Geographic range
of west African freshwater fishes:
role of biological characteristics
and stochastic processes

Bernard Hugueny

Antenne ORSTOM,
Laboratoire d'Ichtyologie générale et appliquée.
Muséum national d'Histoire naturelle.
43, rue Cuvier, 75231 Paris Cedex 05

ABSTRACT

The geographic range of freshwater fishes in the Nilo-Sudanian part of West Africa was investigated. The size of the geographic range (range size) of a species is defined here as the number of rivers in which the species is present. The frequency distribution of this feature is described by a negative power function. A stochastic model in which all species are assumed to have the same probability of extinction in each river and the same probability of immigration from one river to another was developed to test the possibility of reconstituting a frequency distribution close to that observed. It was possible to adjust a negative power function to frequency distributions for certain parameter values, but the variance given by the model was in all cases smaller than the observed value. The hypothesis according to which, species have the same colonization ability is rejected. Multiple reg ession analysis was carried out to identify the biological characteristics associated with a wide geo raphic range. The characteristics analysed are body length, trophic level, possession of an accessory spiratory device and tolerance to sea water. The log of body length was correlated significantly and positively with the log of the number of rivers inhabited. This relation is interpreted envisaging a connection between body size and dispersion ability. When they are of the same length, predators feeding mainly on invertebrates displayed the widest geographic range, followed by predators with ichthyophagous tendencies. omnivores and then herbivores-detritivores. There is an inverse relation between the species richness of a river and the average range size of the species which live in it. This relation is nevertheless compatible with that given by a Monte Carlo model. The data as a whole lead us to consider that the effect of extinction-related factors is negligible with regard to that of immigration-related factors to explain the distribution of range sizes in Nilo-Sudanian fishes.

KEYWORDS: West Africa, freshwater fishes, geographic range. dispersal, selective extinction. insular biogeography.

RÉSUMÉ

Une étude de l'amplitude de répartition géographique des poissons d'eau douce de la zone sahélo-soudanienne en Afrique de l'ouest a été entreprise. L'amplitude de répartition géographique d'une espèce est définie ici comme le nombre de rivières où cette espèce est présente. La distribution de fréquence des amplitudes de répartition géographique est bien décrite par une fonction puissance négative. Un modèle stochastique où toutes les espèces sont supposées avoir les mêmes probabilités d'extinction dans chaque rivière et les mêmes probabilités d'immigration d'une rivière à l'autre est développé afin de tester la possibilité de reconstituer une distribution de fréquence proche de celle

observée. Pour certaines valeurs des paramètres on obtient des distributions de fréquence auxquelles il est possible d'ajuster une fonction puissance négative. mais dans tous les cas la dispersion de l'amplitude de répartition du modèle est inférieure à celle observée. L'hypothèse selon laquelle les espèces ont les mêmes capacités de colonisation est rejetée. Une analyse de régression multiple a été entreprise pour identifier les caractéristiques biologiques associées à une amplitude de répartition élevée. Les caractéristiques analysées sont la longueur corporelle, le niveau trophique, la possession d'un organe de respiration accessoire, la tolérance à l'eau de mer. Le log de la longueur corporelle est corrélé significativement et positivement au log du nombre de rivières habitées. Cette relation est interprétée en envisageant un lien entre taille corporelle et capacité de dispersion. A longueur égale les prédateurs consommant essentiellement des invertébrés ont la plus grande amplitude de répartition, suivis des prédateurs à tendance ichtyophage, des omnivores puis des herbivores-détritivores. Il existe une relation inverse entre la richesse spécifique d'une rivière et l'amplitude de répartition moyenne des espèces qui y résident, cependant cette relation est compatible avec celle générée par un modèle Monte Carlo où les espèces sont réparties aléatoirement dans les rivières. L'ensemble des données laisse penser que l'action des facteurs liés à l'extinction est négligeable en regard de celle des facteurs liés à l'immigration pour expliquer l'amplitude de répartition des poissons de la zone sahélo-soudanienne.

INTRODUCTION

Geographic range of a species is a characteristic which has been studied in various ways. It is possible for example to investigate the physical or climatic factors which set or have set a limit to the range of one or more species. In this approach, it is assumed that all species cannot occupy the whole of the geographic space studied and there are or have been barriers to their dispersion. A large number of examples of such barriers can be found in the literature. Keeping to the subject of freshwater fishes, LEGENDRE & LEGENDRE (1983) observed that a large number of range boundaries of fishes in Québec coincided with climatic, botanical or geomorphological limits. In a different context, DAGET & ILTIS (1965) identified among West African fishes "Sudanian" species "which live exclusively or principally in peneplain savanna" and "Guinean" species "which are found only or mainly in forest regions".

Another approach is to consider in contrast that all the species are potentially capable of occupying the whole of the geographic zone studied and that the existence of species with more or less extensive geographic ranges is essentially a question of chance, as has been assumed in certain models (SEPKOSKI & REX, 1974; ANDERSON, 1985), or results from differences in intrinsic characteristics of species such as the probability of extinction of populations, dispersion capacity, etc. (REAKA, 1980; BROWN, 1981; BROWN & MAURER, 1987) or from interspecific interactions (e. g. competition or predation).

It is obvious that rather than being incompatible, these two approaches are complementary, but use of one or the other may be more or less pertinent according to the level of perception used. According to BLONDEL (1986), distinction can be made between a number of levels of geographic perception running from the continental level to that of the individual site, each accompanied by levels of biological organization and different problematics. The continental perception level mainly involves problems of the delimitation of biogeographic subdivisions and/or centres of endemism, and the characteristics of the geographic distribution of the species are determined to a great extent by the presence of past or present barriers to dispersion. As a general rule, an approach in which stress is laid on random

processes and the biological features of species should only be used at the level of a region where one has good reasons to believe that the climatic, physical or biogeographic barriers have only a small effect on the distribution of species, i.e. at levels of perception smaller than that of the continent. This is probably the case for freshwater fishes in the region described as "sahélo-soudanienne" (DURAND & LÉVÊQUE, 1980) or "Nilo-Sudan" (ROBERTS, 1975) in West Africa which are the subject of this study. This region runs from west to east from the Senegal basin to the Omo basin and includes the Niger, Chad, Nile, Senegal, Gambia and Volta catchment areas. It forms one of the three main centres of endemism in west and central Africa, the two others being the western and eastern Guinean regions (HUGUENY, 1989 b). The boundaries of these zones probably result from the combined effect of geographic barriers (mountainous country) and the existence of Pleistocene refuges. There is no doubt as regards the existence of present and past barriers to dispersion between the three regions. In contrast, the fauna of the Nilo-Sudanian region displays considerable homogeneity, reported on several occasions (MATTHES, 1964; ROBERTS, 1975), leading to assuming that there were frequent contacts between the river catchments in the past. This supports the hypothesis that the whole of this region was potentially colonizable by all the species. A further argument is the existence of several species found in most of the rivers in the region.

A set of rivers can be considered as a system of biogeographic islands with the catchments separated from each other by barriers (dry land, marine environment) which are difficult for strictly freshwater organisms to cross (SEPKOSKI & REX, 1974). In this context, African rivers have already been the subject of several studies centred essentially on fish species richness (DAGET & ILTIS, 1965; WELCOMME, 1979; LIVINGSTONE et al., 1982; HUGUENY, 1989 a). It has thus been shown that in West Africa the fish species richness of a river is related to the surface area of its catchment and to its discharge (HUGUENY, 1989 a). The "island" nature of the rivers examined in this article led to discussion of the size of geographic range of species mainly in terms of immigration and extinction.

Attention is concentrated here on the size of the geographic range (range size) of species and other aspects such as the concordance of geographic ranges or the existence of species with exclusive or vicariant distribution are not examined. It is attempted to find answers to three main questions concerning the geographic range of Nilo-Sudanian fishes.

It was first examined whether the distribution of range sizes can be explained using a stochastic model in which all the species have equivalent colonization ability. Indeed, SEPKOSKI & REX (1974) showed that a Monte Carlo model based on the hypothesis of species with equal probability of extinction and immigration could be used to generate frequency distributions of the number of rivers inhabited which were similar to those observed for North American freshwater mussels. Study of the extent to which range size can be explained by purely stochastic processes should precede examination of factors related to this feature. The stochastic model proposed here can thus be considered as a null or neutral reference model constructed from a minimum number of assumptions.

The second point approached is that of determining whether certain biological characteristics are related to a large geographic range. For example, there is a significant correlation between body size and the area of geographic range in a

number of zoological groups (VAN VALEN, 1972; REAKA, 1980; BROWN, 1981;
BROWN & MAURER, 1987; McALLISTER et al., 1986). The second part of the article
discusses the correlations between a number of biological characteristics and range
size. These characteristics are chosen in such a way that they can be associated
generally — or more particularly for West African fishes — with probabilities of
extinction and immigration.

The third point examined is the preponderance in low species-rich communities
of species with a large geographic range which has been reported several times
(ROSENZWEIG, 1975; BLONDEL, 1986; PATTERSON & ATMAR, 1986). The simulations
carried out by PATTERSON & ATMAR (1986) show that a similar trend is to be
expected in communities generated in a random manner from a set of species with
varied range sizes. We thus attempt firstly to verify whether the average range size
of the species inhabiting a river increases if the species richness decreases and
secondly to compare this evolution with that obtained with random species distribu-
tion.

METHODS

BASIC DATA AND DEFINITIONS

This study is based on data on the absence or presence of freshwater fishes in 11 catchments in
the Nilo-Sudanian region as defined by DURAND & LÈVÈQUE (1980): Senegal, Gambia, Niger, Comoe,
Volta, Oueme, Mono, Ogun, Chad, Nile and Omo. I have added the following rivers in Ivory Coast:
Bandama, Sassandra, Agnebi, Mé, Boubo, Bia, San Pedro, Nero and Dodo. From a biogeographic
point of view, these rivers form a relatively homogeneous set (HUGUENY, 1989 b). Data on absence and
presence were drawn from LÈVÈQUE et al. (in preparation) and TEUGELS et al. (1988). The Meme and
Tabou catchments were not retained even though they are located in the region in question because of
their low species richness (clearly underestimated). Although this set of 20 rivers does not truly form
the Nilo-Sudanian region, it is referred to as such henceforth. Figure 1 shows the geographic zone
covered by the research. Table VI gives the species richness of the 20 rivers studied, 18 of which are
discussed in HUGUENY'S study (1989 a) which shows that the surface area of the catchment and the
discharge at the river mouth are positively related to species richness.

363 species were considered. Analysis did not include those capable of travelling long distances at
sea even if they have been reported in freshwater. Endemic species in lakes connected with the Nile
and those in lake Turkana (Omo catchment) were not taken into account.

The number of rivers in which each species is represented was calculated. The figure was then
considered as a geographic range size index. This measurement is therefore not the same as the surface
area of geographic range, but has two advantages in the present case. Firstly it is better-suited to the
presence/absence per river data used here from which it is difficult — if not impossible — to calculate the
surface area of geographic range. In addition, given the mode of dispersion of freshwater fishes, such a
measurement probably integrates more biogeographically pertinent information than simple measure-
ment of the surface area. Although dispersion within a catchment does not generally present any
particular difficulty in the absence of noteworthy physical barriers (e. g. falls), movement to a neighbour-
ing catchment is more difficult. It requires either the ability to cross the watershed on dry land or the
ability to survive in sea water to swim from one river mouth to another, or contact between two
catchments (lagoon, flood plain, capture) (cf. MATTHES, 1964). Presence of a species with good
colonization ability would therefore be expected in a large number of rivers. However, the index has
the disadvantage of giving the same weighting to rivers whose catchments have very varied areas, as is
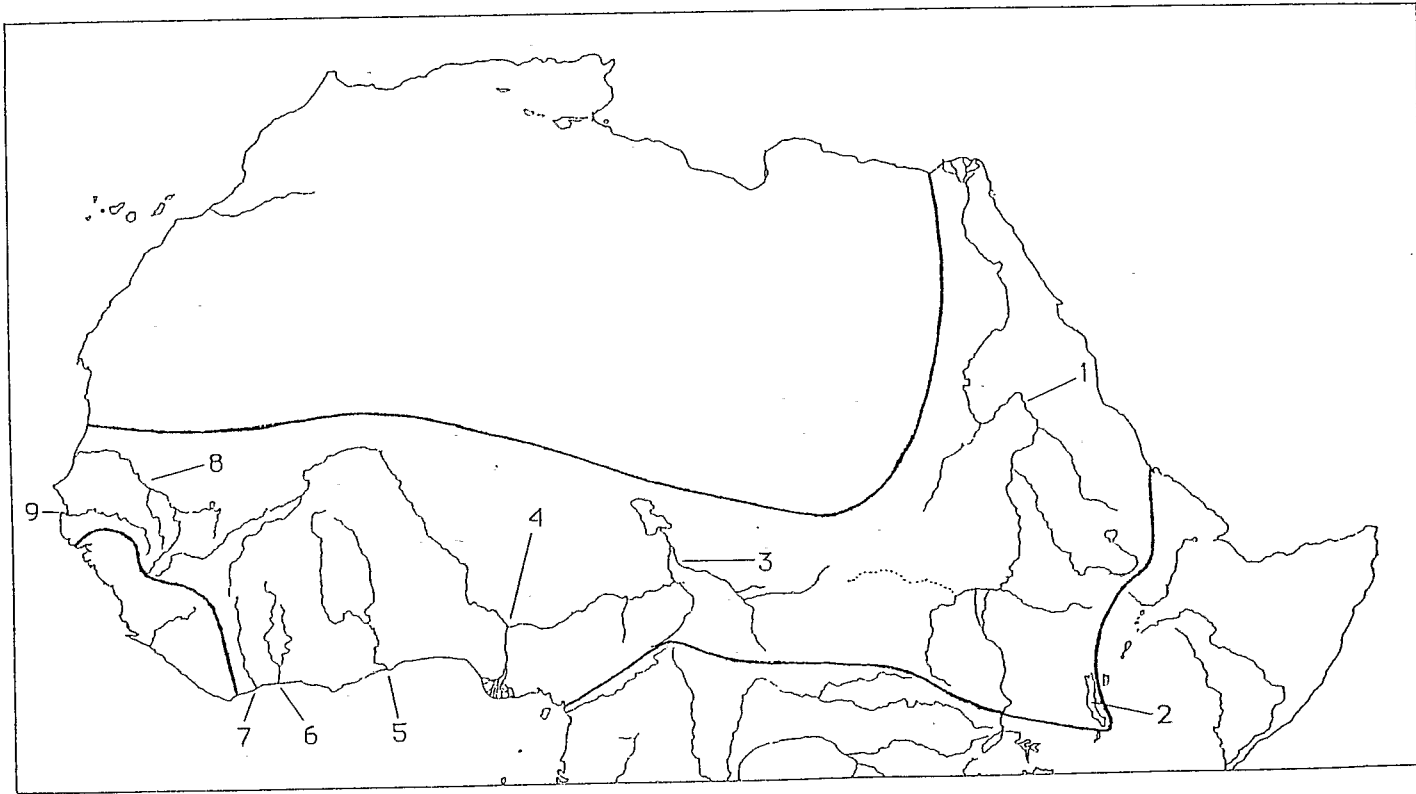the case in the sample discussed here.

FIG. 1. — Map of West Africa showing the geographic zone investigated during the study and main catchment areas covered: Nile (1), Omo (2), Chad (3), Niger (4), Volta (5), Bandama (6), Sassandra (7), Senegal (8) and Gambia (9).

Correlations were sought between four biological characteristics and range size. Body size was retained since in many groups, including fishes, positive correlations has been reported with area of geographic range (VAN VALEN, 1972; REAKA, 1980; BROWN, 1981; MCALLISTER et al., 1986; BROWN & MAURER, 1987). It is also generally considered that risk of extinction of a species increases with body size (FOWLER & MACMAHON, 1982; GLAZIER, 1987; MARSHALL, 1988). The maximum standard lengths described by DAGET et al. (1984; 1986) were used to evaluate body length in centimetres. The second variable was trophic level, which is often considered to be related to risk of extinction (FOWLER & MACMAHON, 1982; GLAZIER, 1987; MARSHALL, 1988). I used four trophic levels: (1) herbivore-detritivores, (2) omnivores, (3) micro-predators (feeding mainly on invertebrates) and (4) top predators (with ichthyophagous tendency). Distribution of species in these categories was mainly carried out using LAUZANNE's synthesis (1988) which gives the trophic positions of the main genera of African fishes.

ROBERTS (1975) stressed the importance that possession of an accessory respiratory device might have in the distribution of freshwater fishes; this enables the fish to use atmospheric oxygen. Distinction was made here between species possessing an accessory respiratory device and those without according to the data given by ROBERTS (1975).

Distinction is made between peripheral, secondary and primary species of freshwater fishes (MYERS, 1938). Peripheral species are of marine origin, spend part or all of their life cycle in fresh water and have kept their ability to move easily in sea water. These species are not included in this analysis. Secondary species live in fresh water but may occasionally move for varying distances in sea water. Finally, primary species are not tolerant to sea water. The classification was drawn up according to the position given to the African families by ROBERTS (1975).

Among the 363 species forming the initial sample, 68 were excluded from analysis because of lack of data on one of the four biological characteristics selected. All the data analysed in this article are available from the author on request (or in HUGUENY, 1989 b).

MONTE CARLO SIMULATIONS

The purpose was to create communities generated by random distribution of the species respecting two constraints. The first was that each river conserved the same number of species and the second was that each species should conserve the same range size. The values used were those in the observed presence/absence matrix (363 species × 20 rivers). Maintaining these constraints is justified firstly because the rivers display differences in species richness caused not by chance but by their characteristics (area and discharge) (DAGET & ILTIS, 1965; WELCOMME, 1979; LIVINGSTONE et al., 1982; HUGUENY, 1989 a) and also because the species display differences in range size not caused by random fluctuations (present study).

Simulations were carried out using the algorithm of CONNOR & SIMBERLOFF (1979). A large number of presence/absence matrices were created by the following procedure. At each iteration the algorithm permuted a species present in river A but absent in river B with a species present in river B but absent in river A. Rivers A and B and the species exchanged were selected at random. The two constraints described above were thus respected. Once a certain number of permutations had been effected, the average range size of the species living in each river was recorded. The same number of permutations was then carried out and the characteristics studied were recorded again. This was continued until a sample of the size desired was obtained.

Numerous criticisms have been made of this type of approach which was originally devised to test the compatibility of patterns of distribution of species with the existence of intense interspecific competition. The discussion concerns epistemological problems (how should hypotheses be tested in ecology?), theoretical problems (what is the role of interspecific competition in the structuring of communities?) and technical questions. Only the latter point is examined briefly here, and readers are referred to articles in the literature for a deeper critical view (GILPIN & DIAMOND, 1982; HARVEY et al., 1983; QUINN & DUNHAM, 1983; ROUGHGARDEN, 1983; TOFT & SHEA, 1983; COLWELL & WINKLER, 1984; GILPIN & DIAMOND, 1984).

· One of the problems raised in the procedure described above is that if the number of permutations between two samplings is not high enough it is difficult to consider the two values sampled as being independent from each other (GILPIN & DIAMOND, 1982, 1984). The following procedure was used to determine the number of permutations necessary. The initial composition of the richest basin (the Niger) was recorded. At each permutation, the species composition of the Niger was compared with the initial composition and the number of common species was recorded. As the number of permutations increased, the number of common species decreased and then stabilized. Stabilization means that from a certain number of permutations the simulated composition becomes independent of the initial composition. There were about 10,000 permutations for the Niger, and it is probable that the figure is lower for rivers with less species richness.

Sample size was fixed at 100, the level at which the simulated averages stabilized with 10,000 permutations. In addition to the simulated average range size, the proportion of times in which the simulated values were greater than the observed value (p_{sup}) was recorded for each river. This measurement is better than a standard deviation since it gives the real dispersion of observed values in relation to that of simulated values. If there is significant positive correlation between the number of times that the simulations have given higher values than the value observed (p_{sup}) and species richness, the average range size decreases faster with species richness than forecast by the Monte Carlo model. The opposite occurs with negative correlation.

STOCHASTIC MODEL

The model described here and as an appendix was inspired to a great extent by that proposed by SEPKOSKI & REX (1974), although resolution is different, using Markov processes instead of Monte Carlo simulations.

The processes leading to increasing or decreasing the number of rivers inhabited by a fish species are shown diagramatically in figure 2. Two parameters are important: pe(A, i, t1, t2), which is the
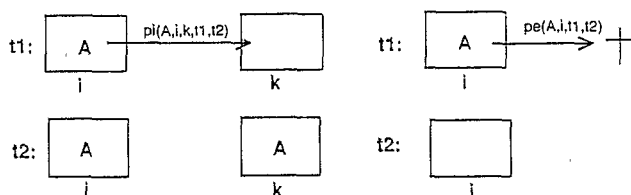

FIG. 2. — Diagram of the processes which can lead to an increase or decrease in the number of rivers inhabited by a fish species.

probability of species A dying out in river i between time t1 and time t2, and pi (A, i, k, t1, t2), which is the probability of colonization of river i by species A from river k between time t1 and time t2. The following assumptions are made: pe and pi are independent of a, i and k. This means that it is assumed that in a given time interval all the species have the same probability of extinction and immigration whatever the rivers in which they are present. My model is therefore based on the two parameters pe, the probability of extinction of a species in a river during a time interval, and pi, the probability that a species will immigrate from a river in which it is present to a river in which it is absent during the interval of time in question.

Using these two parameters, and assuming that the number of species is constant in time, it is possible to use a stochastic model described in more detail in the appendix to determine a stable frequency distribution of range sizes, which is the characteristic examined here. The model described is based on a number of assumptions whose validity might be debatable. If, as is stated in the equilibrium theory of insular biogeography (MACARTHUR & WILSON, 1967), the risk of extinction of populations increases when the surface area of the island (here the catchment) decreases, it cannot be considered (as is done here) that pe is independent of the river, especially as a sample of catchments with very different areas is investigated. Consideration that there is a strict balance of species richness in time in

all the rivers studied is probably an approximation of reality. It is nevertheless probable that there is a trend towards balance insofar as strong area-species relations have been reported in African rivers (WELCOMME, 1979; LIVINGSTONE et al., 1982; HUGUENY, 1989 a), leading to considering that the number of species cannot exceed a certain ceiling in a given geographic zone.

The purpose of the model described here is not strict modelling of the distribution of fishes in a particular system of rivers, but to serve in a way as an ideal reference situation in which a minimum of factors are involved for use as comparison for better interpretation of real data.

MULTIPLE REGRESSION

Search for biological characteristics correlated with range size was carried out using two regression models. The first consists of regression of the number of rivers inhabited in relation to the four explanatory variables used: length (Lg), trophic category (Tr), possession of an accessory respiratory device (Re) and tolerance to sea water (To). Qualitative variables were coded as follows. Re is 1 if the species possesses an accessory respiratory device and 0 if it does not. To is 1 if the fish belongs to the primary species group and 0 if it is a secondary species. Tr has four values from 1 to 4 according to position in the food-web: 1 if it is herbivore-detritivore. 2 if it is omnivore. 3 if it is a micro-predator and 4 if it is a top predator. This coding makes it possible to test whether there is a linear relation between the number of rivers inhabited and the position in the food-web. The second model is identical to the first except for the coding of variable Tr which is carried out so that it is possible to test the effect of belonging to a trophic category on the size of geographic range. For this, Tr was replaced by three dummy variables which each had a value of 0 or 1 (DRAPER & SMITH. 1966): $DTr1$, $DTr2$. $DTr3$. Variables $DTr1$, $DTr2$ and $DTr3$ are 0, 0 and 0 if the species is omnivorous, 1, 0 and 0 if it is a top predator, 0, 1 and 0 if it is a herbivore-detritivore and 0, 0 and 1 if it is a micro-predator.

The F test below was used to find out if all the dummy variables of the trophic categories have a significant contribution over and above the possible action of other variables:

$$F(p-q, n-p-1) = \frac{(R_p^2 - R_q^2)/(p-q)}{(1-R_p^2)/(n-p-1)}$$

where p represents the total number of variables integrated in the analysis, R_p^2 is the coefficient of determination of the model with p variables. q is the number of variables minus the three trophic variables, R_q^2 is the coefficient of determination without the trophic variable and n is the number of observations.

Variables were also selected for each model using a forward stepwise procedure. At each iteration, the variable displaying the strongest partial correlation with the dependent variable was sought and included in the model only if the contribution was significant at the 0.05 level. The procedure was terminated when no variable could be added to the model. In the case of model 2, the three trophic category variables were included or withdrawn from the model together and their common contribution was tested as described below.

RESULTS

STOCHASTIC MODEL

A number of pe and pi values were studied. It was not surprising to observe that average range size increased when probability of extinction (pe) decreased. The same applied when the probability of immigration (pi) increased.

Evolution of frequency distribution of range size as the probability of immigration increases is summarized in figure 3. It appears that for small average range
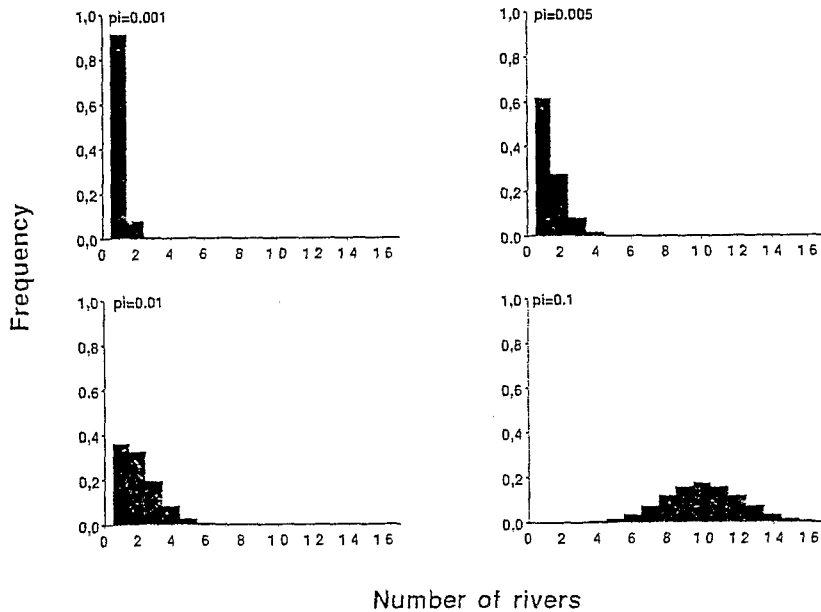

FIG. 3. — Frequency distributions of range sizes obtained
from the stochastic model for four values of *pi.* with *pe* being 0.1.

size, frequency distribution is approximately a negative power function and then it becomes symmetrical and unimodal as the average range size increases. Similar evolution is observed when probability of immigration is kept constant and if the probability of extinction decreases.

TABLE 1. — *Species distribution according to the number of rivers inhabited.*
Only values represented by at least one species are shown.

Number of rivers	Number of species	Number of rivers	Number of species
1	134	10	9
2	49	11	9
3	35	12	6
4	22	13	5
5	19	14	7
6	20	15	7
7	12	16	4
8	8	18	3
9	14		

The distribution of range sizes observed in Nilo-Sudanian fishes (table I) is shown in figure 4 and is well-represented by a negative power function ($r = 0.98$, 15 d. f.). The coefficients were calculated after double logarithmic transformation
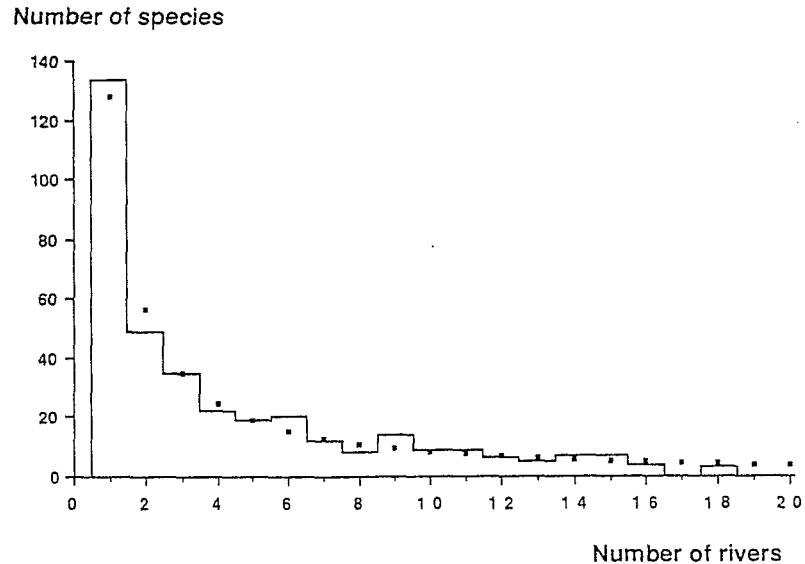
Number of species

FIG. 4. — Distribution of species according to their range size. The dots represent adjustment of data using the equation: number of species = $128.065 \times (\text{number of rivers})^{-1.184}$.

excluding size classes with null distribution. It is noted that there was an abundance of species with a small geographic range. The stochastic model only gives distribution close to a power function for small average range sizes.

Figure 5 shows the distribution observed and distribution generated by the stochastic model with an average of 4.3. that is to say identical to the observed average. It seems that (1) the distribution given by the model is symmetrical and unimodal and hence very different to the observed distribution, and (2) the variance given by the model is smaller than the observed value. An average of 4.3 can be obtained by an infinite number of pairs of *pe* and *pi*, but scanning parameter space did not reveal a pair of parameters giving very different distribution to that described above.

SEARCH FOR CHARACTERISTICS RELATED TO A LARGE GEOGRAPHIC RANGE

As can be seen in figure 4 the size of geographic range is not normally distributed, a log transformation was applied to this variable. As body length was no longer distributed normally but more lognormally (EADIE *et al.*, 1987), this variable was also log-transformed. The other variables were not transformed.

The results of regression of the log of range size against the four explanatory variables (regression model 1) are given in table 2. Only the log of body length displays a significant partial correlation coefficient. Consequently, large fishes tend to have a large geographic range (fig. 6). Once the effect of size has been taken into account by the model, the fact of belonging to the primary or secondary species group does not have a significant effect on range size. The possession or not of an accessory respiratory device does not affect range size. The regression
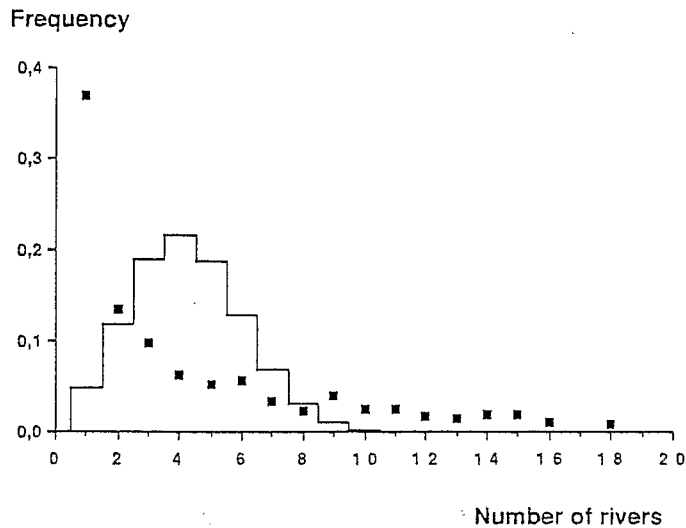
Frequency

Number of rivers

FIG. 5. — Comparison of frequency distribution of observed range sizes (dots) with frequency distribution of the same average obtained using the stochastic model with $pe = 0.1$ and $pi = 0.027$ (histogram).

TABLE II. — *Results of regression of the log of range size against four biological characteristics in model 1 (cf. text). Abbreviations for variables are explained in the text.*

Variables	Coefficients	p (%)
log Lg	0,306	<0,01
Re	-0,064	39,56
To	-0,001	98,69
Tr	0.058	5,09
Intercept:	0,006	
Multiple R:	0,339	
p (%):	<0,01	

coefficient associated with *Tr* is (only just) not significant and there is therefore no linear relation between position in the food-web and range size. The result is not changed by forward stepwise regression since only the log of the length is integrated in the model (table III).

The results are the same in regression model 2, whether all the variables are included (table IV) or the stepwise procedure applied (table V): the log of the
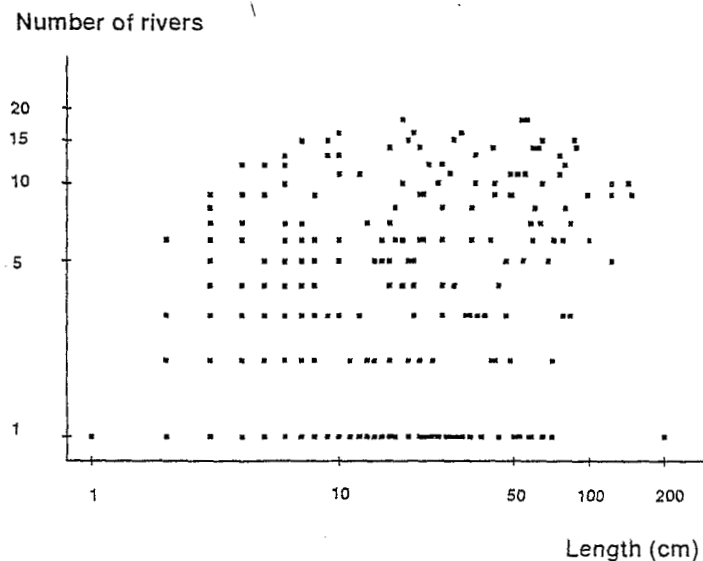
Number of rivers

FIG. 6. — Relation between the number of rivers inhabited and maximum body length in 295 species of fishes in the Nilo-Sudanian region. Abscissae and ordinates are shown on log-scale.

TABLE III. — *Results of stepwise regression of the log of range size against four biological characteristics according to model 1 (cf. text). The equation contains one variable, log Lg. Abbreviations for variables are explained in the text.*

Variables	Coefficients	p (%)
log Lg	0,282	<0,01
Intercept:	0,166	
r	0,319	
p (%):	<0,01	

length and the trophic category both contribute significantly to the variation of the log of range size. Examination of correlation coefficient appears to show that at equivalent lengths micro-predators have the largest geographic range followed by top predators, omnivores and finally herbivore-detritivores.

AVERAGE RANGE SIZE AND SPECIES RICHNESS

Table VI shows the species richness and average range size of resident species and Monte Carlo simulations for the 20 rivers studied. Calculation of the average range size of resident species for each river shows that it varies inversely with the species richness of the river. The fewer species in a river, the more it contains species distributed among a large number of rivers (fig. 7).

TABLE IV. — *Results of the regression of the log of range size against biological characteristics according to model 2 (cf. text). Abbreviations for variables are explained in the text.*

Variables	Coefficients	p (%)
log Lg	0,320	<0,01
Re	-0,060	43,21
To	0,005	92,55
DTr1	0,079	42,99
DTr2	-0,027	74,25
DTr3	0,094	7,12
Intercept:	0,085	
Multiple R:	0,342	
p (%):	<0,01	
Contribution of the trophic variables		
F(288,3):	2,92	
p(%):	<5	

However, when Monte Carlo simulations are carried out according to the procedure described in the Methods section, it is seen here as well that the average range size decreases as species richness increases. Simulated values can be adjusted by an exponential function. The very high correlation coefficient ($r = 0.99$) suggests that the number of simulations carried out was sufficient to reveal a clear relation between average range size and species richness and that this can be summarized very well by an exponential function. The coefficient of regression between the number of simulations giving values higher than the values observed and species richness is not significant ($r = 0.20$; 18 d.f.) and the relation between average range size and species richness observed in the 20 rivers studied does not differ from that generated by the Monte Carlo model. Further demonstration of this is given by comparison of the exponential function adjusted to the data observed with that adjusted to simulated data; the curves for these are almost superimposed (fig. 7).

DISCUSSION

FREQUENCY DISTRIBUTION OF RANGE SIZES

Frequency distributions of range sizes have been published for various zoological groups, including freshwater fishes, amphibians, reptiles and mammals of the

TABLE V. — *Results of stepwise regression of the log of range size against biological characteristics according to model 2 (cf. text). Log Lg and all the trophic variables are integrated in the equation. Abbreviations for variables are explained in the text.*

Variables	Coefficients	p (%)
log Lg	0,302	<0,01
DTr1	0,086	38,60
DTr2	-0,015	84,82
DTr3	0,093	7,10
Intercept:	0,100	
Multiple R:	0,339	
p (%):	<0,01	
Contribution of the trophic variables		
$F_{(290,3)}$:	2,85	
p (%):	<5	

United States (ANDERSON, 1985) and the birds of Australia (SCHOENER, 1987). These distributions resemble each other and are generally grouped under the heading of "hollow curves". These are curves which can be represented more or less by an exponential function or by a negative power function. The frequency distribution of range sizes of freshwater fishes in the Nilo-Sudanian region is similar to these hollow curves, thus confirming that this type of distribution is common [referred to by SCHOENER (1987) as a "macroscopic rule"].

It is possible for certain extinction and immigration values of the stochastic model to obtain distributions which approach a negative exponential function. The model thus makes it possible to plot distributions in which many species are not very widely distributed, as is frequently observed. It can therefore be suggested that hollow curves displaying little flattening at the end of distribution might be explained in terms of random processes playing on a pool of "equivalent" species. This is not the case of the present data since the model does not account for all the variability in range size of fishes in West Africa.

As in any model, a number of assumptions may seem unrealistic or only approximations of reality at best. Some can be found in the model, as was mentioned in the description. However, in the light of the results, and especially as regards the over-dispersion of observed values in comparison with those of the model, the assumption to which most objection can be made is that in which the immigration capacity and risk of extinction are considered to be equivalent in all species. Examination of other hollow curves published appear to lead to a similar conclusion.

TABLE VI. — *Number of species, observed and simulated average range size of resident species, proportion of times that simulated range size was greater than observed range size (p_{sup}) for the 20 rivers studied. With the exception of the Nile, the Chad and the Omo, rivers are in order of the positions of their mouths along the Atlantic coast.*

Rivers	Species richness	Observed average range size	Simulated average range size	psup (cf text)
Nile	126	5,61	7,64	1,00
Chad	125	7,12	7,61	1,00
Omo	50	6,76	9,78	1,00
Senegal	109	8,19	8,05	0,33
Gambia	84	8,70	8,80	0,68
Dodo	18	10,22	11,37	0,89
Nero	21	10,76	10,89	0,48
San Pedro	26	11,61	11,06	0,24
Sassandra	74	9,83	9,07	0,02
Boubo	45	11,08	10,17	0,03
Bandama	86	10,12	8,75	0,00
Agnebi	56	10,48	9,83	0,06
Me	52	10,67	9,90	0,02
Comoe	88	9,78	8,70	0,00
Bia	44	10,72	10,05	0,09
Volta	137	7,78	7,35	0,00
Mono	50	10,84	10,06	0,04
Oueme	91	8,71	8,54	0,31
Ogun	68	8,60	9,35	0,97
Niger	212	5,85	5,90	0,73

The Monte Carlo model used by SEPKOSKI & REX (1974) can also generate distributions whose trends are similar to observed distribution. However, although the authors did not make such a comparison, it appears that here too the model does not account for all the variability observed. ANDERSON (1985), using Markov processes in a different approach to mine, succeeded in obtaining frequency distributions of range sizes with a very similar trend to those observed. His model was not based on simple biological processes (which can be reduced to terms of colonization ability) and so it is difficult to draw a lesson from it.

It appears to me that hollow curve type distribution must result from another macroscopic law which states that small species are more numerous than large ones (VAN VALEN, 1972). Figure 8 shows body length distribution of the 295 species covered by this analysis. Comparison shows that the trend is similar to that of the
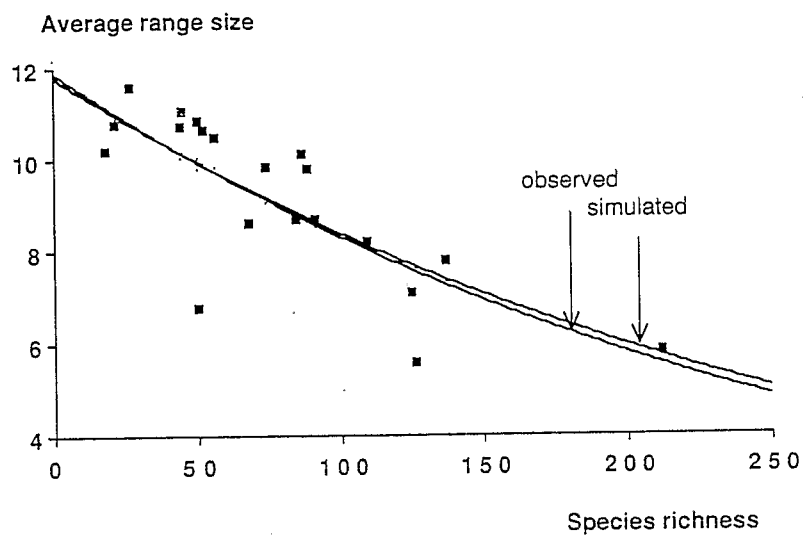
Average range size

FIG. 7. — Average range size of resident species in relation to species richness in 20 Nilo-Sudanian rivers. The points represent observed values. The curves represent adjustments of exponential functions to observed data and simulated data (not shown).
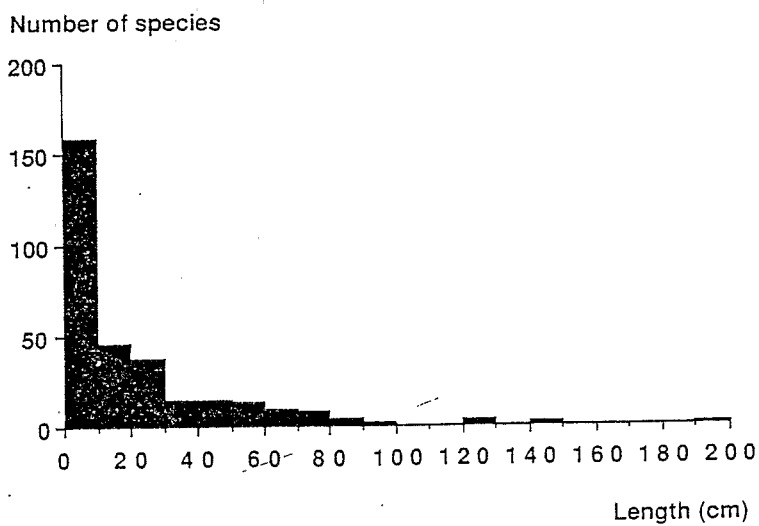
Number of species

FIG. 8. — Distribution in body length classes of 295 fish species in the Nilo-Sudanian region.

curve representing range sizes (fig. 4). This is not surprising as it has been seen above that body length and range size are correlated. It is possible that the hollow curves reported in the literature may be the result of similar processes since in many groups there is a correlation between body size and geographic range size (VAN VALEN, 1972; REAKA, 1980; BROWN, 1981; McALLISTER et al., 1986; BROWN & MAURER, 1987).

RANGE SIZE AND BIOLOGICAL CHARACTERISTICS

The results of the stochastic model lead the examination of all the species studied not as a homogeneous group with regard to colonization ability. Confirmation can be obtained by finding the biological characteristics correlated with range size and which could be combined with differences in rates of extinction or immigration. Significant correlation between range size and body size has been shown. This appears to agree with the results found by BROWN (1981), McALLISTER et al., (1986) and BROWN & MAURER (1987) who reported significant correlation between geographic range size and body size in North American land mammals, birds and freshwater fishes. As is discussed below, there is only partial coherence insofar as it probably does not result from the same factors in all these groups.

McALLISTER et al., (1986) did not suggest an explanation for the relation that they showed between body length and geographic range size in North American freshwater fishes. However, BROWN (1981) put forward a hypothesis based on the risks of extinction of populations to account for the positive relation between weight and geographic range size in North American mammals. He suggested that large mammals had a larger geographic range because they were more sensitive to risk of extinction. It can be considered that the probability of extinction of a species decreases as the number of individuals increases. This number depends on density and geographic range size. Species of large size display low density (PETERS, 1983) and consequently species with a small geographic range are more likely to become extinct than species with the same range but smaller body size. As a result, as body size increases only the species with wider geographic ranges survive. However, this explanation cannot be used to account for the relation between body size and range size observed in Nilo-Sudanian fishes. Indeed, the mechanisms described by BROWN do not operate if the geographic range is divided into regions between which there is little immigration, as is the case for the freshwater fishes distributed in different catchments. Figure 9 shows diagramatically a situation in which BROWN's hypothesis operates: species B has a small geographic range and dies out, whereas the geographic range area of species A is greater than the critical threshold and continues to be present. The same figure illustrates a situation in which two species A and B have the same range areas as in the previous situation, but species A is located in three regions between which there is very little immigration. In contrast with the previous situation, this leads to the extinction of species A since the three regions occupied by the species are below the critical threshold of geographic range size. High risks of extinction for large fishes should result in smaller geographic range. Consequently, the data are not compatible with an important role for extinction processes as for land vertebrates.

It should be stressed that this reasoning is based essentially on the hypothesis that large species have smaller populations or reach lower densities than small
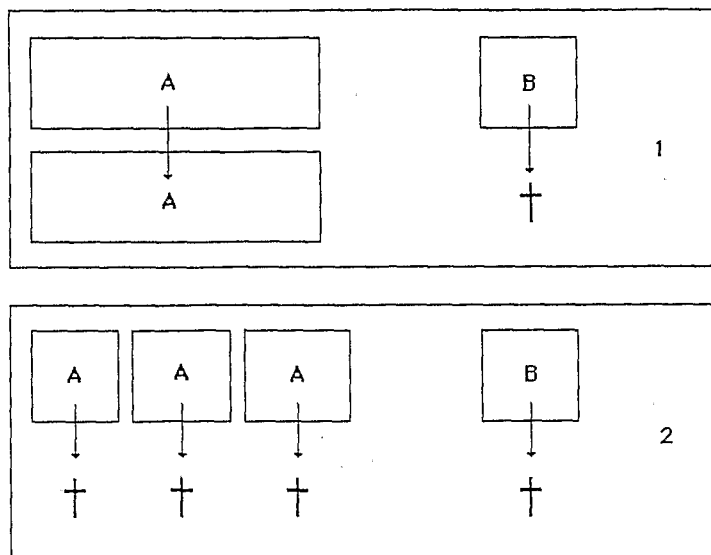
FIG. 9. — (1) Diagram illustrating BROWN's hypothesis (cf. text). The area of the rectangles is proportional to the distribution area of species A and B. (2) BROWN's hypothesis applied to fragmented distribution areas.

species. Data on fishes are rare and contradictory. BROWN & MAURER (1986) found no connection between body size and density whereas DUARTE *et al.* (1987) reported a significant link.

I propose as a hypothesis that the dispersion ability of West African fishes — and fishes in general — are positively related to body size. This would account for the larger geographic range of large species. There is some supporting information for this hypothesis, as is seen below. One feature which can increase the dispersion ability of a species is the ability to cross hostile environments rapidly (sea or low-oxygen environment) to limit exposure time to poor conditions. Size probably plays an important role here since the swimming speed of fishes is correlated with their size (BAINBRIDGE, 1958). Another important characteristic is the ability to travel long distances. Here again, large fishes have an advantage since with the same expenditure of energy they can travel further than small species (BEAMISH, 1978). A study by ROFF (1988) showed that large species of marine fishes frequently migrate more than small ones. This also appears to be the case for freshwater fishes in West Africa. For example, only 2 of the 23 species in Chad known for long or medium range reproduction migration are less than 20 cm long (BENECH & QUENSIÈRE, 1988).

The results of multiple regression of range size against biological characteristics of species make it possible to reject three hypotheses. The first is that the risk of extinction of a population is higher in species at the end of a food-web (FOWLER & MACMAHON, 1982; GLAZIER, 1987; MARSHALL, 1988) because their populations do not generally attain high densities. If rates of extinction per river are low and all the other variables are assumed to be constant, this must result in

large geographic range. As a result, the species at the beginning of the food-web, such as herbivores, should have greater geographic ranges than species such as predators which are at the end of the food-web. This is not the case of fishes in West Africa. Indeed, the results of the regressions carried out show that — size for size — predators have a greater geographic range, i.e. the opposite of what would be expected according to the hypothesis.

The second hypothesis not confirmed by the data is that in which the fishes which possess an accessory respiratory device have better dispersion ability (ROBERTS, 1975; LOWE MCCONNELL, 1988). Flood zones and marshy springs, which form points of exchange between catchments, are generally not well oxygenated. Possession of accessory respiratory device can aid in crossing these environments and thus increase dispersion capability. However, species which possess accessory respiratory devices are not geographically more widespread than those which do not, once body size has been taken into account. The importance of accessory respiration in dispersion of species was underlined by LOWE MCCONNELL (1988) who considers that this accounts for the large geographic range of many species of *Clarias*. She even considered that accessory respiratory devices enhanced dispersion between Africa and SE Asia since many genera common to both regions possess them. These hypotheses remain to be validated quantitatively.

Finally, the third hypothesis which can be rejected is that in which "secondary" fish species have better dispersion ability. If colonization from one catchment to another from the sea is an important immigration process, secondary species have an advantage and should display greater geographic range. The data gathered in West Africa do not confirm this; it would seem that secondary species do not have better colonization ability than primary species once body size has been taken into account. It should nevertheless be noted that division into primary and secondary species at family level is a fairly rough generalization (RIVAS, 1986) and it is obvious that sea water tolerance should be defined at species level. For example, *Brycinus longipinnis*, which belongs to the *Characidae* and is thus a "primary" species according to ROBERTS (1975), probably colinized rivers on the West coast of Africa from the sea (PAUGY, 1986); it is tolerant to high salinity as it is found in lagoons in Ivory Coast (PAUGY, 1986). There are probably many other examples of species which belong to families classified as "primary" but which are nonetheless tolerant to sea water.

SPECIES RICHNESS OF RIVERS AND AVERAGE RANGE SIZE

An inverse relation between species richness of a community and the average range size of the constituent species was observed for the 20 rivers investigated here. Similar results are known in continental (turtles and bats in North America; ROSENZWEIG, 1975) and island areas (birds in Mediterranean islands; BLONDEL, 1986) where it has been observed that communities with few species consist of species with very large geographic range. PATTERSON & ATMAR (1986) observed that mammal species in island environments (true or "continental") tended to display nested distributions with all the species forming the community on each island being a subset of the communities found on islands with greater species richness. ROSENZWEIG (1975) does not dwell at length on the mechanisms which may account for the relation that he demonstrates, but simply suggests that "perhaps the decline results from more intense habitat selection in more diverse areas". The

interpretation made of this phenomenon in island situations is that island coloniz-
ation is not a random phenomenon but that the species which are most widespread
geographically are favoured. Indeed, the most widespread species are often those
capable of attaining high densities (BROWN. 1984) or are species capable of occupy-
ing a large range of habitats. Both characteristics can be an advantage in island
environments where they reduce risk of extinction through increasing the density.
PATTERSON & ATMAR (1986) suggested that the nested distributions that they obser-
ved were the result of a selective extinction process related to area. The species
most liable to extinction are those which cannot attain high densities and hence
disappear preferentially from small "islands" where they cannot maintain large
enough populations.

Simulations taking into account the range size of each species (i. e. in each
simulation the species conserves the same range size as that observed) and assuming
random distribution of species in different rivers show that species with a large
geographic range are more numerous in rivers with fewer species. This agrees with
the result of the simulations carried out by PATTERSON & ATMAR (1986). If the
widely distributed species have a lower risk of extinction than the other species
because they are able to attain high densities, observed average range sizes should
fall faster with species richness than simulated values as species with a limited
geographic range should have higher probability of extinction than those with large
ranges. As this is not the case, it would seem that the greater representation of
species with a large geographic range in the small catchments is the result of a
statistical property of the presence/absence matrices.

It remains to be known whether this result is universal and in particular
whether the examples mentioned above require biological explanation or can be
interpreted in the same way. Only the distributions of mammals in island environ-
ments studied by PATTERSON & ATMAR (1986) were compared with distributions
obtained by Monte Carlo simulation, showing that the higher numbers of widely
distributed species in small "islands" is not the result of a random phenomenon.

The biological properties favourable for a large geographic range do not give
fish in small catchments increased probability of survival. This is not particularly
surprising since in the fishes studied the biological characteristic (large body size)
principally associated with a large geographic range in West Africa is probably
related to dispersion capability enhancing immigration from one catchment to
another but not to risk of extinction as seen above.

HISTORICAL FACTORS

Discussion has so far concerned interpretation of extent of geographic range
related to the biological characteristics of the species and historical processes have
hardly been mentioned. Their importance is not under-estimated, but the data
available is inadequate for all but speculation. The main historical processes to be
taken into account are nevertheless described.

The geographic range of a species may be conditioned by the possibilities of
transfer from one catchment to another which are available over a period of time.
Unfortunately, there is little solid information to demonstrate a connection between
two specific catchments during a given period. The existence of species widely
distributed in the zone in question shows that connections must have existed at

one time or another between most of the catchments and that if certain species were not very widespread, factors other than lack of connections between basins should be sought.

A historical factor which must have had a considerable effect on the geographic ranges of fishes in West Africa is the alternance of dry and wet climatic periods during the Pleistocene (HAMILTON, 1982). It is probable that contacts between catchments were easier during wet periods and that it was possible for fishes to extend their geographic range. It is probable that geographic range was reduced during dry periods as some rivers must have dried out sufficiently for some species to die out. The last dry period was about 12,000 years ago. It is therefore possible that species which used to be widespread now have only relict distribution. This may mask relations between biological characteristics and geographic range.

Another important factor is the date of appearance of species. It can be considered *a priori* that "older" species have had more opportunity to increase their geographic range than more recent species. However, the situation is certainly not as simple as this. For example, the existence of a taxon cycle has been described in island birds (RICKLEFS & COX, 1972) and ants (WILSON, 1961). This hypothesis holds that species go through different stages of geographic distribution during their history. The first stage would be limited distribution at speciation or colonization followed by a period of extension. The final stage would consist of regression of the distribution area. If such a process exists in fishes, it would be illusory to show a relation between geographic range and "age" of the species. In addition, in the absence of sufficient data on the phylogeny and paleontology of ichthyofauna in West Africa, these questions cannot be answered with any accuracy.

ACKNOWLEDGEMENTS

APPENDIX: STOCHASTIC MODEL

The following random variables are defined:

N_t: number of rivers occupied at time t

N_{t+1}: number of rivers occupied at time $t+1$

NC_{t+1}: number of rivers colonized at time $t+1$

NE_{t+1}: number of rivers with an extinction at time $t+1$.

The two parameters *pe* and *pi* described in the text are used to define the probability that a species will be present in m rivers at time $t+1$ if it is present in n rivers at time t: $P(N_{t+1} = m/N_t = n)$.

The probability that nc rivers would be colonized at time $t+1$ using the situation in which n rivers are inhabited at time t is determined first: $P1(NC_{t+1} = nc/N_t = n)$.

If N is the total number of rivers, it is assumed that $N-n$ rivers are potentially accessible.

The probability of river i being colonized from river j during a period time is pi by definition.

The probability that river j will not be colonized from any of the n rivers is deduced: $(1-pi)^n$.

The probability that river j is colonized from at least one of the n rivers is therefore $1-(1-pi)^n$. This probability is called pc.

The probability that $nc\,(0\leqq nc\leqq N-n)$ rivers would be colonized during a period of time from n rivers is given by the binomial distribution:

$$P1\,(NC_{t+1}=nc/N_t=n)=C_{N-n}^{nc}\,pc^{nc}\,(1-pc)^{N-n-nc}.$$

The probability that extinctions will occur in ne rivers at time $t+1$ from n rivers inhabited at time t is now explained: $P2\,(NE_{t+1}=ne/N_t=n)$.

If pe is the probability of extinction in 1 river, the probability that extinction occurs in $ne\,(0\leqq ne\leqq n)$ rivers is given by the binomial distribution:

$$P2\,(NE_{t+1}=ne/N_t=n)=C_n^{ne}\,pe^{ne}\,(1-pe)^{n-ne}.$$

$P1$ and $P2$ can be combined to know the probability that at time $t+1$, m rivers are occupied if n are occupied at time t: $P\,(N_{t+1}=m/N_t=n)$.

It is assumed that $m\geqq 0$, which means considering that if a species dies out in all N rivers it is immediately replaced by another species by immigration from neighbouring zones or by speciation in such a way that the number of species remains strictly constant in time throughout the N rivers.

This leads to probability $P\,(N_{t+1}=m/N_t=n)$ being given by

$$P'\,(N_{t+1}=m/N_t=n)=\Sigma'\,P1\,(NC_{t+1}=i/N_t=n)\,P2\,(NE_{t+1}=j/N_t=n)$$

$$P\,(N_{t+1}=m/N_t=n)=P'\,(N_{t+1}=m/N_t=n)\quad\text{if }m\geqq 2$$

and

$$P\,(N_{t+1}=1/N_t=n)=P'\,(N_{t+1}=0/N_t=n)+P'\,(N_{t+1}=1/N_t=n)$$

where

$$\Sigma'=\sum_{i=0}^{N-n}\sum_{j=0}^{N}\quad\text{respecting the constraint: }i-j=n-m$$

It is thus possible for each value of n to find out the probability that m rivers are occupied at time $t+1$. If the probabilities are independent of time the process is described by a time-homogeneous Markov chain. The values of P for the different combinations of n and m can be grouped in a matrix $N\times N$ whose elements give the probability of changing from the number of rivers given by the column to the number of rivers given by the line.

$$M = \begin{bmatrix} P(N_{t+1}=1/N_t=1) & P(N_{t+1}=1/N_t=2) & \ldots & P(N_{t+1}=1/N_t=N) \\ P(N_{t+1}=2/N_t=1) & P(N_{t+1}=2/N_t=2) & \ldots & P(N_{t+1}=2/N_t=N) \\ \ldots & \ldots & \ldots & \ldots \\ P(N_{t+1}=N/N_t=1) & P(N_{t+1}=N/N_t=2) & \ldots & P(N_{t+1}=N/N_t=N) \end{bmatrix}$$

Matrix M is a transition matrix since if one knows the frequency distribution of range sizes at time t, represented by a vector of size N, it is possible to find out the distribution at time $t+1$ by using the following matrix calculation:

$$M \times V_t = V_{t+1}$$

in which

$$V_t = \begin{bmatrix} f_1 \\ f_2 \\ \vdots \\ f_N \end{bmatrix}$$

and f_i are the frequency of the species present in i rivers at time t.

In a general manner:

$$M^t \times V_0 = V_t.$$

If the matrix is ergodic, it approaches a matrix consisting of identical columns as t increases. Whatever the initial vector, the vector of the final state will therefore be the same when t approaches infinity. This means that here it is possible to find stable frequency distribution of range sizes which depends only on *pe* and *pi*. Study of the graph for matrix M shows that M is irreducible and non-periodic and hence ergodic. Stable frequency distribution for a given *pe* and *pi* was sought by raising to successive powers until the transition matrix columns were identical to within the accuracy threshold allowed. These operations were carried out with $N = 20$ rivers, which corresponds to the size of the sample for which there was data.

REFERENCES

ANDERSON S., 1985. — The theory of range size (RS) distributions. *American Museum novitates*, No. 2833, 1-20.

BAINBRIDGE R., 1958. — The speed of swimming of fish as related to size and the frequency and the amplitude of the tail beat. *J. Exp. Biol.*, 35, 109-133.

BEAMISH W. H., 1978. — Swimming capacity. *In:* HOARD W. S. & RANDALL D. J., eds., *Fish physiology*, Vol. 7, Academic Press, 101-187.

BENECH V. & QUENSIÈRE J., 1988. — *Dynamique des peuplements ichtyologiques de la région du lac Tchad (1966-78) — Influence de la sécheresse*. Thèse d'État, Université de Lille.

BLONDEL J., 1986. — *Biogéographie évolutive*. Masson, Paris. 221 p.

BROWN J. H., 1981. — Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Am. Zool.*, 21, 877-888.

BROWN J. H., 1984. — On the relationship between abundance and distribution of species. *Am. Nat.*, 124, 255-279.

BROWN J. H. & MAURER B. A., 1986. — Body size, ecological dominance and Cope's rule. *Nature*, 324, 248-250.

BROWN J. H. & MAURER B. A., 1987. — Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the north american avifauna. *Am. Nat.*, 130, 1-17.

COLWELL R. K. & WINKLER D. W., 1984. — A null model for null models in biogeography. *In:* STRONG D. R., SIMBERLOFF D., ABELE L. G. & THISTLE A. B., eds., *Ecological communities: conceptual issues and the evidence.* Princeton University Press, Princeton N. J., 345-359.

CONNOR E. F. & SIMBERLOFF D., 1979. — The assembly of species communities: chance or competition? *Ecology*, 60, 1132-1140.

DAGET J. & ILTIS A., 1965. — Les poissons de Côte d'Ivoire (eaux douces et eaux saumâtres). *Mém. Inst. Fr. Afr. Noire*, 74, 385 p.

DAGET J., GOSSE J. P. & THYS VAN DEN AUDENAERDE, eds., 1984. — *Check-list of the freshwater fishes of Africa*, Vol. 1. ORSTOM, Paris, & MRAC, Tervuren, 410 p.

DAGET J., GOSSE J. P. & THYS VAN DEN AUDENAERDE, eds., 1986. — *Check-list of the freshwater fishes of Africa*, Vol. 2. ORSTOM, Paris, & MRAC, Tervuren, 520 p.

DRAPER N. R. & SMITH H., 1966. — *Applied regression analysis.* Wiley, New York, 407 p.

DUARTE C. M., AGUSTI S. & PETERS H., 1987. — An upper limit to the abundance of aquatic organisms. *Oecologia*, 74, 272-276.

DURAND J. R. & LÉVÊQUE C., eds., 1980. — *Flores et faunes aquatiques de l'Afrique sahélo-soudanienne*, tome 1. Éditions de l'ORSTOM, Paris, 389 p.

EADIE J. McA., BROEKHOVEN L. & COLGAN P., 1987. — Size ratios and artifacts: Hutchinson's rule revisited. *Am. Nat.*, 129, 1-17.

FOWLER C. W. & MAC MAHON J. A., 1982. — Selective extinction and speciation: their influence on the structure and functioning of communities and ecosystems. *Am. Nat.*, 119, 480-498.

GILPIN M. E. & DIAMOND J. D., 1982. — Factors contributing to non-randomness in species co-occurrences on islands. *Oecologia*, 52, 75-84.

GILPIN M. E. & DIAMOND J. D., 1984. — Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology. *In:* STRONG D. R., SIMBERLOFF D., ABELE L. G. & THISTLE A. B., eds., *Ecological communities: conceptual issues and the evidence.* Princeton University Press, Princeton N. J., 297-315.

GLAZIER D. S., 1987. — Energetics and taxonomic patterns of species diversity. *Syst. Zool.*, 36, 62-71.

HAMILTON A. C., 1982. — *Environmental history of East Africa — a study of the Quaternary.* Academic Press, London.

HARVEY P. H., COLWELL R. K., SILVERTOWN J. W. & MAY R. M., 1983. — Null models in ecology. *Ann. Rev. Ecol. Syst.*, 14, 189-211.

HUGUENY B., 1989 a. — West African rivers as biogeographic islands: species richness of fish communities. *Oecologia*, 79, 236-243.

HUGUENY B., 1989 b. — *Biogéographie et structure des peuplements de poissons d'eau douce d'Afrique de l'Ouest : approches quantitatives.* Thèse de Doctorat de l'Université Paris-VII. Paris.

LAUZANNE L., 1988. — Les habitudes alimentaires des poissons d'eau douce africains. *In:* LÉVÊQUE C., BRUTON M. N. & SSENTENGO G. W., eds., *Biology and ecology of African freshwater fishes.* Éditions de l'ORSTOM, Paris, 221-242.

LEGENDRE P. & LEGENDRE V., 1983. — Postglacial dispersal of freshwater fishes in the Québec peninsula. *J. Fish. Aquat. Sci.*, 41, 1781-1802.

LIVINGSTONE D. A., ROWLAND M. & BAILEY P. E., 1982. — On the size of African riverine fish faunas. *Am. Zool.*, 22, 361-369.

LOWE MCCONNELL R. H., 1988. — Broad characteristics of the ichtyofauna. *In:* LÉVÊQUE C., BRUTON M. N. & SSENTENGO G. W., eds., *Biology and ecology of African freshwater fishes.* Éditions de l'ORSTOM, Paris, 93-110.

MCALLISTER D. E., PLATANIA S. P., SCHUELER F. W., BALDWIN M. E. & LEE S. D., 1986. — Ichthyofaunal patterns on a geographic grid. *In:* HOCUTT C. H. & WILEY E. O., eds., *The zoogeography of north American fishes.* Wiley, New York, 17-51.

MAC ARTHUR R. H. & WILSON E. O., 1967. − *The theory of island biogeography*. Princeton Univ. Press, N.J.

MARSHALL L. G., 1988. − Extinction. *In:* MYERS A. A. & GILLER P. S., eds.. *Analytical biogeography: an integrad approach to the study of animal and plant distributions*. Chapman & Hall, London. 217-254.

MATHES H., 1964. − *La zoogéographie des poissons dulçaquicoles africains*. Thesis of Amsterdam Museum. 32 p.

MYERS G. S., 1938. − Fresh-water fishes and West Indian zoogeography. *Smithson. Rep.*. 1937. 339-364.

PATTERSON B. D. & ATMAR W., 1986. − Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.*, 28, 65-82.

PAUGY D., 1986. − *Révision systématique des* Alestes *et* Brycinus *africains* (Pisces, Characidae). Éditions de l'ORSTOM, Paris, 295 p.

PETERS R. H., 1983. − *The ecological implications of body size*. Cambridge University Press, 324 p.

QUINN J. F. & DUNHAM A. E., 1983. − On hypothesis testing in ecology and evolution. *Am. Nat.*, 122, 602-617.

REAKA M. L., 1980. − Geographic range, life history patterns and body size in a guild of coral dwelling mantis shrimps. *Evolution*, 34. 1019-1030.

RICKLEFS R. E. & COX G. W., 1972. − Taxon cycles in the West Indian avifauna. *Am. Nat.*, 106, 195-219.

RIVAS L. R., 1986. − Comments on Briggs (1984): freshwater fishes and biogeography of central America and the Antilles. *Syst. Zool.*. 35, 633-639.

ROBERTS T. A., 1975. − Geographical distribution of African freshwater fishes. *Zool. Journal Linnean Soc.*, 57, 249-319.

ROFF D., 1988. − The evolution of migration and some life history parameters in marine fishes. *Environmental biology of fishes*, 22. 133-146.

ROSENZWEIG M. L., 1975. − On continental steady state of species diversity. *In:* CODY M. L. & DIAMOND J. M., eds., *Ecology and evolution of communities*. Harvard Univ. Press. Cambridge, Mass., 121-140.

ROUGHGARDEN J., 1983. − Competition and theory in community ecology. *Am. Nat.*, 122. 583-601.

SCHOENER T. W., 1987. − The geographical distribution of rarity. *Oecologia*. 74, 161-173.

SEPKOSKI J. J. & REX M. A. − Distribution of freshwater mussels: coastal river as biogeographic islands. *Syst. Zool.*, 23, 165-188.

TEUGELS G., LÉVÊQUE C., PAUGY D. & TRAORE K., 1988. − État des connaissances sur la faune ichtyologique des bassins côtiers de Côte d'Ivoire et de l'Ouest du Ghana. *Revue d'Hydrobiol. Tropicale*, 21, 221-237.

TOFT C. A. & SHEA P. J., 1983. − Detecting community-wide patterns: estimating power strengthens statistical inference. *Am. Nat.*, 122. 618-625.

VAN VALEN L., 1972. − Body size and numbers of plants and animals. *Evolution*, 27, 27-35.

WELCOMME R. L., 1979. − *Fisheries ecology of floodplain rivers*. Longman, London & New York, 317 p.

WILSON E. O., 1961. − The nature of the taxon cycle in the melanesian ant fauna. *Am. Nat.*, 95, 169-193.