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# Reproductive strategies of fishes in a tropical temporary stream of the Upper Senegal basin: Baoulé River in Mali

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**Abstract**

In the tropics, there is very little information on fish reproduction in intermittent streams and most of the studies are from the neotropic regions. In temporary rivers, environmental conditions are sharply contrasted and the variation amplitude of hydrological and physicochemical characteristics is high. In the Baoulé River (Mali), during the peak of the dry season, the remaining pools comprise only 10% of the total length of the river. During the wet season, there is a short (three months) but intense period of flooding. In this study, the reproductive strategies of 18 species of fishes were investigated in the upper reach of the Baoulé drainage. They belong to eight families, show variation in feeding guilds, and vary in size and habitat preferences. Fishes were collected from February 1985 to November 1988 using gillnets. Two main types of spawning strategies may be distinguished among these species. The first, the 'total spawners', have generally a short annual spawning period just before the flood. The second, the 'small-brood spawners', produce small batches of eggs at frequent intervals for most of the year. Most of the species inhabiting the Baoulé River exhibit a breeding strategy in relation to the flood seasonality. This type of strategy, common in harsh but predictable environments, favours a synchronous reproduction in phase with the optimal environmental conditions and the production of large number of juveniles that require no parental care. Concerning the Baoulé River, 12 variables related to life-history theory were measured for 18 species. Clustering of these species based on Euclidean distances resulted in two groups. The first corresponds to developed parental care, large oocytes and low fecundity (about a hundred eggs). Two species, *Chrysichthys auratus* and *Sarotherodon galilaeus*, belong to this 'equilibrium strategy'. Others species have a 'seasonal strategy', which is adapted to the harsh local conditions. In the Nilo-Sudanian area, most fishes appeared to be associated with a seasonal life history strategy that exploits an annual expansion of aquatic production. In the Baoulé River, the 'seasonal strategy'is characterised by high fecundity, absence of parental care, limited breeding season and for some species large adult size and upstream spawning migrations to floodplains. 

**Résumé**

**Stratégies de reproduction des poissons d'un cours d'eau temporaire du bassin du haut Sénégal (la Baoulé au Mali).** En zone tropicale, il existe peu d'informations qui concernent la reproduction de poissons peuplant les cours d'eau temporaires et la majorité des études existantes concerne la région néotropicale. Dans ce type de rivière, les conditions environnementales sont très contrastées car l'amplitude des variations hydrologiques et des caractéristiques physico-chimiques est généralement très importante. Sur la Baoulé (Mali), au maximum de la saison sèche, les mares résiduelles ne constituent plus 10% de la longueur totale de la rivière. Au moment de la saison des pluies, la crue est courte (trois mois) mais intense. Dans cette étude, les stratégies de reproduction de dix-huit espèces de poissons d'eau douce ont été examinées dans le cours supérieur du Baoulé. Elles appartiennent à huit familles, ne font pas partie des mêmes guildes alimentaires, ne fréquentent pas les mêmes habitats et sont de taille différente. Les poissons ont été collectés à l'aide de filets maillants de février 1985 à novembre 1988. Ces espèces présentent deux principales stratégies de reproduction. Les espèces "à ponte annuelle unique" possèdent généralement une période de reproduction assez courte qui se situe juste avant la crue; les espèces "à pontes multiples" pondent des petits lots d'œufs à intervalles fréquents pendant presque toute l'année. La majorité des espèces qui peuplent la Baoulé ont une stratégie qui leur permet de se reproduire au moment de la période d'inondation. Ce type de stratégie, la plus fréquente dans des environnements contraignants mais prévisibles, favorise le synchronisme entre la reproduction et la période durant laquelle les conditions environnementales sont optimales. Une telle stratégie est généralement accompagnée d'une fécondité élevée et d'absence de soins à la descendance. Douze

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variables ont été identifiées pour chacune des dix-huit espèces. L'analyse des distances ordonnée selon une classification hiérarchique ascendante basée sur des distances Euclidiennes permet de distinguer deux groupes. Le premier correspond aux espèces qui prodiguent des soins parentaux, possèdent de grands ovocytes et ont une faible fécondité (quelques centaines d'œufs). Deux espèces, *Chrysichthys auratus* et *Sarotherodon galilaeus* présentent ce type de "stratégie équilibrée". Les autres espèces ont une stratégie de type "saisonnière" qui est parfaitement adaptée aux contraignantes conditions locales. Dans le secteur Nilo-Soudanien, la plupart des poissons semblent adopter une stratégie vitale saisonnière pour mieux exploiter la meilleure production annuelle. La stratégie périodique se caractérise dans la Baoulé par une fécondité élevée, l'absence de soins parentaux, une période de ponte réduite et pour quelques espèces par des adultes de grande taille qui effectuent des migrations anadromes de reproduction. 

*Keywords:* Freshwater fishes; Environment; Reproductive strategies; Senegal basin; Western Africa

## 1. Introduction

There have been many recent studies demonstrating an influence of environmental conditions on the reproductive strategies of tropical fish in Africa (Munro et al., 1990; Lévêque, 1997; Lévêque and Paugy, 1999), but the timing of reproduction of tropical riverine fishes has been investigated mainly in floodplain rivers and permanent streams. For seasonal floodplain rivers, most of the fishes have breeding periods that coincide with the annual flood (Welcomme, 1979; Lowe McConnell, 1987; Munro et al., 1990; Lévêque and Paugy, 1999), while in stable habitats such as permanent forest streams, fishes may have much more extended breeding seasons (Albaret, 1982). However, in a stream or a geographic zone, reproductive patterns may differ between species, suggesting the influence of both environmental and biotic factors. For the neotropical stream fishes studied by Winemiller (1989), it was possible to discern three different reproductive strategies among fishes: equilibrium, opportunistic and seasonal.

In the tropics, there is very little information on fish reproduction in intermittent streams and most of the studies are from neotropic regions (Alkins-Koo, 2000 for a review). In temporary rivers, environmental conditions are sharply contrasted and the variation amplitude of hydrological and physicochemical characteristics is high. During the dry season, there may be only a few isolated lentic pools.

In the Baoulé River in tropical West Africa (Mali), the remaining pools comprise only 10% of the total length of the river during the peak of the dry season (Fig. 1). During the wet season, there is a short but intense period of flooding. Finally, lotic conditions resume during some months and the cycle restarts. Given such drastic seasonal changes, it may be expected that breeding should be highly seasonal. However, it may be difficult to predict the most appropriate breeding season, even if flood conditions appear the best. Indeed, in some case, if channel shape and space limit the access of the floodplain habitats floods may even have a negative impact on juveniles or availability of food resources.

In this study, the reproductive strategies of 18 species of freshwater fishes were investigated in the upper reach of a temporary stream within the Baoulé drainage, with complete seasonal records on nine species. They belong to eight families, show variation in feeding guilds, and vary in size and habitat preferences (Table 1).

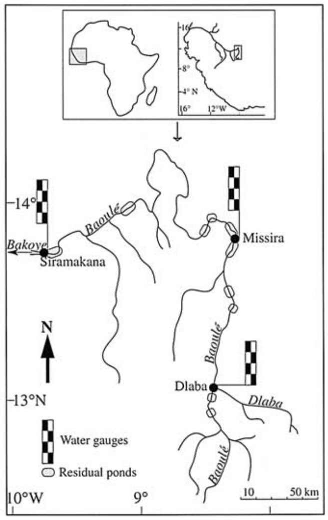


Fig. 1. Baoulé: geographical situation, position of the sample sites and residual ponds during the maximal low water.

## 2. The study site

The Baoulé River is a tributary of the upper Senegal basin in southwest Mali (Fig. 1). The total length of the river is about 550 km with a 59,500 km$^2$ drainage area (for a complete description see Paugy, 1994). The river is situated in the Nilo-Sudanian zone influenced by the tropical climate, which is characterised by two main seasons, one short wet season and one long dry season.

### 2.1. Hydrological features

Climatic alternation characterises the hydrological regime that is typical of a tropical water body (Rodier, 1964). The dry season is very severe. During this period up to 90% of the stream channel dries out, leaving a few isolated pools or chains of pools which represent scarcely 10% of the total stream length (Fig. 1). At the end of the dry season, the water reaches temperatures of 35 °C, the conductivity

Table 1
Biological characteristics of the 18 fish species studied. MSL: maximum standard length (source: Paugy, 1994; Lévêque and Paugy, 1999), N: number of fish examined in the present study.

| Species | Family | MSL(mm) | N | Feeding habits | Habitat |
|---|---|---|---|---|---|
| *Hyperopisus bebe* | Mormyridae | 510 | 27 | insectivorous | benthic dweller |
| *Marcusenius senegalensis* | | 321 | 280 | insectivorous | benthic dweller |
| *Mormyrops anguilloides* | | 1 500 | 20 | insectivorous and ichthyophagous (large adults) | benthic dweller |
| *Mormyrus rume* | | 870 | 29 | insectivorous | benthic dweller |
| *Petrocephalus bovei* | | 100 | 69 | insectivorous | benthic dweller; schools |
| *Alestes baremoze* | Characidae | 425 | 256 | omnivorous | pelagic dweller; schools |
| *Brycinus leuciscus* | | 119 | 151 | omnivorous | pelagic dweller; schools |
| *Brycinus macrolepidotus* | | 530 | 79 | omnivorous (mainly allochthonous feeder) | surface dweller |
| *Brycinus nurse* | | 218 | 229 | omnivorous | pelagic dweller; schools |
| *Hydrocynus forskalii* | | 780 | 90 | ichthyophagous | pelagic dweller |
| *Labeo senegalensis* | Cyprinidae | 550 | 55 | algae and 'aufwuchs'grazer | bottom dweller |
| *Chrysichthys auratus* | Claroteidae | 270 | 269 | invertivorous | bottom dweller |
| *Schilbe intermedius* | Schilbeidae | 500 | 1 399 | omnivorous | pelagic dweller; schools |
| *Schilbe mystus* | | 350 | 30 | omnivorous | pelagic dweller; schools |
| *Clarias anguillaris* | Clariidae | 1 500 | 36 | omnivorous | benthic dweller |
| *Synodontis ocellifer* | Mochokidae | 370 | 68 | invertivorous | bottom dweller |
| *Synodontis schall* | | 400 | 451 | invertivorous | bottom dweller |
| *Sarotherodon galilaeus* | Cichlidae | 340 | 72 | microphagous | along the river banks |

reaches 120 µS and the oxygen levels drop to very low levels (2.1–3.0 mg/l between March and May). These conditions are reversed during the rainy season, which begins early in July and lasts about two months up to mid-September. During this period the water temperature and the conductivity fall to 25 °C and 40 µS. At the end of the rainy season, the water level decreases very quickly. In fact, depending on the year, the period of actual flow lasts only four to five months (July to November) (Fig. 2).

### 2.2. Sampling sites and fish fauna

The lower reaches of these streams tend to be completely dry during the dry season because of a slope inversion (for details see Michel, 1973), so two perennial pools were chosen in the upper and middle course of the river, namely

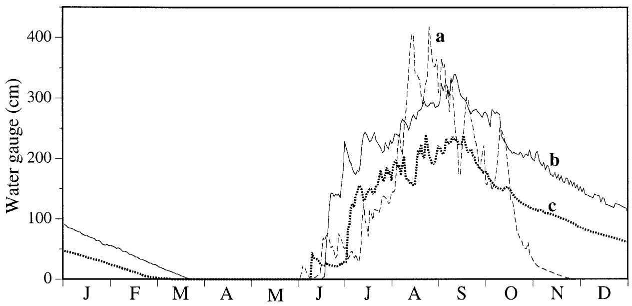


Fig. 2. Baoulé River: hydrological regime (weekly average from 1984 to 1988) for the upper, medium and lower course (see the sites position on (Fig. 1). **(a).** Dlaba (≠ 5 000 km$^2$); **(b).** Missira (11 400 km$^2$); **(c).** Siramakana (58 000 km$^2$).

Dlaba and Missira (Fig. 1). No aquatic macrophytes were recorded, but a narrow gallery forest fringes both sites. Beyond a savannah zone there are only scattered small trees in short stretches constituting a characteristic Sahelian landscape.

The fish fauna of this river is typically Nilo-Sudanian (Hugueny and Lévêque, 1994; Paugy et al., 1994). In the Senegal River basin, 120 species are currently known, but fewer than 100 species have been caught in the Baoulé River (Daget, 1961 and own observations). Of these only 50 have been regularly collected during the period studied. Eighteen species were common enough to be investigated for reproductive strategies (Table 1).

## 3. Materials and methods

### 3.1. Samples

Fishes were collected monthly (October to June) or twice a month (July to September) from February 1985 to November 1988 using three sets of gillnets (mesh sizes of 10, 12.5, 15, 17.5, 20, 22.5, 25, 30 and 40 mm knot-to-knot). All nets were 2.0 m deep and 25 m long. Sometimes, in some particular biotopes and when gillnets catches were insufficient, they were supplemented by cast nets (mesh size: 12.5 mm knot-to-knot). Catch-effort was approximately 12 hours, from 6: 00 P.M. to 6: 00 A.M. After the first night of fishing, gillnets were removed during the day and set elsewhere the second night. During the flood (July to

September), when the fishes are collected twice a month, gillnets were set only one night to avoid overfishing.

With regard to fishes, the drift is a poorly known phenomenon. Therefore, in this study the goal is not to understand or explain the reason of the drift, but to use this method to sample young fishes. In this way a massive catch of young fishes may demonstrate that adults of species have spawned some days before. As observed for insects, there is a circadian periodicity in the drift of fishes inhabiting the rivers of western Africa (Elouard and Lévêque, 1977). According to previous observations, drift nets were used during 12 hours, from 18h30–19h00 until 6h30–7h00. The drift net is 3 m long with a $40 \times 70$ cm opening, and the mesh size is 1.5 mm (knot-to-knot). This gear is used only during the flood period for capturing young fishes. It is not a quantitative method and it is only used to get information about the presence of species.

### 3.2. *Reproductive parameters*

Size at (50%) sexual maturity was determined during the maximum breeding period (ripe or spent) when 50% of the adults stock of a species are mature. Nevertheless, when the number of specimens is insufficient for a species, the smallest specimen estimates the size at first maturity. Because males and females sometimes have a different growth pattern, we considered each sex separately.

All fishes caught were immediately identified, standard length measured to the nearest mm and weighed (whole fish and gonads to the nearest 0.1 g). All the fishes were then dissected and sexed. For females, gonads were weighed individually, but for males, all the gonads of a same length group are weighed because of their very low individual weight (the gonado-somatic index [GSI] always less than 2% and for numerous species less than 1%). The GSI is calculated with the following formula:

$GSI = GW / W - GW$ where GW is the gonad weight and W the total fish weight.

Because of the prediction of the climatic seasonality, data were pooled monthly across years to calculate mean GSI value (i.e., we have calculated the means of the different years for each month).

In order to establish the ordination of species function of their life-history traits, the factorial correspondence analysis (CoA) for which salient points have been described elsewhere (Benzecri, 1973; Legendre and Legendre, 1984) was used. Then a UPGMA (agglomerative algorithm: average link) distance analysis was carried out on the factorial coordinates (species) of the CoA to check species relationships. We used the ADE-4 software (Chessel et al., 1995) for the whole analysis.

Oocytes are measured with a reticle fitted into an adjustable eyepiece ($10\times$). All oocytes larger than the minimum mature oocyte size were taken into account (i.e., only oocytes belonging to the last clutch of the frequency distribution of oocyte diameter). Ovarian fecundity was estimated using two methods: for small ovaries, complete counts were made; for large ones, a two-gram subsample was taken, counted, and extrapolated to the total ovaries'weight.

## 4. Results

### 4.1. *Size at first sexual maturity*

For most of the species discussed here, females tend to have a faster growth rate than males, and tend to have a larger body size at sexual maturity. Nevertheless, as the general pattern is approximately the same for the two sexes, we have only considered females in this study. There is a significant difference between the two sites. The median length at first sexual maturity is smaller at Dlaba (upstream) than at Missira (downstream) (Table 2 and 3). In fact, it is certainly a difference linked to the growth rate of the species between the two sites and related to most harsh conditions in Dlaba. Indeed, in this site the dry season is more severe because the refuge zones (residual ponds) are less numerous and of very small sizes. In fact, the poorer the environment is, the lower the growth rate is (greater for Missira, weaker for Dlaba).

### 4.2. *Reproduction seasonality*

#### 4.2.1. *Species with a short spawning period*

Two main groups can be distinguished: the flood-spawning species, and those which are not influenced by the flood cycle.

#### 4.2.1.2. *Flood spawners species*

Whatever the species, a peak in mean monthly GSI of females is identified in June– July (Fig. 3). In fact, for the six species, *Marcusenius senegalensis* (Mormyridae), *Alestes baremoze*, *Brycinus nurse* (Characidae), *Schilbe intermedius* (Schilbeidae), *Synodontis ocellifer* and *S. schall* (Mochokidae), the ovaries start to mature in May and continue their development up to June or July depending on the species and/or the individual. For all the species reproduction seems to be over in August, except for *B. nurse*, for which a large proportion of specimens is still mature at this date. Finally, reproduction is over by September for all species in our sample. When we compare the changes in GSI and the hydrological cycle, we note that these species lay during a short period (approximately one month) just before the maximum impact of the flood (Fig. 3). In this flood spawners group, most fish are egg-scattering pelagic spawners. If not ancestral, this reproductive style seems to be general and unspecialised (Balon, 1990).

Table 2
Median size (standard length, in mm) or age (year) at first maturity for 18 species of the Baoulé River, and at two other West African sites for comparison (* indicates smallest [and not median] size observed). RCI: Côte d'Ivoire. Sources: (1) Bénech and Dansoko, 1994; (2) Albaret, 1982 .

| Species | Baoulé at Dlaba | Baoulé at Missira | Niger at Mopti (1) | RCI (2) |
|---|---|---|---|---|
| *Hyperopisus bebe* | 255* | 324* | 320 | |
| *Marcusenius senegalensis* | 140 | 150 | | |
| *Mormyrops anguilloides* | | 346* | | 210 |
| *Mormyrus rume* | 252* | 325* | 330 | |
| *Petrocephalus bovei* | one year | one year | | one year |
| *Alestes baremoze* | 140 | 185 | | 175 |
| *Brycinus leuciscus* | one year | one year | | |
| *Brycinus macrolepidotus* | | 190 | | 185 |
| *Brycinus nurse* | 100 | 95 | | 80 |
| *Hydrocynus forskalii* | | 165 | | 100* |
| *Labeo senegalensis* | 206* | 201* | 210 | 175 |
| *Chrysichthys auratus* | 86 | 108 | | |
| *Schilbe intermedius* | 100 | 110 | | 100 |
| *Schilbe mystus* | | 185* | | |
| *Clarias anguillaris* | | 288* | 150 | 235* |
| *Synodontis ocellifer* | 135* | 151* | | |
| *Synodontis schall* | 105 | 175 | | 150 |
| *Sarotherodon galilaeus* | 111* | 137* | 140 | 145* |

For some species, data are insufficient (lack of data for some months) to give a general survey of the GSI variations. But, we expect that *Mormyrus rume*, *Hyperopisus bebe* (Mormyridae), *Brycinus leuciscus* (Characidae) and *Labeo senegalensis* (Cyprinidae) belongs to the same flood spawners category (Fig. 3). Finally, from the scarce data collected on *Petrocephalus bovei* (Mormyridae), it seems that this species has the same type of reproduction.

Table 3
Maximum median gonado-somatic index for females and males of 18 species in the Baoulé river.

| Species | Females | Males |
|---|---|---|
| *Hyperopisus bebe* | 8.0 | 0.2 |
| *Marcusenius senegalensis* | 18.7 | 0.5 |
| *Mormyrops anguilloides* | 7.5 | |
| *Mormyrus rume* | 11.8 | 0.2 |
| *Petrocephalus bovei* | 21.4 | 0.4 |
| *Alestes baremoze* | 13.4 | 1.3 |
| *Brycinus leuciscus* | 17.0 | 1.2 |
| *Brycinus macrolepidotus* | 19.8 | 6.7 |
| *Brycinus nurse* | 26.1 | 2.0 |
| *Hydrocynus forskalii* | 9.4 | 2.1 |
| *Labeo senegalensis* | 17.2 | 2.0 |
| *Chrysichthys auratus* | 27.5 | 0.7 |
| *Schilbe intermedius* | 23.4 | 1.1 |
| *Schilbe mystus* | 16.2 | |
| *Clarias anguillaris* | 14.4 | |
| *Synodontis ocellifer* | 26.3 | 1.5 |
| *Synodontis schall* | 16.7 | 2.1 |
| *Sarotherodon galilaeus* | 4.8 | |

#### *4.2.1.2. Other species*

Two Characidae, *Hydrocynus forskalii* and *Brycinus macrolepidotus* don't belong to the flood spawners species. In contrast to the species mentioned above, the predatory tiger fish, *H. forskalii*, seems to reproduce both before (March to April) and at the end (August to September) of the high water period (Fig. 3). We may expect an adaptive strategy that allows the predator to benefit from an important diet supply. Indeed, juveniles of the predator feed on insects or large invertebrates (Lauzanne, 1975). Two or three months later, the young tiger fish have reached a sufficient size to feed on the newborn juveniles of the other species.

The spawning period of *Brycinus macrolepidotus* is not clearly delimited. Mature individuals are found in each sample period, from February to September, yet each individual spawns only once a year. Nevertheless, we observe a peak in May just at the end of the dry season. Among large common species, *B. macrolepidotus* is the only known species that does not spawn during a restricted period just before the flood.

### *4.2.2. Small-brood spawners*

In the Baoulé River, small-brood spawners seem to be limited to a few Cichlid species. Among the five Cichlidae inhabiting the area two are rather common but reproduction data are available only for *Sarotherodon galilaeus* (Fig. 4). The mean monthly GSI of this mouth brooder is always reduced, and the standard deviation generally high. Further more, throughout the year ripe and spent individuals are found and the frequency distribution of oocytes in the

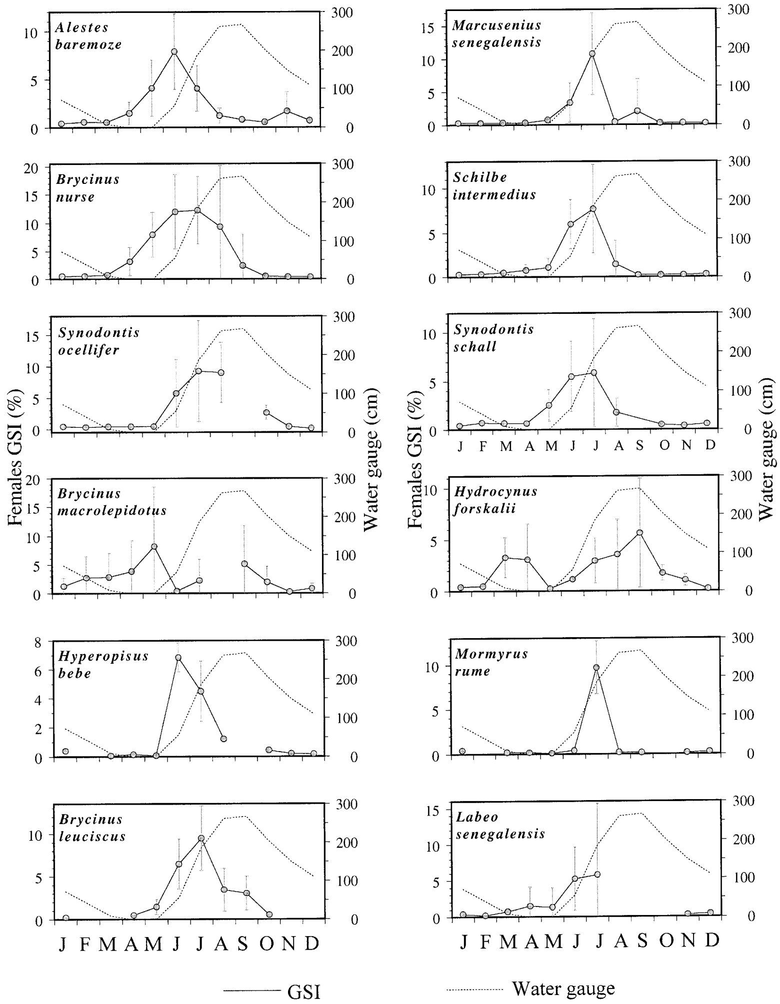


Fig. 3. Baoulé River: hydrological cycle and changes in females gonado-somatic index (GSI) of different 'non-guarding' fishes.

ovaries is multimodal. All these factors strongly suggest a multiple spawning strategy.

### 4.3. Fecundity

#### 4.3.1. Egg diameter

Most of the species encountered in the Baoulé River have small eggs (Fig. 5). Within a given family, egg size is more or less similar for all the species. There is an inverse relation between egg size and fecundity. The optimal egg size is that which maximises the number of offspring to become reproductively active. So, egg size could be considered as a tradeoff between fecundity and young survival. Bigger eggs, which produce larger larvae, seem to be an adaptational advantage when food supply is variable or limited. Conversely, in the Baoulé River the minimisation of egg size would tend to maximise fecundity.

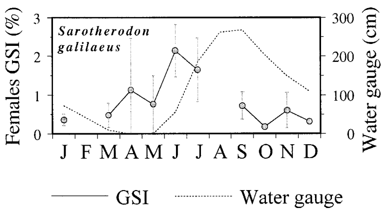


Fig. 4. Baoulé River: hydrological cycle and changes in females gonado-somatic index (GSI) of the 'small-brood' spawner *Sarotherodon galilaeus*.

#### 4.3.2. Size distribution of oocytes

There are three main patterns of the size distribution of oocytes within the ovaries of the different species. The first group shows a unimodal distribution (Fig. 6). Most species belong to this group: Characidae, Cyprinidae and catfishes (*Chrysichthys*, *Synodontis* and *Schilbe*). The second group, which includes the Mormyridae (Fig. 6) has a multimodal distribution of eggs, with a peak of high diameter values and a second batch of very small oocytes. We have no information about the structure of the ovary during the non-breeding season so that we do not know if the smaller eggs develop

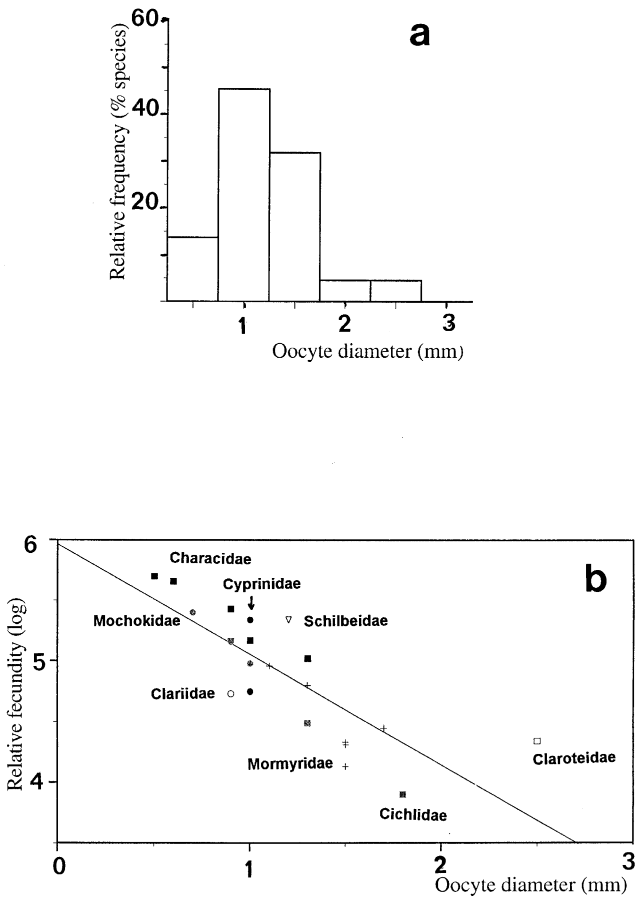


Fig. 5. **(a)** Frequency distribution of oocyte mean diameter; **(b)** relationship between relative fecundity and oocyte mean diameter for species from the Baoulé River ($r^2 = 0.648$).

during a second breeding season, or whether they are held in reserve for the following year. Finally the third group is that of the multiple spawners species (Fig. 6). In the particular case of the Baoulé River this group is represented by Cichlidae like *Chromidotilapia guntheri* (multimodal structure).

### *4.4. Drift*

Following the hydrograph, drift of organisms begins in July and lasts up to November-December. Nevertheless, if the catches are mainly composed of very young fishes (10–35 mm SL) at the beginning, sub-adults are more and more numerous from October– November. In fact, the maximum of juveniles drift from July to September with a mean of 100–150 individuals per night (Table 4).

The composition of drift catches differs from that in gillnets. Cyprinidae are dominant in driftnets while Characidae, Mormyridae and Mochokidae are more numerous in gillnets. Juveniles first appear during the flood, confirming the conclusion that spawning is timed by the flood period.

## 5. Discussion and conclusion

For most of the species, sizes at first maturity observed in the Baoulé River are comparable to other West African areas with similar climatic regimes (Albaret, 1982; Bénech and Dansoko, 1994). We may therefore consider that in the Baoulé River, the species reach their (50%) sexual maturity at the similar lengths – and ages – than in other zones of West Africa.

For African species, the GSI is generally higher for females than for males (Munro et al., 1990; Paugy and Lévêque, 1999). This observation is confirmed for the fishes of the Baoulé River. For most species the females had a GSI higher than 10% except for Cichlidae, where the value reaches only about 5%.

Based on the relative frequency distribution of oocytes in the ovaries, two main styles of spawning strategies (sensu Lowe McConnell, 1987) may be distinguished among the considered species. The first, the ‘total spawners’, generally have a short annual spawning period. The second, the ‘small-brood spawners’, give parental care and produce small batches of eggs at frequent intervals for most of the year. In the Baoulé River, the two species of Cichlidae studied, *Sarotherodon galilaeus* and *Tilapia zillii*, belong to this second group while the remainder belong to the ‘total spawners’group; most of the species spawn just before the flood.

The ichthyophagous *Hydrocynus forskalii* seems to reproduce both before (March to April) and at the end (August to September) of the high water period. For an open water feeder (Jackson, 1961; Winemiller and Keslo-Winemiller, 1994), there is a huge advantage of being born some months before other species to reach a sufficient size to eat juveniles when they leave their birth sites. This reproductive pattern of predators is also observed in temperate regions where the pike (*Esox lucius*) spawns some weeks before the others species (Billard, 1996). In the Chad basin (lake and rivers), *H. forskalii* has also two spawning periods (Srinn, 1976; Bénech and Quensière, 1985). The first takes place in March and concerns most of the individuals (more than 90% of the females); the second takes place in August and concerns the remaining population. In the rivers of Côte d’Ivoire the frequency distribution of oocytes in the ovaries is multimodal (Albaret, 1982), which suggests that each female is able to spawn twice a year if the environmental conditions are favourable.

Most of the species encountered in the Baoulé River have small eggs. This minimisation of egg size would tend to maximise fecundity. That is to say, that for most of the species, food supply would not be a limitative variable during the flood. This result is generally similar to that observed for European freshwater species, which also show a frequency distribution skewed towards the smaller diameters (Wootton, 1991). Nevertheless, some European species have eggs, which diameter (up to 6–7 mm) has never been observed in West Africa, where the maximum egg size

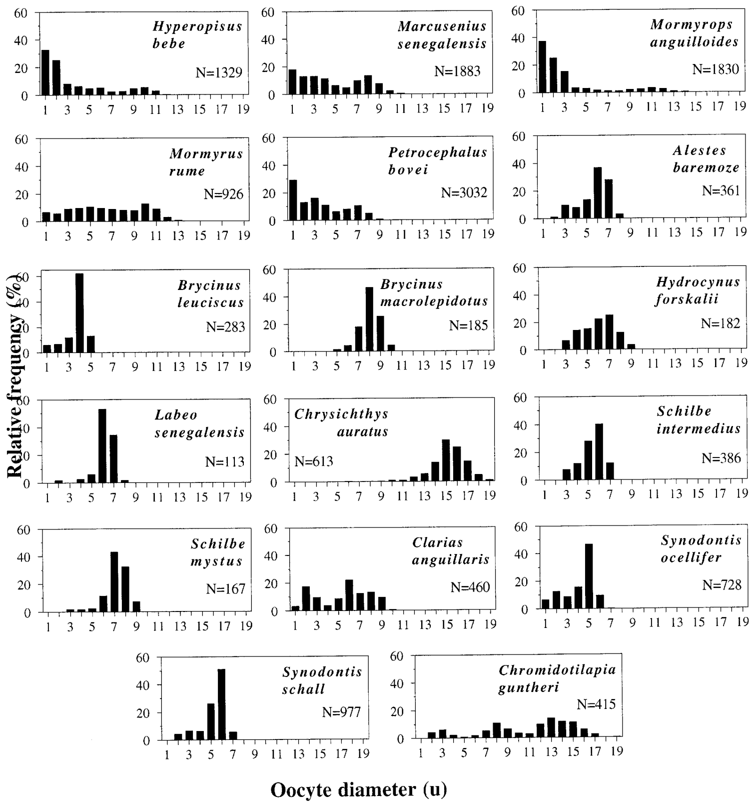


Fig. 6. Relative frequency distribution of clutches sizes. Unit of x-axis (u = 0.165 mm) is that of the reticle fitted into an adjustable eyepiece (10 ×).

is 2.5 mm for *Chrysichthys auratus*. Generally speaking, two major groups in which the ripe females have more or less the same gonado-somatic index may be distinguished: the first, the ‘egg-number group’, which invested heavily in higher fecundity (West African Characidae, for example), and the second, the ‘egg-size group’, which invests in egg size (West African *Chrysichthys*, for example).

Most of the species inhabiting the Nilo-Sudanian region exhibit a breeding strategy in relation to flood seasonality. This type of strategy (high density-independent mortality), called “r-selection” (McArthur and Wilson, 1967), is common in harsh and unpredictable environments and selects early reproduction, high fecundity and short life expectancy. According to Balon (Balon, 1977), ‘r’strategists are more or less similar to altricial species. Finally, as a result of previous studies Winemiller (1989 and 1992) and Winemiller and Rose (1992) identified three types of strategies fitted into a triangular continuum: 1) small size, rapidly maturing, short-lived fish (opportunistic strategists); 2) larger, highly fecund fish with longer lifespans, often associated with spawning migrations (periodic strategists); and 3) fish that often exhibit parental care and produce fewer but larger offspring (equilibrium strategists). These different strategies are evaluated from different life-history traits.

Concerning the Baoulé River, 12 variables (see appendix) related to life-history theory were measured, coded or estimated (bibliographic data from the same zone when original data were unknown) for 18 species. In order to establish the ordination of species function of their life-history traits, we carried out a correspondence analysis (CoA) on log-transformed data [Log ($x$+1)] so as to normalise the variances. Then a UPGMA (agglomerative algorithm: average link) distance analysis was carried out on the factorial coordinates (species) of the CoA to check species relationships.

Clustering of 18 species based on Euclidean distances resulted in two groups (Fig. 7). The first corresponds to developed parental care, large oocytes and low fecundity. Two species, *Chrysichthys auratus* and *Sarotherodon galilaeus*, belong to this ‘equilibrium’strategy. Others species have a ‘seasonal’strategy which is adapted to the harsh local conditions. In fact most fishes in the Nilo-Sudanian area appeared to be associated with a seasonal life-history strategy that exploits an annual expansion of aquatic production. The seasonal strategy is characterised by high fecundity, absence of parental care, limited breeding season and, for some species, large adult size (i.e., *Alestes baremoze*, *Synodontis schall*, *Hyperopisus bebe*) and upstream spawning migrations to floodplains (Daget, 1954, 1957; Bénech and Quensière, 1985).

The lack of ‘opportunistic’species has to be underlined. The ‘opportunistic’life-history strategy in fishes appears to place a premium on early maturation, frequent and extended spawning, rapid larval growth, and rapid turnover rates. This type corresponds to small fishes with early maturation

Table 4
Monthly drift (number of fishes per night) in the Baoulé River.

| Species | Family | July | August | September | October |
|---|---|---|---|---|---|
| *Polypterus bichir* | Polypteridae | 0.4 | 0.3 | | |
| *Mormyrops anguilloides* | Mormyridae | | 0.3 | | 6.0 |
| Mormyrus rume | | 0.6 | 0.3 | | |
| *Alestes baremoze* | Characidae | | | 0.5 | 1.0 |
| *Brycinus leuciscus* | | 51.8 | 75.3 | 4.5 | |
| *Brycinus nurse* | | | 7.7 | | |
| *Distichodus rostratus* | Distichodontidae | | 5.0 | 0.5 | |
| *Nannocharax* sp. | | 0.6 | | 0.5 | |
| *Barbus* cf *macinensis* | Cyprinidae | | | 125.5 | |
| *Barbus macrops* | | | | 16.5 | |
| *Barbus punctitaeniatus* | | | | 6.0 | |
| *Barbus* sp. | | | 0.7 | | |
| *Labeo senegalensis* | | | 1.7 | | |
| *Labeo* sp. | | 7.4 | 24.0 | 1.5 | |
| *Raiamas* sp. | | 8.6 | 3.0 | 0.5 | 3.0 |
| *Bagrus docmac* | Bagridae | 0.2 | 0.3 | | |
| *Auchenoglanis occidentalis* | Claroteidae | | 6.3 | | |
| *Chrysichthys auratus* | | 1.4 | | | |
| *Schilbe intermedius* | Schilbeidae | 1.6 | 4.0 | 0.5 | |
| *Clarias anguillaris* | Clariidae | 6.0 | 3.7 | 0.5 | |
| *Heterobranchus longifilis* | | 17.8 | 1.3 | | |
| *Malapterurus electricus* | Malapteruridae | | 0.3 | 0.5 | 1.0 |
| *Synodontis* sp. | Mochokidae | 3.8 | | | |
| *Epiplatys* sp. | Cyprinodontidae | 3.4 | | | |
| *Lates niloticus* | Centropomidae | 3.0 | 1.0 | | |
| *Hemichromis* sp. | Cichlidae | 0.8 | | | |
| *Sarotherodon galilaeus* | | 1.4 | 2.0 | | |
| *Tilapia zillii* | | 1.0 | | | |

with generally small eggs and small clutches. This suite of life-history traits permits efficient recolonisation of marginal habitats over relatively small spatial scales. Small, short-lived fishes, like *Fundulus* (killifishes) or *Gambusia* (mosquitofishes) in North America, typically have an 'opportunistic'strategy (Winemiller and Rose, 1992). In Africa, killifishes like *Aphyosemion*, *Epiplatys* and *Aplocheilichthys* likely belong to this group. The smallest meshes employed in our set of gillnets do not allow us to catch species as small as killifishes. The lack of 'opportunistic'life-history strategy in fishes of Baoulé River is therefore related to a sample bias. Nevertheless, species that have this type of strategy are not very common in large rivers and are encountered in very small tributaries.

If conditions favourable for species durability are periodic and occur at frequencies smaller that the lifespan, selection will favour the synchronisation between reproduction and optimal climatic conditions for a good recruitment of offspring without parental care. Hydrological conditions of the Baoulé River are very restricting, so most of the species are of course periodic. "In fact, the periodic strategy maximises age-specific fecundity (clutch size) at the expense of optimising turnover time and juvenile survivor

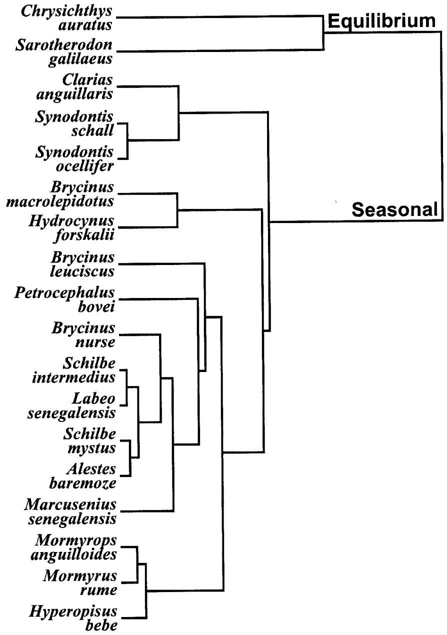


Fig. 7. Hierarchical classification (average link on Euclidean distances) of the center of mass of the factorial coordinates (CoA) of the life-history traits for each species.

ship" (Winemiller and Rose, 1992). Large size of adults enhances their survivorship during poor conditions and permits storage of energy for the next bout of reproduction. Finally, species such as *Alestes baremoze* execute long-distance upstream migrations to spawn during the wet season. Among the studied species, 89% have a periodic strategy and only 11% an equilibrium strategy. The Baoulé River is a nice example where fishes have proved their ability to adapt life histories to very drastic environmental conditions.

The pattern of traits related to the life history of species of the Baoulé River is very close to that observed for example in seasonal environments for neotropical fish species from the Venezuelan llanos (Winemiller, 1989). Most of the fishes have a 'seasonal'life-history strategy associated with synchronised reproduction at the early wet season, high fecundity and absence of parental care. The second important group is that of species that have an 'equilibrium'life-history strategy associated with parental care, low fecundity and large eggs. Finally, the less important group is that of fishes that have an 'opportunistic'life-history strategy associated with early maturation and small clutches.

This study doesn't concern all the species of the system but it constitutes a contribution to a more global matrix where life-history traits will be the foundations of a comparison between different geographical and climatic systems (intercontinental comparison, for example). In this way an interesting goal would be a macro-ecological approach to study the relations between the diversity of the biological strategies (heritability and adaptation) and the environmental variability.

## . Appendix

*List of life-history traits used in statistical analysis.*

Females standard length at maturation (mm)
Maximum length observed (mm)
Longevity in years (from literature)
Maximum clutch size: i.e.; the largest batch fecundity reported (number of eggs per kg)
Oocyte size: mean diameter of mature ovarian oocytes (to nearest 0.01 mm)
Range of oocyte sizes (to nearest 0.01 mm)
Number of spawning bouts per year
Parental care: quantified as ($x1 + x2$) where
$x1 = 0$ (no special placement of zygotes); 1 (zygotes are placed in a special habitat); 2 (zygotes and larvae are placed in a nest)
$x2 = 0$ (no parental protection of zygotes or larvae); 1 (parental period of protection)
Hatch duration:
0 = 1 to 3 months
1 = 4 to 6 months
2 = 7 to 9 months
3 = 10 to 12 months
One-year length (mm)
Maximum GSI
Structure of the ovary: size-frequency distribution of oocytes:
0 = one mode; 1 = two modes; 2 = more than two modes

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