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UNSATURATED FISH COMMUNITIES IN AFRICAN RIVERS

Ricklefs (1990) writes that "a pervasive role of regional and historical processes in shaping local biological communities requires that ecologists expand the spatial and temporal scale of their concepts in order to address community phenomena" (p. 775). In particular, the fact that the local richness of communities is not strictly dependent on local conditions but is also affected by regional richness has been stressed (Cornell and Lawton 1992; Cornell 1993; Schluter and Ricklefs 1993). According to Cornell and Lawton (1992), local species richness can be related to regional species richness in different ways, and two endpoints on this continuum can be distinguished: proportional sampling (linear relationship between the two variables; Type I curve) or ceiling (local species richness increases with regional species richness but reaches an asymptote; Type II curve). Proportional sampling reveals unsaturated communities in which species interactions are not sufficient to limit local species richness. Cornell and Lawton (1992) suggest that this pattern is probably ubiquitous in nature, but too few assemblages have been studied to confirm this assumption unambiguously.

Here we discuss a case of local species richness that cannot be accounted for by local conditions alone but that requires knowledge of factors involved on a larger spatial scale: aquatic communities in particular habitat patches within a river catchment.

For aquatic organisms, rivers can be considered as biogeographical islands since they are separated from each other by barriers difficult to cross (sea, dry land), and, as for real islands, a positive relationship between the species richness observed in a river and the size of its catchment area (measured by surface, discharge at the river mouth, or a combination of these two variables) has been reported on several occasions (Daget and Iltis 1965; Daget 1968; Sepkoski and Rex 1974; Daget and Economidis 1975; Welcomme 1979; Brönmark et al. 1984; Eadie et al. 1986; Hugueny 1989). The insular nature of rivers—that is, the lack of communication between them—means that the number of species available to colonize a given local habitat is the same as the number of species found in the catchment area.

In order to test the hypothesis of proportional sampling (linear relationship between local species richness and river species richness), we analyzed the data on fish communities sampled in "pools" in 10 rivers located in Côte d'Ivoire (West Africa), a country for which Teugels et al. (1988) give river species lists. With regard to their fish species composition, these rivers belong to the same biogeographical unit (Hugueny and Lévêque 1994). Species richness per river ranges from 18 to 95 and is well explained by catchment area ($r = 0.96$, from data in table 1, after log transformation). Species composition displays low variability

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TABLE 1

RIVER SPECIES RICHNESS, MEAN LOCAL SPECIES RICHNESS (RANGE IN PARENTHESES) AND SURFACE OF CATCHMENT AREA FOR 10 RIVERS LOCATED IN CÔTE D'IVOIRE

Rivers	Local Species Richness	Number of Samples	River Species Richness	Catchment Area (km^2)
Agnebi	21	1	61	8,520
Bandama	24 (18–35)	23	95	97,000
Boubo	15 (12–18)	2	46	4,690
Cavally	15.2 (13–18)	4	63	28,850
Comoe	27.2 (19–34)	7	91	78,000
Nero	8.5 (8–9)	2	24	985
Nipoue	15.2 (13–18)	4	60	11,920
San Pedro	10.5 (10–11)	2	32	3,310
Sassandra	25	1	76	75,000
Tabou	5	1	18	800

between pools within the same drainage area (see de Mérona 1981 for the Bandama River). These communities can display a high temporal stability in species composition. For instance, in a pool located in the Comoe River, 18 species occurred in at least seven of the nine samples collected between 1977 and 1979 (the period considered in this study; see below). This value has to be compared with the 19.1 species per sample average, which suggests that most of the populations constituting pool communities are permanent during this period. This relatively high spatiotemporal stability provides evidence that most of the fish species sampled are pool-dwelling species instead of transient species. Communities were studied as part of a monitoring program for rivers treated with insecticides during the onchocerciasis control program sponsored by the World Health Organization (Lévêque et al. 1988). Experimental fishing was carried out using sets of gill nets 25 m long and 2 m deep with various mesh sizes (15, 20, 25, 30, and 40 mm) during two consecutive nights (Lévêque et al. 1988). Results are expressed as catch per unit effort (CPUE), which is the number of fish caught in 100 m^2 of net per day. In the Bandama River, for which a great number of samples was available, it appeared that species richness per sample increased with CPUE, probably as a result of a passive sampling process. However, for CPUE greater than 200, species richness leveled off. Consequently, only samples having a CPUE higher than 200 have been included in the data analyzed to provide reliable estimates of local species richness in the 10 rivers studied. The gill net catches do not reflect the whole community since, given the selectivity of the method, some species are never caught. Given the standardization of the procedure, the species richness of different sites can nevertheless be compared. In order to avoid, as much as possible, long-term changes in species richness, only samples occurring between 1977 and 1979 were considered. Sampling can take place or be efficient only in pools that are more than 1 m deep, 20 m wide, and 500 m long, with no or low current velocity (less than 0.2 m/s). In addition to their relative homogeneity of size and current velocity, the habitats sampled displayed small variability in the

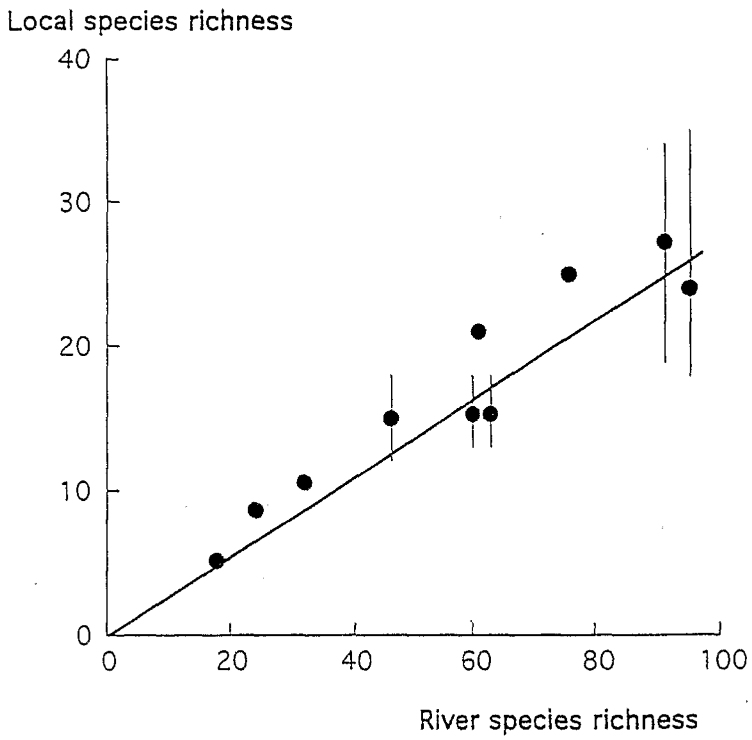

FIG. 1.—Relationship between local species richness and the number of fish species present in the catchment area. Mean local species richness (*points*) and range (*bars*) are figured for each river. The regression line is constrained to pass through the origin and fitted using the 47 samples. The best fit is obtained with the following relationship: local species richness = 0.269 × river species richness ($r = 0.970$). A second order does not contribute significantly to this equation when integrated ($P = .224$).

type of substrate: muddy with scattered rocks and rarely sandy (de Mérona 1981; D. Paugy, personal observation). For each locality we measured distance from source in order to include this variable in the analyses. Samples have been distributed between two categories: rainy season (sampling dates from July through December) and dry season (from January through June).

Analysis of the 47 samples retained (presented in table 1) demonstrates a strong relationship between local species richness that is not improved when a second-order term is integrated in the regression equation. This suggests a linear model is the best representation of the relationship (fig. 1). In a multiple regression model (table 2), season and distance to source have no significant effect on local species richness, and river species richness remains the only significant predictive variable. This result is concordant with the work of de Mérona (1981), in which no relationship between local species richness (either in pools or riffles) and distance from river mouth was observed. Conversely, the suggestion that there is seasonal variation in species richness (de Mérona 1981) is not verified. The absence of a relationship between year and local species richness suggests that

TABLE 2

RESULTS OF A GENERAL LINEAR MODEL EXPLAINING LOCAL SPECIES RICHNESS AS A FUNCTION OF LOG(CPUE), RIVER SPECIES RICHNESS, DISTANCE FROM SOURCE, SEASON (TWO CATEGORIES), AND YEAR (THREE CATEGORIES)

Source	df	*F* Ratio	*P*
Log(CPUE)	1	1.411	.241
River species richness	1	27.289	<.001
Distance from source	1	1.208	.278
Season	1	<.001	.985
Year	2	.513	.602

long-term changes observed in species richness in some localities (B. Hugueny, unpublished manuscript) do not affect our data over a 3-yr period. The absence of a relationship between local species richness and log(CPUE) demonstrates that we were successful in removing bias due to sampling effort. Our results strongly support a Type I relationship between local and regional richness. However, the action of an uncontrolled variable positively related to river species richness and local species richness can produce a similar pattern. It is commonly recognized that fish community structure in a river is mainly determined by its position along two environmental gradients: the upstream-downstream gradient and the riffle-pool gradient (Schlosser 1987). The effect of these two gradients on local species richness cannot explain our observed pattern because our samples are located at the end of the first gradient, and the position along the second one is controlled. During the onchocerciasis control program, detailed descriptions of river habitats were not made, so pools can differ between rivers in some habitats in an unknown fashion. However, considering the reduced range of variation imposed by the sampling criteria on habitat structure, some habitat variables are unlikely to have a strong effect on species richness. For instance, current speed, river width, and river depth are uncorrelated with local species richness in a set of 23 pools within the Konkoure River (Guinea, West Africa) for which a habitat description is available and that were sampled in the same way as Ivoirian pools (B. Hugueny, unpublished data). We have no reason to believe that this result is not applicable to Ivoirian rivers. Reanalysis of the data provided by Daget et al. (1973) gives more weight to this claim. Sampling was conducted by poisoning large pools ($n = 22$) of the Bandama River, and no relationship can be found between local species richness and volume sampled, current speed, depth, or substrate composition. Pool length (distance between upstream and downstream riffles) seems also to have no perceptible effect on species richness, if pools are large enough. In our data set from the Bandama River, mean species richness in some "small" pools (500–1,000 m long) is similar to the mean species richness observed in other pools (24 vs. 20 species, respectively). Variation in substrate composition can affect local species richness; it was observed in Guinean pools in which rock abundance in the riverbed is positively correlated with species richness. However, as seen before, no relationship between substrate composition and local species richness has been found in the analysis of data from the Bandama River. Moreover, we are unable to find any argument in favor of a correlation between this variable and river species richness (or catchment area), a required condition for the occurrence of a systematic bias. Moreover, although pool habitats have not been quantitatively described, no obvious systematic differences in substrate and current speed were observed between rivers during sampling (D. Paugy, personal observation).

In conclusion, many factors known to affect local species richness in rivers, which could have potentially biased our results, can be discarded considering the following arguments. First, the effects of some variables have been controlled during the study. This is the case for temporal variation and distance from source and its correlates (such as river width and depth). Second, given that variation in habitat structure is constrained within a limited range by the sampling scheme used in pools, the effects of some habitat variables are unlikely to be perceptible, as was demonstrated in two other studies. This is the case for river width, river depth, pool length, current speed, and, to a lesser extent, substrate composition. Finally, some variables are unlikely to be correlated with river species richness and to introduce a systematic bias in the analysis. This is the case for substrate, current speed, and pool length. These arguments lead us to conclude that the relationship observed between local and regional richness in our data set is real and not spurious, and it will now be discussed as such.

Studies of the species diversity of riverine fish communities have thus far been conducted assuming that community structure is determined mainly by the local structure of the habitat (see, e.g., Gorman and Karr 1978). The results reported here show the limits of an approach that does not take into account the factors involved at a higher integration level. The factors that affect the overall richness of a river determine in large part local community structure. As in most islands, surface area plays an important role. It is therefore necessary to find out what mechanisms are responsible for the species-area relationships observed among rivers and especially the contribution of population extinction processes related to area. These processes have been reported many times for island vertebrates but have not yet been analyzed for freshwater fish communities.

In a saturated community it is not possible to add a species unless it replaces (and eliminates) another (Ricklefs 1990). In such a community, local species richness is governed by processes that occur on a small spatial scale and do not require a hierarchical approach. Conversely, if local species richness increases linearly with the species richness of the regional pool of potential colonists (proportional sampling), then it can be concluded that communities are not saturated. Note that a curvilinear (Type II) relationship between local and regional richness does not imply that community saturation occurs, and some processes, such as pool exhaustion, can drive a nonsaturated community to display this pattern (Cornell and Lawton 1992). The positive and linear relationship between local species richness and regional species richness demonstrated here suggests that the communities studied are not locally saturated with species and are shaped by processes operating on a broader spatial scale, the most probable being recolonization from neighboring sites, which prevents long-term interspecific exclusion. The importance of these phenomena has been stressed in river systems because of the seasonal and interannual hydrological variability that disturbs communities, causing local population extinction or displacement or promoting species coexistence (Horwitz 1978; Grossman et al. 1982; Power et al. 1988; Resh et al. 1988). This is particularly true in intertropical rivers, which show high seasonal variation in flow regime. The importance of interdrainage immigration in shaping community structure, particularly the relationship between distance to colonization source and local species richness, has been emphasized in recent studies on riverine fish assemblages (Detenbeck et al. 1992; Osborne and Wiley 1992). As community structure on one scale is influenced by processes that operate on a larger scale, it can be assumed that nonsaturation goes hand in hand with community openness. In fish communities, openness can be favored by ontogenetic changes in habitat selection, migration for reproduction, and wandering individuals. Some of these processes are probably acting in the communities studied in this note. The young of species found at the adult stage in pools frequently inhabit riffles. Some examples are *Petrocephalus bovei, Brycinus imberi, Barbus waldroni, Chrysichthys maurus* and some *Tilapia* (sensu lato) species (de Mérona et al. 1977). For species having a short reproduction period, the complex length frequency distribution in a pool makes cohort analysis difficult and suggests a mixing of individuals from different origins (Lévêque et al. 1977). In Lake Chad, reproductive migrations or large-scale movements are undertaken by the following species, which also occur in Ivoirian rivers: *Alestes baremoze, Distichodus rostratus, Petrocephalus bane, Labeo senegalensis, Synodontis schall,* and *Mormyrus rume* (Benech and Quensière 1988).

The present study demonstrates that riverine fish communities may be unsaturated but contrasts with the only other study dealing with freshwater fishes (Tonn et al. 1990). In that case, the authors claimed that the community was saturated, but this conclusion was based on only two data points (small nordic lakes in America and Europe) and so is debatable. A compromise view is that the occurrence of unsaturated communities is more likely in habitats with high temporal variation such as rivers. Other studies suggest a dependency between regional and local richness in riverine fish communities (Smith and Miller 1986; Beecher et al. 1988) but do not provide data allowing the separation between Type I and Type II curves.

Knowledge of the degree of saturation of a community provides an important basis for understanding how the community reacts or will react to the introduction of new species. Some rivers around the world are subjected to a large number of biological introductions (Welcomme 1988), and it is important to analyze or forecast the consequences. The data analyzed here suggest that nonsaturation is locally possible in rivers. In other words, an increase in local species richness is expected after the number of species in a river has been increased by biological introductions, although some extinctions of native species are likely to occur. Such a situation has been described in some North American rivers, the coexistence between native and exotic species being apparently favored by spatial or temporal disturbances (Minckley and Meffe 1987). This does not mean that there is no risk in introducing new species but rather that the examination of this problem should be shifted from the local to the catchment scale and from short-term to long-term effects.

Finally, if our results are representative of riverine communities, we are faced with the obligation to understand which factors regulate species richness on the catchment scale, if we want to preserve and manage biodiversity in these insular habitats.

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