Environmental Biology of Fishes **65:** 327–339, 2002.

An analysis of fish species richness in natural lakes

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Received 14 February 2001 Accepted 17 December 2001

Key words: biological diversity conservation, empirical models, fish assemblages, fish biodiversity, inland waters, species-area relationships, temperate lakes, tropical lakes

Synopsis

There is a growing recognition of the need to conserve biodiversity that has been conceptualised in the Convention of Biological Diversity. Maintenance of fish species richness is particularly important, because habitat degradation in inland waters continues to accelerate on a global scale. Here we develop empirical models for predicting fish species richness in natural lakes in various geographical regions of the world. In tropical lakes where fish biodiversity is richer than in temperate lakes, fish species richness can be predicted by a few variables such as lake area and altitude. Low fish species richness in most temperate lakes might be due to the effect of glaciation on colonisation and speciation of fishes. In US, Canadian and northern European lakes, lake acidification is one of the important factors influencing fish species richness. Although limnological characteristics influence fish species richness in temperate lakes, lake area and altitude have greater predictive power. This is in contrast to fish species richness in rivers, which can be reliably predicted by basin area. In the power curves, which describe the relationship between fish species richness and habitat size in lakes and rivers, the exponent is always greater in tropical regions than in temperate regions. Because fish biodiversity is greater in the tropics threats to fish biodiversity through habitat degradation are greater than those in temperate inland waters.

Introduction

The growing recognition of biodiversity conservation has led to the Convention of Biological Diversity (CBD) in 1993 (UNEP 1995). According to the CBD information base [http://www.biodiv.org], 178 countries and European Union were parties to the CBD as of November 2000. The general objectives of the CBD are the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilisation of genetic resources. Conservation of biodiversity implies knowledge of the number and distribution of the flora and fauna of any particular area. Because of the complexity of living organisms and the number of species, many of which have yet to be described, it is rarely possible to count individual species in a particular habitat. There is therefore, a need for generalised models for biological diversity assessment, which can easily be utilised as reliable predictors of number of species on a regional basis. Such generalised models for biological diversity assessment are particularly useful because of the logistical and financial difficulties involved in comprehensive surveys.

As habitat degradation continues to accelerate on a global scale, maintenance of species richness has become a central issue of conservation biology. This is particularly the case with the fish fauna of inland waters. There is a great diversity in the form and function in inland aquatic systems, presenting a wide range of habitats for fish. Unlike rivers and flood plains, natural lakes have relatively uniform habitats in a given area

(Fernando & Holčík 1991). As environments change, the species composition of fish communities is reported to change (Cowx 1994). From the conservation point of view, studies of fish populations which focus on the static relationships between fish and their habitats are of particular importance because of their value in quantifying the effects of habitat supply limits, that by some means, control the size and dynamics of fish populations.

Environmental changes are either due to natural causes or human activity. At present, most lakes and rivers in the world are used by people for multiple purposes such as waste disposal, industrial processes, fisheries, recreation, etc. Thomas (1994) identified habitat alteration and destruction as the major cause of most extinctions of freshwater fishes. Fish communities are different in individual freshwater lake systems, hence site-specific management is important in fishery biology and fish biodiversity conservation. Because of this the abundance and community composition of freshwater fishes have long been subjects of interest in fishery ecology (Tonn et al. 1983, Marshall & Ryan 1987, Evans et al. 1987).

Most available data from inland waters on almost all aspects ranging from morphometric and edaphic characteristics to biological characteristics such as structure of biotic communities are poor in quality and quantity. Simple models to describe inland fish biodiversity are among the basic tools in the conservation and management of biological diversity of inland water bodies. This is of particular importance because inland fish biodiversity is one of the biological resources most vulnerable to environmental changes including those caused by mankind.

The number of species present or species richness is one way of characterising a community, although it ignores the numerical structure of communities (Begon et al. 1996). However species richness is valuable in describing and comparing communities, and can serve as a baseline for measuring future changes in community structure to assess the success of conservation and management strategies. The present paper develops empirical models for predicting fish species richness in natural lakes in various geographical regions of the world.

Material and methods

The data used in the present study were gleaned from various publications, through personal communications with researchers, from literature survey and from databases maintained by one of us (R.L.W.) and by MRAG Ltd., London. Summary of the types of data used to analyse species richness in lakes and their sources are given in Table 1. The complete data set used in this analysis may be obtained from the authors.

As species richness is bound to be problematic in characterising a community for various practical reasons, such as presence of undescribed species and inadequacy of sampling (Begon et al. 1996), care was taken to minimise such effects. For example, it is likely that underestimation of species richness occurs as a result of extinctions during the recent past, and as a result of inadequate sampling efforts. On the other hand, as evident from the FAO[1] database on the introductions of aquatic species (DIAS), intercontinental fish introductions have taken place in an extensive scale. The fish species richness in inland waters may be overestimated if some species have been recently introduced into lakes and rivers. Extinction of endemic fish species may also be possible due to the introduction of exotic species, as has happened in Lake Victoria (East Africa) following introduction of *Lates niloticus* (Coulter et al. 1986, Moreau 1995). Effects of introduced species on native fish fauna are however site-specific. Whittier & Kincaid (1999) have indicated that it was not immediately clear that species introductions into lakes of the north-eastern USA have had a large effect on native species richness in general. Care was taken as far as possible, to minimise errors arising from recent introductions in selecting data for the present analysis. The available data from Africa (summarised by Vanden Bossche & Bernacsek[2] and backed by an extensive scientific literature) is known to be better and more reliable than in other tropical regions because there has been an accumulation of data on various aspects of ecology and fisheries of inland waters through internationally funded projects in the continent. In situations where data are available from various sources such as sampling in

[1] FAO. 1998. Database on the introductions of aquatic species (DIAS). Accessible via, http://www.fao.org/waicent/faoinfo/fishery/statist/ fisoft/dias/index.htm.

[2] Vanden Bossche, J.-P. & G.M. Bernacsek, 1990a. Source book for the inland fishery resources of Africa, Vol. 1. CIFA Tech. Pap. 18/1. 411 pp.
Vanden Bossche, J.-P. & G.M. Bernacsek. 1990b. Source book for the inland fishery resources of Africa, Vol. 2. CIFA Tech.l Pap. 18/2. 240 pp.
Vanden Bossche, J.-P. & G.M. Bernacsek. 1991. Source book for the inland fishery resources of Africa, Vol. 3. CIFA Tech. Pap. 18/3. 219 pp.

Table 1. Summary of types of data on species richness in natural lakes used in the present analysis and their sources.

Location of lakes (latitude range)	Number of lakes	Area of lakes (range in km^2)	Fish species richness (range)	Source of data
USA and Canada enskip (34-66N)	315	0.0062-82 367	1-114	Barbour & Brown 1974, Harvey 1975, Rahel 1986, Pierce et al. 1994, Randall et al. 1995, Kelso & Minns 1996, Marshall 1996, EMAP data*
Central America (11-20N)	6	8-8264	5–48	Barbour & Brown 1974
South America Peru/Bolivia (16S)	1	9065	18	Barbour & Brown 1974
Argentina (24.12-54.65S)	67	0.0009-8.16	1–9	Quirós 1988, ARLARE data**
Africa (13.5N-19S)	30	30-68 800	3–245	Vanden Bossche and Bernacsek 1990a, 1990b, 1991
Europe & Asia (temperate region) (24.6-74.5N)	42	1.8-436 000	3–156	Zhadin & Gerd 1961, Barbour & Brown 1974, Maitland et al. 1981, Giles 1994
Tropical Asia (5-17.7N)	13	2.06-900	2–29	Barbour & Brown 1974, Moreau & De Silva 1991

*EMAP data – Database of the Environmental Monitoring and Assessment Programme of the U.S. Environmental Protection Agency (T.R. Whittier personal communication); also accessible via EMAP website, http://www.epa.gov/emap/html/dataI/surfwatr/data/nalakes/

**ARLARE data – Argentinean lake and reservoir database collected from 1984 to 1987 (R. Quirós personal communication)

specific projects, and information accumulated over a long period in various fisheries and environmental authorities as is the case of North American great lakes (Kelso & Minns 1996), the highest value of species richness was used. It is known that in many lakes, fish species in the littoral zone makes up the bulk of the total fish community (Werner et al. 1977, Pierce et al. 1994). Data used from the lakes in Southern Quebec, Canada (Pierce et al. 1994) consist of species richness in the littoral zones of the lakes only although it is doubtful that many species were missed in this way.

A database on world lakes has been developed by the International Lake Environment Committee Foundation (ILEC) in cooperation with the United Nations Environment Programme (UNEP) and Environment Agency of Japan. This is accessible via the worldwide web, http://www.ilec.or.jp. Data on geographical location, morphometric features and edaphic characteristics of most lakes were obtained from this website.

The relationships between fish species richness in natural lakes and various habitat variables were determined using linear, power, logarithmic and exponential regression techniques. Where necessary, second order polynomial regression techniques were also used to determine the most significant and biologically reasonable relationship between species richness and the independent variable. The independent variables, which are themselves not directly related, were also related to fish species richness using multiple regression analysis. The independent variables used in the present analysis were lake area, altitude, latitude, mean depth, Secchi disc depth, pH. In South American temperate lakes (Argentinean lakes), limnological characteristics such as conductivity, Chlorophyll-a and total nitrogen content were also used as independent variables. The coefficient of determination (R^2) was used to examine the degree to which the independent variable explained variations in fish species richness. In all relationships, the two-tail level of significance for rejection of null hypothesis was $\alpha(2) = 0.05$. All factors used as independent variables were however, not available for all lakes. It is thought that the effect of absence of data from all lakes on the models derived from the multiple regression analysis is negligible because databases with wide ranges of variables were used to derive models.

The morphometric, geographical and limnological characteristics of the lakes in a given geographical region, which appear to have at least marginal influences on fish species richness in lakes, were used to separate water bodies using Principal Component

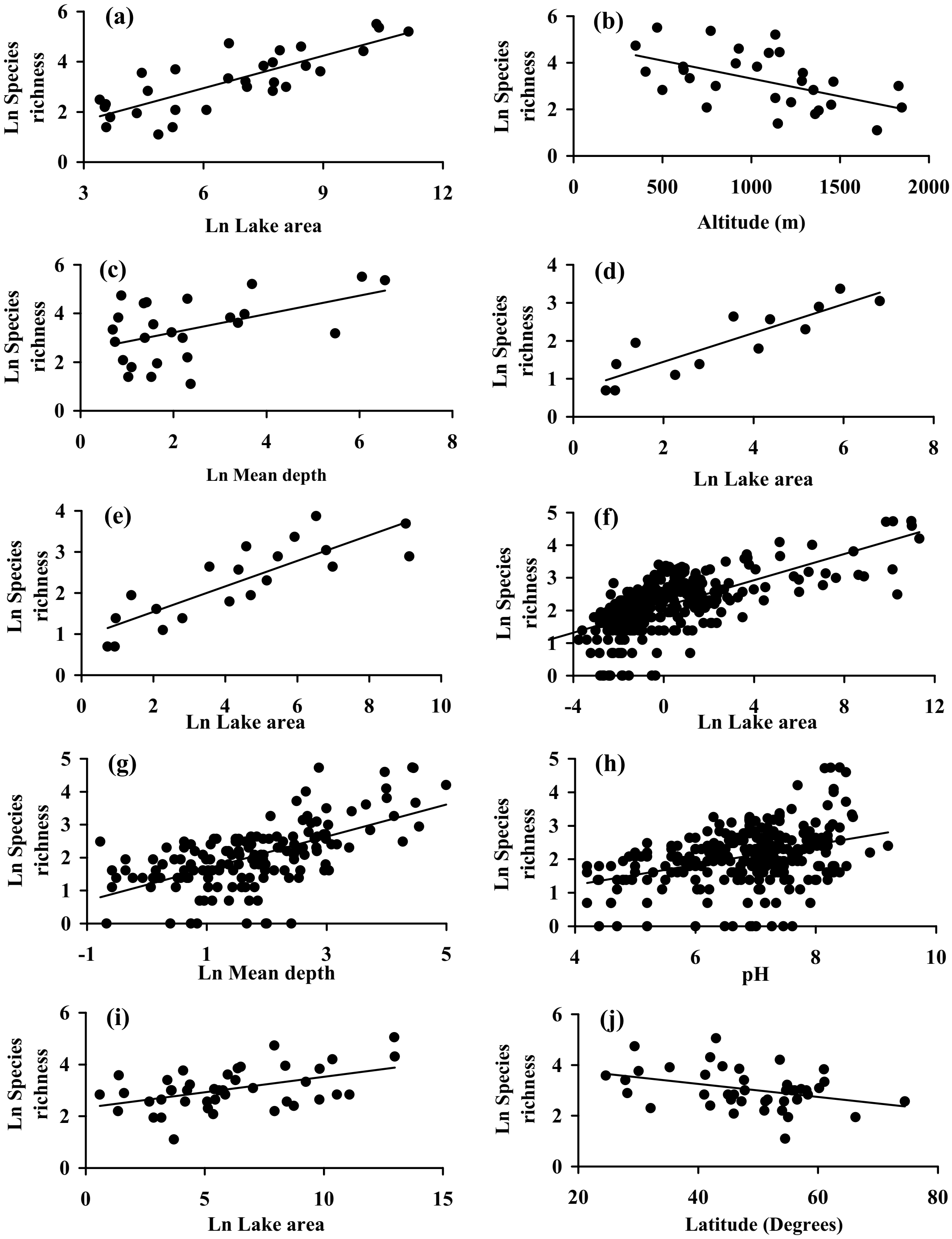

Figure 1. Relationship of fish species richness to various independent variables in lakes of different geographical regions: a–c – African lakes; d – tropical Asian lakes; e – Pooled data for tropical Asian and tropical American lakes; f–h – North American temperate lakes; i–m – European and Asian temperate lakes; n–t – Argentinean lakes. Lake area in km^2; altitude in m; mean depth in m; Secchi disc depth (SDD) in m; catchment area (CA) in km^2.

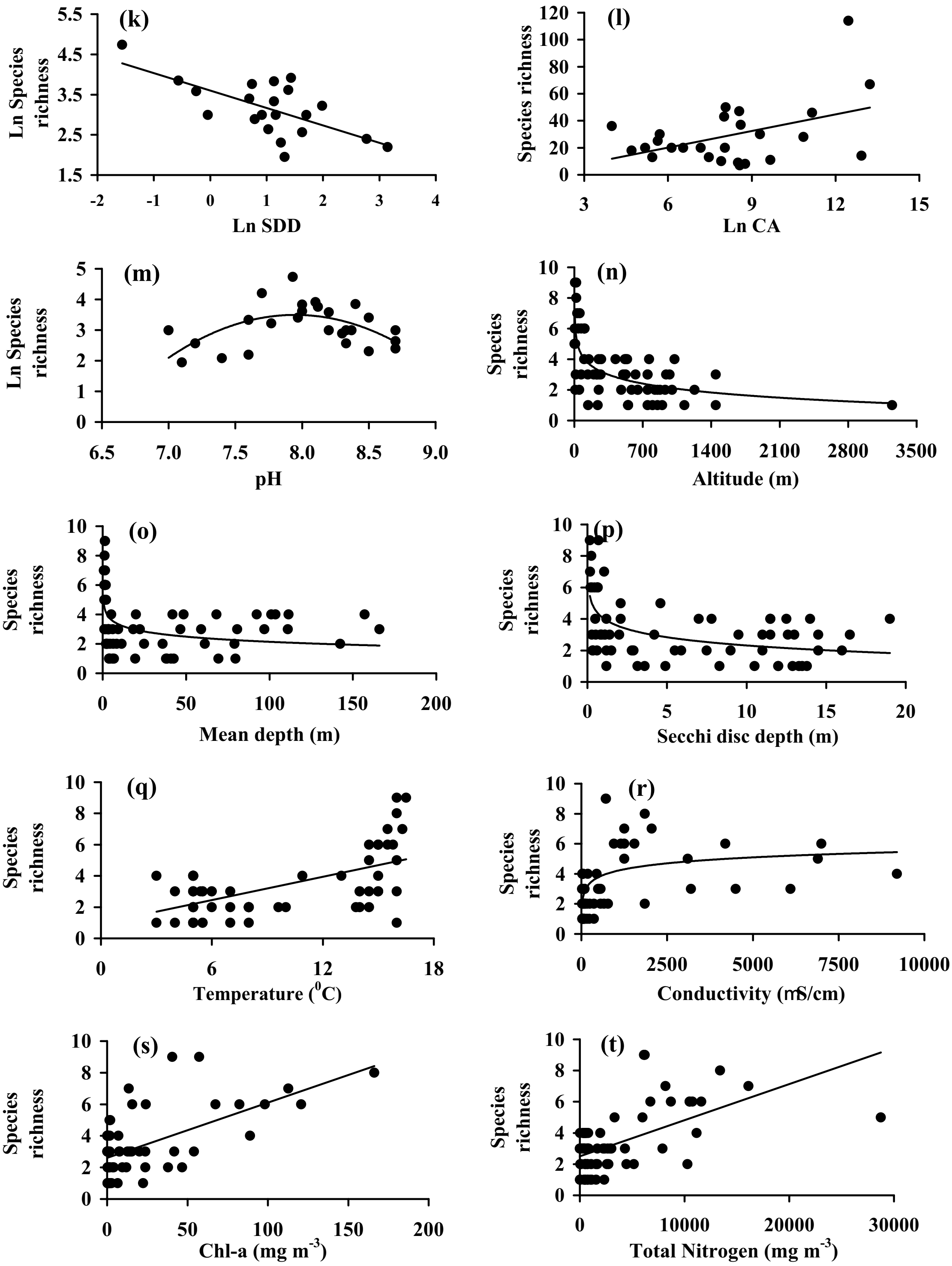

Figure 1. Continued.

Analysis (PCA) ordination. All variables with the exception of pH and latitude were log transformed prior to the analyses in order to reduce non-normality. The scores of the first principal component (PC1) were then related to Ln species richness. This is in conformity with Clarke & Warwick (1994), who suggested that the summary provided by a principal component from a PCA of environmental variables can be related to a simple univariate measure of biotic data. However, due to the paucity of natural lakes in Asian and American tropical regions, data bases for these regions used in the present analysis are not sufficient for PCA analysis. All statistical analyses were carried out using the MINITAB Version 13.1 for Windows statistical software package.

Results

The statistically significant relationships between fish species richness and various independent variables in African and Asian/American tropical lakes, North American and European/Asian temperate lakes and South American temperate lakes are shown in Figure 1. These statistical relationships are given in Table 2. Also given in Table 2 are multiple regression relationships of fish species richness with various independent variables, which have regression coefficients significantly different from zero (t-test; $\alpha(2) = 0.05$). Results of the PCA ordination of lakes based on the morphometric, geographical and limnological characteristics are shown in Figure 2. In all cases, analysis of morphometric, geographical and limnological data produced the first two principal component axes with eigenvalues greater than one. The relationships between the scores first principal component (PC1) and Ln species richness in different geographical regions are shown in Figure 3.

African lakes

The significant relationships of fish species richness and various independent variables are shown in Figures 1a–d. Species-area relationship (SAR) appears to be valid for African lakes because about 65% of variation in Ln species richness are explained by the variation in Ln lake area (Figure 1a). There is a significant negative relationship between Ln species richness and altitude (Figure 1b), and a positive relationship between Ln species richness and Ln mean depth (Figure 1c). It is evident from the multiple regression analysis that addition of Ln mean depth of lake as an independent variable does not result in a significant contribution to the model.

PCA ordination of lakes on the basis of lake area, altitude, mean depth, conductivity, latitude and pH (Figure 2a) resulted in a widely scattered pattern of lakes. Here altitude was used without log-transformation as an input variable in ordination in order to conform to its relationship with species richness (Figure 1b). The eigen values, variance explained and coefficients of the variables of the first two principal components are given in Table 3.

The first Principal Component (PC1) explained 37.8% variance (eigenvalue – 2.2685) and the second Principal Component (PC2) explained 27.4% of variance (eigenvalue – 1.6422). The scores of PC1 are positively influenced by logarithmic values of lake area, mean depth and conductivity and negatively influened by altitude. Ln species richness is positively correlated ($r = 0.592$, $p < 0.01$) with the PC1 (Figure 3a). This substantiates the results of the regression analysis, which indicate that Ln lake area explains most of the variation in Ln species richness in African lakes.

Asian and American tropical lakes

In tropical Asian lakes, Ln fish species richness is better predicted by Ln lake area (Figure 1d). The data from the present analysis did not show significant relationships of species richness and altitude, latitude and mean depth ($p > 0.05$). In tropical American lakes too, Ln lake area seems to have a positive relationship with Ln species richness (Table 2). More data are needed to investigate whether SAR describes fish species richness in lakes in tropical America. The data pooled for both geographical regions (tropical America and tropical Asia) show that Ln lake area describes over 70% variations in Ln species richness (Figure 1e). The regression relationships are given in Table 2.

North America

The relationships between native fish species richness and lake area, mean depth and pH are shown in Figures 1f–h. The statistically significant regression relationships between the species richness and various independent variables are given in Table 2.

PCA ordination of lakes derived on the basis of lake area, altitude, mean depth, latitude and pH is shown in Figure 2b and Table 4. PC1 (eigenvalue – 2.2162)

Table 2. Regression relationships between species richness (S) and various independent variables in the lakes of different geographical regions. A = area in km^2; Alt = altitude in m; Z = mean depth in m; Lat = latitude in °N; SDD = Secchi disc depth in m; CA = catchment area in km^2; Temp = temperature in °C; Cond = conductivity in μS/cm; Chl-a = chlorophyll-a in mg m^{-3}; TN = total nitrogen in mg m^{-3}. N = number of lakes; R^2 = coefficient of determination; r = correlation coefficient; p = probability level.

Geographical region/Relationship	N	R^2	r	p
Africa				
Ln S = 0.4308 Ln A + 0.3602	30	0.653	0.808	<0.001
Ln S = −0.0015Alt + 4.8665	30	0.266	−0.516	<0.005
Ln S = 0.3780 Ln Z + 2.4620	25	0.238	0.488	<0.02
Ln S = 0.3813 Ln A − 0.0007Alt + 1.4722	30	0.705	0.840	<0.001
Tropical Asia				
Ln S = 0.3791 Ln A + 0.6889	13	0.774	0.880	<0.001
Tropical America				
Ln S = 0.2210 Ln A + 1.4621	7	0.454	0.674	>0.05 (ns)
Pooled data for both regions				
Ln S = 0.3107 Ln A + 0.9205	20	0.705	0.840	<0.001
US & Canadian lakes				
Ln S = 0.2014 Ln A + 2.1183	315	0.435	0.659	<0.001
Ln S = 0.4866 Ln Z + 1.1768	156	0.371	0.609	<0.001
Ln S = 0.3016 pH + 0.0291	280	0.138	0.372	<0.001
European & Asian temperate lakes				
Ln S = 0.1195 Ln A + 2.3260	42	0.224	0.474	<0.002
Ln S = -0.0257 Lat + 4.2965	42	0.130	−0.361	<0.02
Ln S = -0.4324 Ln SDD + 3.5994	21	0.441	−0.664	<0.002
Ln S = 4.1045 Ln CA − 4.4850	26	0.195	0.442	<0.05
Ln S = -1.5551 pH2 + 24.7210 pH − 94.75	26	0.326	0.571	<0.005
Ln S = 0.0963 Ln A − 0.2158 Ln Alt − 0.0394 Lat + 5.5208	25	0.500	0.707	<0.001
South American temperate lakes				
S = -0.8415 Ln Alt + 7.9287	67	0.450	−0.671	<0.001
S = -0.5121 Ln Z + 4.4924	67	0.189	−0.435	<0.001
S = -0.7447 Ln SDD + 4.0351	67	0.308	−0.555	<0.001
S = 0.2488 Temp + 0.9621	67	0.354	0.595	<0.001
S = 0.5709 Ln Cond + 0.2322	67	0.258	0.508	<0.001
S = 0.035 Chl-a + 2.6054	66	0.362	0.602	<0.001
S = 0.0002 TN + 2.4634	67	0.326	0.571	<0.001
S = 0.2504 Ln A − 0.6031 Ln Alt − 0.4177 Ln SDD − 0.4503 Ln Cond + 0.1703 Temp + 7.256	67	0.568	0.753	<0.001

and PC 2 (eigenvalue – 1.1723) explained 44.3% and 67.7% of cumulative variance respectively.

Contributions of individual factors to the first two principal components indicate that small, shallow, relatively high altitude lakes situated in high latitudes seem to aggregate in the principal component space. There is a significant negative correlation (r = -0.698, $p < 0.0001$) between Ln species richness and PC1 (Figure 3b), which substantiates the findings that fish species richness in North American lakes is influenced not only by lake area but also by mean depth and pH of lake.

European and Asian temperate lakes

The relationships between fish species richness and various independent variables as determined by linear and polynomial regressions are shown in Figures 1i–m. These relationships indicate that in addition to lake area, latitude, Secchi disc depth (SDD) and catchment

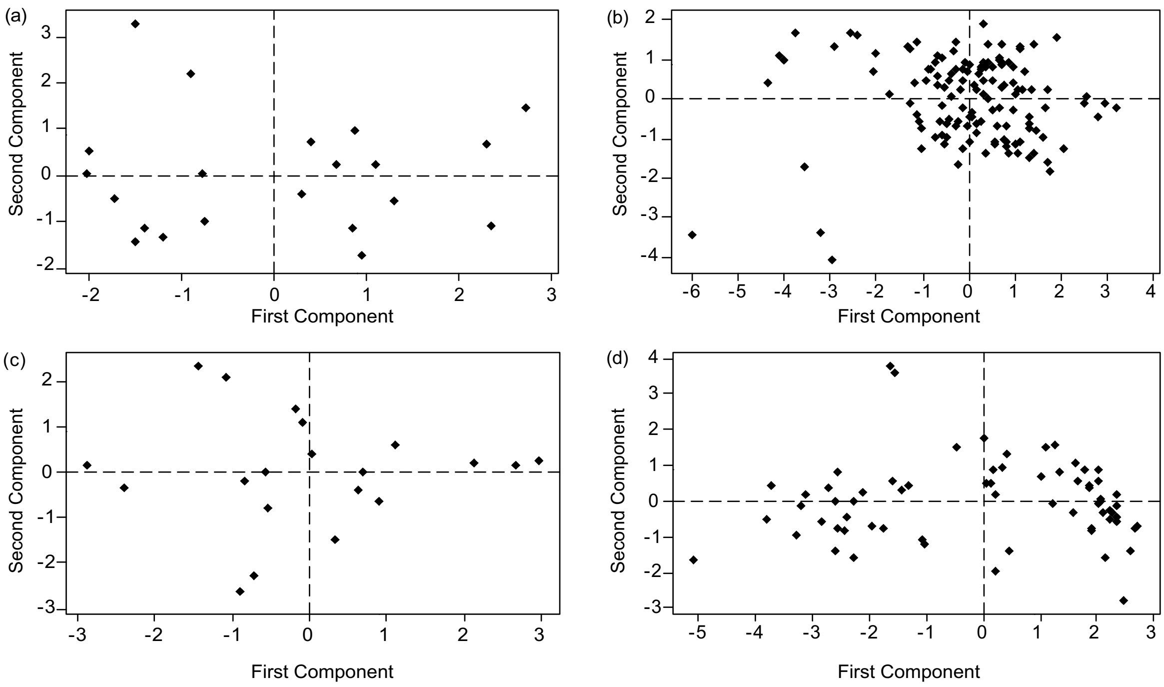

Figure 2. PCA ordination of lakes based on the morphometric, geographical and limnological characteristics: a – African lakes; b – North American temperate lakes; c – European and Asian temperate lakes; d – Argentinean lakes. Contributions of individual variables to the first and second principal components in each geographical area are given in Tables 3–6.

area also have significant influences on fish species richness. Also as shown in Figure 1m, there appears to be an optimal pH level for fish species richness in European and Asian temperate lakes within the range of pH in the present data set. It must be noted however, most SDD data fall within a narrow range so that the relationship between Ln species richness and Ln SDD is not fully qualified. The statistically significant regression relationships, including multiple regressions, which gave coefficient of independent variables of significant difference from zero are given in Table 2.

PCA ordination of lakes, which was based on the Ln lake area, Ln altitude, Ln catchment area (CA), Ln Secchi disc depth (SDD), latitude and pH is shown in Figure 2c. The cumulative variance explained by the PC1 (eigenvalue – 2.2869) and PC2 (eigenvalue – 1.5832) is 38.1% and 64.5% respectively. PC1 is dominated by Ln lake area, Ln catchment area, Ln altitude and latitude and the dominant factors in the PC2 are latitude and lake pH (Table 5). There is no significant relationship between Ln species richness and PC1 (Figure 3c) possibly due to highly scattered ordination of lakes produced by PCA (Figure 2c). As the PC1 is dominated by morphometric characteristics, but not by limnological features, non-significance of the relationship between PC1 and Ln species richness perhaps indicates that limnological features are also of equal importance for predicting fish species richness in European and Asian temperate lakes. It is also possible that this is due to high variability among lakes.

South America

The lake data that were used in the present study for South America, were essentially from the central-western and northwestern arid regions of Argentina, Pampa Plain, the Patagonian Plateau, the Patagonian Andes, and Tierra del Fuego, located between 25 and 55°S latitude (Quirós personal communication.). The relationships of fish species richness in these lakes with several lake morphometric and limnological charactestistics are shown in Figures 1n–t. The regression relationships are given in Table 2. Although lake area alone is not significantly related to species richness, Ln lake area together with Ln altitude, Ln Secchi disc depth, Ln conductivity and pH is multiply correlated with the species richness (Table 2) and the coefficients are significantly different from zero.

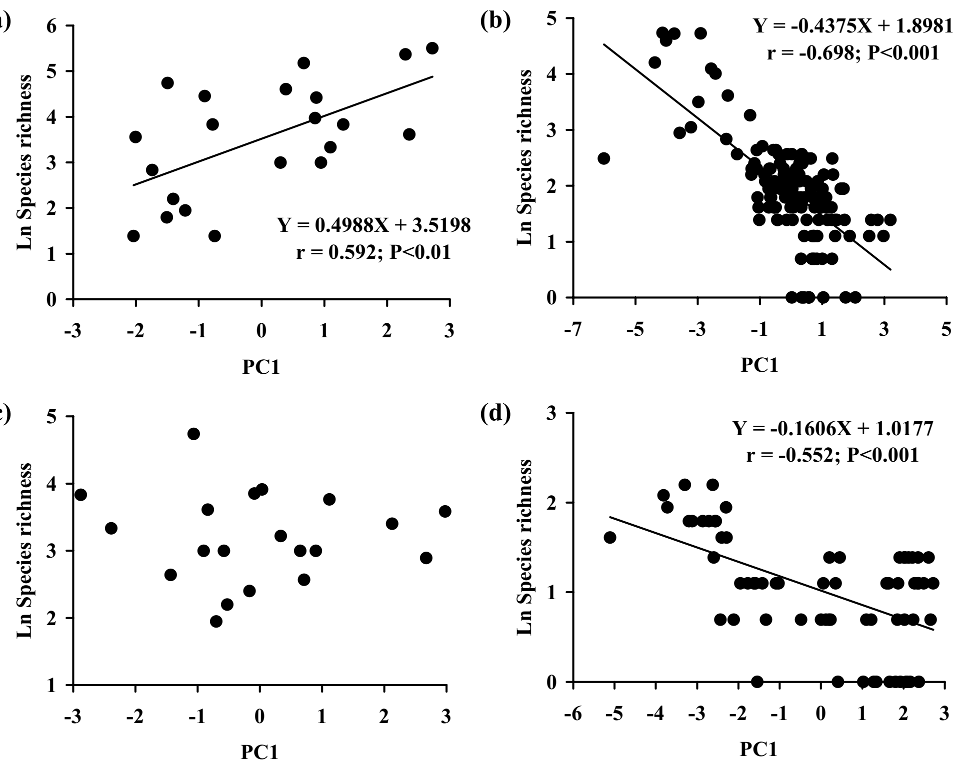

Figure 3. The relationship between the first principal component (PC1) and Ln species richness: a – African lakes; b – North American temperate lakes; c – European and Asian temperate lakes; d – Argentinean lakes. For details, see text.

Table 3. Eigen values, percentage variance explained and coefficients of the principal component analysis of different morphometric and limnological parameters for African lakes. The coefficients which are mainly responsible for the positive principal component scores in each PC are indicated as bold italics and those responsible for negative principal component scores are indicated in non-italic, bold.

Variable	PC 1	PC 2
Eigen value	2.2685	1.6422
% cumulative variance explained	37.8	65.2
Variables		
Ln lake area	*0.551*	0.234
Altitude	**−0.394**	**−0.368**
Ln mean depth	*0.492*	−0.065
Ln conductivity	*0.392*	**−0.509**
Latitude	0.284	*0.342*
pH	0.253	**−0.639**

Table 4. Eigen values, percentage variance explained and coefficients of the principal component analysis of different morphometric and limnological parameters for North American lakes. The coefficients which are mainly responsible for the positive principal component scores in each PC are indicated as bold italics and those responsible for negative principal component scores are indicated in non-italic, bold.

Variable	PC 1	PC 2
Eigen value	2.2162	1.1723
% cumulative variance explained	44.3	67.7
Variables		
Ln lake area	*0.592*	0.028
Altitude	0.050	**−0.789**
Ln mean depth	**−0.585**	0.108
Latitude	**−0.311**	**−0.588**
pH	**−0.456**	0.140

PCA ordination of the lakes on the basis of data on lake area, altitude, mean depth, Secchi disc depth, conductivity, chlorophyll-a latitude, pH and latitude is shown in Figure 2d. Here all variables with the exception of Chlorophyll-a, temperature and altitude, were log transformed according to regression relationships of species richness and different independent variables. PC1 (eigenvalue – 4.5945) explained 57.4%

Table 5. Eigen values, percentage variance explained and coefficients of the principal component analysis of different morphometric and limnological parameters for European and Asian temperate lakes. The coefficients which are mainly responsible for the positive principal component scores in each PC are indicated as bold italics and those responsible for negative principal component scores are indicated in non-italic, bold.

Variable	PC 1	PC 2
Eigen value	2.2869	1.5832
% cumulative variance explained	38.1	64.5
Variables		
Ln lake area	**−0.548**	0.354
Ln altitude	*0.427*	0.179
Ln catchment area	**−0.540**	0.397
Ln Secchi depth	−0.090	−0.341
Latitude	**−0.426**	**−0.436**
pH	0.188	*0.615*

Table 6. Eigen values, percentage variance explained and coefficients of the principal component analysis of different morphometric and limnological parameters for South American temperate lakes. The coefficients which are mainly responsible for the positive principal component scores in each PC are indicated as bold italics and those responsible for negative principal component scores are indicated in non-italic, bold.

Variable	PC 1	PC 2
Eigen value	4.5945	1.2806
% cumulative variance explained	57.4	73.4
Variables		
Ln lake area	0.099	**−0.790**
Ln altitude	*0.325*	*0.365*
Ln mean depth	*0.420*	−0.171
Ln Secchi depth	*0.427*	−0.007
Ln conductivity	**−0.416**	−0.211
Chlorophyll-a	−0.295	−0.168
Temperature	**−0.436**	−0.002
Latitude	0.276	**−0.375**

variance and PC2 (eigenvalue – 1.2806) explained 16% of variance (Table 6).

PC1 reflects Ln mean depth, Ln SDD and altitude positively and Ln conductivity and temperature negatively, whereas Ln lake area, latitude (positive loading) and Ln altitude (negative loading) are reflected by PC2. Ln species richness is negatively correlated ($r = -0.552$, $p < 0.001$) with the PC1 (Figure 3d), substantiating the relationships of species richness and various independent variables. Although this relationship is statistically significant, the data points are highly scattered indicating that the predictive power of all independent variables for fish species richness in South American temperate lakes is very poor.

Discussion

Empirical models for the prediction of fish production in inland waters have been developed in various parts of the world with considerable success (Ryder 1965, Henderson[3] & Welcomme 1974, Oglesby 1977, Matuszek 1978, Hanson & Leggett 1982, Downing et al. 1990), mainly due to the fact that inland water resources are particularly important for recreational fisheries in temperate regions and for food fish production in the tropical world. All these models indicate the importance of habitat characteristics for the management of fisheries. Models have also been developed for fish biodiversity based on various ecological theories such as species-area theory (Preston 1962, McArthur & Wilson 1967) and species-energy theory (Wright 1983). However these models are likely to be specific for the climatic zones from whence the data set originates.

In the broad sense, there are marked differences between tropical and temperate fish communities. In contrast to temperate fishes, tropical lake fishes exhibit continuous growth and year-round reproduction that shortens generation times. Furthermore, in tropical inland waters, especially lakes, many of the commercially important fishes are herbivores. This results in a more efficient transfer of energy fixed by photosynthesis to the fish biomass. From the point of view of geological history, it is known that rivers are generally old and lakes young. Also in most lakes of previously glaciated areas in Europe, North America and Argentina, colonisation and speciation processes of fishes are also relatively younger than those in tropical lakes. Presence of a large number of endemic fish species in the major African lakes (Coulter et al. 1986, Lévêque 1997), and Lake Baikal in Russia (Kozhova & Izmest'eva 1998) gives evidence for the influence of the age of lakes for colonisation and speciation of fishes in the habitats.

From the present analysis, it is evident that the number of fish species in tropical lakes (especially in

[3] Henderson, H.F. & R.L. Welcomme. 1974. The relationship of yield to morphoedaphic index and numbers of fishermen in African inland waters. CIFA Occ. Pap. 1. 19 pp.

Africa and Asia) can be predicted from a few variables such as lake area and altitude. In US and Canadian temperate lakes, lake acidification (Scheider et al. 1979, Dillon et al. 1987) is shown to be one of the important factors influencing fish species richness (Rahel 1986, Rago & Wiener 1986). The present study also shows that there is a significant positive influence of lake pH on fish species richness. According to results of the studies on the North American lakes (Harvey 1975, 1978, Tonn & Magnuson 1982), it is evident that several independent variables in addition to lake area influence fish species richness even when the data are used on a regional basis.

It is a fact that in shallow lakes, as the littoral zone occupies a larger percentage of the total bottom area and because critical nutrients are recycled more rapidly there, fish biomasses and yields are higher than in deep lakes with the similar nutrient status (Hanson & Leggett 1982, Wetzel 1983). It can therefore be expected that when comparing waters of similar nutrient status, lakes with a greater portion of the bottom area as littoral zone have higher fish productivity. However fish species occurrence in lake ecosystems is related to habitat affinities of fish species. Fish generally avoid deoxygenated hypolimnion. As such, although fish yield and fish biomass are negatively correlated to mean depth of lakes (Rawson 1952, Hanson & Leggett 1982), the positive log-log relationship between the species richness and mean depth in African and North American lakes perhaps reflects the extent of available habitats for fishes in the lake ecosystem. Absence of highly significant relationships between the lake area and the mean depth of lakes in Africa and North America further also supports this contention. Fish species richness in European and Asian temperate lakes on the other hand, shows a negative log-log relationship with SDD, possibly due to the influence of primary productivity-related factors or organic pollution on fish species richness. The negative influence of altitude on fish species richness in African and Argentinean lakes may be, amongst others, due to the differences in trophic status between high altitude and low altitude lakes (Wetzel 1983).

Argentinean lake systems include a wide diversity of aquatic systems ranging from ultraoligotrophic and oligotrophic deep lakes in the Andean Patagonia and Tierra del Fuego, mesotrophic or eutrophic lakes in the Patagonian Plateau to very shallow eutrophic, hypertrophic or salt lakes in the Chaco-Pampa Plain (Quirós & Drago 1999). In these lakes there are distinct relationships between nutrient levels and biological standing stocks and the differences in fish community composition among lakes are due to the limnological conditions among lakes (Quirós 1998). As such, in the lakes where limnological characteristics have pronounced influences on fish species communities, as in Argentinean lakes, species-area relationships are of little use for predicting fish species richness. As in the present analysis, fish species richness is considered as the dependent variable, underestimated values of number of fish species may have influenced the results of the analysis. The predictive models for fish species richness for Argentinean lakes need to be refined, as more accurate data on number of fish species present in the lakes become available.

In contrast with lakes, the single predictor variable of basin area is highly significant in rivers to predict species richness. The relationship between fish species richness and basin area in rivers is according to a power curve (Table 7). Welcomme[4] has shown that when the data sets in individual geographical regions are analysed separately, in most cases coefficient of variation (R^2) of the power curves of the form, $S = cA^z$ (where S = fish species richness, and A basin area in km^2) is over 0.83. The results of the analyses of data from small rivers in Portugal and Greece (Daget & Economidis 1975) also showed the same. Oberdorff et al. (1995) have shown however, that basin area and mean annual river discharge, and to a lesser extent, energy availability are the most important factors influencing fish species richness patterns in rivers on a global scale. The sample of 292 rivers from around the world (Oberdorff et al. 1995) gave a relationship, Log_{10} species richness $= 0.478+0.266\,Log_{10}$ drainage

Table 7. The relationships between number of fish species and river basin area in different geographical regions. The relationship for African rivers is from Welcomme (2000). The other relationships were derived based on the information from the database maintained by one of us (R.L.W.). The data on Asian rivers were supplemented by the information on Sri Lankan rivers (Pethiyagoda 1991).

Geographical region	Relationship ($Y = Log_{10}$ species richness; $X = Log_{10}$ river basin area)
Africa	$Y = 0.485X–0.561$ ($R^2 = 0.876$)
Asia	$Y = 0.263X + 0.770$ ($R^2 = 0.824$)
Europe	$Y = 0.248X + 0.428$ ($R^2 = 0.672$)
South America	$Y = 0.505X–0.491$ ($R^2 = 0.910$)

[4] Welcomme, R.L. 1985. River fisheries. FAO Fish. Tech. Pap. 262. 330 pp.

basin area (km^2), with an R^2 of 0.439. According to Welcomme (2000), when relationships are calculated for rivers in each continent, higher R^2 values are given (Table 7). The robustness of the relationship between basin area and fish species richness to describe fish biodiversity in rivers might be due to the greater diversity of habitas for fish in larger river systems than in small ones. Usually fish species communities in small tributaries of rivers are different from those in the main channel.

The present analysis shows that lake area and altitude are by and large, the two major determinants, which have greater predictive power for fish species richness. In the SAR in lakes and the relationships between species richness and drainage basin area in rivers, the exponent is always greater in tropical (lower latitude) regions than in temperate regions. This indicates that fish species richness in lakes and rivers increases with the habitat size faster in tropical regions than in temperate regions.

As it has already been mentioned, taxonomy is a major problem in modelling fish species richness in inland waters. In Lake Victoria, East Africa for example, the taxonomic status of some cichlid species as well as non-cichlid species is problematic (De Vos[5], Fuerst & Mwanja[6]). The fish community in Lake Malawi too contains about five hundred hitherto undescribed haplochromines (Turner 1995, Turner et al. 1995). The exponent of the SAR for African lakes must therefore be greater than the value obtained in the present analysis, when actual number of species are used. As such, habitat conservation can be considered as an extremely important issue in the conservation of fish biodiversity particularly in African lakes.

Acknowledgements

The authors wish to thank T.R. Whittier, US Environmental Protection Agency and R. Quirós, Universidad de Buenos Aires for sending us data of northeastern USA lakes, and Argentinean lakes respectively. This analysis was carried out while the first author was in Imperial College of Science, Technology and Medicine, University of London under a postdoctoral fellowship awarded by Association of Commonwealth Universities, UK.

[5] De Vos, L. 2000. The non-cichlids of Lake Victoria system: diversity, taxonomy and identification problems. Paper presented at the International conference on 'Lake Victoria 2000: a new beginning', 16–19 May 2000, Jinja. (abstract only).

[6] Fuerst, P.A. & W.A. Mwanja. 2000. The opportunities and challenges to conservation of genetic biodiversity of the fishery of the Lake Victoria region, East Africa. Paper presented at the International conference on 'Lake Victoria 2000: a new beginning', 16–19 May 2000, Jinja (abstract only).

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