Fish species richness in lakes of the northeastern lowlands in Germany

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Abstract Fish species richness was assessed by electrofishing and gillnetting in 16 lakes of the northeastern lowland in Germany (the Schorfheide biosphere reserve). The lakes range from 0.03 to 10.55 km² and support between 5 and 14 fish species. Species richness is significantly correlated with lake area in an exponential and a power model. Richness is also correlated with shoreline development and total dissolved solids. This supports the hypothesis that larger areas contain more species within a taxonomic group due to increased habitat diversity. The slope of the species-area curve is low compared with most other studies of fish species richness in lakes, and the intercept value is high. This is interpreted as the result of high habitat and food diversity, lack of stress from abiotic factors, and the small regional species pool from which these lakes can be colonized. Two species inventories, one from the beginning of this century and one from the 1950s, are available for comparison. Average species richness did not change during the last decades. Species turnover rates were not related to the degree of anthropogenic eutrophication or to the intensity of fishery exploitation in these lakes. On the species level, however, one effect of accelerated eutrophication is apparent, the disappearance of 4 bottom-living species from one to 6 of the study lakes.

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Introduction

There are 3 major hypotheses as to why more species within a taxonomic group exist in larger areas (Angermeier & Schlosser 1989). The first, the area-per se hypothesis, is derived from island biogeography (Mac Arthur & Wilson 1967) and considers species richness as the result of an equilibrium between immigration and extinction rates, which are both dependent on habitat size (Magnuson 1976). The second, the habitat diversity hypothesis (Williams 1964), suggest that larger habitats contain more subdivisions of habitat configurations and resources and, thus, maintain more species. The third, the sampling hypothesis (Connor & McCoy 1979), views species number as the result of passive sampling from the available species pool, whereby larger habitats receive more individuals and, ultimately, more species.

Species-area curves were first documented for terrestrial organisms on islands. Subsequently, the similarities between ocean islands and lakes have

been pointed out (Barbour & Brown 1974; Magnuson 1976) and species-area curves documented for a variety of aquatic taxa including littoral zooplankton (Fryer 1985), pelagic zooplankton (Dodson 1991), snails (Brönmark 1985), and fish (Barbour & Brown 1974; Browne 1981; Eadie & Keast 1984; Eadie et al. 1986; Harvey 1978, 1981; Matuszek & Beggs 1988; Matuszek, Goodier & Wales 1990; Rahel 1986; Somers & Harvey 1984; Tonn & Magnuson 1982). These studies show that, in lacustrine fish communities, parameters other than lake area may also be significantly correlated with species richness. These include latitude, altitude, lake depth, shoreline development, pH, winter oxygen concentrations and lake connectedness, substrate diversity, submerged macrophyte complexity, and invertebrate prey diversity.

The purpose of this article is to investigate relationships between fish species richness and morphometry (area, depth, shoreline development) and indices of trophic state (conductivity/total dissolved solids, total P, chlorophyll a) for a set of 16 lakes of

glacial origin in the northeastern lowland in Germany. Additionally, since many of these lakes have suffered from severe anthropogenic impact during the last decades (eutrophication, intensive fish production, stocking with exotics), it should be tested whether species richness or species composition were persistently affected by these perturbations.

Material and methods

Sixteen lakes in the Schorfheide biosphere reserve, situated about 100 km north of Berlin, were used in these analyses. They were primarily selected to include the range of lake sizes available in this region, and secondarily to represent wide arrays of trophic state and human impact. Surface area and shoreline length were measured from digitized areal photographs or ordnance maps. Maximum and mean depth were taken from files of a state-wide assessment of the fish production potential in lakes of the German Democratic Republic carried out in the 1950s. Vertical temperature and oxygen profiles (Syland model 4002 F) and Secchi depth were measured parallel to each fishing operation. Conductivity and total dissolved solids (TDS) were determined on two occasions in 14 lakes. From the linear relationship $\text{TDS [mg/l]} = 28 + 0.68 \text{ conductivity [\mu S/cm]}$ ($n=27$, $R^2=0.96$), TDS was estimated for the two lakes for which only conductivity measurements were available. Total phosphorus and chlorophyll-a concentrations were measured 3 times during the growing season in representative samples from the epilimnetic water column. The extent of the reed belt, abundance of submersed macrophytes and presence of connections with other waterbodies were assessed by visual inspection. Winterkills were reported by fishermen and residents and by personal observations. These sources were also used to assess type and severity of human impact during the last decades.

Fish sampling was carried out in 2 consecutive years. In 1992, each lake was fished once in summer with 4 bottom-set gill nets of 12, 18, 26 and 32 mm bar mesh, 1.2 to 2.4 m height and 10 to 25 m length. Additionally, several littoral sites per lake were sampled by electrofishing and with a 30-m beach seine of 6-mm mesh size. During the growing season 1993, the 12 smaller lakes were fished once and the four larger ones twice with a new fleet of eight gill nets of 12, 16, 20, 25, 32, 40, 50 and 60 mm bar mesh, 1.2 to 2.4 m height and 10 to 25 m length. Electrofishing was done as in the previous year, but the beach seine was not used. Fish caught in gill nets were easily identified, except small individuals of bream and white bream whose identity was verified by scale and fin ray counts. Whenever the identity of small fish

sampled by electrofishing was doubtful, samples were preserved for later identification in the laboratory. Only the species that were present in our samples were included in the species list, except for coregonids, whose presence was confirmed by professional catches. Accidentally or intentionally introduced exotics (*Oncorhynchus mykiss*, *Cyprinus carpio* and *Aristichthys nobilis*), which do not reproduce in the recipient lake, were not counted. Scientific and common names of fish species are given in the Appendix. Historical species lists for 14 of the 16 study lakes were available for the beginning of this century (Eckstein 1908) and for the 1950s (files from the former Inland Fisheries Institute of the German Democratic Republic).

Results

The lakes range in surface area from 0.03 to 10.55 km² and from 2 to 50 m maximum depth (Table 1). In 12 permanently stratified lakes, however, oxygen depletion in the hypolimnion ($\leq 1 \text{ mg O}_2/\text{l}$) restricts fish distribution to only two thirds of maximum depth on average during the growing season. Winterkills have only been reported for the two smallest lakes. Most lakes are either completely isolated from other water bodies or are only temporarily connected to small ditches, and only 3 lakes have a permanent outlet creek or ship canal that permits fish movements. The lakes' trophic states range from mesotrophic ($< 10 \text{ } \mu\text{g chl-a/l}$) to heavily polluted (around $100 \text{ } \mu\text{g chl-a/l}$). Reed stands (mainly *Phragmites* and *Typha*) are usually present, and in some lakes they occupy a large portion of the littoral zone. Submerged vegetation (*Potamogeton*, *Myriophyllum*, *Ceratophyllum*, *Chara* and also *Stratiotes*) is present in almost all lakes, but in the most turbid lakes it is not abundant or even rare. During the last decades, 10 lakes were managed by fisheries cooperatives, including 3 lakes with intensive net-cage culture using pelleted food, whereas 6 lakes were only fished by hook and line (Table 1).

A total of 19 fish species were found, which could be classified as either being ubiquitous (present in 11 to 16 lakes) or nonubiquitous species (present in only 1 to 6 lakes) (Table 2). Species numbers per lake range from 5 to 14. If the species number that was documented after two years of fishing is set to 100, then an average of 86% of all species records had already been obtained after the first study year. The highest numbers of new species per lake that were observed in the second study year belong to the largest lakes, except for Kleinvätersee, which was sampled inappropriately in the first year, and Tiefer See, which was sampled in the second year only. If the number of species

Table 1. Basic morphometric and limnological data for the 16 study lakes.

	Kleiner Döllnsee	Teutzen- see	Kleinväter- see	Großväter- see	Großer Krinertsee	Duester- see	Klarer See	Luebbe- see	Werbellin- see	Wolletz- see	Grimnitz- see	Rederns- walder See	Parsteiner See	Kleiner Plunzsee	Großer Plunzsee	Tiefer See
area (km ²)	0.24	0.03	0.09	0.12	0.75	0.42	0.47	3.14	8.04	3.29	7.93	0.53	10.5	0.04	0.22	0.10
shoreline (km)	2.3	0.8	1.4	1.5	7.1	4.5	4.2	22.1	27.2	16.0	13.1	6.0	32.0	0.9	2.2	1.5
SLDF	1.3	1.3	1.3	1.2	2.3	2.0	1.7	3.5	2.7	2.5	1.3	2.3	2.8	1.3	1.3	1.3
max. depth (m)	8	2	14	13	10	8	7	12	50	18	11	12	27	4	10	33
TDS (mg/l)	236	196	194	200	438	405	310	309	250	416	372	199	347	473	290	233
total-P (µg/l)	21	80	17	23	27	48	98	37	40	150	65	36	n.d.	1270	148	n.d.
chlorophyll-a (µg/l)	9.8	6.8	2.8	4.2	7.6	21.9	42.6	9.1	4.7	11.8	10.2	8.8	n.d.	100	15.0	n.d.
in/outflow	(+)				(+)	(+)	—	+	+	+	(+)		(+)	(+)	(+)	
hypolimnetic anoxia	+	—	+	+	+	+	+	+	—	+	+	+	+	+	+	—
winterkill	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
reed belt	+	+	+	+	++	+	—	+	+	+	++	+	++	+	+	+
submerged vegetation	++	+	+	—	++	+	++	+	+	+	+	++	+	—	—	+
human impact	hl	hl	hl	eu	hl	eu	eu	ts	ts	cc	bc,cc	ts	cc	eu	bc	hl
				hl	ts	ts	ts	ts	ts	eu,ts	eu,ts	ts	eu,ts	hl	eu,ts	

SLDF: shoreline development factor. TDS (total dissolved solids), total-P and chlorophyll-a are means from 2–3 epilimnetic measurements during summer stagnation. in/outflow: — absent; (+) present but generally not passable to fish; + regularly passable to fish. hypolimnetic anoxia: assessed during summer stagnation. reed belt: — absent or only small isolated stands; + present, of moderate width; ++ broad belt occupying large parts of shallow bays. submerged vegetation: — almost absent; + regularly present; ++ abundant. human impact: bc – stocked with bighead carp; cc – cage culture, use of pelleted feedstuff; eu – eutrophication due to sewage input and/or runoff from agricultural soils; hl – fished with hook and line; ts – fished commercially with trap and seine nets

Table 2. Occurrence of 19 fish species in 16 lakes of northeastern Germany according to electric and gillnet fishing (total number). The number of species that were found in each study year are indicated as well as the number of species that were only discovered during the second year (new in 93)

	Kleiner Döllnsee	Teutzen- see	Kleinväter- see	Großväter- see	Großer Krinertsee	Duester- see	Klarer See	Luebbe- see	Werbellin- see	Wolletz- see	Grimnitz- see	Rederns- walder See	Parsteiner See	Kleiner Plunzsee	Großer Plunzsee	Tiefer See	Σ
<i>Anguilla ang.</i>	•			•	•	•	•	•	•	•	•	•	•			•	11
<i>C. albula/lavaret.</i>								•	•	•			•			•	5
<i>Esox lucius</i>	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	15
<i>Abramis brama</i>	•		•	•	•	•	•	•	•	•	•	•	•		•	•	14
<i>Alburnus albur.</i>	•			•	•	•	•	•	•	•	•	•	•		•	•	13
<i>Blicca bjoerkna</i>	•			•	•	•	•	•	•	•	•	•	•				11
<i>Carassius car.</i>		•	•	•							•						4
<i>Gobio gobio</i>								•		•			•				3
<i>Leucaspis del.</i>		•						•	•		•			•			5
<i>Rhodeus s. am.</i>					•												1
<i>Rutilus rutilus</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	16
<i>Scardinius ery.</i>	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	14
<i>Tinca tinca</i>	•	•	•	•	•	•		•	•		•	•	•	•	•		13
<i>Gasterosteus a.</i>									•		•						2
<i>Perca fluviatilis</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	16
<i>Gymnoceph. c.</i>	•		•		•	•	•	•	•	•	•		•		•		11
<i>Stizostedion lu.</i>					•		•			•	•		•		•		6
<i>Lota lota</i>									•	•							2
total number	10	6	8	10	12	10	10	13	13	13	14	9	13	5	9	7	
No. of species in 1992	9	5	4	10	9	10	10	11	11	9	13	8	10	5	9	—	
No. of species in 1993	7	6	8	8	12	9	7	12	11	12	10	9	13	3	7	7	
new in 93	1	1	4	0	3	0	0	2	2	4	1	1	3	0	0	7	

per lake is estimated as a function of fishing effort (number of study years) according to $S = a - 1/\text{fishing effort}$, one would expect an average asymptotic richness of 11.7 species per lake, excluding Tiefer See, instead of 10.3 species that have been found after two years of fishing.

The presence of 5 species (*Anguilla anguilla*, *Tinca tinca*, *Gobio gobio*, *Rhodeus sericeus amarus* and *Perca fluviatilis*) was documented by electrofishing and the presence of 5 species by gill-netting alone (*Coregonus* spp., *Abramis brama*, *P. fluviatilis*, *Stizostedion lucioperca* and *Gymnocephalus cernua*), but the combination of both methods was necessary to obtain the complete species inventory for each lake. Beach seining was not necessary to complement the record obtained by the other two fishing methods. Correlation analyses showed significant relationships between species richness and surface area (Fig. 1), species richness and shoreline development factor (the quotient of actual lake circumference and the perimeter of a circle of equal area) ($P < 0.01$), and species richness and TDS ($P < 0.01$). The last relationship is only significant if the second smallest lake (Kleiner Plunzsee) is deleted from the data set.

This lake has received sewage from a large animal farm for at least the past 20 years, and its TDS content of more than 470 mg/l in relation to its species number (5) must be considered as an outlier.

Regression analysis showed that shoreline development is no longer significantly correlated with species richness in a linear model where lake area is the other predictor variable. Similarly, TDS is not significant together with lake area as predictor

variable for species richness. There was no correlation between species richness and either lake depth, total phosphorous content (excluding Kleiner Plunzsee) or chlorophyll a content. Species-area curves were fitted using an exponential model and a power function. The equations are:

$$S = 10.99 + 3.07 \log_{(10)} A \quad (R^2 = 0.874)$$

$$\text{and } S = 10.67 \times A^{0.141} \quad (R^2 = 0.808)$$

where S is species richness and A is lake area in km^2 .

Discussion

Species richness is significantly correlated with lake area in the present data set (Fig. 1). The slope of the log species/log area regression line (0.14), however, is low compared with most other studies on fish species richness in lakes (Table 3). If species richness is the result of an equilibrium between colonization and extinction, then the slope value should fall in the range 0.2–0.4 (Preston 1960). Higher slope values can be attributed to increased habitat diversity with area, and lower values may be the result of sampling nonisolated areas (Connor & McCoy 1979). In the latter situation, many transient species will be encountered, independent of habitat size, thereby increasing species richness in small areas and depressing the slope of the species-area curve. It is unlikely that the presence of transient species is the reason for the low slope value in the present data set. These lakes, which were formed some 10,000 years ago, were highly connected initially by runoff from the retreating ice shield, allowing colonization from the available fish species pool. The lakes then became increasingly isolated, and contemporary colonization rates are probably very low and transient species insignificant.

An alternative explanation for low slope value is the asymptotic nature of species numbers for large areas (Connor & McCoy 1979). This fundamental characteristic of species-area curves is masked when power functions are fitted to the data but is evident when exponential models (species/log area curves) are used. In the present case, the exponential model gives a better fit to the data ($R^2 = 0.87$) than the power function ($R^2 = 0.81$), and the asymptotic nature of the species-area relation is obvious: for every 10-fold increase in area, richness is expected to rise by roughly 3 species, i.e., even for a 1000 km^2 lake we would expect only 20 fish species.

Species richness levels off at relatively low values, probably because the regional fish species pool is small. Of the 83 freshwater fish species that have been reported for Germany (Ladiges & Vogt 1979), 6 are exotics, 9 live in brackish waters, 16

Fig. 1. Fish species richness in relation to lake surface area in 16 glacial lakes of the northeastern lowland in Germany

Table 3. Regression equations used to predict fish species richness (S) from lake area (A), and predicted richness for lakes of 0.1, 1, and 10 km² surface area. Original equations were modified if necessary, so that the area unit is km² in all cases. Logarithms are to the base 10. Predicted richness values in parentheses are either extrapolated beyond the area range of the studied lakes, or the area range was unknown.

Regression equation	Area range	No. of lakes	R^2	Predicted richness for x km ²			Source
				0.1	1	10	
$S = 10.42 * A^{0.143}$	0.8...436 000	70	0.298	(7.5)	10.4	14.5	Barbour & Brown (1974) ^a
$S = 3.86 * A^{0.39}$	~0.04...~40	70	0.56	1.6	3.9	9.5	Eadie & Keast (1984)
$S = 7.52 * A^{0.209}$	~0.001...~10 000	82	0.796	4.6	7.5	12.2	Eadie et al. (1986) ^b
$S = 6.46 * A^{0.2}$	0.009...31.6	40	0.94	4.1	6.5	10.2	Matuszek & Beggs (1988) ^c
$S = 9.77 * A^{0.2}$	0.1...15.85	11	0.94	6.2	9.8	15.5	Matuszek et al. (1990) ^d
$S = 9.68 + 5.63 \log A$	<0.1...100	51	0.656	4.0	9.7	15.3	Harvey (1978)
$S = 12.72 + 5.29 \log A$	<0.1...~10	57	0.23	7.4	12.7	18.0	Harvey (1981)
$S = 15.61 + 8.68 \log A$	0.05...15.66	100	0.496	6.9	15.6	24.3	Rahel (1986) ^e
$S = 10.9 + 5.8 \log A$	0.06...1.78	34	0.34	5.1	10.9	(16.7)	Somers & Harvey (1984)
$S = 9.76 * A^{0.346}$	0.02...0.9	18	0.50	4.4	9.8	(21.6)	Tonn & Magnuson (1982) ^f
$S = 8.65 + 4.33 \log A$	?	54	0.63	(4.3)	(8.6)	(13.0)	Beamish et al. (1976), cited in Rahel (1986)
$S = 12.91 + 5.98 \log A$	?	34	0.45	(6.9)	(12.9)	(18.9)	Keller (1984), cited in Rahel (1986)
$S = 10.99 + 3.07 \log A$	0.03–10.55	16	0.87	7.9	11.0	14.1	Present study

^a Recalculated from the data provided in the paper. ^b Geometric mean regression (all other models are based on model I least-squares regression). ^c Mean number of species in 40 subsets of lakes, grouped according to area (total number of lakes: 1928, excluding lakes with pH < 6.4). ^d Mean number of species in 11 subsets of lakes, grouped according to area (total number of lakes: 213, excluding lakes pH < 6.0). ^e Low and high alkalinity lakes combined. ^f Recalculated from the data provided in the paper, summer assemblages only

are almost exclusively confined to running waters. 4 depend on lake tributary streams for reproduction and 20 are not present in northeastern Germany at all. Of the remaining 28 species, 19 have been found in our study lakes. Of the remaining 9 species, 5 are in danger of extinction or are severely threatened (Rote Liste Brandenburg 1992). The more species from a given species pool that are already present in a habitat, the lower is the probability that later arrivals belong to a new species. This effect is more pronounced when the regional species pool is small, and even more so when the species that are not present in the habitat are rare.

Even so, the slope of the species-area curve could be high if the smallest lakes contained only few species, i.e., the intercept of the species-area curve was low. Species richness for the smallest lakes in this study, however, is high as compared with other studies (Table 3). There are only 4 of 12 studies in which predicted species richness for a 0.1 km² lake is similar to, or higher than, the value (7.9 species) for the present set of lakes. For a 10 km² lake, however, 8 of 12 studies predict higher richness than the present model (14.1 species). High species richness in the smallest lakes in this study is probably due to a set of factors: winters are not severe, so that the lakes sometimes do not freeze at all or they freeze only for some weeks, and winterkills do not occur in most lakes; reed belt and submersed vegetation provide ample spawning, feeding and hiding habitats; food resources are varied, although benthic food can be partly inaccessible due to hypolimnetic anoxia during summer stagnation; and fish are not stressed

by low pH values (pH is around 8). Thus, habitat and food diversity and lack of stress from abiotic conditions in even the smallest lakes, together with the small regional pool of 28 species, are probably the main reasons for a low slope value combined with a high intercept value of the species-area relationship in the present data set.

The importance of habitat diversity for species richness is evidenced by the correlation between richness and shoreline development. Eadie & Keast (1984) reported a similar observation for a combined set of northern and southern Ontario lakes. In the present study, however, the influence of shoreline development, and thus habitat complexity, is masked by the strong influence of area on species richness, because shoreline development is correlated with area. The narrow range of shoreline development (1.2–3.5) does not allow the unequivocal separation of the influences of both factors on species richness.

Total dissolved solids are an indicator of the productivity level of a lake (Ryder et al. 1974). A high correlation between species richness and TDS was found for 15 lakes in this study. This is an indication that more productive lakes, where more food is available and resources can be finer subdivided, support more species (MacArthur 1972). A similar observation is reported by Tonn & Magnuson (1982) for centrarchid-*Esox* assemblages in northern Wisconsin lakes, where conductivity was significantly related to fish species richness. No direct measures of food abundance or diversity are available for the present set of lakes, so the prediction that more productive lakes support more fish

Table 4. Comparison of the fish species inventories from the first six decades of this century (early studies) and from the present study for 14 of the 16 study lakes. No. of species lost: species that were reported in at least one of the earlier studies but not found in the present study. No. of species gained: species found in the present study but not reported in either of the two earlier studies. Species turnover rate: sum of lost and gained species.

	Kleiner Döllsee	Teutzen- see	Kleinväter- see	Großväter- see	Großer Krinertsee	Düster- see	Klarer See	Luebbe- see	Werbellin- see	Wolletz- see	Grimnitz- see	Rederns- walder See	Parsteiner See	Kleiner Plunzsee	Großer Plunzsee	Tiefer See
Early studies*	9	8	9	11	12	13	12	9	16	12	14	12	13	10	10	-
Present study	10	6	8	10	12	10	10	13	13	13	14	9	13	5	9	7
No. of species lost	-2	4	-3	-2	3	3	3	-2	4	2	-3	3	-3	-7	3	-
No. of species gained	13	12	12	11	0	0	1	16	11	13	13	0	13	12	12	-
Species turnover rate	5	6	5	3	3	3	4	8	5	5	6	3	6	9	5	-

*Eckstein (1908) and files from the former Institute of Inland Fisheries (German Democratic Republic) combined.

species cannot be tested rigorously at the moment. Additionally, the influence of TDS content (range: 194–438, $n=15$) is masked by the overwhelming influence of lake area in a multiple linear regression model.

It is often claimed in public discussion, and even some scientists favor the view, that fish communities in lakes of northeastern Germany were severely affected by human impact during the last decades. For 14 lakes, 2 earlier species inventories are available for comparison. Both studies were carried out before these lakes were anthropogenically affected, mainly by nutrient input from domestic sewage, animal farming, intensive agriculture and intensive fish production. The main disadvantage with these studies is that the occurrence of fish species was not assessed by adequate sampling but recorded as personal communications from professional fishermen and residents. Therefore, the true species numbers might have been underestimated in these studies. To alleviate this potential bias, all fish species reported in either of these two studies were combined and compared with the present species list (Table 4). In 1992–1993, these 14 lakes had, on average, one species less than during the first half of this century. Since it has been estimated from a simple asymptotic model that contemporary species richness may be underestimated by roughly one species, this difference is negligible.

It is interesting that almost all lakes lost and gained fish species during the last decades, although average species richness remained unchanged. This might be considered further evidence for the strong correlation between species richness and lake area. There is, however, no relationship between the total number of lost and gained species per lake (i.e., species turnover rates) and the severity of human impact. The lakes that are most strongly polluted nowadays (Düstersee, Klarer See, Wolletzsee, Grimnitzsee and Großer Plunzsee) did not lose or gain more species (average turnover rate: 4.6) than the other lakes (average turnover rate: 5.1). Similarly, the lakes that were fished intensively with trap and seine nets are characterized by an average species turnover rate of 5, which is not significantly different from the value of 4.8 for the lakes that were only fished with hook and line. An outstanding species loss occurred in Kleiner Plunzsee, a shallow, polytrophic lake, where nowadays in summer the living space for fish is compressed to 1.5–2 m and where winterkills are frequent.

Another argument is that specialist species are easier lost from a local species pool and replaced by generalist species. This argument is supported by the present data. Four bottom-living species (*Lota lota*, *Silurus glanis*, *Cobitis taenia* and *Mis-*

gurnus fossilis) disappeared from 1–6 lakes but did not appear anew in any of the 16 lakes. This pattern is interpreted as a direct result of eutrophication-mediated habitat degradation, to which these species might be particularly susceptible. Apart from changes of species number or species composition, human impact may alter the relative abundance of particular species in a lake. Fish communities in most of the study lakes are nowadays dominated by roach, perch and bream. This is often attributed to anthropogenic impact, but precise data are lacking to support this contention.

In summary, neither changes in species richness or species turnover rates provide conclusive evidence that the fish communities in the study lakes were negatively affected by human influences during the last decades. On the species level, however, these influences are apparent: accelerated eutrophication was likely the ultimate cause for the disappearance of 4 bottom-living species, and it might have changed relative species abundances as well.

Appendix. Common and scientific names of fish species mentioned in this study

Scientific name	English	German
<i>Anguilla anguilla</i> (L.)	eel	Aal
<i>Oncorhynchus mykiss</i> (Walbaum)	rainbow trout	Regenbogenforelle
<i>Coregonus albula</i> (L.)	vendace	Kleine Maräne
<i>Coregonus lavaretus</i> (L.)	whitefish	Große Maräne
<i>Esox lucius</i> L.	northern pike	Hecht
<i>Cyprinus carpio</i> L.	common carp	Karpfen
<i>Abramis brama</i> (L.)	common bream	Blei, Brachsen
<i>Alburnus alburnus</i> (L.)	bleak	Ukelei
<i>Aristichthys nobilis</i> Richardson	bighead carp	Marmorkarpfen
<i>Blicca bjoerkna</i> (L.)	white bream	Güster, Blicke
<i>Carassius carassius</i> (L.)	crucian carp	Karausche
<i>Gobio gobio</i> (L.)	gudgeon	Gründling
<i>Leucaspius delineatus</i> (Heckel)	?	Moderlieschen
<i>Rhodeus sericeus amarus</i> (Bloch)	bitterling	Bitterling
<i>Rutilus rutilus</i> (L.)	roach	Plötze, Rotaue
<i>Scardinius erythrophthalmus</i> (L.)	rudd	Rotfeder
<i>Tinca tinca</i> (L.)	tench	Schleie
<i>Cobitis taenia</i> L.	spined loach	Steinbeißer
<i>Misgurnus fossilis</i> (L.)	?	Schlammpeitzger
<i>Silurus glanis</i> L.	European catfish, wels	Wels
<i>Gasterosteus aculeatus</i> L.	three-spined stickleback	Dreistachliger Stichling
<i>Perca fluviatilis</i> L.	Eurasian perch	Barsch, Flußbarsch
<i>Gymnocephalus cernua</i> (L.)	ruffe	Kaulbarsch
<i>Stizostedion lucioperca</i> (L.)	zander	Zander
<i>Lota lota</i> (L.)	burbot	Quappe, Trüsche

Resumen

1. La abundancia de especies de peces se ha estudiado en 16 lagos del noreste de Alemania (reserva de la biosfera "Schorfheide") mediante pesca eléctrica y redes de enmalle. La superficie de los lagos oscila entre 0.03 y 10.55 km², donde habitan de 5 a 14 especies.
2. La abundancia de especies está significativamente correlacionada con la superficie de los lagos, el desarrollo de la orilla y la cantidad de sólidos disueltos. Dichas correlaciones respaldan la hipótesis de que en los grandes lagos habitan más especies de un mismo grupo taxonómico debido a una mayor diversidad de hábitats.
3. La pendiente de la relación número de especies-superficie de los lagos es menor que la obtenida en estudios similares, siendo mayor el punto de corte. Esto se debe a la alta diversidad de hábitats y de las fuentes de alimentación, a la ausencia de alteraciones de orden abiótico y al bajo número de especies presentes en la región.
4. Si se compara con la información existente, la abundancia media de las especies no ha cambiado durante las últimas décadas.
5. La tasa de renovación de las especies parece que no está relacionada con el grado de eutrofización antropogénica ni con la intensidad de la explotación pesquera. Sin embargo, a nivel de especie, cuatro especies bentónicas han desaparecido en 6 lagos por causa de la eutrofización.

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References

- Angermeier, P.L. & Schlosser, I.J. 1989. Species-area relationships for stream fishes. *Ecology* 70: 1450–1462.
- Barbour, C.D. & Brown, J.H. 1974. Fish species diversity in Lakes. *The American Naturalist* 108: 473–489.
- Brönmark, C. 1985. Freshwater snail diversity: effects of pond area, habitat heterogeneity, and isolation. *Oecologia* 67: 127–131.
- Browne, R.A. 1981. Lakes as islands: the biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *Journal of Biogeography* 8: 75–83.
- Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species-area relationship. *The American Naturalist* 113: 791–833.
- Dodson, S. 1991. Species richness of crustacean zooplankton in European lakes of different sizes. *Verhandlungen der internationalen Vereinigung für Limnologie* 24: 1223–1229.
- Eadie, J.M.A. & Keast, A. 1984. Resource heterogeneity and fish species diversity in lakes. *Canadian Journal of Zoology* 62: 1689–1695.
- Eadie, J.M.A., Hurly, T.A., Montgomerie, R.S. & Teather, K.L. 1986. Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. *Environmental Biology of Fishes* 15: 81–89.
- Ecksten, K. 1908. Die Fischerei-Verhältnisse der Provinz Brandenburg zu Anfang des 20. Jahrhunderts. II. Teil. Berlin: Verlag des Fischerei-Vereins für die Provinz Brandenburg. 275 pp.
- Fryer, G. 1985. Crustacean diversity in relation to the size of

- water bodies: some facts and problems. *Freshwater Biology* 15: 347–361.
- Harvey, H.H. 1978. Fish communities of the Manitoulin Island lakes. *Verhandlungen der internationalen Vereinigung für Limnologie* 20: 2031–2038.
- Harvey, H.H. 1981. Fish communities of the lakes of the Bruce Peninsula. *Verhandlungen der internationalen Vereinigung für Limnologie* 21: 1222–1230.
- Ladiges, W. & Vogt, D. 1979. *Die Süßwasserfische Europas bis zum Ural und Kaspischen Meer*. 2nd edn. Hamburg: Paul Parey. 299 pp.
- MacArthur, R.H. 1972. *Geographical ecology. Patterns in the distribution of species*. New York: Harper & Row. xviii+267 pp.
- MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton, N.J.: Princeton University Press. xi+203 pp.
- Magnuson, J.J. 1976. Managing with exotics – a game of chance. *Transactions of the American Fisheries Society* 105: 1–9.
- Matuszek, J.E. & Beggs, G.L. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1931–1941.
- Matuszek, J.E. Goodier, J. & Wales, D.L. 1990. The occurrence of cyprinidae and other small fish species in relation to pH in Ontario lakes. *Transactions of the American Fisheries Society* 119: 850–861.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41: 611–627.
- Rahel, F.J. 1986. Biogeographic influences on fish species composition of Northern Wisconsin lakes with applications for lake acidification studies. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 124–134.
- Rote Liste Gefährdete Tiere im Land Brandenburg. 1992. Potsdam: Ministerium für Umwelt, Naturschutz und Raumordnung. 288 pp.
- Ryder, R.A., Kerr, S.R., Loftus, K.H. & Regier, H.A. 1974. The morphoedaphic index, a fish yield estimator – review and evaluation. *Journal of the Fisheries Research Board of Canada* 31: 663–688.
- Somers, K.M. & Harvey, H.H. 1984. Alteration of fish communities in lakes stressed by acid deposition and heavy metals near Wawa, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 20–29.
- Tonn, W.M. & Magnuson, J.J. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63: 1149–1166.
- Williams, C.B. 1964. *Patterns in the balance of nature*. London: Academic Press. 324 pp.