Assessing the Potential Extent of Damage to Inland Lakes in Eastern Canada due to Acidic Deposition. III. Predicted Impacts on Species Richness in Seven Groups of Aquatic Biota

C. K. Minns and J. E. Moore

Department of Fisheries and Oceans, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Bayfield Institute, 867 Lakeshore Road, P.O. Box 5050, Burlington, Ont. L7R 4A6 Canada

and D. W. Schindler[1]

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6 Canada

and M. L. Jones[2]

Environmental and Social Systems Analysts Ltd., Suite 102 - 66 Isabella Street, Toronto, Ont. M4Y 1N3 Canada

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Linked regional chemical and biotic models predicted that at least 20% of all lakes in 15 of 38 secondary watersheds in eastern Canada had lost at least 20% of their potential species richness given 1980 acidic sulphate deposition levels; 20% of lakes in 15 watersheds represents circa 55 000 lakes. Fish and molluscs were the most affected of seven aquatic taxonomic groups, and rotifers the least. Mean percent loss of potential richness in all of eastern Canada ranged from 5.0 to 9.5% for the seven groups of biota under 1980 acidic deposition. Sulphur dioxide emission reductions of 42% in Canada and the United States were predicted to reduce the number of affected watersheds to seven, leaving circa 25 000 lakes with 20% or more loss of potential richness. Greater acidic deposition reductions will be needed to minimize the biotic damage affecting large areas of eastern Canada.

Selon des modèles régionaux faisant le lien entre les conditions chimiques et biotiques, au moins 20 % de tous les lacs de 15 des 38 bassins hydrographiques secondaires de l'est du Canada, soit environ 55 000 lacs, ont perdu au moins 20 % de leur diversité biologique potentielle, en termes d'espèces, à cause des retombées acides sulfatées de 1980. Parmi les sept groupes taxonomiques aquatiques étudiés, les poissons et les mollusques étaient les plus touchés tandis que les rotifères étaient les moins touchés. La perte moyenne de diversité biologique potentielle due aux retombées acides de 1980 dans tout l'est du Canada variait de 5,0 à 9,5 % pour les sept groupes à l'étude. La réduction de 42 % des émissions d'anhydride sulfureux au Canada et aux États-Unis devrait faire passer le nombre de bassins touchés à sept; dans ces conditions, il y aurait encore environ 25 000 lacs dont la diversité biologique potentielle serait diminuée de 20 %. Il faudra que les retombées acides, touchant de vastes régions de l'est du Canada, diminuent davantage pour que les dommages environnementaux dont elles sont responsables soient réduits au minimum.

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Damage suffered by aquatic biota is a major consequence of lake acidification for both ecosystems and humans. Models must be used to assess this damage because acidic deposition is falling on vast areas and it is impossible to directly measure the conditions in every lake. While there are many models describing the link between acidic sulphur deposition and lake chemistry (cf. Reuss et al. 1986), there are few linking sulphur emissions and biotic damage. Predictions from models of biotic damage in conjunction with those of the chemical status of regional populations of lakes can provide measures of total impact on the resource. The resource considered here includes the more than 700 000 lakes in Canada east of the Ontario–Manitoba border and south of latitude 52 (Minns and Kelso 1986) and all the biota they contain now or contained prior to acidification. (This total number of lakes is most likely an underestimate as it is based on incomplete data — R. Helie, pers. comm., Environment Canada, Hull, Quebec). Only when the impact on the whole of this resource has been assessed, can the trade-offs between controlling the sources of acidic deposition and allowing receptor resource losses to be assessed for aquatic ecosystems. Thus, models linking cause and effect are the ecological component of a broad framework for impact assessment wherein the 'costs' (ecological, social, and economic) of controls are compared with the 'costs' of damage.

In this paper, we have used a model of biotic damage due to lake acidification developed by Schindler et al. (1989) to predict the potential magnitude and extent of damage by acidic deposition to the population of lakes in eastern Canada. The model

[1]Present address: Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9.

[2]Present address: Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, Box 5000, Maple, Ont. L6A 1S9.

is also used to predict the effects of different levels of sulphur dioxide emissions. An integrated regional model of lake acidification (DFO-ESSA) which links sulphur emissions through deposition to lake chemistry, is described in two earlier papers in this series; a chemical 'site' model for lake acidification was derived (Marmorek et al. 1990) and applied in a regional model of lakes' chemistry in eastern Canada (Jones et al. 1990). We have also assessed the regional model's sensitivity to parameter uncertainties (M. L. Jones, K. J. Heltcher, D. R. Marmorek, and C. K. Minns, unpubl. data).

The regional chemical modelling predicted an uneven distribution of chemical effects due to differences between the distributions of sensitive lakes and acidic deposition across eastern Canada (Jones et al. 1990). The degrees of chemical impact were characterized using a variety of pH and alkalinity threshold criteria. The various emission reduction scenarios did not produce a uniform response in all watersheds because of the uneven distribution of emission sources in North America. Overall, the watersheds with the highest proportion of lakes with alkalinity ≤ 0 $\mu eq \cdot L^{-1}$ or pH ≤ 5.5 were concentrated in south-central Ontario, south-eastern Quebec, and the southern Maritimes. The predictions of lake chemistry also indicated that proposed emission reductions of 42% at all Canadian and United States sources would not eliminate the problem of lake acidification in eastern Canada. In this paper, we have used the predicted chemical changes in lakes to predict the effects on lake biota.

Materials and Methods

Site Acidification Model

The derivation and analysis of the site model was described in detail by Marmorek et al. (1990). The model is based on principles of mass and charge balance applied to the prediction of alkalinity. The steady state prediction of alkalinity associated with a given level of acidic deposition ($[Alk]_\infty$) consists of two parts in the site model: predicting the original alkalinity before acidic deposition ($[Alk]_0$) and predicting the change in alkalinity due to acidic deposition ([Alk]). Acidic deposition (D_a) was defined as the sum of total wet and dry sulphate deposition less the equivalent of the base cation (calcium + magnesium + sodium + potassium) wet deposition minus wet chloride deposition (D_n). Nitrogen was not considered in the site model.

Changes in alkalinity were assumed to be the sum of three components: the acidity (negative alkalinity) expected if all the acidic deposition appeared in runoff, plus the alkalinity due to the proportion (F_w) of acidic deposition falling on the watershed that was neutralized via cation exchange processes in the soils, and the alkalinity due to the reduction of sulphate in the lake sediments. The proportion (F_L) of in-lake sulphate reduction is a function of lake flushing rate (Baker et al. 1986; Kelly et al. 1987); the higher the flushing rate, the lower the proportion of sulphate reduced in the lake.

The original alkalinity was calculated from a charge sum balance; current base cations corrected for the increase from the watershed due to acidic neutralization (F_w) less original chloride which was assumed to equal current chloride and less original sulphate which was assumed to be equivalent to base cation minus chloride deposition divided by runoff and reduced by in-lake neutralization. The watershed neutralization factor (F_w) was assumed to be a simple function of original base cations such that F_w rose linearly from zero at zero base cations concentration to one at 200 $\mu eq \cdot L^{-1}$. Above 200 $\mu eq \cdot L^{-1}$, F_w was one. The 200 $\mu eq \cdot L^{-1}$ level was chosen as a conservative figure and reduces lake acidification considerably except when the watershed to lake area ratio (r) is small (< 5:1).

Regional Acidification Model

Jones et al. (1990) described in detail the use of the 'site' model in the context of an integrated regional model of acidification. The site model was applied to the estimated total population of lakes in each of 38 secondary watersheds in eastern Canada (Fig. 1). The application to each watershed was achieved by deriving estimates of the distributions of original alkalinity ($[Alk]_0$), runoff (R), watershed to lake area ratio (r), and deposition (D). The alkalinity and r-ratio distributions were derived from regional surveys of lakes between 1979 and 1982 (Kelso et al. 1986). The data were assumed to be representative of all lakes by region and to represent the 'current' condition of lakes in this study. The runoff data were obtained from summaries produced by the Water Survey of Canada. The 1980 deposition fields for sulphate were provided by Atmospheric Environment Service (AES), and for base cations and chloride were obtained by the interpolation from network data provided by AES.

The distributions of model input variables were considered to be independent and for a given deposition scenario all combinations weighted by their relative frequency were used to predict the cumulative percentage distribution of steady state alkalinity (Jones et al. 1990). The alkalinity distributions were converted to pH distributions using the standard equations (Stumm and Morgan 1981) fitted to the survey data (Kelso et al. 1986). We used a pCO_2 of 2.8 to obtain the best fit between measured pH and alkalinity values (Jones et al. 1990).

The consequences of different emission control scenarios were predicted using a source–receptor model linking 1980 sulphur dioxide emissions to the observed 1980 regional pattern of acidic sulphate deposition (Olson et al. 1983). Differences between observed and predicted 1980 sulphate deposition were used to adjust the depositions predicted under other scenarios where emissions were changed. Four scenarios were considered: (1) 1980 deposition, (2) a Canada-only emission control program modelled on the existing federal–provincial agreement and equivalent to a 42% reduction at all Canadian sources from 1980 levels (Young 1988), (3) a Canada–United States emission control program equal to a 42% reduction at all sources in both countries, and (4) a worst case of 10% increase in emissions at all sources. The regional pattern of nonacidic sulphate deposition was assumed to be constant in all scenarios. The nonacidic sulphate deposition values were used to estimate original lake sulphate concentrations which were then used in conjunction with the lake survey chemistry data to estimate original alkalinity distributions.

The predictions for secondary watersheds were pooled for regions (Ontario, Quebec, and Maritimes) and all of eastern Canada using estimates of the number of lakes in each watershed as weights (Jones et al. 1990).

Potential Richness Model

From published lists of species occurrences in lakes and streams, Eilers et al. (1984) compiled lists of species' pH-minima, i.e. the minimum pH at which a species has been observed to survive in field conditions. They compiled lists for eight taxonomic groups of aquatic biota including algae (field minima

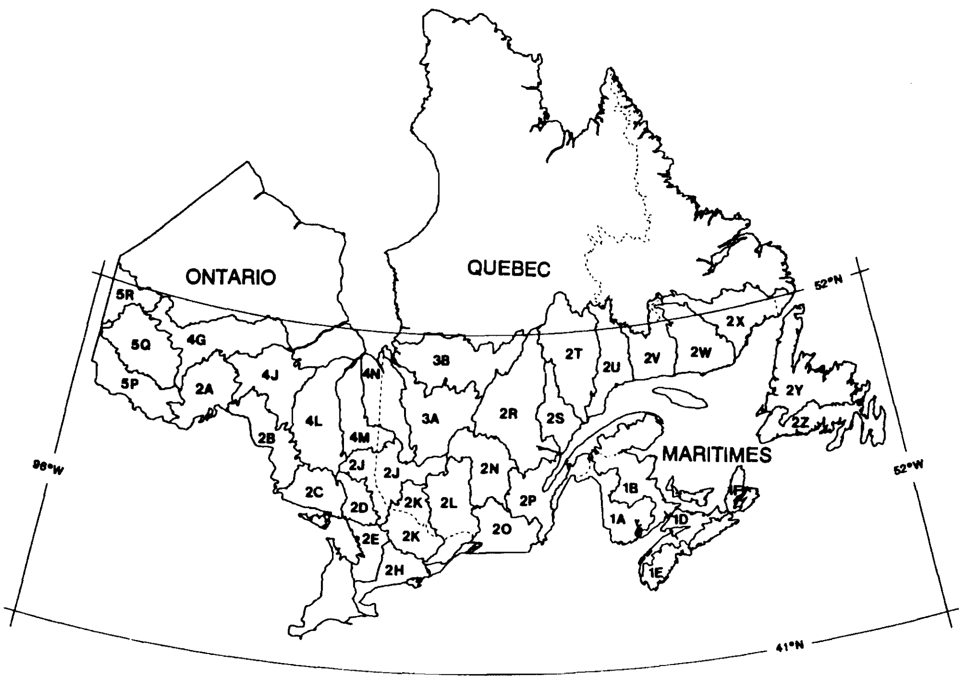

FIG. 1. Location of the 38 secondary watersheds.

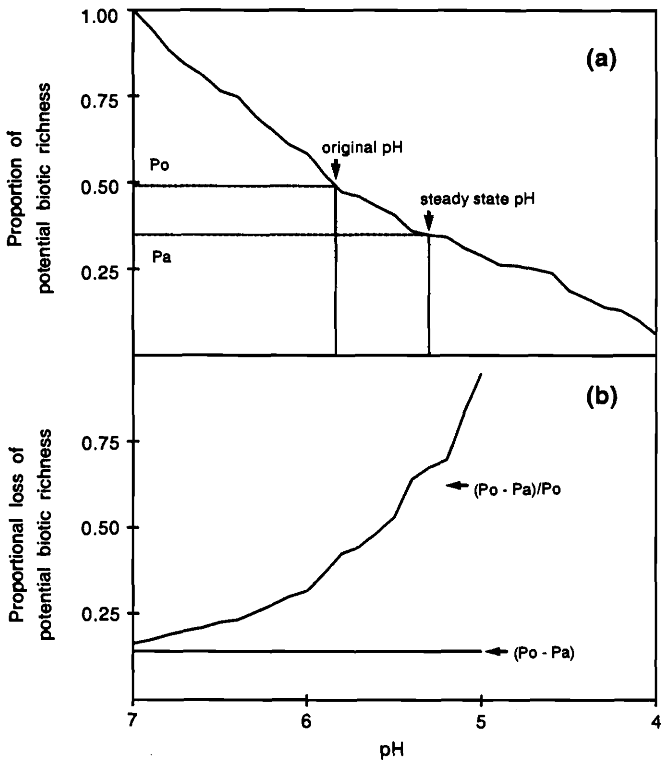

FIG. 2. An illustration of the percentage richness model showing: (a) the average response curve for seven taxonomic groups of aquatic biota and the calculation of percentage loss, $(P_0 - P_a)$ and (b) the contrast in calculated loss values with and without relative scaling.

for 264 species), rotifers (67), leeches (46), molluscs (92), crustaceans (185), insects (370), fish (66), and sponges (14). The data were obtained primarily from North American sources, particularly the north-eastern quadrant of the continent. They found that laboratory minima based on experimental data were typically about 1 pH unit lower than field values and that lake minima were usually lower than corresponding stream minima for the same or similar orders or families of biota. By taxonomic group, they graphed the proportion of species found at various pH's from 7.0 to 4.0 in 0.1 intervals; the proportion at pH 7.0 was assumed to be 1.0 (100%). If the observed pH minimum for a species in the field is 6.0, the species is considered extinct at 5.9. The curves for each group followed a sigmoid trend with declining pH. Joseph Eilers (pers. comm., Northrop Services, Corvallis, Oregon) provided us with the original database allowing us to reconstruct the pH-minima curves rather than interpolate from a graph in the published report. The data on sponges were not used here because of the small number of species.

Mills and Schindler (1986) brought the curves of Eilers et al. (1984) to a wider audience. They showed that the compiled curves mirrored the biotic response to declining pH at the ELA Lake 223 acidification experiment. Subsequently, Schindler et al. (1989) developed a model of biotic damage based on the curves of Eilers et al. (1984). The pH-minima curves are used to estimate the percentage loss of potential richness when a lake's pH is changed from an original, nonacidified, level to that resulting from the input of acidic deposition as shown in Fig. 2a where the curve is the mean of the sigmoid curves for the seven taxonomic groups considered. Schindler et al. (1989) divided the proportional loss of potential richness $(P_0 - P_a)$ by the original proportion (P_0) to estimate the relative damage (Fig. 2b). A 20% loss applied at various points along the curve (Fig. 2a) results in a rising relative value with declining pH thereby exaggerating damage in lakes which had a low pH originally and producing a measure of damage which is not comparable at different points along the pH axis. Here we have used the actual percentage loss of potential richness $(P_0 - P_a)$ as a measure of biotic damage. This latter value is directly proportional to numbers of species if the actual original richness is known.

We have used the phrase 'potential richness' to highlight the fact that we are not predicting changes in actual richness in individual lakes. The assemblage of species found in a partic-

TABLE 1. Predicted mean percentage loss of richness for seven groups of aquatic biota and the mean percentage loss of the seven groups using the 1980 deposition scenario by secondary watershed and region in eastern Canada. Highest and lowest regional means with asterisk and underline, respectively.

Region	Algae	Rotifers	Leeches	Molluscs	Crustaceans	Insects	Fish	Groups' mean
Ontario mean	5.9	4.3	5.3	6.2	4.2	5.6	6.6*	5.4
2A	0.1	0.0	0.3	0.2	0.1	0.2	0.0	0.2
2B	1.9	0.9	1.9	2.2	1.3	2.1	1.8	1.7
2C	22.6	17.5	18.8	22.0	16.3	20.3	25.8	20.5
2D	25.4	18.3	22.4	25.7	17.7	23.5	28.0	23.0
2E	27.7	20.2	23.7	27.5	19.3	25.2	30.5	24.9
2H	17.5	15.9	13.7	16.6	14.7	15.3	21.8	16.5
2J	9.8	4.6	10.0	10.1	5.6	9.9	8.2	8.3
2K	18.2	13.8	13.7	16.7	12.8	15.7	20.8	16.0
4G	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4J	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4L	0.4	0.4	0.6	0.7	0.4	0.6	0.5	0.5
4M	0.4	0.4	0.6	0.7	0.4	0.6	0.5	0.5
4N	0.3	0.1	0.5	0.5	0.3	0.4	0.3	0.3
5P	0.8	0.4	0.6	0.6	0.4	0.7	0.6	0.6
5Q	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5R	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quebec mean	11.0	5.7	10.6	12.4*	6.4	11.1	10.7	9.7
2J	9.3	1.6	9.8	8.0	3.7	9.0	4.5	6.6
2K	12.8	4.7	7.8	8.8	5.2	10.0	10.5	8.5
2L	7.7	4.0	8.4	8.4	5.0	8.0	6.5	6.9
2N	17.7	6.8	16.3	16.8	8.5	17.1	13.2	13.8
2O	4.8	1.0	6.3	5.2	2.5	5.4	2.2	3.9
2P	14.7	5.8	12.9	14.0	6.7	13.6	12.0	11.4
2R	8.4	3.4	9.0	9.9	4.8	8.9	6.8	7.3
2S	14.4	12.3	14.7	18.2	11.5	14.9	19.0	15.0
2T	10.5	7.3	9.8	12.7	7.0	10.8	11.5	9.9
2U	11.5	8.1	10.8	14.0	7.9	11.8	12.9	11.0
2V	12.9	6.2	11.0	14.8	6.7	12.4	13.4	11.1
2W	11.4	5.2	9.9	12.9	6.0	10.9	11.6	9.7
2X	10.5	4.6	8.8	11.6	5.4	9.9	10.6	8.8
3A	10.6	5.5	11.0	12.2	6.5	11.1	9.6	9.5
3B	7.4	2.6	8.0	8.1	4.0	7.8	5.4	6.2
Maritimes mean	8.6*	4.6	7.4	8.6*	4.6	8.2	7.6	7.1
1A	21.7	17.2	21.3	24.5	16.2	21.5	25.1	21.1
1B	16.1	10.8	15.5	19.5	10.5	16.7	17.4	15.2
1D	18.8	12.2	14.6	22.0	11.3	18.0	21.8	17.0
1E	17.7	21.6	17.5	26.9	14.6	19.6	29.3	21.0
1F	15.2	9.0	12.3	17.8	8.6	14.8	17.0	13.5
2Y	6.0	3.7	6.0	6.7	3.6	6.0	6.0	5.4
2Z	10.2	3.7	7.6	8.3	4.5	9.0	7.2	7.2
E. Canada mean	8.9	5.0	8.3	9.5	5.3	8.6	8.5	7.7

ular lake is a subset of the pool of species present in the region and actual richness may be determined by other factors such as lake size (Matuszek and Beggs 1988; Minns 1990).

We predicted biotic damage using predicted cumulative distributions of pH in populations of lakes by watershed and emission–deposition scenarios in combination with the potential richness model. The distribution of original pH values was used to derive P_0 values at each percentile point from 1 to 100 with an interval of 1. Then for each scenario, the same procedure was used to derive P_a values. Percentiles from both the original and scenario distributions were paired and subtracted to give the predicted percentage loss of richness $(P_0 - P_a)$ distribution by percentiles. The percentile distributions of percentage loss were summarised in three ways: (1) tabulation of the mean percent loss of potential richness $(P_0 - P_a)$ by secondary watershed, (2) plots of cumulative percentiles of lakes ordered by decreasing values of $(P_0 - P_a)$, and (3) shaded regional maps showing those secondary watersheds meeting dual criteria of $(P_0 - P_a)$ values and cumulative percentage of lakes affected.

Results

Given the predicted percentile distributions of pH for lakes by secondary watershed under the 1980-base deposition scenario and prior to the occurrence of acidic deposition (Jones et al. 1990), the mean percentage richness loss $(P_0 - P_a)$ ranged from 0.0 to 30.5 across the seven taxonomic groups of aquatic biota and 38 watershed areas (Table 1). The seven groups showed a similar response pattern across watersheds. Rotifers and crustaceans were predicted to have the lowest losses and molluscs, algae, and fish the highest losses with the other two groups (leeches and insects) being closer to the highest values.

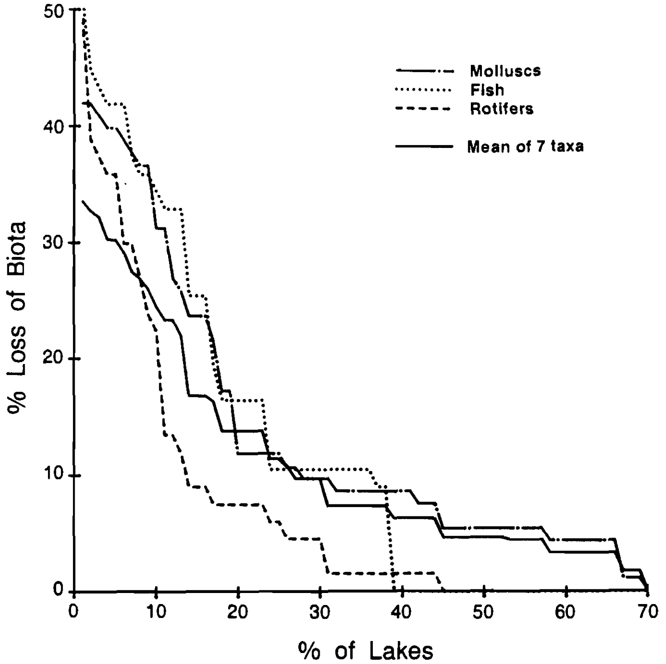

FIG. 3. Cumulative percentage of lakes in eastern Canada (X axis) predicted to have a given or greater percentage loss of richness (Y axis) given the 1980 deposition scenario: Molluscs, fish, rotifers, and the mean of seven taxonomic groups.

Molluscs were predicted to have the highest mean losses among groups in 16 of 38 watersheds and fish in eight of 38. Within watersheds, the unweighted mean loss was representative of the range, e.g. 24.9 versus 19.3 to 30.5% in Ontario watershed 2E and 15.0 versus 11.5 to 19.0% in Quebec watershed 2S. Therefore the unweighted groups' mean percent loss of richness for the seven groups was considered to be a good indicator of the losses for each watershed.

Across eastern Canada, the groups' mean losses showed considerable variation as was expected from the variations in the distribution of lake chemical sensitivity and in the level of acidic deposition. In Ontario, watersheds with the highest group means were clustered in the south-central portion of the province on the Canadian Shield, e.g. watersheds 2C, 2D, 2E, 2H, and 2K had mean losses of 16.0 to 24.9%. In Quebec, the range of losses was less than in Ontario with the highest values occurring in watersheds 2P (groups' mean 11.4%), 2N (13.8), and 2S (15.0). Groups' mean values were higher in the Maritimes than in Quebec with the highest mean losses being in watersheds 1A (21.1%) in New Brunswick and 1E (21.0) in Nova Scotia. Over all of eastern Canada south of latitude 52, the predicted groups' mean potential loss of aquatic biota was 7.7 with a range of mean losses among the seven taxonomic groups of 5.0 to 9.5%.

While the mean response may be a good indicator, the distribution of responses within a watershed may be uneven with some lakes sustaining more damage and others less. Within a region, lakes with high original alkalinities (> 150 $\mu eq \cdot L^{-1}$) are relatively unaffected while lakes with low ones (< 50 $\mu eq \cdot L^{-1}$) are altered considerably. To examine this situation, we ordered the percentiles of lakes by their percentage loss of richness and plotted the cumulative percentage of lakes having a given or greater level of damage to show the distribution of damage under the various deposition scenarios. While the groups' mean loss was predicted to be 7.7% for all of eastern Canada, losses greater than 30% were predicted in about 5% of lakes (Fig. 3). Rotifers were predicted to be the least affected taxonomic group and molluscs and fish the most affected with losses of more than 10% in more than 25% of lakes. Although the pH minima curve for molluscs begins to decline at higher pH's than does the fish curve (Eilers et al. 1984), there are relatively few high pH lakes (Jones et al. 1990). Therefore when the chemical status distributions were linked to the biological response curves of the potential richness model, the damage distributions showed fish and molluscs were affected to similar levels in more than 35% of lakes but fish were unaffected in more than 60% of lakes. The mean curve for the seven groups of biota fell below the mollusc curve for the first 20% of lakes and followed the mollusc curve thereafter.

While the cumulative damage curves illustrate the distribution of damage among populations of lakes in a region, they cannot be used to illustrate the spatial pattern of biotic damage. However, these results did suggest that dual criteria incorporating two percentage values might be used to prepare a statement of biotic damage: the percentage of lakes in each area exhibiting a given or greater percentage loss of potential richness.

We examined a range of dual percentage criteria, from 10 to 50%, to find a combination which highlighted the contrast between the various deposition scenarios and between taxonomic groups. We arbitrarily selected 20:20, i.e. 20% or more of lakes predicted to have 20% or more loss of potential richness, on the grounds that 20% is a significant portion of any resource. Taking the 1980 deposition scenario, we looked at the geographical distribution of secondary watersheds meeting the criteria for fish, molluscs, rotifers, and the mean of seven taxonomic groups (Fig. 4). The map for molluscs (Fig. 4B) showed a large proportion (53%) of watersheds met the 20:20 criteria, whereas the map for rotifers (Fig. 4D) showed a substantially smaller proportion (26%). The groups' mean and fish maps showed similar but intermediate extents of effect. Lake resources in large portions of eastern Canada were predicted to have 20:20 damage given levels of acidic deposition prevailing in 1980. As indicated (Table 1), the affected areas were mainly south-central Ontario, Quebec along the north shore of the St. Lawrence, and the southern Maritimes (Fig. 4).

Using the groups' mean percent loss of richness, we examined the mean losses predicted as a result of the three emission control scenarios relative to the 1980 deposition scenario and the current conditions (Table 2). For the 42% reduction in Canadian emissions, the biggest recoveries were predicted for south-central Ontario and the smallest for the Maritimes. When emissions were reduced by 42% in both Canada and the United States, there were further recoveries in all three regions, especially in Ontario. A 10% increase in emissions caused the mean loss of richness in affected watersheds to increase slightly (1–2%). The estimated current mean loss of richness based on the regional lake survey data was the lowest of all scenarios for most watersheds. Watersheds in Ontario around Sudbury (2C and 2D) and in Nova Scotia (1D, 1E, 1F) had current values similar to or worse than those predicted for 1980 emission levels. Most watersheds were predicted to sustain further lake acidification and therefore further biotic losses as they came into a steady state with 1980 emission levels. According to the lake survey data (Kelso et al. 1986), current lake sulphate concentrations were lower than values predicted from sulphate deposition in 1980 and therefore were not in steady state with deposition chemistry. Therefore predicted lake conditions under

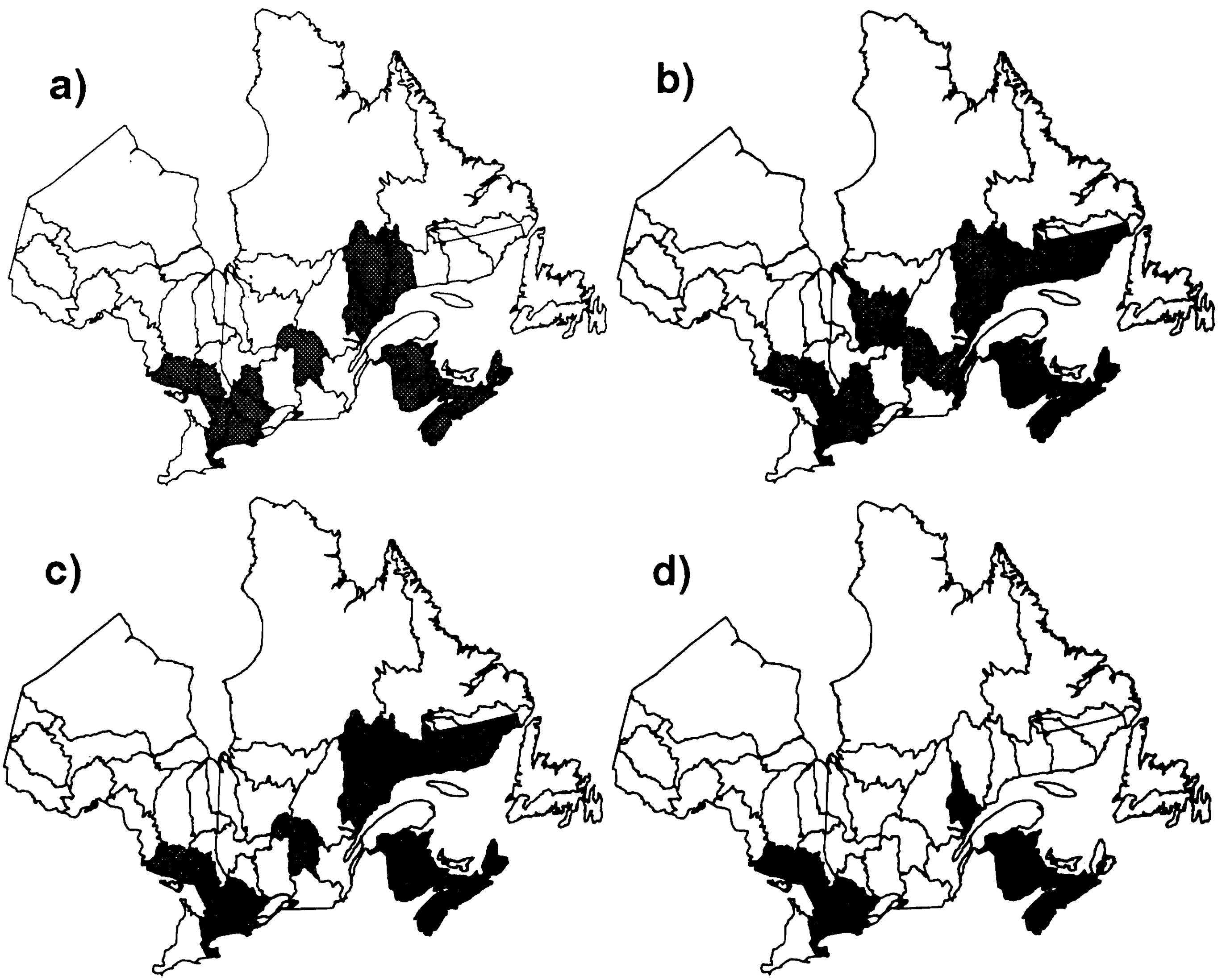

FIG. 4. Secondary watersheds in eastern Canada predicted to have 20% or more richness loss in 20% or more of lakes given the 1980 deposition scenario: (a) the mean of seven taxonomic groups, (b) molluscs, (c) fish, and (d) rotifers.

different emission control scenarios must be assessed against the predicted steady state conditions under the levels of acidic deposition prevailing in 1980 and not against the current conditions measured in the surveys.

The percentile distributions of damage showed the response to the emission control scenarios was largely confined to about 30% of the lakes with the most affected portions of the lake populations showing the greatest improvements (Fig. 5). None of the emission reductions reduced the level of percentage loss below 25% for all portions of the lake population; varying percentages of the lake populations exhibited levels of loss greater than 20%.

When the dual criteria were applied, the patterns of watersheds predicted to have 20% or more mean losses in 20% or more of lakes varied considerably under the various deposition scenarios (Fig. 6). The current chemical conditions predicted that those damage levels were present in a few south-central Ontario watersheds and throughout New Brunswick and Nova Scotia. The pattern expanded to include more watersheds in Ontario and a large part of Quebec under the 1980 deposition scenario. The Canadian emission controls were predicted to reduce the affected areas by three watersheds in Quebec and by one each in Ontario and the Maritimes. Adding United States controls removed the remaining effects from Nova Scotia (1D, 1E) and one watershed in Ontario. Increased emissions expanded the area affected, particularly in Quebec.

Discussion

Uncertainties in the Chemical Predictions

The predictions of the site model have been shown to be most sensitive to uncertainty in the values of acidic sulphate deposition and original sulphate (M. L. Jones, K. J. Heltcher, D. R. Marmorek, and C. K. Minns, unpubl. data). Deposition monitoring networks in Canada are few in number and deposition rates for most areas are obtained by interpolation. There is also evidence of considerable variation at individual sites depending on the placement of collectors. There are no data sets describing either the original sulphate concentrations in lakes prior to the occurrence of acidic deposition or original sulphate deposition from the atmosphere plus any inputs from soils in the watersheds. Yet, it is essential that we be able to estimate the change in lake sulphate or the change in sulphate

TABLE 2. Predicted mean percentage loss of richness for the mean of seven groups of aquatic biota given five emission scenarios by secondary watershed and region in eastern Canada.

		42% Decrease			
Region	1980	Canada	Canada + United States	10% Increase	Current
Ontario mean	5.4	4.5	3.4	6.0	4.2
2A	0.2	0.2	0.1	0.2	0.2
2B	1.7	1.5	1.0	1.8	1.5
2C	20.5	18.3	14.2	21.8	21.8
2D	23.0	16.9	12.0	25.2	23.1
2E	24.9	17.6	12.3	27.1	10.6
2H	16.5	13.8	11.4	17.4	4.1
2J	8.3	5.8	4.0	9.3	7.1
2K	16.0	12.5	9.5	17.1	3.5
4G	0.0	0.0	0.0	0.0	0.0
4J	0.0	0.0	0.0	0.0	0.0
4L	0.5	0.5	0.4	0.6	0.1
4M	0.5	0.5	0.3	0.6	0.1
4N	0.3	0.3	0.1	0.4	0.1
5P	0.6	0.6	0.5	0.6	0.2
5Q	0.0	0.0	0.0	0.0	0.0
5R	0.0	0.0	0.0	0.0	0.0
Quebec mean	9.7	7.8	6.0	10.6	7.4
2J	6.6	4.2	3.0	7.3	6.9
2K	8.5	4.6	2.4	9.9	6.0
2L	6.9	5.4	4.2	7.4	4.5
2N	13.8	10.5	7.8	15.1	8.2
2O	3.9	3.1	2.2	4.5	4.2
2P	11.4	9.3	7.1	12.3	10.6
2R	7.3	5.9	4.7	8.1	7.1
2S	15.0	12.7	10.7	16.0	8.9
2T	9.9	8.0	6.2	11.0	9.5
2U	11.0	8.9	7.2	11.6	9.5
2V	11.1	9.0	6.7	12.2	6.5
2W	9.7	8.1	6.6	10.7	6.5
2X	8.8	7.3	6.0	9.5	6.3
3A	9.5	7.2	5.3	10.4	6.8
3B	6.2	5.1	4.3	6.6	7.2
Maritimes mean	7.1	6.4	5.5	7.6	6.6
1A	21.1	19.4	16.0	22.1	14.7
1B	15.2	13.4	10.4	16.3	15.0
1D	17.0	14.5	9.9	19.0	24.2
1E	21.0	18.0	12.5	23.0	36.8
1F	13.5	12.1	10.4	14.5	24.2
2Y	5.4	4.9	4.3	5.8	2.6
2Z	7.2	6.5	5.6	7.5	9.8
E. Canada mean	7.7	6.5	5.2	8.4	6.3

deposition if we are to predict the degree of acidification. Other factors, like F_w and runoff, affect the lake chemistry predictions, but to a lesser degree. Taken alone F_w, the proportion of neutralization in the watershed, is important but not in the aggregate if one accepts that F_w varies monotonically in some fashion with original cation levels which ought to reflect background cation release rates from the rocks and soils of the watershed.

Our ability to predict the chemistry of lakes in relation to varying levels of acidic sulphate deposition hinges on a number of assumptions. Many of those assumptions are not readily tested but represent the prevailing consensus and err in a conservative manner, e.g. F_w varies with our estimates of original base cation levels but reaches a maximum value of 1

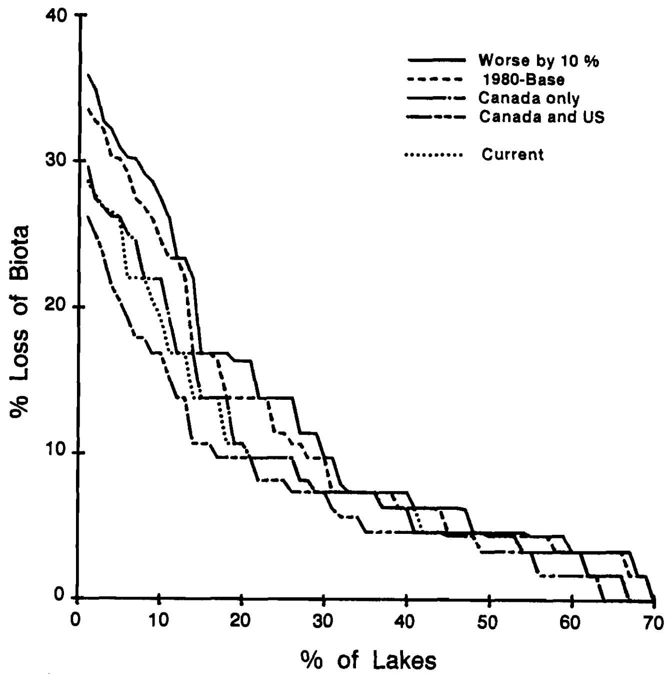

FIG. 5. Cumulative percentage of lakes in eastern Canada predicted to have a given or greater percentage richness loss for the mean of seven groups of aquatic biota given: a 10% increase of emissions, 1980 deposition, a 42% reduction of Canadian emissions, a 42% reduction of Canadian and United States emissions, and current conditions.

at a relatively low level of base cations. At the very least, the predictions may be considered useful on a relative scale. This view is probably too conservative, since the disagreements between values predicted from 1980 deposition levels and the 'current' condition as measured in surveys were not substantial (Jones et al. 1990).

In connection with our evaluation of emission control scenarios relative to predicted 1980 and observed 1979 to 1982 lake chemistry in eastern Canada, we must note that decreases in deposition and improvements in lake chemistry have been observed in the Sudbury area of Ontario between 1974 to 1976 and 1981 to 1983 (Keller and Pitblado 1986) and in the Algoma district in Ontario between 1979 and 1985 (Kelso and Jeffries 1988). Kelso and Jeffries (1988) also found evidence of reinvasion and expansion of fish stocks in some lakes where pH had increased. Thus the situation now, in 1990, likely lies somewhere between the conditions predicted in 1980 and those predicted with a 42% emission reduction in Canada and the United States.

Percent Loss of Species Richness

The model of biotic damage used here could overstate the amount of loss because potential compensatory mechanisms are ignored. If, as is proposed in the theory of island biogeography (MacArthur and Wilson 1967), the species richness in a lake, another sort of island, is a result of the balancing of immigration and extinction rates, lake acidification will increase the extinction rate and thereby reduce richness. There may be a delay in the establishment of a new richness equilibrium due to low rates of immigration and/or an associated lag in the increase of the immigration rate. Observed species richness may fall below the equilibrium point. After the initial rise, extinction rates will gradually decline to an intermediate level with the arrival of acid-tolerant species and the lessened extinction rates for the

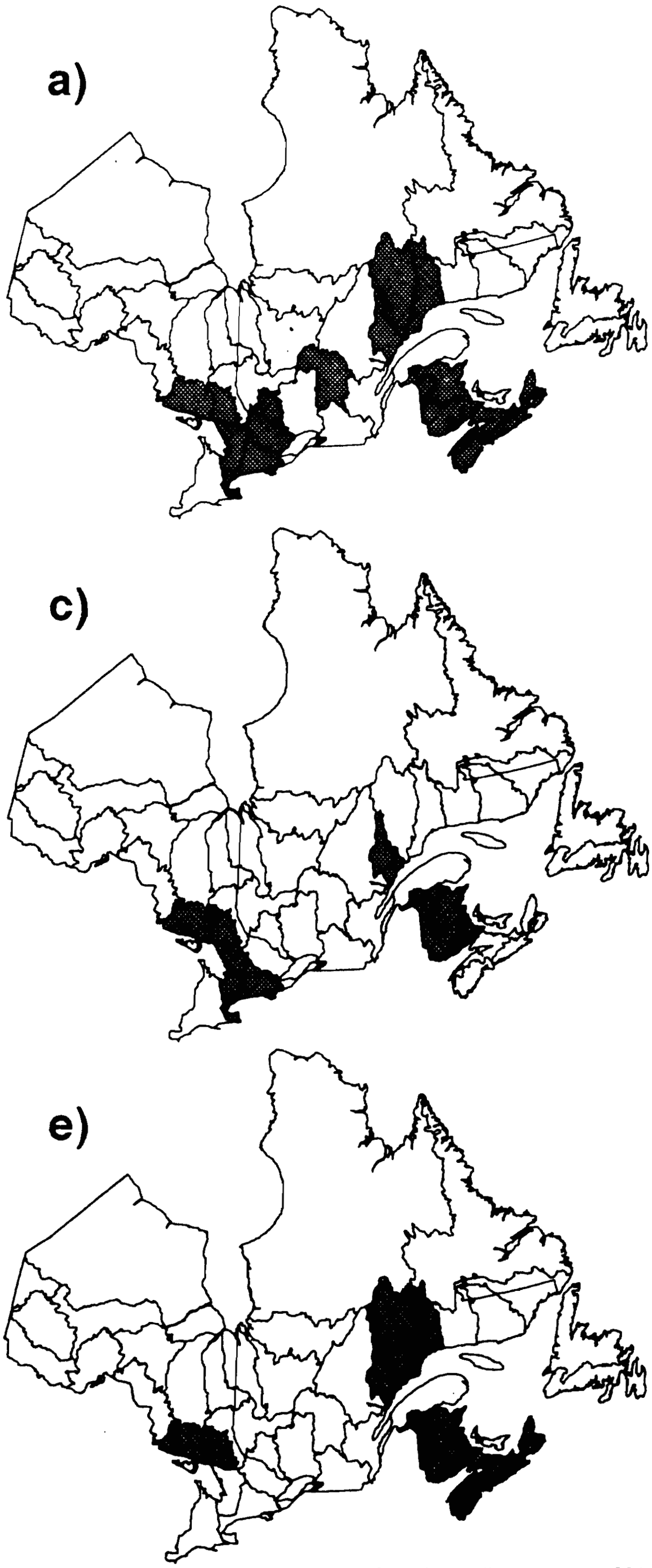

FIG. 6. Secondary watersheds in eastern Canada predicted to have 20% or more richness loss in 20% or more of lakes for the mean of seven groups of aquatic biota given: (a) 1980 deposition, (b) a 42% reduction of Canadian emissions, (c) a 42% reduction of Canadian and United States emissions, (d) a 10% increase of emissions, and (e) current conditions.

species persisting in the lake. However, if acidification is a regional problem affecting large numbers of lakes, as is predicted for eastern Canada, immigration rates might also be reduced through a widespread reduction in species richness that limits the supply of immigrants to acid-tolerant species, thereby decreasing compensation. This would be true if the size of the regional species pool influences the level of immigration. Southwood and Kennedy (1983) distinguished between immigrants and colonizers; the former include many species which enter new ecosystems but fail to persist and the latter include those which arrive and succeed. Among the immigrants will be acid-intolerant species. Extinction only applies to those species 'established' in the ecosystem. Where lake acidification occurs, there may be many immigrants but few colonizers. Thus it is likely the percentage loss of biotic richness may overestimate the level of damage but unlikely immigration can completely replace acid-related losses.

The percent loss of richness model can be used to describe both loss and recovery but only at steady state. Long-lived species may linger in a lake long after reproduction has ceased. As noted above, recovery may be long-delayed by low immigration rates particularly in larger forms such as fish which have fewer opportunities to move between lakes and take longer to mature and produce a population compared to smaller organisms like insects and algae.

Among the disadvantages of the biotic damage model used here are the equal treatment of all species within a taxonomic group and the inability to reflect the differential values humans attach to different species. Within taxonomic groups a lake's biomass and production are unevenly allocated among the species present and the acid-sensitive species may account for a large portion of the total. Humans selectively exploit piscivores such as lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*) and loss of populations of these and similar species is considered to be of far greater importance than the loss of less valued species.

The species richness losses considered here and in Eilers et al.'s (1984) compilation are more closely linked to regional species pools than to the richness of individual lakes. Minns (1990) has shown that local (i.e. lake) richness is usually a small proportion of regional (i.e. secondary watershed) richness. In keeping with island biogeography concepts (MacArthur and Wilson 1967), local richness is related to lake size and associated habitat constraints. Regional richness is tied to evolutionary and geological events (Ricklefs 1987). A next step in the development of richness models as a basis for measuring the impact of acidification and other stresses should be the development of local richness models. Lake richness models tied to the potential richness model should provide a basis of making absolute estimates of the numbers of species populations lost or recovered in relation to changing emission levels.

Predicted Scale and Extent of Biotic Damage

We have chosen relatively high damage criteria as a basis for damage assessment: 20% or greater percentage loss of richness in 20% or greater of lakes in a watershed or region. Dual criteria are needed to allow consideration of both the level of response and the absolute magnitude and extent of effects. In percentage terms, the predictions shown here are little different from the chemical predictions reported earlier (Jones et al. 1990). However, measuring the damage in biological units directly addresses the primary basis for our concern about the potential impacts of acidic deposition. Schindler et al. (1989) predicted comparable levels of biotic damage in lakes across the northeastern United States. The predictions shown here indicate there was already a large area showing the effects of lake acidification and that if 1980 acidic deposition levels had prevailed, more losses would have occurred. The emission reduction scenarios predict that the expected level of damage can be reduced. Indeed in Ontario, Kelso and Jeffries (1988); Keller and Pitblado (1986); and Beggs and Gunn (1986) have already reported improvements in lake chemistry and biota in Algoma and Sudbury area lakes in response to decreases in acid deposition. However, the scenarios presented here also indicate further emission reductions beyond those already achieved, being implemented, or proposed will be needed if biotic losses are to be reduced to a minimum.

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We wish to note the work of our colleagues, Dave Marmorek and Floyd Elder, on the integrated regional model of acidification. We thank John Kelso and Ken Mills in Sault Ste. Marie and Winnipeg, respectively for comments and suggestions on an earlier draft. The comments of the reviewers (Mark Hansen and Anonymous) helped polish the final draft.

References

Baker, L. A., P. L. Brezonik, and C. D. Pollman. 1986. Model of internal alkalinity generation: sulphate retention component. Water Air Soil Pollut. 31: 89–94.

Beggs, G. L., and J. M. Gunn. 1986. Response of lake trout (*Salvelinus namaycush*) and brook trout (*Salvelinus fontinalis*) to surface water acidification in Ontario. Water Air Soil Pollut. 30: 711–718.

Eilers, J. M., G. L. Lien, and R. G. Berg. 1984. Aquatic organisms in acidic environments: a literature review. Wisc. Dep. Nat. Resourc. Tech. Bull., 150: 18 p.

Jones, M. L., Minns, C. K., D. R. Marmorek, and F. C. Elder. 1990. Assessing the potential extent of damage to inland fisheries in eastern Canada due to acidic deposition. II. Application of the regional model. Can. J. Fish. Aquat. Sci. 47: 67–80.

Keller, W., and J. R. Pitblado. 1986. Water quality changes in Sudbury area lakes: a comparison of synoptic surveys in 1974–76 and 1981–83. Water Air Soil Pollut. 19: 285–296.

Kelly, C. A., J. W. M. Rudd, R. H. Hesslein, D. W. Schindler, P. J. Dillon, C. T. Driscoll, S. A. Gherina, and R. E. Hecky. 1987. Prediction of biological acid neutralization in acid-sensitive lakes. Biogeochem. 3: 129–140.

Kelso, J. R. M., C. K. Minns, J. E. Gray, and M. L. Jones. 1986. Acidification of surface waters in eastern Canada and its relationship to aquatic biota. Can. Spec. Publ. Fish. Aquat. Sci. 87: 42 p.

Kelso, J. R. M., and D. S. Jeffries. 1988. Response of headwater lakes to varying atmospheric deposition in north-central Ontario, 1979–85. Can. J. Fish. Aquat. Sci. 45: 1905–1911.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Marmorek, D. R., M. L. Jones, C. K. Minns, and F. C. Elder. 1990. Assessing the potential extent of damage to inland fisheries in eastern Canada due to acidic deposition. I. Development and evaluation of a simple 'site' model. Can. J. Fish. Aquat. Sci. 47: 55–66.

Matuszek, J. E., and G. L. Beggs. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

Mills, K. H., and D. W. Schindler. 1986. Biological indicators of lake acidification. Water Air Soil Pollut. 30: 779–789.

Minns, C. K. 1990. Factors affecting fish species richness observed in Ontario's inland lakes. Trans. Am. Fish. Soc. 118: 533–545.

Minns, C. K., and J. R. M. Kelso. 1986. Estimates of existing and potential impact of acidification on the freshwater fishery resources and their use in eastern Canada. Water Air Soil Pollut. 31: 1079–1090.

Olson, M. P., E. C. Voldner, and K. K. Oikawa. 1983. Transfer matrices from the AES-LRT model. Atmosphere-Ocean. 21(3): 344–361.

Reuss, J. O., N. Christopherson, and H. M. Seip. 1986. A critique of models for freshwater and soil acidification. Water Air Soil Pollut. 30: 909–930.

Ricklefs, R. E. 1987. Community diversity: relative role of local and regional processes. Science (Wash., DC) 235: 167–171.

Schindler, D. W., S. E. M. Kasian, and R. H. Hesslein. 1989. Biological impoverishment in lakes of the midwestern and northeastern United States from acid rain. Environ. Sci. Technol. 23(5): 573–580.

SOUTHWOOD, T. R. E., AND C. E. J. KENNEDY. 1983. Trees as islands. Oikos 41: 359–371.

STUMM, W., AND J. J. MORGAN. 1981. Aquatic chemistry (2nd ed.). John Wiley and Sons, New York, NY. 780 p.

YOUNG, J. W. S. 1988. Source–receptor relationships: the Canadian experience, p. 151–163. *In* Acid rain: the relationship between sources and receptors. J. C. White [ed.] Elsevier, New York, NY.