris* and *Clarias grandisquammis* and constituted 18.7% of the total catches. Caracins comprised 13.6% of the total with *Brycinus leuciscus* (6.2%), *Hydrocynus brevis* and *Hydrocynus forskalii* (5.2%), and *Alestes* sp. (2.2%). Other families contributing were the Bagridae catfishes with 11% (*Chrysichthys* sp., 5.4%, *Bagrus* sp., 2.8% and *Auchenoglanis* sp., 2.7%), the Cyprinidae (5.3%) with only one genus, *Labeo* and the Centropomidae with only one species *Lates niloticus* (3.8%).

The specific distribution of the catches showed seasonal variations linked to the hydrological cycle of the delta. The Shannon index computed from monthly specific catches, by weight, reached its highest level during the flood and at the beginning of the falling water (*fig.* 5). Catches were at their lowest in November. This is a special case because of the specialization in the fishing way, that reduces the number of species caught. That month 3 species represent 60% of the fish landing instead of 6 the other months. The lowest values of the Shannon index occurred at the end of the low-water period in April and May. The decrease in specific diversity when the delta dries up is interesting as it could help to understand larger time scale processes (*i.e.* during drought periods).

In most cases, the largest catches occur during fall water (*fig.* 6), except for *Labeo senegalensis* and *Synodontis* sp., whose maxima coincide with high water level and *Oreochromis niloticus* which was most abundant at low water level. Regardless of the amount caught, there was a marked seasonal variability in the relative abundance of the various species (*fig.* 7). For example *Brycinus leuciscus* occupied the third rank in landings during falling water when it formed 10% of the catch as compared to only 14th position with 2% of the catch during low water. The same was true of *Hydrocynus brevis* and *Hydrocynus forslali* which are predators of *Brycinus leuciscus*. In contrast, species such as *Chrysichthys auratus* or *Labeo senegalensis* were more numerous during rising water or during the floods. Some families like the Cichlidae (*Sarotherodon galilaeus*, *Oreochromis niloticus*, *Oreochromis aureus*)

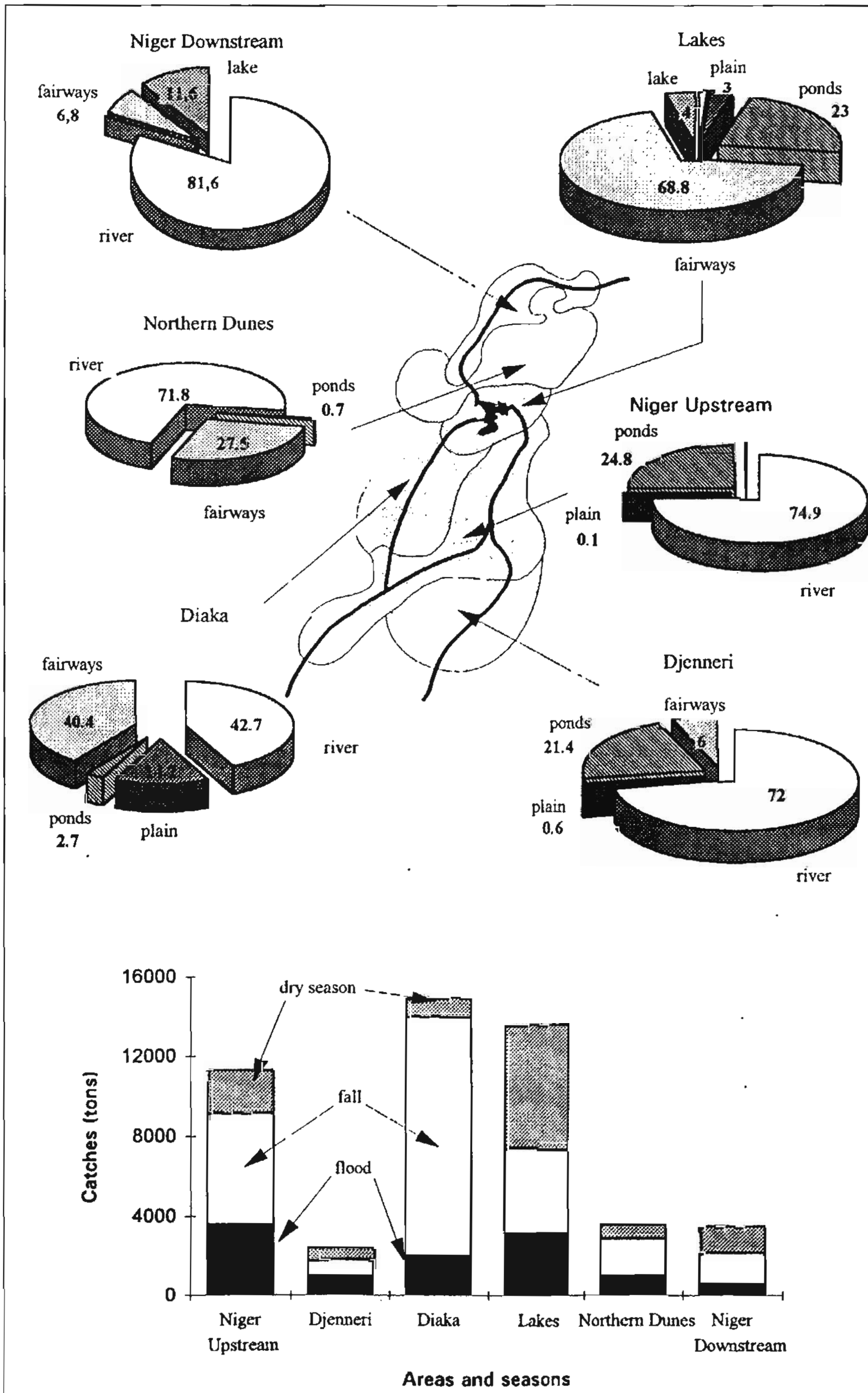

Figure 4. – Seasonal fish landings of the six statistical areas of the delta and catch distribution per biotope.

or Centropomidae (*Lates niloticus*) were relatively more abundant during low water. Finally, other species such as *Clarias anguillaris*, *Tilapia zillii*, *Mormyrus rume* and *Schilbe mystus* were relatively stable over time.

Besides differences in abundance between the six areas of the delta, there were differences in the composition of the catches (*fig.* 8). For instance, catches of *Alestes* sp., *Hydrocynus* sp., *Brycinus leuciscus*, *Auchenoglaris* sp. and *Labeo senegalensis*

Table 2. – Annual catches (metric tons) in 1990-1991 and biological features of fish species in the Central Delta of the Niger (H.W = High water, L.W. = Low water, M.H. = Mouth Hatching).

Families	Species	Breathing	Reproduction	Habitat	Catches
Clariidae	*Clarias anguillaris*	aerial	extensible	pond + river	8 891
Cichlidae	*Oreochromis niloticus*	endurance	mulyiple M.H.	river + floodplain	4 950
Cichlidae	*Tilapia zillii*	endurance	nest L.W.	river + pond	4 057
Cichlidae	*Sarotherodon galilaeus*		multiple M.H.	river + floodplain	3 003
Characidae	*Brycinus leuciscus*		H.W.	river + floodplain	3 003
Cyprinidae	*Labeo senegalensis*		H.W.	river + floodplain	2 468
Bagridae	*Chrysichthys auratus*			river + pond	2 292
Characidae	*Hydrocynus brevis*		flood	river + pond	1 912
Centropomidae	*Lates niloticus*		flood	river + pond	1 853
Bagridae	*Bagrus macropterus*		H.W.	river	1 273
Bagridae	*Auchenoglanis occidentalis*		H.W.	river + pond	1 121
Cichlidae	*Oreochromis aureus*			floodplain	907
Schilbeidae	*Schilbe mystus*	endurance	H.W.	river + pond	780
Characidae	*Hydrocynus forskali*		flood	river	614
Mormyridae	*Hyperopsius bebe*		H.W.	pond	576
Characidae	*Brycinus nurse*		H.W.	river + floodplain	565
Mormyridae	*Mormyrus rume*		H.W.	muddy bottom	537
Mochokidae	*Synodontis schall*	endurance	end L.W.	pond	471
Protopteridae	*Protopterus annectens*	aerial	nest	floodplain	444
Characidae	*Alestes dentex*		H.W.	river + floodplain	403
Bagridae	*Chrysichthys nigrodigitatus*		H.W.		349
Tetradontidae	*Tetroadon lineatus*		H.W.	river + pond	292
Mochokidae	*Synodontys nigrita*	endurance			267
Mochokidae	*Hemisynodontys membranaceus*		H.W.	river + pond	225
Schilbeidae	*Siluranodon auritus*		H.W.?	river + pond	224
Bagridae	*Auchenoglanis biscutatus*				207
Bagridae	*Clarotes laticeps*				186
Mormyridae	*Petrocephalus bane*		H.W.	river	170
Distichodontidae	*Distichodus brevipinnis*		H.W.	river + floodplain	142
Cyprinidae	*Barbus donaldsonsmithi*			floodplain	140
Cichlidae	*Hemichromis fasciatus*		H.W.	river + floodplain	129
Cichlidae	*Tilapia dageti*		nest multiple	river + floodplain	125
Characidae	*Alestes baremoze*		H.W.	river + floodplain	122
Scilbeidae	*Eutropius niloticus*		H.W.	river	99
Claridae	*Heterobranchus bidorsalis*		end L.W.	pond + river	98
Cyprinidae	*Raiamas senegalensis*				96
Cyprinidae	*Labeo coubie*		H.W.	rock + mud	88
Bagridae	*Bagrus docmac*				80
Malapteruridae	*Malapterurus electricus*			floodplain	71
Citharinidae	*Citharinus citharus*		H.W.	river + pond	64
Mormyridae	*Marcusenius senegalensis*		H.W.	pond	61
Clariidae	*Heterobranchus longifilis*				30
Clariidae	*Hemichromis bimaculatus*		H.W.	river + floodplain	21
Distichodontidae	*Distichodus rostratus*		H.W.	river + floodplain	21
Clupeidae	*Pellonula miri*		multiple	river	17
Cichlidae	*Tylochromis jentinki*		H.W.		14
Mochokidae	*Synodontys clarias*	endurance	H.W.	river + pond	13
Schilbeidae	*Physailia pellucida*				11
Mochokidae	*Synodontys filamentosus*		H.W.	rock	11
Osteoglossidae	*Heterotis niloticus*		nest H.W.	pond	9
Mochokidae	*Synodontys courteti*			river	7
Mormyridae	*Mormyrops oudoti*			rock	6
Mormyridae	*Mormyrops deliciosus*				5
Cyprinidae	*Barbus occidentalis*			river + floodplain	5
Bagridae	*Clarotes macrocephalus*				5
Mochokidae	*Brachysynodontys batensoda*		H.W.	river + pond	4
Cichlidae	*Chromidotilapia guntheri*				4
Mormyridae	*Mormyrus macrophtalmus*				3
Polypteridae	*Polypterus senegalus*	aerial	H.W.		2
Characidae	*Brycinus macrolepidotus*				1
Mochokidae	*Synodontys sorex*			river	1
Gymnarchidae	*Gymnarchus niloticus*	air bladder	nest H.W.	pond	+
Others					1 655

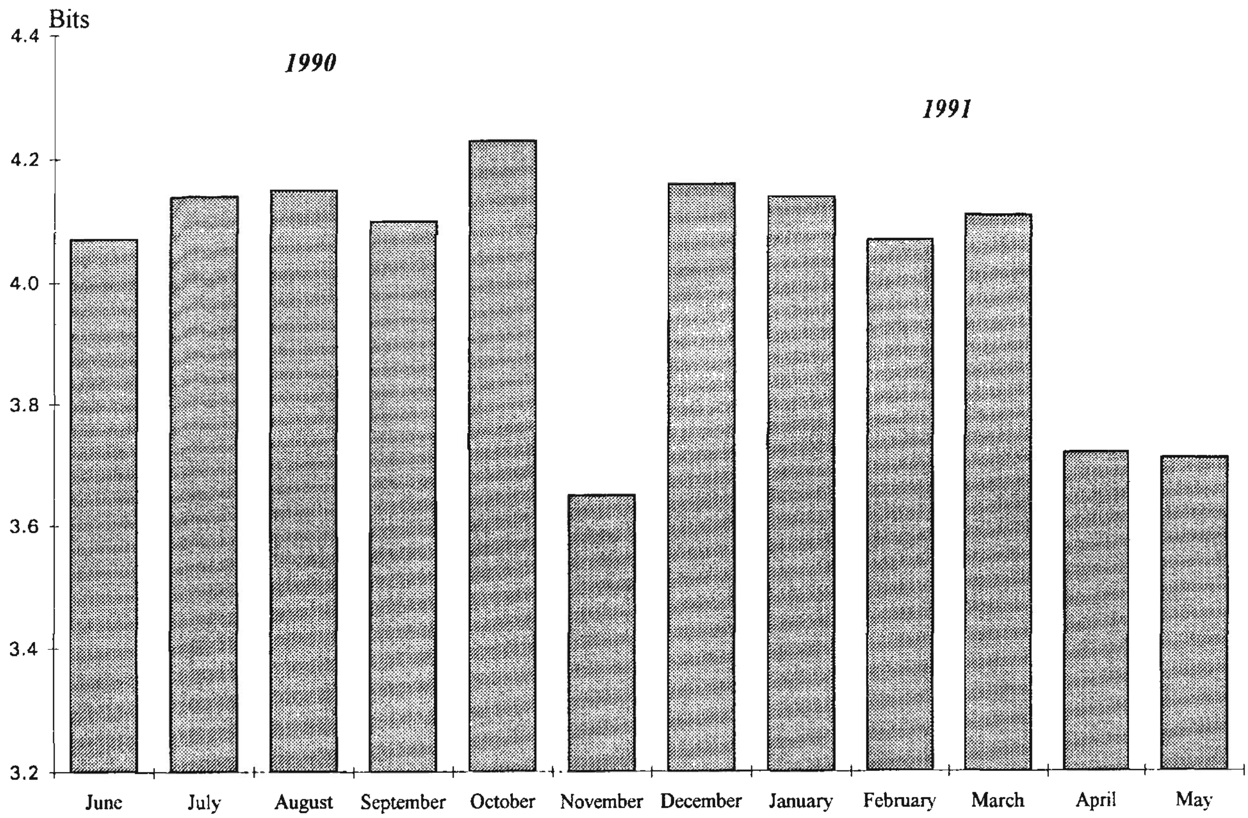

Figure 5. – Monthly evolution of Shannon diversity index in the Central Delta of the Niger River from June 1990 to May 1991.

were higher in the Niger river upstream of the lakes than in the rest of the delta. There were large concentrations of *Clarias anguillaris* and *Brycinus leuciscus*, *Bagrus bayad*, *Sarotherodon galilaeus* and *Tilapia zillii* in the Diaka sector. *Chrysichthys auratus*, *Hydrocynus* sp., *Hyperopsius bebe*, *Lates niloticus* and cichlids especially *Oreochromis niloticus*, were more abundant in the sector of the lakes. Downstream of the lakes in the Niger river *Hydrocynus* sp., *Hyperopsius bebe* and *Oreochromis niloticus* were caught in greater numbers than in sectors south of the lakes. In the Djenneri and Northern dunes sectors the relative distribution of catches was more regular, though in these two areas *Clarias anguillaris* was strongly dominant. In general *Brycinus leuciscus*, *Alestes* sp., *Labeo senegalensis* and *Auchenoglanis* sp., seemed to be more abundant upstream of the lakes than downstream where *Bagrus* would be more numerous.

Such heterogeneity actually reveals differences in fish affinity. Migratory species are mainly associated with flooded areas during rising water and the beginning of falling water, while opportunist species frequently visit floodplains or rivers during low-water. As ascending hierarchical classification was used to cluster the sectors according to their fish communities. We worked out a two order momentum using specific catches per area of each site. The resulting dendrogramm (*fig.* 9) joins the Upstream Niger and the Djenneri area which is now reduced to the Bani river. The Diaka and Northern dune sectors show similar fish communities as the lakes and downsteam Niger sectors.

Evolution of yields

From 1950 to 1970, the growth of fishing lead to an increase in annual fish landings from 45 000 tons to 90 000 tons. Thereafter fish production showed large fluctuations with a general downward trend from 87 000 tons in 1969-1970 to 37 000 tons in 1984-1985 (Laë, 1992 *a*). This drop in catch was directly linked to the decrease in flooded area in the delta and more generally to the drought period that prevailed in West Africa.

During the same period, yields per hectare, computed from annual average flooded areas, showed a rising trend from 40 kg/ha in 1968 to 120 kg/ha in 1990 (*fig.* 10). The reason for the rise in fish yield is attributed to the disappearance of large species living in floodplain areas and to the increase in productivity caused by the shift of the fishery to younger and smaller fish. This, in turn, is a consequence of rising fishing pressure which is in part due to the smaller area flooded: actually the number of fishermen grew from 43 000 in 1966 to 63 000 in 1989 and each fisherman increased his efficiency through the import

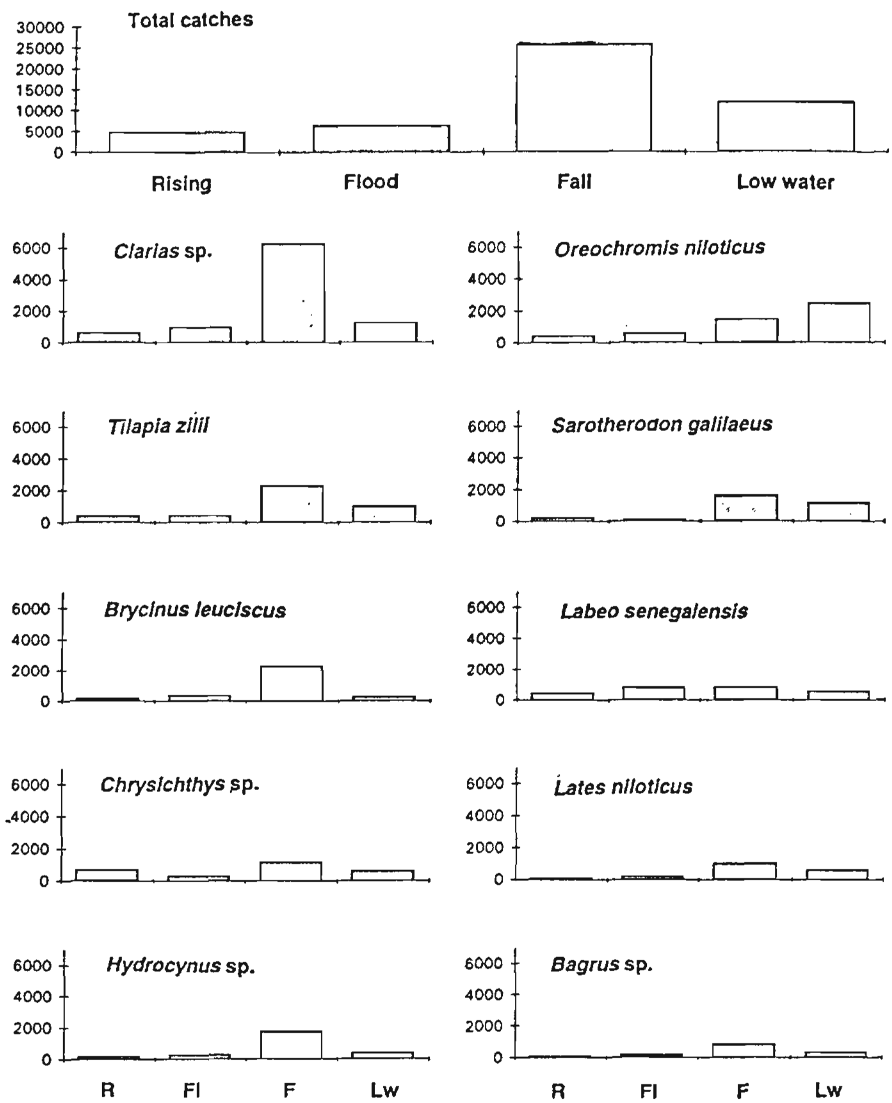

Figure 6. – Seasonal catches of the main species fished in the delta (metric tons).

of modern fishing material. The reduction in floodplain area concentrated the fishing pressure on those areas still flooded.

It is interesting to draw a parallel between the catch composition and the evolution of yields. As no statistics are available for the period between 1950 and 1990, such an analysis in of course limited. Nevertheless, some species which were prominent in the catch in the past (Gallais, 1967), now seem to be rare (*table* 2). For example *Hepsetus odoe* and *Gymnarchus niloticus* were no longer found in landings in 1990-1991, and *Polypterus senegalus* at 2 tons and *Heterotis niloticus* at 9 tons showed very poor catches relative to the past. All these species have reproductive cycles linked closely to flooded areas.

In addition species which frequently visit floodplains such as *Clarotes macrocephalus* (5 tons), *Citharinus citharus* (64 tons), *Malapterurus electricus* (71 tons), *Distichodus brevipinnis* (142 tons), *Clarotes laticeps* (186 tons), *Hemisynodontis membranaceus* (255 tons) and *Synodontis* sp. in general (770 tons) were poorly represented in 1990-1991.

The greater efficiency of the modern fishing gears and the persistent drought have not lead, therefore, to species extinction but rather to changes in the composition of fish communities. There is now a greater abundance of opportunist species with short life-cycles which counterbalances a decline in the long lived species. Because of the shift towards faster growing species there has been a trend to increase biological production which in turn has raised the catch per unit area.

The length characteristics of the catches is also modified. Comparison of data from Daget (1952,

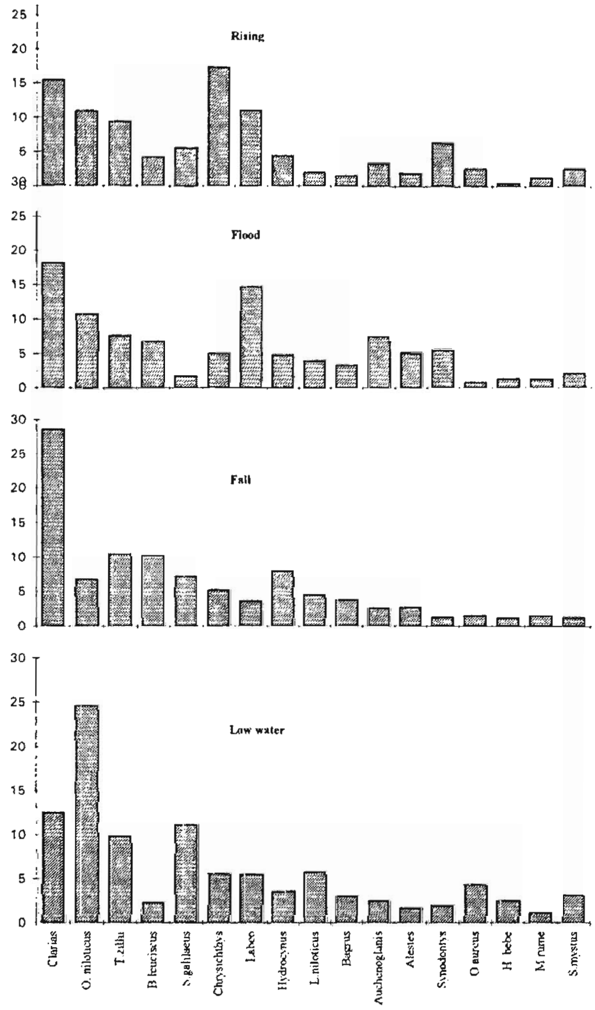

Figure 7. – Relative abundance of the main 17 species in the fish landings of the Delta Central for the 4 defined hydrological seasons.

1956) and Laë *et al.* (1994) for *Tilapia zillii*, *Alestes dentex*, *Alestes baremoze*, *Brycinus nurse* and *Brycinus leuciscus* (*fig.* 11) showed that average catch lengths were appreciably smaller at the time of sampling. Despite the small sample sizes and the sampling procedure used by Daget which are different from ourselves (Laë *et al.*, 1994*a*), some clear trends appear, particularly the sliding of length frequencies towards lower values. This was clearly observed for long life-cycle species such as *Alestes dentex* (disappearance of a 260 mm peak), *Alestes baremoze* (disappearance of a 230 mm peak) and *Tilapia zillii* (disappearance of a 180 mm peak) in which length frequency peaks present in the past had disappeared by 1990. This phenomenon was not noted for short life-cycle species such as *Brycinus nurse* or *Brycinus leuciscus* in which the length characteristics of the catch vary little between Daget's study and the present study. Reduction in mean length towards smaller individuals has a similar effect on the productivity of the community as the trend to smaller species.

DISCUSSION

There was a drop in specific diversity of fish with a relative increase in the various Cichlidae, Clariidae and Centropomidae species between falling water and the end of low-water. The seasonal decrease in flooded area and possibly the intense fishing activity leads to a decrease throughout the year in the abundance of migratory fishes which generally breed only once a year. It may be supposed that this intra-annual observation can be extrapolated to an inter-annual scale whereby the same species are affected by long term drought. Evidence for this can be drawn from the trends in fresh fish traded in Mopti (Quensière *et al.*, 1994) from which three phases in the evolution of the fish communities can be distinguished.

(i) 1969 to 1970: – fish communities were typical of good flood regimes with a remarkable abundance of *Synodontis*, which is usually found during marked seasonal floods. Quensière *et al.* (1994) note that species like *Polypterus senegalus* and *Gymnarchus niloticus* which are typical elements of the fauna of permanent water bodies in areas liable to flooding, were also present.

(ii) 1973 to 1979: – the situation was similar to (i) above in so far as the 9 most abundant species are concerned but secondary species, which are often more typical of the permanent water bodies disappear or become infrequent. At the same time the relative abundance of *Clarias anguillaris*, *Heterobranchus bidorsalis*, *Chrysichthys auratus*, *Bagrus bayad*, *Schilbe mystus* and *Auchenoglanis occidentalis* increases.

(iii) 1985 to 1991: – changes in population structure accelerated and species such as *Citharinus citharus*, *Alestes* sp., *Synodontis* sp. and *Heterotis niloticus* continue to decrease and join the group of secondary species. On the other hand, *Bagrus bayad*, *Clarias anguillaris* and *Chrysichthys auratus* increase in catches.

Similar changes have been described from other parts of Africa. For instance, Benech *et al.* (1983) described the decline of Lake Chad from "Normal Chad" to "Lesser Chad" representing in a diminution of the area of the lake from 22000 km^2 to 6000 km^2 in the space of two years (1971-1972 and 1972-1973). The drying up of the lake led to the concentration of fish and to a strong increase in mortality due to the increased vulnerability to fishing. Furthermore, the degradation of ecological characteristics throughout the basin increased natural mortality. These two phenomena were the principal factor in the change in the populations. The fish population responded with a progressive disappearance of species like *Heterotis niloticus*, *Hydrocynus brevis*, *Citharinus*

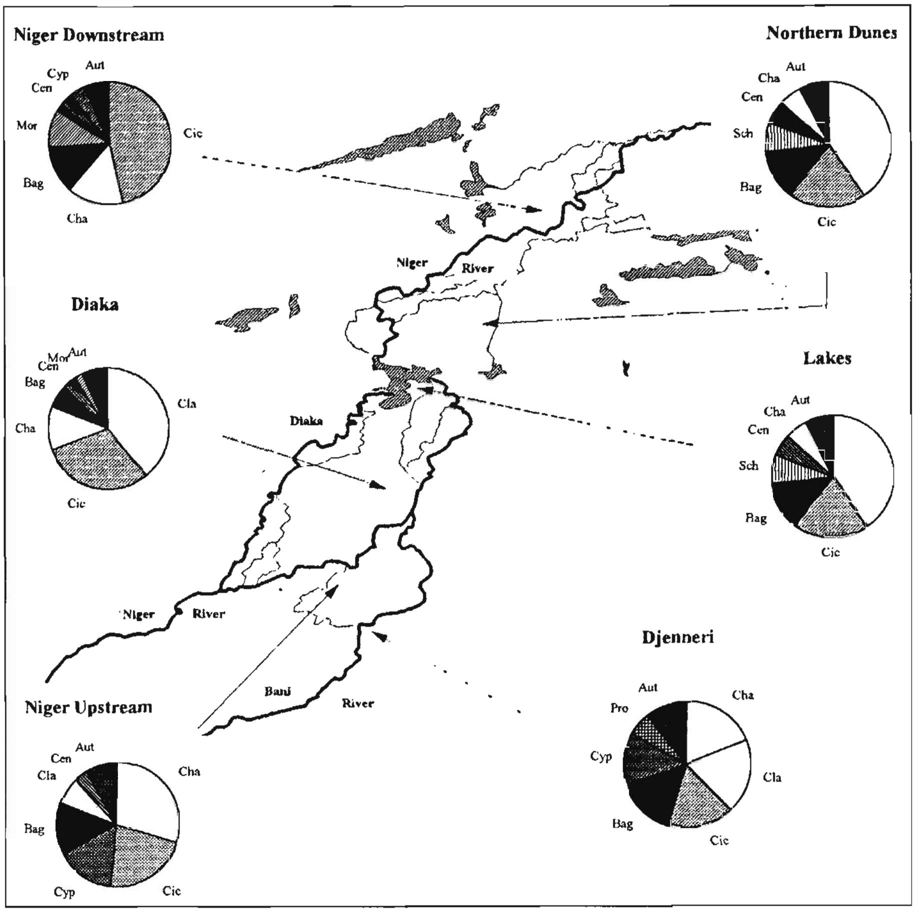

Figure 8. – Fish catch composition for the six statistical areas defined in the Central Delta (Bag = Bagridae, Cen = Centropomidae, Cha = Characidae, Cic = Cichlidae, Cla = Clariidae, Cyp = Cyprinidae, Mor = Mormyridae, Pro = Protopteridae, Sch = Schilbeidae, Aut = Other fish families).

citharus, *Tetraodon fahaka*, *Pollimyrus isidori* and *Mormyrus rume*. Other species described as less abundant in 1971-1972 like *Polypterus senegalus*, *Synodontys schall*, *Brachisynondontis batensoda* became predominant later. Finally, during the drought, *Sarotherodon niloticus* and *Sarotherodon aureus* became increasingly dominant in the catch.

We did not observe any disruption in fish specific richness in the Central Delta of the Niger. Species no longer caught were of course rare when the flow was high. However, reversion to more normal hydrological regimes would probably lead to the re-invasion of the delta by these species, either because they are still there or because they would migrate back into the delta from upstream or downstream areas. The risk that some species may disappear completely is lessened because the breeding areas are scattered throughout the delta. For this reason Benech and Dansoko (1994) thought that fish breed everywhere in the delta. Moreover, most Niger River species show remarkable flexibility in their length at maturation and first breeding in response to periods of crisis (Benech and Dansoko, 1994).

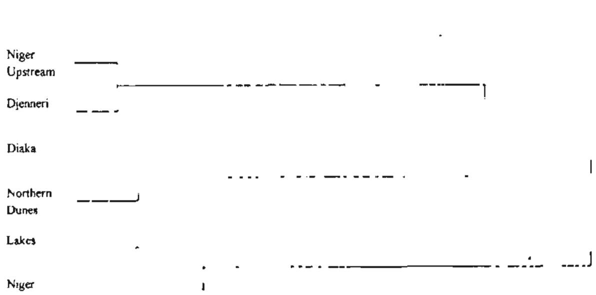

Figure 9. – Similarities dendrogramm of the two order momentum ascending hierarchical classification. Used values are specific catches for each statistical area.

Within the relative stability of the numerical richness in species number the changes recorded in the relative abundance of species were very important. The increase in abundance of the Cichlidae and the Clariidae, which constituted 30% and 20% respectively of total annual catches during the drought illustrate the reaction of the stocks to stress induced by drought and increasing fishing effort. Similar changes were described in Lake Chad by Benech *et al.* (1983) during the drought when the nature of the environment favoured the development of species whose of diet, reproduction and respiration was best adapted to the emergent marshy conditions.

In the Benue River the decrease in flow favoured the Cichlid and Clariid species which are adapted to low dissolved oxygen concentration and which are prolific breeders (Neiland *et al.*, 1990). These observations are akin to those realized by Roberts (1975) on changes in fish communities subject to perturbation of their environment. According to this author, if the biotope can only support a limited number of genera, the evolution of the fish community will favour species like *Barbus*, *Clarias*, Cyprinodonts, Tilapiine cichlids and generally the family Cichlidae. It is difficult to relate these changes to limitations in the food supply without precise data. Moreover, because of the large number of species in African rivers, their trophic flexibility, the excess of food that becomes available during the floods and the general fast that fish undergo during the relative famine of the dry season, it appears that competition for food resources is not a serious factor in determining the composition and abundance of African riverine fish communities in the potamon (Welcomme, 1989). Rather, it would seem that limitations to the extent of breeding areas caused by flood restriction may play a greater role in determining relative abundance of species. However this needs to be exploited in more detail.

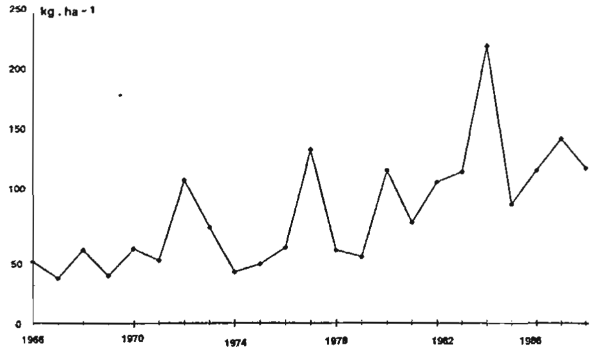

Figure 10. – Yearly evolution of fish yields in the Central Delta of the Niger River.

One particular response of the fish community to various stress in the Central Delta of the Niger River was the increase in importance of tilapias. The particular success of this group merits closer examination and has already been observed, for example by Holding (1993) in Lake Turkana (Kenya) who explains the importance of tilapias in catches by their high individual growth, high fecundity (although the survival rate may be the restricting factor for tilapias production), and by their resistance to low oxygen concentration. The balance is quite complex because oxygen concentration must be low enough to exclude predators but not so low as to threaten tilapia survival.

As tilapias have developed great flexibility towards abiotic factors, it may be supposed that they have developed similar adaptations towards biotic factors and particularly in their ability to resist predators. This

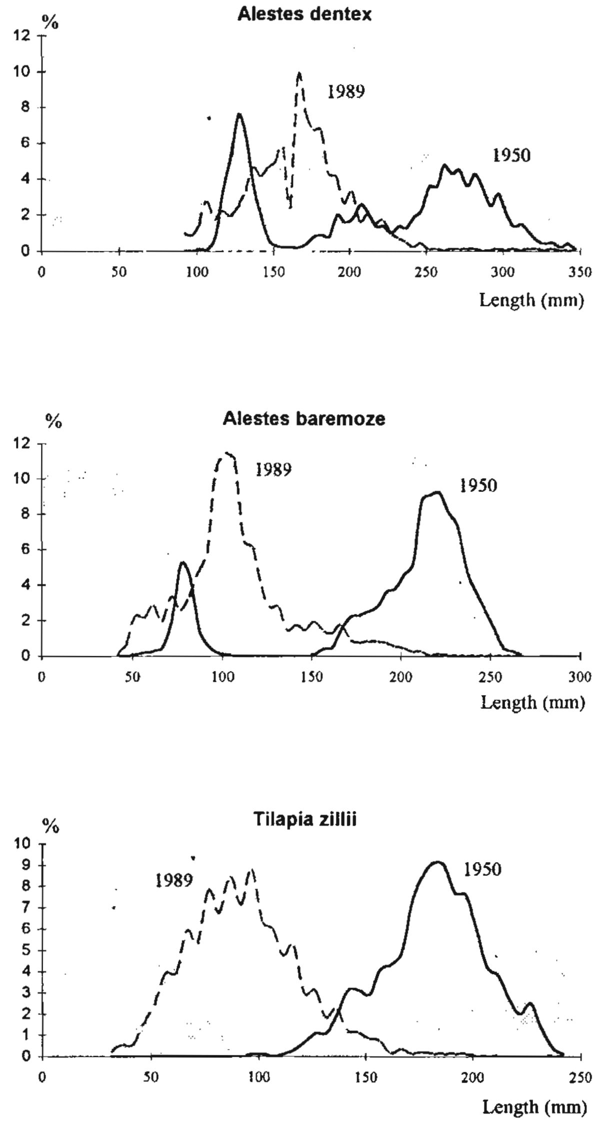

Figure 11. – Evolution of catch length for *Alestes dentex*, *Alestes baremoze* and *Tilapia zillii* from 1950 to 1989 in the Central Delta of the Niger River.

would be possible, for example, by growth regulation when the balance between reproduction and growth is determined by the ratio of adults to juveniles. Tilapias are well adapted to variable ecosystems. They adjust to changes using their remarkable flexibility, in contrast with migratory species of floodplains which react to changes by their mobility.

The limited changes observed in the delta come from the relative heterogeneity of biotopes which act favourably on biological richness (landscape ecology). Biological diversity is linked to the nature of the ecological ecosystem, to their history, and their heterogeneity. During the drought the existence of refuge areas allow the re-settlement of the ecosystem upon the reappearance of more normal flood regimes.

This is typical of biotopes with very marked space and time variability.

The increase in fish yields observed during the drought period, especially between 1972-1973 (111 g ha^{-1}) and 1984-1985 (216 kg ha^{-1}), results from various causes including the increase in fish concentration and the increase of fish vulnerability to fishing gear. Moreover the progressive increase in yields from 1966-1967 (47 kg ha^{-1}) to 1988-1989 (121 kg ha^{-1}) comes from the trend to the increasing dominance of young fish in the fish stocks. In 1950 the average age at capture of *Alestes dentex* and *Alestes baremoze* was over 2 years (Daget, 1952), and those of *Tilapia zillii* was almost 3 (Daget, 1956). In 1990, fishing was much more intense and many species were being caught in their first year life (Laë, 1992*a*) including: *Labeo senegalensis* (86% of 0^+ in catches), *Brycinus leuciscus* (82%), tilapias (82% for *Sarotherodon galilaeus*, 78% for *Tilapia zillii* and 68% for *Oreochromis niloticus*), *Lates niloticus* (76%) and *Chrysichthys auratus* (72%). By contrast, other species such as *Chrysichthys nigrodigitatus*, *Alestes dentex*, *Auchenoglanis biscutatus*, *Brycinus nurse* and *Alestes baremoze* seem to be fished at a greater age as the percentage of 0^+ fish in the catches vary between 20% and 40%. The weighted average of all landings showed that 69% were 0^+ fish.

The increase in fish concentration and fish vulnerability has been observed elsewehere especially in lake Chad where Durand (1983) recorded a rapid increase of fish yield from 104 kg ha^{-1} in 1972 to 245 kg ha^{-1} in 1974 corresponding to the reduction in lake area. On the whole the increase of fish yield in lake Chad from 34 kg ha^{-1} in 1969 to 120 kg ha^{-1} in 1978 were attributable to the development of the fishery and the common occurrence of small and probably immature individuals in the catches.

The increase in yields which occurs concurrently with the decrease in the area of floodplains, is probably due to more intensive exploitation of fish stocks, leading to an increase in productivity. The growth rate declines and longevity increases with fish weight (Peters, 1983). Consequently, large fish species are less productive per unit of biomass unit than smaller ones. For example Downing and Plante (1993) estimate production by 100 fish populations living in 38 various lakes around the world. They observed that the ratio P/B (P=production and B=Biomass) of a 5 g per unit population would be more than three times on average than of a 5 kg population with the same residual biomass. As a fish population moves towards a dominance of short lived species there is a decrease in population life expectancy which produces an increase in the P/B ratio. In addition the emergence of short lived species is a good adaptation to environmental fluctuations because these species take advantage of micro habitats which are not available to species of large size.

In other respects, the behaviour of a multi-species fish community, faced with high fishing effort is completely different to that of a simple stock (Welcomme, 1989). For example, in the Nile River, fish catches remained at about 8400 tons for ten years despite a threefold increase in boat number. Nevertheless, if the catches are in a stagnant phase, fish communities composition are highly modified during the same period. These changes lead to a gradual elimination of large size species which are replaced by a sequence of small size and more productive species (Welcomme, 1986). In general, the fisheries in the Central Delta of the Niger River have followed the fishing up process described by Regier and Loftus (1972) and Welcomme (1992). They also conform to the general pattern of communities subject to stress as described by Rapport *et al.* (1985). In the earlier phases of the fishery the yield rose sharply as effort increased. Then, the yield reached a plateau at which further increases in effort produced a constant total catch. The level of the plateau is linked to the flow which determine the breeding and the feeding of fishes in the floodplains. This plateau is made possible by increases of the P/B ratio and conceals adjustements in species dominance and composition. The biodiversity of fishes decreases as effort increases. In an ultimate phase, only a few small species remain to be exploited by the fishery and when fishing effort exceeds the capacity of the fish stock to breed, catches become unstable from one year to the next and may be followed later by the rapid collapse of catches.

CONCLUSION

The Central Delta of the Niger river is a typical heterogeneous ecosystem which is characterized by highly diversified fish communities. These species are able to tolerate serious environmental disturbances. Even when flooded surfaces are only 25% of those during more normal flood regimes there still exist favourable areas for breeding and the species which are associated with floodplains continue to breed even if they are less abundant. This is all the more true because breeding areas in the delta are scattered and because species adapt various strategies mixing parental care and adopting a diversity of breeding sites. Fish communities, therefore, have considerable adaptive capacities and the individual fish species are very robust (Benech and Dansoko, 1994).

Unfavourable climatic conditions are associated with a very intensive fishing effort which mainly affects large fishes and the migratory species. Drought leads to an overall drop in residual ichthyomass by lessening the renewal rate of some species during the flood and by reducing the carrying capacity of the river during low-water while fishing acts mainly act on the age composition of stock.

Under these conditions of combined stress fish communities are able to attain new stability.

Specialized species seem to be more sensitive to change because their adaptive capacities with respect to changes in diet or breeding sites are poor. Generalist species proliferate because they are more flexible and are free from competitors and predators. *Clarias anguillaris* and the tilapias which spawn in various biotopes for a major part of the year and are very resistant to poor dissolved oxygen concentrations are particularly successful.

While changes in species composition occur, the average length at capture of the fishes declines as their life expectancy decreases. This together with the suppression of the largest species, which have a poor coefficient of transformation, leads to an increase of the P/B rate. Moreover, the trend to a greater percentage of young fish in the catch acts on the trophic level because young fishes are rarely final consumers. Consequently, fish productivity increases even if the residual biomass decreases. This process leads to an increase of fishing yields and a decrease in the diversity of the catch.

Thus, in the Central Delta of the Niger, biodiversity, due to contrasted seasons, allows fish communities to react in an appropriate way to each stress without a collapse in fish production.

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REFERENCES

Benech V., D. Dansoko, 1994. La reproduction des espèces d'intérêt halieutique. *In*: La pêche dans le Delta Central du Niger, Annibal, éd. J. Quensière, ORSTOM, 10-25.

Benech V., J. R. Durand, J. Quensière, 1983. Fish communities of Lake Chad and associated rivers and floodplains. *In*: Lake Chad, ecology and productivity of a shallow tropical ecosystem, J. P. Carmouze *et al.*, eds., Junk, The Hague, 293-356.

Blanc M., J. Daget, F. d'Aubenton, 1955. Recherches hydrobiologiques dans le bassin du moyen Niger. *Bull. Inst. fr. Afr. noire*, **17A**, 17 p.

Brunet-Moret Y., P. Chaperon, J. P. Lamagat, M. Molinier, 1986. Monographie hydrologique du fleuve Niger. Tome II: cuvette lacustre et Niger moyen. *ORSTOM, Coll. Monogr. Hydrol.*, **8**, 506 p.

Daget J., 1949*a*. La pêche dans le delta central du Niger. *J. Soc. afr.*, **19,** 79 p.

Daget J., 1949*b*. Le tineni: poisson migrateur des eaux douces africaines. *Cybium*, **4,** 6 p.

Daget J., 1952. Mémoire sur la biologie des poissons du moyen Niger. Biologie et croissance des poissons du genre *Alestes. Bull. Inst. fr. Afr. noire*, **14A**, 191-225.

Daget J., 1954. Les poissons du Niger supérieur. *Mém. Inst. fr. Afr. noire*, **36,** 391 p.

Daget J., 1956. Mémoire sur la biologie des poissons du moyen Niger. Recherches sur *Tilapia zillii* (Gerv.). *Bull. Inst. fr. Afr. noire*, **18A**, 165-233.

Daget J., 1973. La pêche dans le fleuve Niger. *Afr. J. Trop. Hydrobiol. Fish.*, spec. issue II, 107-114.

Durand J. R., 1983. The exploitation of fish stocks in the lake Chad region. *In*: Lake Chad, ecology and productivity of a shallow tropical ecosystem, J. P. Carmouze *et al.*, eds., Junk, The Hague, 425-481.

Downing J. A., C. Plante, 1993. Production des populations de poisson dans les lacs. *Can. J. Aquat. Sci.*, **50,** 110-120.

Gallais J., 1967. Le delta intérieur du Niger. Étude de géographie régionale. *Inst. fr. Afr. noire*, Dakar, 2 tomes.

Gallais J., 1984. Hommes du Sahel, le delta intérieur du Niger, 1960-1980. *Flammarion*, Paris, 289 p.

Holding J., 1993. Population dynamics and life history steps of Nile Tilapia, *Oreochromis niloticus*, in Ferguson's gulf, lake Turkana, Kenya. *Environ. Biol. fish.*, **37,** 25-46.

Laë R., 1991. L'échantillonnage des pêches artisanales dispersées: nécessité d'opérations préalables. L'exemple du Delta Central du Niger. *In*: La Recherche Face à la Pêche Artisanale, Symp. Int. ORSTOM-IFREMER, Montpellier, France, 3-7 juillet 1989, J. R. Durand, J. Lemoalle, J. Weber, éds., Paris, ORSTOM, 1991, t. I, 395-407.

Laë R., 1992*a*. Influence de l'hydrologie sur les pêcheries du Delta Central du Niger de 1966 à 1989. *Aquat. Living Resour.*, **5,** 115-126.

Laë R., 1992*b*. Impact des barrages sur les pêcheries artisanales du delta central du Niger. *Cahiers Agricultures*, **1,** 256-263.

Laë R., P. Morand, C. Herry, J. Y. Weigel, 1994. Méthodes quantitatives: Echantillonnage et traitement des données. *In*: La pêche dans le Delta Central du Niger, éd. J. Quensière, ORSTOM, 30 p.

Lévêque C., 1995. Role and consequences of fish diversity in the functioning of African freshwater ecosystems. *Aquat. Living Resour.*, **8**, 59-78.

Lowe-McConnell R. H., 1975. Fish communities in tropical freshwaters. Their distribution, ecology and evolution. Longman, London and New York, 317 p.

Morand P., J. Quensière, C. Herry, 1990. Enquête pluridisciplinaire auprès des pêcheurs du delta central du Niger: plan de sondage et estimateurs associés. ORSTOM éd., SEMINFOR, **4**, 195-211.

Neiland A. E., J. P. Goddard, G. M. Reid, 1990. The impact of damming drought and overexploitation on the conservation of marketable fish stocks of the River Benue. *J. Fish. Biol.*, **37A**, 203-205.

Peters R. H., 1983. The ecological implications of body size. Cambridge University Press, Cambridge, U.K., 329 p.

Raimondo P., 1975. "Monograph on operation fisheries, Mopti", in consultation on fisheries problems in the Sahelian Zone, Bamako, Mali, 13-20 Nov. 1974, *CIFA Occas. Pap.*, **4**, 294-311.

Quensière J., 1988. Études halieutiques du delta central du Niger. Enquête Statistique auprès des Pêcheurs. *In*: INRZFH-ORSTOM, Actes de l'atelier de Bamako, 7-9 juin 1988, 180 p.

Quensière J., 1994. Écologie des poissons d'eau douce tropicaux. *In*: La pêche dans le Delta Central du Niger, éd. J. Quensière, ORSTOM.

Quensière J., V. Benech, D. Dansoko, 1994. Évolution de la composition des peuplements de poissons du Delta Central. *In*: La pêche dans le Delta Central du Niger, éd. J. Quensière, ORSTOM, 211-227.

Rapport D. J., H. A. Regier, T. C. Hutchinson, 1985. Ecosystem behaviour under stress. *Am. Nat.*, **125**, 617-640.

Regier H. A., K. H. Loftus, 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. *J. Fish. Res. Board Can.*, **29**, 959-968.

Roberts J. R., 1975. Geographical distribution of African freshwater fishes. *Zool. J. Linn. Soc.*, **57**, 249-319.

Welcomme R. L., 1986. The effects of the sahelian drought on the fishery of the central delta of the Niger river. *Aquac. Fish. Manage.*, **17**, 147-154.

Welcomme R. L., 1989. Review of the present state of knowledge of fish stocks and fisheries of African Rivers. *In*: Proc. Int. River Symp., D. P. Dodge ed., *Can. Spec. Publ. Fish. Aquat. Sci.*, **106**, 515-532.

Welcomme R. L., 1992. The conservation and environmental management of fisheries in inland and coastal waters. *Neth. J. Zool.*, **42**, 176-189.

Welcomme R. L., R. A. Ryder, J. A. Sedell, 1989. Dynamics of fish assemblages on river systems-a synthesis. *In*: Proc. Int. River Symp., D. P. Dodge ed., *Can. Spec. Publ. Fish. Aquat. Sci.*, **106**, 569-577.