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Growth in four populations of *Leporinus friderici* (Bloch, 1794) (Anostomidae, Teleostei) in French Guiana

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The growth rates of *Leporinus friderici* (Bloch, 1794) in four populations from four rivers of French Guiana are compared. According to a statistical analysis of growth curves using the method of maximum likelihood with the Gauss–Markardt algorithm, a marked difference is observed in the growth of the different samples which is attributed to the year of capture rather than to the geographical origin of fishes. It is demonstrated that the main factor affecting growth performances is the length of the rainy season, which corresponds for this species to the feeding period.

Key words: *Leporinus friderici*; South America; French Guiana; growth; skeletal chronobiology.

I. INTRODUCTION

In previous studies (Meunier *et al.*, 1985; Lecomte *et al.*, 1985, 1986, 1989), an annulus was shown to be formed at each of the two dry seasons of the year in three species of fish from French Guiana [*Leporinus friderici*, *Arius proops* (Val., 1839), *A. couma* (Val., 1839)]. These growth zones are particularly obvious on the opercular bone and in the first ray of the pectoral fin. They were used to describe the growth of these species using the von Bertalanffy (1938) model.

Several authors have already used the von Bertalanffy model to describe the growth of tropical fish which exhibit two growth zones per year triggered by seasonal cycles (Garrod, 1959; Poinsard & Troadec, 1966; Okedi, 1969; Bruton & Allanson, 1974; Hureau & Ozouf, 1977; Blacke & Blacke, 1978; Warburton, 1978; Robben & Van Den Audenaerde, 1984; Moreau & Moreau, 1987). However, the existence of such growth cycles, and the manner in which they are formed do not provide any information on the total growth rate of individuals. Indeed, this growth rate can be affected quite independently by environmental parameters.

In the present study, the growth performance of four populations of *L. friderici*, an omnivorous fish with a wide geographical distribution (Boujard *et al.*, 1988), was examined to determine first whether growth performances are different between the populations, and second, whether growth periods are related to the duration of access to flooded forest, since this appears to be an important factor for feeding in this species (Boujard *et al.*, 1990).

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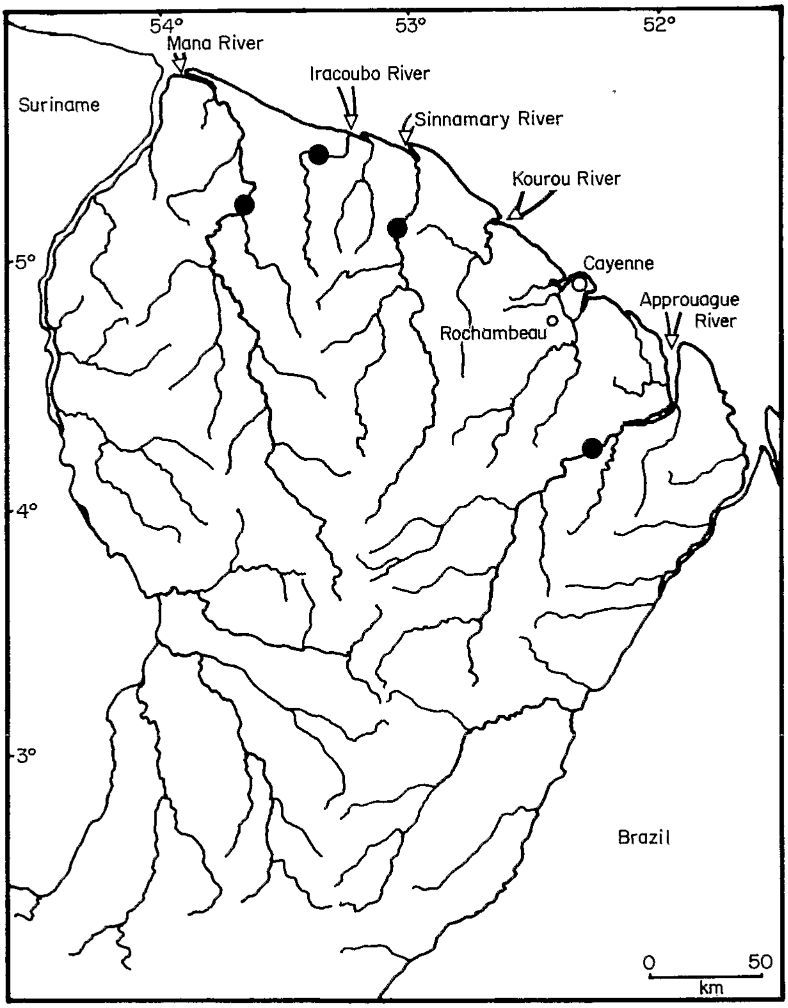

FIG. 1. Sampling sites.

II. MATERIALS AND METHODS

SAMPLING

Samples were collected in four rivers of French Guiana (Fig. 1): the Approuague, between St Esprit and the Athanase rapids; the Sinnamary, in the vicinity of the Petit-Saut; the Iracoubo, downstream of the Genipa rapids and the Mana, downstream of the Valentin rapids. The waters of these rivers, acid and with low conductivity, were classified as ' black waters ' by Sioli (1967).

Thirty-two sampling visits between June 1982 and October 1984 were made to the Sinnamary River, and between May 1986 and September 1987 to the other rivers, apart from the Mana River in which fish were collected in March 1988 (Table I). Each sampling visit involved 4 days of fishing using 25- to 50-m long trammel nets graded from 10 to 60 mm bar mesh. The net-setting procedure has already been described (Boujard & Rojas-Beltran, 1988*a*). All captured specimens were measured (standard length, S.L.) to the nearest millimetre and their sex determined by microscopic examination of gonads.

TABLE I. Temporal distribution of catches of *L. friderici* in the rivers studied

Date	Sinnamary	Approuague	Iracoubo	Mana	Total
1982:					
Jun.	1	—	—	—	1
Oct.	1	—	—	—	1
Dec.	5	—	—	—	5
1983:					
Jan.	4	—	—	—	4
Mar.	9	—	—	—	9
Apr.	14	—	—	—	14
May	12	—	—	—	12
Jun.	5	—	—	—	5
1984					
Oct.	1	—	—	—	1
1986:					
May	—	—	29	—	29
Jun.	1	—	—	—	1
Aug.	—	4	—	—	4
Sept.	—	1	—	—	1
Nov.	2	—	—	—	2
Dec.	1	—	—	—	1
1987:					
Jan.	—	6	—	—	6
Apr.	6	—	—	—	6
May	11	—	—	—	11
Sept.	—	14	—	—	14
1988:					
Mar.	—	—	—	41	41
Total	73	25	29	41	168

For each river, except for the Sinnamary, data were pooled irrespective of the date of capture. In the Sinnamary, a first group of data was for captures made between June 1982 and October 1984, a second group was for those made between June 1986 and May 1987.

PROCEDURE FOR READING SKELETAL GROWTH MARKS

The opercular bones were cleaned and air-dried. They were examined under reflected light on a black background with a dissecting microscope, using a 20% glycerol solution as a refracting medium. Two independent observations were made for every preparation. Results of observations proved to be similar in 55% of the cases. Most discrepancies (78%) concerned the presence (or absence) of the first growth zone, often indistinct because of bone remodelling. However, the percentage of agreement for the first reading reached 90% within about one growth mark. One specimen was discarded because age determination was not possible.

In order to avoid an abnormal distribution of the residuals (i.e. a normal distribution of the differences between the observed and the predicted data is a necessary condition for a regression analysis), we attempted to estimate the time between the last growth mark deposit and the date of capture. For this, we measured the distance between the last growth mark and the margin of the opercular bone to the nearest 0·1 mm, and divided it by the distance between the two last growth marks.

MATHEMATICAL MODEL

The relationship between age and size has been adjusted previously to the von Bertalanffy model (Lecomte *et al.*, 1986). Data used concerned the Sinnamary River (from June 1982 to October 1984). The equation was

$$\text{S.L.} = 409\,(1 - e^{-0{\cdot}248\,(t+0{\cdot}07)})$$

with S.L. in millimetres and t in years.

The von Bertalanffy logistic model can be applied to the growth of this species, but can be replaced by a simple linear relation provided that only fishes exhibiting two to 10 growth zones are taken into account (Fig. 2) (Weatherley, 1972).

STATISTICAL ANALYSIS

The relationship between age (number of growth zones) and size was estimated using CS-NL software (Bouvier *et al.*, 1985) based on the maximum likelihood method and the Gauss–Marquardt algorithm. The use of this method described by Kimura (1980) and Francis (1988), allows the comparison of growth curve parameters of several populations by means of the likelihood ratio. This corresponds to a χ^2 test on the likelihood ratio logarithms of the general model and of a submodel. This test permits the simultaneous use of all pairs of data and thus, allows the comparison with populations that comprise only a few individuals. This method allows the estimation of the parameters of the equations assuming that the growth of each population is different. This gives the likelihood which is used as reference for the submodels to be tested. For instance, if all growth curves are different except two, another likelihood is obtained after an estimation of the equation parameters. Using the χ^2 test on the likelihood ratio logarithms, it is possible to evaluate the relevance of the proposed submodel.

III. RESULTS

COMPARISON OF GROWTH RELATED TO SEX

When the data of each population are treated separately, there is no difference between the growth of males and females, probably because of the small number of males in our samples. However, when the data are treated simultaneously, the distribution of the residuals of the age–size relation is not homogeneous relative to sex (Fig. 3). This shows that beyond 3 years of age, the growth of females is faster than that of males ($P > 0{\cdot}01$; Student's t-test). As a result, only females, which constitute the major part of the samples, will be used in further analyses.

COMPARISON OF GROWTH BETWEEN POPULATIONS

The general model consisting of five different regression lines leads to the smallest residual variance with a standard error of 20·0 mm.

The hypothesis that the five samples have a similar growth rate is discarded ($X_{2\text{obs}} = 117{\cdot}58 > X_{2\text{th}95\%} = 15{\cdot}51$; 8 d.f.) to the benefit of the general model. The standard error of the residuals is 33·6 mm.

The hypothesis that two samples from the Sinnamary River have the same growth and that each population of different origin exhibits a different growth is also discarded ($X_{2\text{obs}} = 43{\cdot}88 > X_{2\text{th}95\%} = 5{\cdot}99$ with 2 d.f.). The residuals have then a standard error of 24·4 mm.

COMPARISON OF GROWTH ACCORDING TO THE PERIODS OF CAPTURE

All samples from the Iracoubo and Approuague Rivers and part of those collected in the Sinnamary River were captured between May 1986 and September

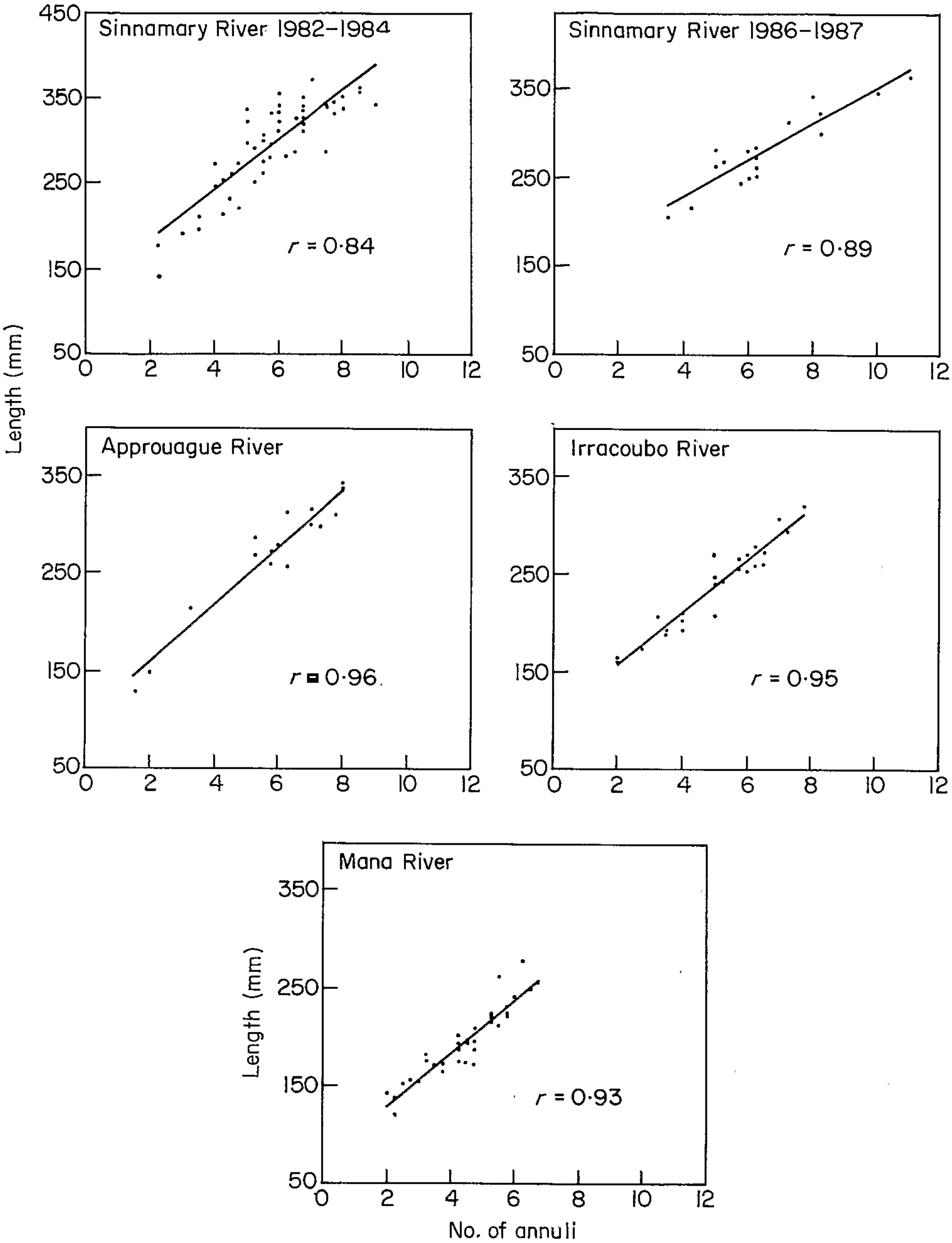

FIG. 2. Linear relationships between number of growth annuli and standard length for the five groups studied.

1987. Thus, the growth of these three samples can be described by the same equation. Fish collected in the Sinnamary River between June 1982 and October 1984, as well as those captured in the Mana River in March 1988, were assumed to have distinct growth. This hypothesis was accepted ($X_{2obs} = 6{\cdot}94 < X_{2th95\%} = 9{\cdot}49$ with 4 d.f.). The standard error of residuals was then 20·8.

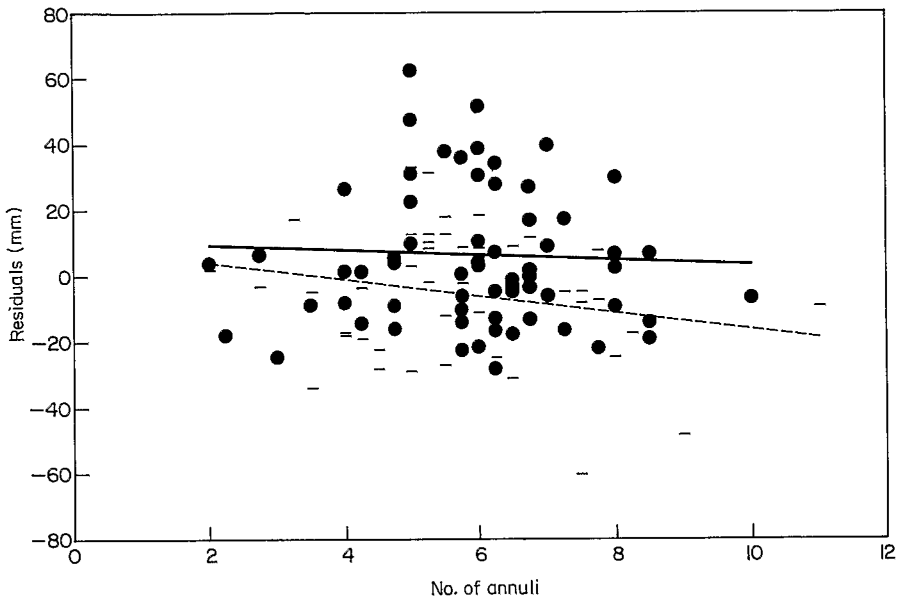

FIG. 3. Distribution of male and female residuals indicating a difference in growth between sexes. Fish for which sex determination was not possible were not used. ●, Females; —, males.

TABLE II. Yearly rainfall (mm) at Rochambeau, data supplied by the National Meteorology Office

Year	Water height	Year	Water height
1971	4931	1980	3618
1972	3896	1981	3620
1973	4060	1982	3483
1974	4011	1983	3210
1975	3576	1984	4276
1976	5429	1985	3524
1977	3724	1986	3300
1978	3500	1987	2377
1979	3615	1988	2880

Consequently, pooling should be done on the basis of the capture date rather than on the geographical location. Three groups can be established: samples collected between June 1982 and October 1984 (Sinnamary River); samples collected between May 1986 and September 1987 (Sinnamary, Approuague and Iracoubo Rivers); samples collected in March 1988 (Mana River).

EFFECT OF THE LENGTH OF THE RAINY SEASON ON GROWTH

In French Guiana as a whole, there are large variations in rainfall between successive years (from 2377 to 5429 mm year^{-1} between 1971 and 1988, Table II).

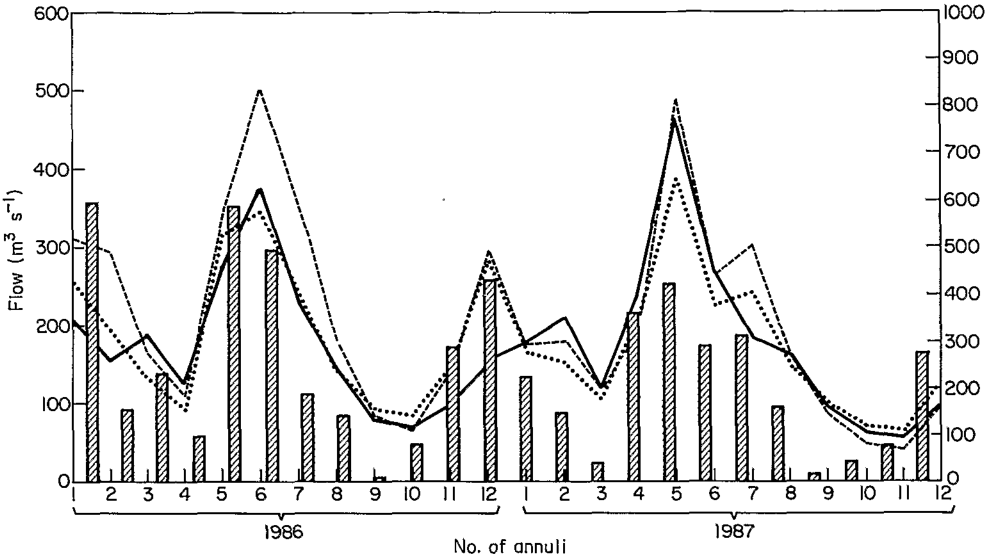

FIG. 4. Influence of monthly rainfalls (measured at Rochambeau, data supplied by the National Meteorology Office) on the flow rate of the rivers Mana (– – –), Sinnamary (· · · ·) and Approuague (———) between January 1986 and December 1987 (data supplied by ORSTOM-Hydrology, Cayenne, France).

This could account for the large variations in growth performance from one year to another, irrespective of the river basin. To test if the duration of the rainy season has an effect on growth, in addition to the amount of rain, it is possible to use the rainfall data recorded by the national meteorology centre of Rochambeau, since the climatic conditions are relatively homogeneous in the area studied (Fig. 4).

The number of months when rainfall is high, i.e. above the 10-year monthly mean, can be used as an indicator. It is then possible to express the age of each fish not in terms of years, but in terms of number of rainy months. Thus, the 'age' would be proportional to the length of time of flood periods.

This model is based on the assumption that the five samples correspond to five different regression lines, the age being expressed in terms of number of rainy months. The residual variance is as small as possible, with a standard error of 19·3 mm i.e. inferior to the previous general model.

The hypothesis that the growth of the five samples can be assimilated to a single regression line is accepted ($X_{2\text{obs}} = 6{\cdot}94 < X_{2\text{th}95\%} = 15{\cdot}51$ with 8 d.f.). It leads to a residual variance of 21 mm and to the following general equation:

$$\text{S.L.} = 11{\cdot}3\,M + 110{\cdot}6$$

with S.L. in millimetres and M, the number of rainy months, $r = 0{\cdot}95$ (Fig. 5).

IV. DISCUSSION

FACTORS AFFECTING GROWTH PERFORMANCE

Populations of *L. friderici* captured in the different rivers of French Guiana were compared by electrophoresis of 15 enzymatic systems corresponding to 21 loci

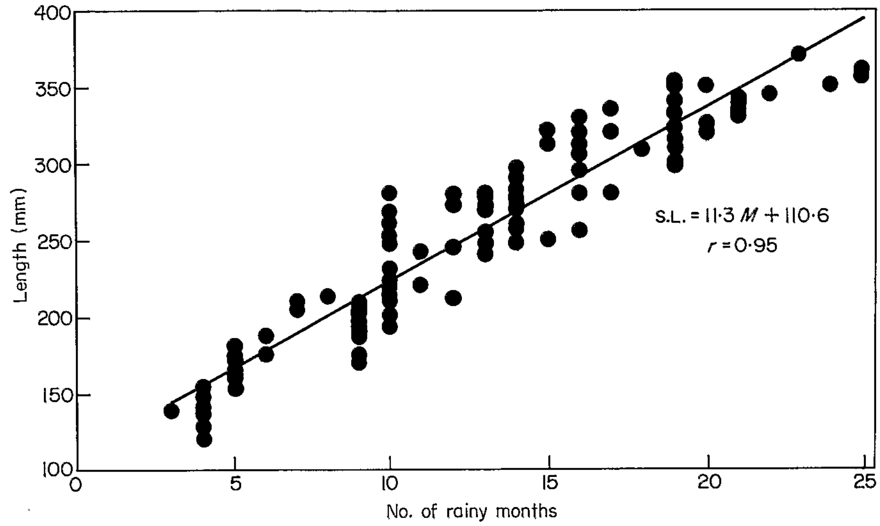

FIG. 5. Relationship between the number of rainy months and the standard length of fish, for all populations grouped together.

(Renno *et al.*, 1989, 1990). This showed that the populations of French Guiana can be pooled in two groups located on each side of the Kourou River. The population of the Approuage seems to be genetically well differentiated from that of the other rivers (Fig. 1), but this is not the case for growth rate. Although genetic differences affect the growth of these populations, this influence is masked by another factor which seems to be highly correlated with the year of capture.

Although *L. friderici* is an omnivorous fish, it mainly ingests seeds and fruits. Its feeding is mainly allochtonous. Stomach repletion is high during the rainy season, while during the dry season most of the sampled stomachs are empty (Boujard *et al.*, 1990).

Goulding (1980) reports that *L. friderici* populations from the Rio Madeira are captured mainly during the rainy season in flooded forests. Similar observations were made in French Guiana (Boujard & Rojas-Beltran, 1988*b*). Goulding (1980) also notes that during this period their stomachs are full whereas during the dry season they are empty. This confirms the observations of Lowe-McConnell (1964) on *L. friderici* and other large-sized characoids in the Rupununi savanna (Guyana). This author assumed that the growth rate decreased with the water subsidence. She also observed that the stomachs of many fishes were empty during the dry season, but that their fat reserves were highly developed, suggesting that feeding was abundant and rich during the flood period. Since 1964, these observations have been confirmed by several studies (Lowe-McConnell, 1979, 1987; Welcomme, 1979; Angermeier & Kar, 1983; Winemiller, 1987). Accordingly, an ecological division between flood and drought periods is generally accepted.

Junk (1985) proposed a more precise division. He observed that growth is especially high during the period of river overflow. Fish accumulate large fat reserves during this period, whereas, food intake is negligible or reduced when the water drains back into the rivers toward the end of the rainy season. Moreover, some short-lasting water run off may even take place during the rainy season. According to Junk *et al.* (1983) the access to food is then temporarily limited by the formation of anoxic areas. More recently, Bayley (1988) showed that the growth performance of fry from many species of Central Amazonia depended on the length of the inundation season.

From these data, it may be concluded that the length of the inundation season has an effect on growth performances because during this period the banks are flooded enabling the fish to exploit available food resources.

ACCURACY OF THE RESULTS

The interpretation of these results relies on the assumption that growth in each bone zone actually takes place according to an intrinsic rhythm synchronized by the alternation of wet and dry seasons. Monthly observation of the deposition of these growth zones in the natural environment have shown that deposition in the bony structures of this species occurs twice a year (Lecomte *et al.*, 1986). Of course, this has to be verified in strictly controlled environments (Beamish & McFarlane, 1983; Casselman, 1983), a requirement which, to our knowledge, has never been satisfied so far for any tropical species.

Although the deposition of an annulus at each dry season has been established, it cannot be asserted that this deposit is laid down at each dry season. The occurrence of false growth marks is still possible, this source of error existing in any age determination study based on the number of growth marks.

With this limitation in mind, the study reported here shows that the main factor affecting growth performance is of trophic origin. Results obtained recently in ponds for farm-reared *L. friderici* show that it is possible to obtain a mean live weight of 420 g at 1 year of age with a daily level of feeding corresponding to 3·5% of live weight (unpublished data). In the natural environment, the mean live weight of 1-year-old fish is only 125 g. This difference between actual and potential growth performances explains why genetic differences between populations of this species have no effect on the growth performance in a natural environment.

Using the number of rainy months as a factor of physiological correction of the actual age in relation with growth is not very satisfactory. It would be better to know for each trapping area the threshold-flow rate of flood in adjacent areas. This is in agreement with other studies conducted in Africa (Daget, 1952, 1957, in the River Niger, Johnels, 1952, 1954, in the Gambia River), in Central Amazonia (Junk *et al.*, 1983; Junk, 1985, Bayley, 1988), in deep Amazonia (Goulding, 1980) or in Guyana (Lowe-McConnell, 1964).

In temperate environments, the growth rate generally appears to be affected mainly by temperature. The rhythm of deposit of the growth marks is also generally synchronized to the annual variations of the photoperiod. In tropical environments where temperature and photoperiod are relatively constant throughout the year, growth performances are thus mainly limited by feeding resources. However, the precise physiological factors which play a role in the synchronization of bone growth zone deposition are still poorly known.

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References

Angermeier, P. L. & Kar, J. R. (1983). Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fish* **9**, 117–135.

Bayley, P. B. (1988). Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. *Environmental Biology Fish* **21**, 127–142.

Beamish, R. J. & McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* **112**, 735–743.

Bertalanffy, L. von. (1938). A quantitative theory of organic growth. *Human Biology* **10**, 181–213.

Blacke, C. & Blacke, B. F. (1978). The use of opercular bones in the study of age and growth in *Labeo senegalensis* from Lake Kainji, Nigeria. *Journal of Fish Biology* **13**, 187–295.

Boujard, T. & Rojas-Beltran, R. (1988*a*). Zonation longitudinale du peuplement ichtyque du fleuve Synnamary (Guyane Française). *Revue d'Hydrobiologie Tropicale* **21**, 47–61.

Boujard, T. & Rojas-Beltran, R. (1988*b*). Description des captures au filet tramail sur le cours supérieur du Sinnamary (Guyane Française). *Revue d'Hydrobiologie Tropicale* **21**, 349–356.

Boujard, T., LeBail, P. Y. & Planquette, P. (1988). Données biologiques sur quelques espèces continentales de Guyane Française d'intérêt piscicole. *Aquatic Living Resources* **1**, 107–113.

Boujard, T., Sabatier, D., Rojas-Beltran, R., Prevost, M. F. & Renno, J. F. (1990). The food habits of three allochtonous feeding characoids in French Guiana. *Revue d'Ecologie (Terre & Vie)* **45**, 247–258.

Bouvier, A., Gelis, F., Huet, S., Messean, A. & Neveu, P. (1985). *Manuel d'Utilisation CS-NL.* Paris: INRA.

Bruton, M. N. & Allanson, B. R. (1974). The growth of *Tilapia mossambica* Peters (Pisces, Cichlidae) in Lake Sibaya, South Africa. *Journal of Fish Biology* **6**, 701–715.

Casselman, J. M. (1983). Age and growth assessment of fish from their calcified structures. Techniques and tools. *United States Department of Commerce, NOAA Technical Report, NMFS* **8**, 1–17.

Daget, J. (1952). Mémoires sur la biologie des poissons du Niger Moyen. I-Biologie et croissance des espèces du genre *Alestes. Bulletin Francais d'Afrique Noire* **14**, 191–225.

Daget, J. (1957). Données récentes sur la biologie des poissons dans le delta central du Niger. *Hydrobiologia* **9**, 321–347.

Francis, R. I. C. C. (1988). Maximum likelihood estimation of growth and growth variability from tagging data. *New Zealand Journal of Marine and Freshwater Research* **22**, 42–51.

Garrod, D. J. (1959). The growth of *Tilapia esculenta* Graham in Lake Victoria. *Hydrobiologia* **12**, 268–298.

Goulding, M. (1980). *The Fishes and the Forest.* Los Angeles, CA: University of California Press.

Hureau, J. C. & Ozouf, C. (1977). Détermination de l'âge par scalimètrie et croissance du Coelacanthe *Latimeria chalumnae* Smith 1939 (Poisson Crossoptérygien, Coelacanthidé). *Cybium* **2**, 129–137.

Johnels, A. G. (1952). Notes on scale rings and growth of tropical fishes from the Gambia river. *Arkiv foer Zoologi (Stockholm)* (Serie 2) **3**, 363–366.

Johnels, A. G. (1954). Notes on fishes from the Gambia river. *Arkiv foer Zoologi (Stockholm)* (Serie 2) **6**, 327–411.

Junk, W. J. (1985). Temporary fat storage, an adaptation of some fish species to the waterlevel fluctuations and related environmental changes of the Amazon river. *Amazoniana* **9**, 315–351.

Junk, W. J., Soares, G. M. & Carvalho, F. M. (1983). Distribution of fish species in a lake of the Amazon river floodplain near Manaus (Lago Camaleao), with special reference to extreme oxygen conditions. *Amazoniana* **7**, 397–431.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* **77**, 765–776.

Lecomte, F., Meunier, F. J. & Rojas-Beltran, R. (1985). Mise en évidence d'un double cycle de croissance annuel chez un Silure de Guyane, *Arius couma* (Val., 1839) (Teleostei, Siluriforme, Ariidae) à partir de l'étude squelettochronologique des épines des nageoires. *Comptes Rendus de l'Academie des Sciences de Paris* (Serie 3) **300,** 181–184.

Lecomte, F., Meunier, F. J. & Rojas-Beltran, R. (1986). Données préliminaires sur la croissance de deux téléostéens de Guyane, *Arius proops* (Ariidae, Siluriformes) et *Leporinus friderici* (Anostomidae, Characoidei). *Cybium* **10,** 121–134.

Lecomte, F., Meunier, F. J. & Rojas-Beltran, R. (1989). Some data on the growth of *Arius proops* (Ariidae, Siluriforme) in the estuaries of French Guiana. *Aquatic Living Resources* **2,** 63–68.

Lowe-McConnell, R. H. (1964). The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *Journal of the Linnean Society of Zoology* **45,** 103–144.

Lowe-McConnell, R. H. (1979). Ecological aspects of seasonality in fishes of tropical waters. *Symposia of the Zoological Society of London* **44,** 219–241.

Lowe-McConnell, R. H. (1987). *Ecological Studies in Tropical Fish Communities.* Cambridge: Cambridge University Press.

Meunier, F. J., Lecomte, F. & Rojas-Beltran, R. (1985). Mise en évidence de doubles cycles annuels de croissance sur le squelette de quelques téléostéens de Guyane. *Bulletin de la Société Zoologique de France* **110,** 285–289.

Moreau, J. & Moreau, I. (1987). Fitting of von Bertalanffy growth function (VBGF) with two growth checks per year. *Journal of Applied Ichthyology* **3,** 56–60.

Okedi, J. (1969). Observations on the breeding and growth of certain mormyrid fishes of Lake Victoria Basin (Pisces: Mormyridae). *Revue de Zoologie et de Botanique Africaines* **79,** 34–64.

Poinsard, F. & Troadec, J. P. (1966). Détermination de l'âge par la lecture des otolithes chez deux espèces de Sciaenidae Ouest-Africains (*Pseudolithus senegalis* C.V. et *Pseudolithus typus* Blkr.). *Journal du Conseil, Conseil International pour l'Exploitation de la Mer* **30,** 291–307.

Renno, J. F., Guyomard, R., Boujard, T. & Bastide, C. (1989). Evidence for genetic isolation among four morphological species of *Leporinus* (Anostomidae, Pisces) in French Guiana. *Aquatic Living Resources* **2,** 127–134.

Renno, J. F., Berrebi, P., Boujard, T. & Guyomard, R. (1990). Intraspecific genetic differentiation of *Leporinus friderici* (Anostomidae, Pisces) in French Guiana and Brazil: a genetic approach to the refuge theory. *Journal of Fish Biology* **36,** 85–95.

Robben, J. & Van den Audenaerde, D. K. T. (1984). A preliminary study of age and growth of a Cyprinid fish *Barilius moori* (Blgr.) in Lake Kivu. *Hydrobiologia* **108,** 153–162.

Sioli, H. (1967). Studies in Amazonian waters. *Atlas do Simposio Sobre a Biota Amazonica* **3,** 9–50.

Warburton, K. (1978). Age and growth determination in a marine catfish using an otolith check technique. *Journal of Fish Biology* **13,** 429–434.

Weatherley, A. H. (1972). *Growth and Ecology of Fish Populations.* London: Academic Press.

Welcomme, R. L. (1979). *Fisheries Ecology of Floodplain Rivers.* London: Longman.

Winemiller, K. O. (1987). Feeding and reproductive biology of the currito, *Hoplosternum littorale,* in the Venezuelan llanos with comments on the possible function of the enlarged male pectoral spines. *Environmental Biology of Fishes* **20,** 219–227.