



THE UNIVERSITY OF CHICAGO PRESS JOURNALS

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Source: *The American Naturalist*, Vol. 108, No. 962 (Jul. - Aug., 1974), pp. 473-489

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <https://www.jstor.org/stable/2459679>

Accessed: 01-06-2020 14:20 UTC

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FISH SPECIES DIVERSITY IN LAKES

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For ecologists and evolutionary biologists interested in biogeographic patterns and the relationships among species in natural communities, islands and insular habitats (e.g., caves, mountaintops, and desert oases) provide interesting systems for analysis. The number of species of several taxa in some isolated habitats represents a dynamic equilibrium between contemporary rates of colonization and extinction (see MacArthur 1972). Diversity of these biotas can be accounted for with little or no reference to historical events. For certain other taxa, however, barriers between insular habitats prevent colonization except during periods when they are temporarily abolished and the “islands” are connected by bridges of suitable habitat (Brown 1971).

What determines the diversity (the number) of fish species in a lake or inland sea? The number and identity of taxa which have had opportunity to colonize a lake depend on unique, historical events: geological connections with other bodies of water inhabited by fishes and the composition of those faunas. Speciation of the colonizing taxa can also influence the number of species. Ultimately, diversity will be limited if the ability of the species to exist and coexist within a lake results in an equilibrium between the acquisition of species by colonization and speciation and loss by extinction. Our purpose here is to ask whether or not the number of fish species in a lake or sea conforms to the model of island biogeography proposed by MacArthur and Wilson (1967) and to assess the relative importance of certain environmental variables as determinants of the number of species present.

METHODS

Statistical analysis.—The results described below were derived by forward stepwise multiple regression analyses of the number of fish species on a series of independent variables according to the method outlined by Draper and Smith (1966). Similar to Hamilton, Barth, and Rubinoff (1964) we present arithmetic-to-arithmetic and logarithmic-to-logarithmic (log 10) analysis of X 's on Y as fitted by the computer. The study was carried out at the University of Michigan Computing Center utilizing the Michigan Interactive Data Analysis System (MIDAS). In this algorithm,

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variables are added to the regression in order of their partial correlation coefficients; after the selection of the most correlated X with Y , the variable with the highest partial correlation coefficient of those remaining is the next to be entered into the equation as long as its F statistic for its added contribution remains above a predetermined level of significance. When F falls below this value, computations are terminated. Variables are also deleted from the equation if, in the process of adding new Y 's, the significance of the F values for their added contributions falls below a preset level. In our analysis, levels of significance for both inclusion and deletion of variables were set at $\alpha = 1.0$, with the result that variables were added to the regression as long as the number of degrees of freedom was not exceeded.

In tables 1 and 2, r^2 is the coefficient of determination and was derived by squaring the correlation coefficient of each independent variable with the number of fish species. R^2 is the coefficient of multiple determination and indicates the cumulative proportion of variability in the number of fish species accounted for by the independent variables. We stress that the values of R^2 are not independent but are contingent upon the other variables which have been entered into the regression equation and their order of entry.

Data.—Values for the number of fish species, latitude, and surface area of the lakes are from a variety of sources (Appendix). The number of fish species is subject to several sources of error. It may be less than the actual number if collectors failed to obtain some which were present. This surely affects our analysis of the African lakes, as many of them are still poorly known (G. Fryer and P. H. Greenwood, pers. comm.). Species number may also be depressed if extinctions owing directly to human activity occurred before collections were made. For example, the draining of about 50,000 hectares of Lake Chapala, Mexico, between 1909 and 1912 (Goldman 1951) undoubtedly caused local extinctions. The number of species may be greater than the actual number if fishes have been introduced or if the censuses include transients washed in from streams and rivers. We adjusted species number to account for extinctions and introductions wherever possible. Finally, the criteria for recognizing fish species differ among ichthyologists, so that taxonomic treatments may have influenced the data. The objection that we have not rigorously defined a lacustrine species may also be raised. While it is true that there are species restricted to either lakes or streams,

TABLE 1
COMPARISON OF COEFFICIENTS OF DETERMINATIONS (r^2) AND COEFFICIENTS OF MULTIPLE DETERMINATION (R^2) OF TWO ENVIRONMENTAL FACTORS AFFECTING THE NUMBER OF FISH SPECIES IN 70 OF THE WORLD'S LAKES (SEE APPENDIX AND FOOTNOTES TO TABLE 2)

VARIABLE	LINEAR		LOGARITHMIC	
	r^2	R^2	r^2	R^2
Surface area1493+†	.1493+	.3050+	.3050+
Latitude0835—	.2476—	.0652—	.3400—

TABLE 2
COMPARISON OF COEFFICIENTS OF DETERMINATIONS (r^2) AND COEFFICIENTS OF MULTIPLE DETERMINATION (R^2) OF ENVIRONMENTAL FACTORS AFFECTING THE NUMBER OF FISH SPECIES IN 14 NORTH AMERICAN AND 14 AFRICAN LAKES (SEE LEGEND OF FIG. 2)*

LINEAR			LOGARITHMIC		
Variable	r^2	R^2	Variable	r^2	R^2
North America					
Mean annual rainfall5401+†	.54007+	Latitude6437—	.64370—
pH2832+	.73625+	Surface area2521+	.92570+
Altitude2574—	.91261—	Shoreline length .	.1672+	.95386—
Growing season ..	.4805+	.94447+	Altitude3130—	.96470—
Drainage area ..	.0055—	.96243+	Transparency0316—	.97883—
Mean depth0950+	.98069—	Shore develop- ment‡1138—	.98445+
Mean July temperature ..	.4936+	.98972—	Growing season ..	.5374+	.98660—
Total alkalinity .	.2358+	.99216+	pH1409+	.99771+
Latitude4864—	.99526+	Mean annual rainfall5690+	.99899—
Surface area3121+	.99691—	Total alkalinity .	.1452+	.99952—
Morphoedaphic index§0309—	.99905—	Maximum depth .	.0788+	.99996+
Shoreline length .	.1539+	1.00000+	Mean depth1670+	.99998—
Africa					
Maximum depth 6947+	.69474+	Surface area4887+	.48879+
Surface area5909+	.85428+	Conductivity1688—	.70838—
Latitude0051+	.90997+	Maximum depth 4644+	.78408+
Conductivity1992—	.94465—	pH0003+	.78746+
pH94828—	Mean annual rainfall0027+	.79462+
Mean annual rainfall0806+	.95050—	Latitude0017+	.79620+

* See Statistical Analysis section for computational procedures.

† The sign of the correlation coefficient and the partial regression coefficient for each independent variable is indicated to the right of the values for r^2 and R^2 , respectively.

‡ The length of the shoreline of a lake divided by the circumference of a circle with the same area.

§ The measured or estimated total dissolved solids (mg/liter) divided by mean depth (m).

|| See Data section; includes oxygenated depths only of Lakes Tanganyika, Malawi, and Kivu.

there are also many that can exist in both places by being sufficiently generalized or by seeking out similar habitats in both places (Corbet 1961). Some, such as certain salmonids, may be important members of the lake community but spawn in its tributaries. Because lacustrine species are derived from fluvial ancestors, we are dealing with an evolutionary continuum which we have not attempted to subdivide. With the exceptions noted, we have taken the censuses at face value even if they do tend to increase the number of species in the lakes. The patterns we describe below are clear enough to indicate that such imprecision may be tolerated as a first approximation.

The values for latitude are for the center of each lake and are calculated to the nearest decimal tenth of a degree. All lakes were treated as if they were in the same hemisphere. Surface areas varied slightly from reference to reference, representing either real changes in the lake levels or errors of

measurement. The areas of Lakes Chad and Balkhash, widely fluctuating, shallow bodies of water, are means of maximum and minimum values.

Morphometric, physiographic, chemical and physical parameters, most of the climatic data, and numbers of species for our samples of northern North American and African lakes are from Ryder (1972, tables 1-3), Fryer and Iles (1972, tables 1, 2), and Greenwood (1964, table 1). The first two references also contain maps showing the localities of the lakes. These data are subject to the sources of error discussed by those authors (in particular Ryder) or their sources and are not reproduced here; we have accepted them at face value with the exception of the maximum depths of Lakes Tanganyika, Malawi, and Kivu. These bodies of water are permanently stratified and, as a result, anaerobic below depths of about 200, 250, and 65 m, respectively (G. Fryer, pers. comm.; Damas 1937). As these values represent functional maximum depths, they have been substituted for the geological maxima of 1,470, 704, and 465 m. Stratification may also result in loss of oxygen in the deeper waters of Lake Victoria (Fryer and Iles 1972), but we disregard this transitory phenomenon.

All independent variables for African lakes were entered into the regression equation for those basins. For the North American lakes, two variables, total dissolved solids and conductivity, were not included in the analysis because of missing data. It is very doubtful, however, that these parameters are important determinants of fish species diversity in our sample, as the former ranges from 33 to 150 mg/liter and the latter from 40 to 596 micromhos. Of the remaining variables, three were not added to the regression because of the limiting number of degrees of freedom. These were, for the linear regression, maximum depth, shoreline development, and transparency. In the nonlinear regression, drainage area, morphoedaphic index, and mean July temperature were omitted.

Some variables were given as ranges and were averaged for our analysis: mean July temperature, mean annual rainfall and growing season (Ryder 1972), and conductivity and pH (Fryer and Iles 1972). Values for mean annual rainfall for African lakes were estimated from Jackson (1961) and should be considered rough approximations.

RESULTS

Lakes and seas of the world.—Nonlinear multiple regression of species numbers on area and latitude for a sample of 70 of the world's lakes and seas accounts for 34% of the variation in the dependent variable; 30.5% is explained by area and 3.5% by latitude. The linear model is less effective and accounts for only 24.8% of the variability (table 1). The slope of the species-area curve is low ($z = 0.15$, fig. 1), falling below that usually reported for islands ($z = 0.20-0.35$, MacArthur and Wilson 1967).

North American lakes.—Both linear and nonlinear multiple regression of species numbers against 12 independent variables accounts for essentially all the lacustrine variation (table 2) for 14 northern North American Lakes

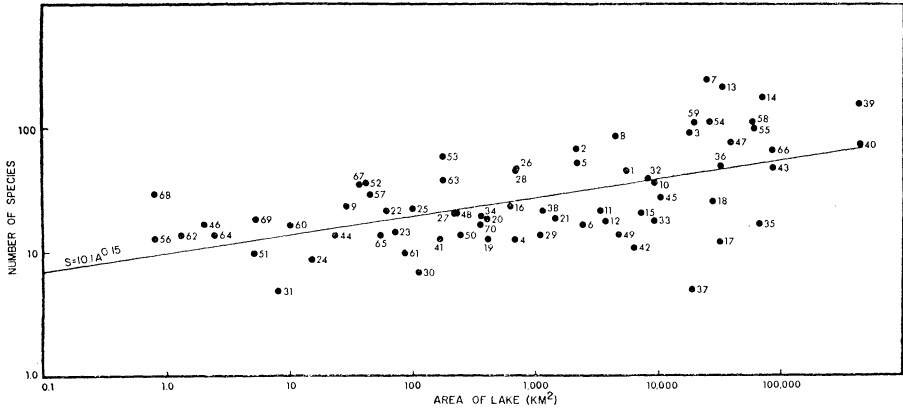


FIG. 1.—The relationship of area to number of fish species for 70 of the world's lakes and seas. The basins are numbered the same as in the Appendix.

(fig. 2). In the former model, mean annual rainfall, pH , and altitude account for 91% while latitude and surface area account for about 92% of the variability in species numbers in the analysis of transformed data. The remaining variables by themselves are inconsequential as determinants of diversity. The slope of the species-area curve ($z = 0.16$, fig. 2) is almost as low as it is for the sample of worldwide lakes.

African lakes.—Linear and nonlinear multiple regression of the number of species against six independent variables for 14 African lakes (fig. 2) accounts for about 95% and 80% of the variation, respectively (table 2). Maximum depth and surface area are the most important factors affecting the species numbers in the linear analysis and together account for about 85% of the variation. Surface area and conductivity explain about 71% in the nonlinear analysis. The slope of the species-area curve ($z = 0.35$, fig. 2) falls in the upper range of the values for islands (MacArthur and Wilson 1967).

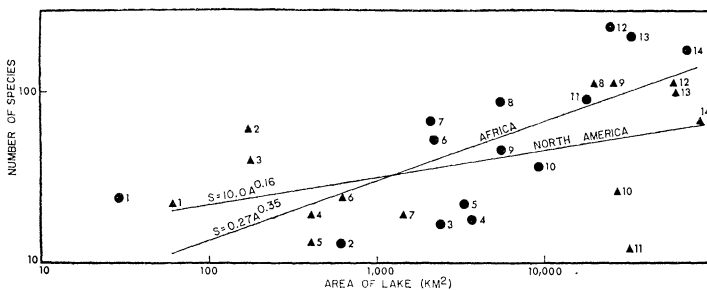


FIG. 2.—Area-species curves for 14 northern North American and 14 African lakes. North America (triangles): Opeongo, 1; Cayuga, 2; Seneca, 3; Kootenay, 4; Keller, 5; Big Trout, 6; La Ronge, 7; Ontario, 8; Erie, 9; Great Slave, 10; Great Bear, 11; Michigan, 12; Huron, 13; Superior, 14. Africa (circles): Nabugabo, 1; Chilwa, 2; Kivu, 3; Tana, 4; Rukwa, 5; Edward, 6; Bangweulu, 7; Mweru, 8; Albert, 9; Rudolf, 10; Chad, 11; Malawi, 12; Tanganyika, 13; Victoria, 14.

DISCUSSION

Lakes are insular habitats. It is tempting to assume that they acquire and lose species in the same manner as oceanic islands or some isolated habitats—so that species diversity represents an equilibrium between rates of contemporary colonization and extinction (MacArthur and Wilson 1967; Simberloff and Wilson 1969; Diamond 1969; Vuilleumier 1970; Culver 1970). However, fishes cannot disperse across terrestrial barriers. They colonize lakes only when suitable bridges of aquatic habitat connect the lakes with other bodies of water containing fishes. Lakes normally are colonized from rivers and streams, but colonists conceivably could immigrate through direct connections with another lake or with the ocean. For most lakes, the rate of contemporary colonization is zero or nearly so. Many lie in interior basins where they are completely surrounded by terrestrial barriers. Others are drained by river systems and must already have been colonized by all of the available fluvial fishes capable of exploiting lacustrine habitats, so there is no significant immigration at present. Fish species diversity in lakes should not represent an equilibrium between colonization and extinction in the sense of MacArthur and Wilson.

The diversity of fishes in lakes depends on the effects of two kinds of events. First, there must be a colonization episode in which the lake is connected by a water bridge to a source of fish species. This connection is normally a river or a stream which acts as a filter, permitting only selected taxa to immigrate into the lake. Lacustrine and marine species must be able to pass through the fluvial habitats, and fluvial species must at least be able to spend most of their lives in lacustrine habitats (even if they reproduce in tributary streams) if they are to colonize the lake. The periods of colonization are likely to be brief and to follow immediately the geological events which establish aquatic connections between a lake and other waters containing fishes. After the colonization episode has provided the original fauna, diversity can be altered by interactions among species, and between species and the lacustrine environment. Extinctions owing to small population size, and often compounded by the effects of competition, predation, or changes in the aquatic habitat, may reduce the diversity of the fauna. However, if there is sufficient time and environmental diversity, additional colonization, intralacustrine speciation, or speciation in satellite lakes (Greenwood 1964) may increase species diversity.

The unique and important role of history in biogeography probably is nowhere better demonstrated than in the distribution of freshwater fishes. This has been repeatedly demonstrated in faunal studies and by the students of particular groups of fishes (e.g., Darlington 1957; Smith 1966; Pflieger 1971; Jenkins, Lachner, and Schwartz 1972). Ancient drainage patterns can often be worked out on the basis of taxonomic relationships of fishes. However, much variation in species diversity between islands or habitat islands can be accounted for on the basis of ecological variables such as island size, climate, and habitat diversity. Are there also general patterns of

lacustrine fish species diversity that can be explained in terms of ecological characteristics of lakes? To what extent can we detect such overall patterns despite the pervasive influence of history on freshwater fish distribution?

We have attempted to answer these questions using multiple stepwise regression to analyze the relationship between the number of fish species and two environmental variables for 70 lakes of the world. We also performed more detailed analyses on two more localized (North American and African) groups of lakes for which additional kinds of environmental data were available. Multiple regression is an a posteriori method, and its results should be interpreted with caution, particularly in inferring causal relationships. In general, our results provide interesting preliminary information on the factors influencing lacustrine fish species diversity.

If we first consider all 70 lakes of the world for which we have data, surface area accounts for about 30% of the variability in fish species diversity. This figure is quite large despite the very wide geographic range and the differences in age, geographic isolation, ecology, and fish taxa among the lakes. However, extremes of some of these factors do account for extreme deviations from the regression line in figure 1. For example, lakes in northernmost North America and Asia such as Great Bear (17; numbers refer to fig. 1 and Appendix) and Taimyr (49) are cold and unproductive. The Aral Sea (35) and Lake Balkhash (37) lie in interior basins of Asia; the latter is partly saline and extremely shallow, while the former has had a complex history which apparently included periods of high salinity (Zenkevitch 1963). Issyk Kul (42) and Lake Titicaca (33) lie in isolated interior basins at high altitudes. Lakes Chapala (29), Pátzcuaro (30), and Zirahuén (31) lie at fairly high elevations on the faunistically depauperate Mesa Central of Mexico. All the above lakes contain relatively few fish species for their size. In contrast, lakes of relatively high diversity include small temperate lakes such as Walnut (68) and Waccamaw (67), which are more productive and lie in faunistically richer areas. The largest number of lacustrine fishes are found in the lakes of tropical Africa such as Malawi (7), Tanganyika (13), and Victoria (14).

It is interesting that latitude accounts for only a small fraction (3.5%) of the total variability in fish species diversity when viewed on a worldwide scale. This may be due in part to the fact that the aquatic environment tends to be climatically buffered by the physical properties of water. Its major cause, however, probably lies in the many physical barriers, some of which were mentioned above, which preclude the easy movement of fishes from drainage to drainage. We would expect a much greater effect of latitude on the diversity of terrestrial organisms on islands or habitat islands.

The species-area relationship is logarithmic and can be described by the exponential equation $S = CA^z$, where S and A are number of species and area, respectively, and C and z are fitted constants. For the lakes of the world, the species-area curve has a low slope ($z = 0.15$) compared with that for other organisms inhabiting islands or isolated habitats (MacArthur and Wilson 1967; Vuilleumier 1970; Brown 1971). This is interesting because

normally isolated sample areas such as islands are thought of as having steeper species-area curves than nonisolated sample areas within continuous habitats (Preston 1962a, 1962b). Fishes in lakes are obviously more isolated than many terrestrial organisms on islands or habitat islands. We suggest two explanations, one ecological and the other historical, for the low slope of the species-area curve. First, lakes may be more homogeneous than isolated terrestrial habitats, so that the diversity of habitats and resources increases more slowly with area in lakes than it does on land. This would obviously affect the ability of lakes to support coexisting fish species. Alternatively, historical events may tend to prevent large lakes from acquiring as many species as they can support ecologically. The filtering nature of the fluvial connections coupled with the slow biogeographic movement of fishes results in a relatively small number of taxa available to colonize a lake; immigrant species may fill small lakes to capacity but not large ones. As a result, speciation is required to fill larger basins, and there simply may not have been sufficient time since the initial colonization episode to reach an equilibrium between speciation and extinction. These alternative explanations are reexamined below, when we discuss diversity in the African lakes.

The lakes in the northern United States and Canada represent a geographically localized subsample of temperate and subarctic lakes for which we were able to obtain data on water quality and climate. The analysis indicates that the number of fish species in these lakes is related to surface area, latitude, and climatic variables correlated with latitude (mean July temperature, growing season, and mean annual rainfall). These variables account for about 90% of the variability in species diversity when log-transformed data are used. When the linear model is used, there are statistically significant correlations (at the .05 level) between species diversity and both pH and altitude. It is unlikely that these correlations are biologically significant because of the small absolute variation in the independent variables. The slope of the species-area curve ($z = 0.16$) is almost the same as for the total sample of lakes throughout the world. Two phenomena probably account for the strong correlation between latitude (or related climatic variables) and species diversity. First, there is probably a direct effect of climate on species diversity of fishes in aquatic habitats just as there is for terrestrial organisms. Compared with the more southern lakes, the northern ones tend to be cold and unproductive, and the growth and reproduction of aquatic organisms are restricted to the midsummer months. Fish must have specialized adaptations in order to tolerate such climatic extremes. For the reasons given below, there has probably not been sufficient time for many taxa to acquire such adaptations. Second, the historical pattern of colonization of these lakes is related to latitude; the more northern lakes have been formed most recently by the retreat of the Wisconsin ice sheet. A few species apparently have colonized these lakes by moving eastward along the margins of retreating glaciers from unglaciated Alaska. However, the major source of colonists has been the diverse faunas of the rivers of the Mississippi Basin and the Atlantic Coast (McPhail and Lindsey 1970). Thus, latitude

tends to be correlated with distance from the source of colonists and the severity of barriers posed by the filter bridges.

The pattern of fish species diversity in the 14 lakes of tropical central and east Africa is very different from that in the North American lakes. In the linear model, maximum depth and surface area account for about 85% of the variability in species numbers, with latitude explaining an additional 5%. In the nonlinear model, surface area and conductivity account for about 71% of the variability, with maximum depth explaining an additional 8%. Of particular interest is the relatively steep slope ($z = 0.35$) of the species-area curve. This figure is similar to the highest values obtained for terrestrial organisms inhabiting oceanic islands (MacArthur and Wilson 1967), and it approximates the value ($z = 0.43$) obtained by Brown (1971) for the mammals on isolated mountaintops where there is no contemporary colonization. The steep slope for the African lakes contrasts with the much shallower slopes ($z = 0.15$ – 0.16) for the lakes of the world and the North American lakes. Compared with many other lacustrine systems, some of the African lakes are relatively old and the center of a great deal of rapid speciation, particularly in the family Cichlidae (Greenwood 1964; Fryer and Iles 1972). They are also situated in the center of a rich faunal area. Apparently time and other conditions (such as the formation of satellite lakes, the heterogeneous distribution of substrate types, and the biological characteristics of cichlids which appear to preadapt them for rapid speciation) have been adequate for speciation to fill the larger of these lakes and at least approach an equilibrium with extinction.

This suggests that the low species-area curves for other lacustrine systems are the result of a small number of initial colonists and inadequate time and opportunities for speciation to fill the large lakes to equilibria. This is supported by the fact that only in the African lakes does depth contribute significantly to determining the number of fish species. The fluvial species which normally colonize lakes initially tend to occupy habitats such as shallow waters, inlets of tributary streams, and surge zones along the shore which are similar to those they previously exploited in the streams (Corbet 1961). One would expect that it would require a period of speciation and adaptive radiation to produce fishes of sufficient ecological diversity to exploit all habitats and resources of large lakes potentially suitable for fishes. Apparently when this stage is reached the diversity of habitats is related to depth as well as surface area.

Conductivity, an estimation of the degree of mineralization of water, varies in the African lakes from 25–26 micromhos for Lake Nabugabo to 1,630–12,000 micromhos for Lake Chilwa. The lakes also vary in their concentrations of individual anions; Lake Nabugabo is very low in Ca, Lakes Rukwa and Rudolf are rich in Na, and Lake Kivu is rich in Mg. These data suggest that osmoregulatory or other physiological difficulties may have prevented the colonization of certain lakes or caused extinctions as minerals slowly accumulated in the basins with time. However, bear in mind that the volcanic and tectonic activity which resulted directly or indirectly in the

increased mineral content of these waters also created geographic barriers to fish movements. Until these factors can be separated, the significance of physiology as a determinant of fish species diversity in this region will remain unclear.

Finally, we emphasize that our subsamples of African and North American lakes were determined by the availability of physical and limnological data. Had many more lakes from both regions been included, we predict that both curves would have shown pronounced toes to the left of their point of intersection. This is the result of there being a relatively greater number of fish species available in both regions to colonize small lakes from streams and rivers. Further, the very high numbers of species present in the smaller North American lakes (fig. 1) suggest that the smaller lakes of the temperate and the tropics will show comparable levels of fish species diversity. To the right of the intersection the tropical curve, for reasons discussed above, will rise much more steeply as space becomes less of a limiting factor. This interpretation is consistent with the findings of Patrick (1966) for tropical and temperate rivers.

It is becoming apparent that there are several distinct patterns of species diversity for organisms distributed on islands or insular habitats. Since all islands lose species by the same process (extinction), the various patterns are determined by how species are acquired. We distinguish four patterns of insular species diversity as follows:

1. Many insular biotas represent equilibria between colonization and extinction (MacArthur and Wilson 1967; Diamond 1969; Simberloff and Wilson 1969; Culver 1970; Vuilleumier 1970). This occurs whenever there is a significant and continual immigration of potential colonists. Colonization-extinction equilibria tend to result in species-area curves with z values in the range 0.20–0.35 (MacArthur and Wilson 1967). The remaining patterns occur when colonization is not continual but confined to periods when the islands were connected by bridges of suitable habitat to an area containing suitable colonists.
2. Some biotas should represent equilibria between speciation and extinction, provided that the area of the island in question is large enough to allow speciation to occur. This takes place when habitat bridges admitted a relatively small number of colonists sufficiently long ago for speciation to reach an equilibrium with extinction. In this case the slope of the species-area curve should be steeper than for colonization-extinction equilibrium biotas because of the slow rate of speciation (relative to colonization) and the high rate of extinction on small islands. We expect fish faunas of the tropical African lakes to be closer to such an equilibrium than any of the other lacustrine assemblages we have studied because of the great amount of speciation which has occurred within the Cichlidae. On the other hand, the smaller lakes of our sample are probably too small to allow extensive multiplication of species; their faunas are largely the result of colonization. It is encouraging, however, that the z value for the African faunas is 0.35, at the upper extreme of the range for colonization-extinction equilibrium

biotas. The two preceding patterns represent equilibrial situations on different time scales. The two remaining patterns represent nonequibrilial situations because the habitat bridges have been relatively recent.

3. Islands have less than equilibrilial numbers of species when small numbers of colonizers crossed the habitat bridges too recently for significant subsequent speciation. In this case, large islands tend to be particularly impoverished and the slope of the species-area curve (at least initially) will be less than that for a colonization-extinction equilibrilial biota. The fish faunas of many large, geologically recent lakes apparently represent such a subequibrilial pattern; for samples including such lakes we obtain z values in the range 0.15–0.16.

4. Islands have more than equilibrilial numbers of species when a large number of species (often an entire “mainland” biota) crossed the habitat bridges too recently for subsequent extinctions to reduce the biotas to equilibrilium. The absence of colonization and the high rate of extinction on small islands combine to produce species-area curves with steeper slopes than for biotas characterized by colonization-extinction equilibrilial. Brown (1971) showed that the boreal mammal fauna of isolated mountains in the western United States represented such a supraequibrilial fauna; he obtained a species-area curve with a z value of 0.43.

SUMMARY

Stepwise multiple regression was used to obtain preliminary insights into the environmental parameters which influence the number of fish species occurring in lakes. Results are summarized as follows:

1. For a sample of 70 lakes and inland seas from throughout the world, surface area and latitude account for about one-third of the variability in fish species diversity.

2. For a subsample of 14 North American lakes, latitude and surface area account for about 90% of the variability in species numbers. The large effect of latitude can be explained in terms of climatic severity and isolation from sources of colonization.

3. For a subsample of 14 African lakes, surface area, depth, and conductivity were primary variables affecting species diversity.

4. For 70 lakes of the world and 14 North American lakes, the slope of the species-area curve was low ($z = 0.15$ – 0.16). Apparently this reflects the fact that, whereas a relatively large number of species are available to colonize small lakes, larger ones are impoverished. Most of the latter are recent enough that there has not been time for endemic speciation to reach an equilibrilium with extinction. We expect the large lakes of tropical Africa to be the closest to such an equilibrilium, and it is encouraging that the slope of the species-area curve for the sample including these bodies of water is quite steep ($z = 0.35$).

5. On the basis of our data and analyses of species distribution in other insular habitats, four patterns of species diversity are distinguished.

ACKNOWLEDGMENTS

Numerous people aided this study with criticism, discussion, suggestions, and in some cases unpublished data. The following were particularly helpful: J. Addicot, R. M. Bailey, W. Y. Brockelman, W. R. Bussing, F. P. Cichocki, G. Fryer, D. M. Gillespie, W. A. Gosline, P. H. Greenwood, J. Kethley, K. Kurawaka, J. D. McPhail, R. R. Miller, N. C. Negus, R. A. Ryder, W. B. Scott, D. J. Stewart, and S. H. Smith. We especially thank H. Wilbur for help in a preliminary analysis of the data. Computer time was made possible by funds made available to R. R. Miller through the University of Michigan Museum of Zoology for that purpose. Finally we thank G. Fryer and T. D. Iles; the original publisher, Oliver and Boyd; and the American publisher, T. F. H. Publications, for permission to analyze data appearing in their book, *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution*.

APPENDIX

NUMBER OF FISH SPECIES, SURFACE AREA, AND LATITUDE FOR 70 LAKES AND SEAS
OF THE WORLD

	Number of Species	Surface Area (km ²)	Latitude
Africa:			
1. Albert	46	5,346.0	1.7° N
2. Bangweulu	68	2,072.0	11.1° S
3. Chad	93	17,500.0	13.0° N
4. Chilwa	13	673.0	15.3° S
5. Edward	53	2,150.0	0.5° S
6. Kivu	17	2,370.0	2.0° S
7. Malawi	245	28,490.0	12.0° S
8. Mweru	88	4,413.0	9.0° S
9. Nabugabo	24	28.5	0.6° S
10. Rudolf	37	9,065.0	3.5° N
11. Rukwa	22	3,302.0	8.0° S
12. Tana	18	3,626.0	12.0° N
13. Tanganyika	214	32,893.0	6.0° S
14. Victoria	177	69,484.0	1.0° S
Canada:			
15. Athabasca	21	7,154.0	59.2° N
16. Big Trout (Ontario)	24	616.0	53.8° N
17. Great Bear	12	31,153.0	66.0° N
18. Great Slave	26	27,195.0	61.4° N
19. Keller	13	406.0	64.0° N
20. Kootenay	19	399.0	49.5° N
21. La Ronge	19	1,425.0	55.0° N
22. Opeongo	22	60.0	45.7° N
Great Britain:			
23. Loch Lomond	15	71.0	56.1° N
24. Windermere	9	15.0	54.3° N
Guatemala:			
25. Petén	23	98.0	17.0° N
26. Yzabal	48	684.0	15.5° N
Italy:			
27. Maggiore	21	212.0	46.0° N
Japan:			
28. Biwa	46	676.0	35.2° N
Mexico:			
29. Chapala	14	1,080.0	20.2° N
30. Pátzcuaro	7	111.0	19.6° N
31. Zirahuén	5	8.0	19.4° N
Nicaragua-Costa Rica:			
32. Nicaragua	40	8,264.0	11.5° N
Peru-Bolivia:			
33. Titicaca	18	9,065.0	16.0° S
Philippine Islands:			
34. Lanao	20	357.0	7.9° N
Soviet Union:			
35. Aral Sea	17	64,500.0	45.0° N
36. Baikal	50	31,500.0	54.0° N
37. Balkhash	5	18,500.0	46.0° N
38. Beloe (Vologda region)	22	1,125.0	60.2° N
39. Black Sea	156	423,488.0	43.0° N
40. Caspian Sea	74	436,000.0	42.0° N
41. Gusinoe	13	165.0	51.2° N
42. Issyk Kul	11	6,206.0	42.0° N

APPENDIX (*Continued*)

	Number of Species	Surface Area (km ²)	Latitude
43. Ladoga	48	18,400.0	61.0° N
44. Leprindo	14	24.0	56.5° N
45. Onega	28	10,340.0	61.5° N
46. Pestovo	17	2.0	58.3° N
47. Sea of Azov	17	38,000.0	46.0° N
48. Seliger	21	221.0	57.2° N
49. Taimyr	13	4,650.0	74.5° N
50. Teletskoe	14	231.0	51.6° N
United States:			
51. Black (North Carolina)	10	5.2	34.7° N
52. Canandaigua	37	41.0	42.8° N
53. Cayuga	60	171.0	42.7° N
54. Erie	113	25,719.0	42.2° N
55. Huron	99	59,596.0	44.5° N
56. Jones (North Carolina)	13	0.8	34.7° N
57. Keuka	30	44.0	42.5° N
58. Michigan	114	58,016.0	44.0° N
59. Ontario	112	19,477.0	43.5° N
60. Otisco	17	10.0	42.8° N
61. Owasco	10	85.0	42.8° N
62. Salters (North Carolina)	14	1.3	34.7° N
63. Seneca	39	174.0	42.6° N
64. Singletary (North Carolina) .	14	2.6	34.6° N
65. Skaneateles	14	54.0	42.8° N
66. Superior	67	82,414.0	47.5° N
67. Waccamaw	36	36.0	34.3° N
68. Walnut (Michigan)	30	0.8	42.6° N
69. White (North Carolina)	19	5.2	34.6° N
Yugoslavia-Romania:			
70. Ohrid	17	347.0	41.0° N

NOTE.—Data in this Appendix are from the following sources. Africa: United States Board on Geographic Names (1955*a*); Greenwood (1964); Fryer and Iles (1972). Canada: Canadian Board of Geographic Names (1953, 1958); Canadian Permanent Committee of Geographic Names (1969); Department of Mines and Technical Surveys, Geographical Branch (1962); McPhail and Lindsey (1970); Ryder (1972). Great Britain: Le Cren, Kipling, and McCormack (1972); Maitland (1972). Guatemala: United States Army Map Service (1940*a*, 1940*b*; surface areas by planimetry); R. R. Miller (personal communication). Italy: United States Board on Geographic Names (1956*b*); Grimaldi (1972). Japan: United States Board on Geographic Names (1955*b*); Horie (1969); K. Kurawaka (personal communication). Mexico: De Buen (1943, 1944); United States Board on Geographic Names (1956*a*); C. D. Barbour (unpublished). Nicaragua-Costa Rica: United States Board on Geographic Names (1956*c*); W. R. Bussing (personal communication). Peru-Bolivia: Eigenmann and Allen (1942); Tehernavin (1944); Brooks (1950). Philippine Islands: Myers (1960); Frey (1969). Soviet Union: Kozhov (1963); Zenkevitch (1963); Zhadin and Gerd (1963); United States Board on Geographic Names (1970). United States: Hankinson (1908); Greeley (1927); Frey (1949); Louder (1962); Ryder (1972). Yugoslavia-Romania: Stankovic (1960). The primary source for surface areas was Gresswell and Huxley (1965). Many of the latitudes were calculated from Bartholomew (1955-1959) or appropriate topographic maps.

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