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# COMMUNITY ANALYSIS OF FISH POPULATIONS IN HEADWATER LAKES OF NEW BRUNSWICK AND NOVA SCOTIA

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Five fish community assemblages, based upon surveys with gill-nets, were identified in Maritime headwater lakes. These were (1) brook trout only, (2) brook trout-white sucker, (3) multispecies with white sucker, yellow perch and brown bullhead most frequent members, (4) yellow perch only and (5) multispecies with smallmouth bass and/or white perch. The two lake physico-chemical parameters most important in determining fish community were pH and lake area. Brook trout-only lakes had the least area, while yellow perch-only lakes were the most acidic (mean pH of 4.60). It is suggested that lakes containing only yellow perch may have once contained assemblage (3), but have become too acidic for any but yellow perch.

Cinq groupements de poissons, bases sur des relevès au moyen de filets, ont été identifiées dans quelques lacs eaux—souches des Provinces Maritimes. Ceux-ci comprenaient (1) l'omble de fontaine seul, (2) l'omble de fontaine et le meunier noir, (3) plusieurs espèces comprenant le meunier noir, la perchaude et la barbotte brune en majorité, et (4) la perchaude seule. Les deux paramètres physico-chimiques de plus grande importance quant aux groupements de poissons sont le pH et la superficie des lacs. Les lacs avec l'omble seul ont la moindre superficie, tandis que les lacs contenant la perchaude seule sont les plus acidiques (un pH moyen de 4.60). On suggère que les lacs contenant seulement la perchaude contenaient dans le passé le groupement (3), mais sont devenus trop acidiques pour maintenir aucune espèce autre que la perchaude.

## Introduction

The possible loss of fish populations has been a primary concern of scientists studying the ecological effects of acid precipitation. The effects of acidification on fish populations are most easily discerned where adequate historical data on both fish populations and water chemistry exists. Beamish and Harvey (1972) reported acidification of La Cloche Mountain lakes in Ontario and associated losses of fish species. Schofield (1976) associated losses of fish populations in lakes in the Adirondack Mountains with acidification of these waters. In Scandinavia, similar relationships have been proposed (Muniz *et al.*, 1976; Snekvik, 1974). Even in the absence of good historical data, lake surveys are useful in examining how physico-chemical parameters of lakes can influence fish populations. Thus, concern about lake and stream acidification has resulted in many surveys of fish populations with concomitant water chemistry analyses. This report presents results of the Maritime portion of a survey of headwater lakes in eastern Canada done to estimate the potential for lake acidification in this region (Kelso *et al.*, 1986).

Recurrent questions asked by those who perform analyses on data sets from large numbers of lakes are whether fish populations can be classified into a few general assemblage types and, if so, whether such assemblages are related to any physico-chemical properties of the lakes where they occur.

Several trends have been shown to consistently occur in published accounts of lake survey data. Species richness (i.e., number of species) tends to increase with increasing lake area (Haines *et al.*, 1986; Eadie *et al.*, 1983; Johnson *et al.*, 1977; Rahel, 1984). MacArthur and Wilson (1967) formulated a general theory to explain the relationship between species richness and island size, wherein under equilibrium conditions a balance is struck between immigration of new species and extinction of those present. The slope relating species richness to lake area has been found to lie within the range of values published for island groups (Matuszek and Beggs, 1988). Whether or not the species richness-lake area relationship reflects immigration-extinction phenomena or reflects increased habitat diversity in larger lakes is a matter of discussion (e.g. Eadie *et al.*, 1983).

Another observed trend is that associated with lake eutrophication (Colby *et al.*, 1972; Leach *et al.*, 1977), where salmonid communities of low diversity are replaced successively by centrarchid and cyprinid communities as eutrophication progresses. Rahel (1984), in an analysis of lakes at various stages of dystrophication, could separate three distinct fish assemblages. An *Umbra*-yellow perch assemblage was characteristic of the most acidic lakes. Two other assemblages "centrarchid" and "cyprinid" were related to lake size, and low winter oxygen tension, respectively. Van Leuven and Oyen (1987), in an analysis of Netherlands' ponds and lakes, also found *Umbra* to be characteristic of very acidic waters. Haines *et al.* (1986) in an analysis of lakes in the northeastern U.S. were able to distinguish three assemblages: "sunfish-sucker," "cyprinid," and "depauperate". The important lake parameters separating those assemblages were lake area, depth and ionic strength. Factors associated with acidity were important in distinguishing fishless lakes. Other studies have found that "fishless" lakes occur frequently at low lake pH (Kelso *et al.*, 1986). It is possible that fish community response to natural dystrophication (Rahel, 1984) is distinct from the response to anthropogenic acidification. The latter process is much more rapid, so that changes in fish assemblages may lack sufficient time to stabilize.

In this paper we analyze the information on fish species collected from 145, mostly headwater, lakes in New Brunswick (N.B.) and Nova Scotia (N.S.) by gill-netting.

## Materials and Methods

The lakes selected for the survey were situated on granitic or metamorphic bedrock materials known to provide low buffering capacity. Lake and catchment areas were measured and catchment: lake ratios calculated. Lakes were selected from this catalogue, based upon low catchment: lake area ratios and relative lack of human disturbance. Most were headwater lakes; however, a few higher order lakes were included and some clustering of selected lakes was done to minimize helicopter expenses.

Information on lake physico-chemical parameters and fish species present was collected in July-August of 1981 and 1982. The methods used in collection of water samples, chemical analyses, and estimation of lake physical parameters are described in Peterson *et al.* (1986), and Kelso *et al.* (1986).

The multifilament experimental gillnets used were of 63.7 m total length, 1.8 m deep, and consisted of seven panels with mesh sizes of 3.8, 5.1, 6.4, 7.6, 8.9, 10.2, and 12.7 cm, respectively. The nets were fished overnight. The nets were fished on the surface, set offshore from a rocky point (where possible) with the smallest mesh size nearest shore.

Since only gillnets were used to sample the lakes, the analysis is confined to specimens (and species) large enough to be collected. Thus several small species (e.g. banded killifish, sticklebacks) are excluded from the analysis. Several other species were excluded due to very low sampling efficiency (e.g. American eel) or very low frequency of collection (e.g. alewife, striped bass).

Lake physico-chemical variables were transformed when necessary to normalize the distributions, with skewness and kurtosis values used to determine the most appropriate transformation (SPSSX, 1986). Lake chloride, lake $SO_4^{2-}$ and pH required no transformation, while the other parameters utilized were transformed as follows: $K^+$, and DOC (log X +1); lake area (log X); and depth (square root).

*Statistical analyses.* A detrended correspondence analysis (DECORANA; Hill, 1979a) was utilized to ordinate lakes on the basis of species sampled from them. Abundance of species was also taken into consideration in the analysis by the use of "pseudo-species." A species could be represented by up to four pseudo-species, thus providing a method of weighting species importance according to abundance. Abundances of 1-4 were assigned a pseudospecies value of 1, 5-14 a value of 2, 15-24 a value of 3 and >24 a value of 4. The detrended correspondence analysis technique is a reciprocal averaging technique with "detrended" orthogonal axes to eliminate any "horseshoe" effect due to compression of the extremes of calculated environmental axes (Gauch, 1982). The results of this lake by species ordination was tabulated, with lakes ranked in order of ordination scores, and the tabulated lake sequence separated into "assemblages" by visual inspection. A polythetic divisive cluster analysis of the data was also performed (TWINSPAN; Hill, 1979b) and clusters delineated were used to assist in separation of the fish communities into assemblages. An eigen value of 0.3 was used as the criterion to terminate level of clustering. The "assemblages" so designated were correlated with various physico-chemical parameters by a multiple discriminant function analysis (MDA:SPSSX). In this analysis, linear combinations of the environmental variables were used to discriminate among groups of lakes, with all variables entered into the functions simultaneously (Green and Vascotto, 1978). The discriminant functions used were based on the statistical significance ($p \leq 0.05$) of the Wilks' lambda statistic. The discriminant functions utilizing the physico-chemical parameters were then used to predict group membership of each lake with respect to species assemblage; thus the accuracy of the functions in allocating group membership could be assessed.

Fish species were also ordinated on the basis of the lakes where they were found, using detrended correspondence analysis — the inverse of the lake ordination procedures described above.

## Results

*Ordination of lakes on the basis of species present.* The lakes were ordinated along four orthogonal axes by detrended correspondence analysis, based on fish species present, with eigen values for axes 1-4 of 0.854 (48% of the variance), 0.556 (31%), 0.254 (14%) and 0.109 (6%). Since axis 1 accounted for nearly 50% of the variance, the various lakes were ranked according to their position along this axis (App. 1). The two most obviously defined assemblages were formed by lakes from which only *Salvelinus fontinalis* (brook trout) were netted (assemblage 1) and those from which only *Perca flavescens* (yellow perch) were netted (assemblage 4). These assemblages were also well defined in the cluster analysis as clusters A and H. The cluster analysis separated the yellow perch assemblage into two clusters (D, H) based upon numbers of perch netted. It seems reasonable to amalgamate them as one assemblage as was done by the ordination scores. The fish communities of the remaining lakes form a graded continuum with various species forming successive maxima in abundances as one proceeds along axis 1. *Catostomus commersoni* (white sucker), *Ictalurus nebulosus* (brown bullhead) and yellow perch form successive maxima in the central portion of the axis. *Morone americanus* (white perch), *Esox niger* (chain pickerel) and *Micropterus dolomieui* (smallmouth bass) have the lowest scores along axis 1 and form the opposite end of the axis from brook trout. Assemblage 2, containing brook trout and white sucker, but usually lacking brown bullhead or yellow perch, forms a fairly discrete segment of the continuum (mainly cluster B). We also delineated assemblage 5 from 3, based on high abundances of one or more of white perch, chain pickerel and smallmouth bass.

The detrended correspondence analysis, as with all ordination procedures averages species along an undefined "environmental" gradient, such that species "abundance" rises and falls in a normal curve exhibiting "optima" at various points along the gradient. The analysis is successful in this regard for the major species: brook trout, white sucker, brown bullhead, *Semotilus corporalis* (fallfish) and yellow perch.

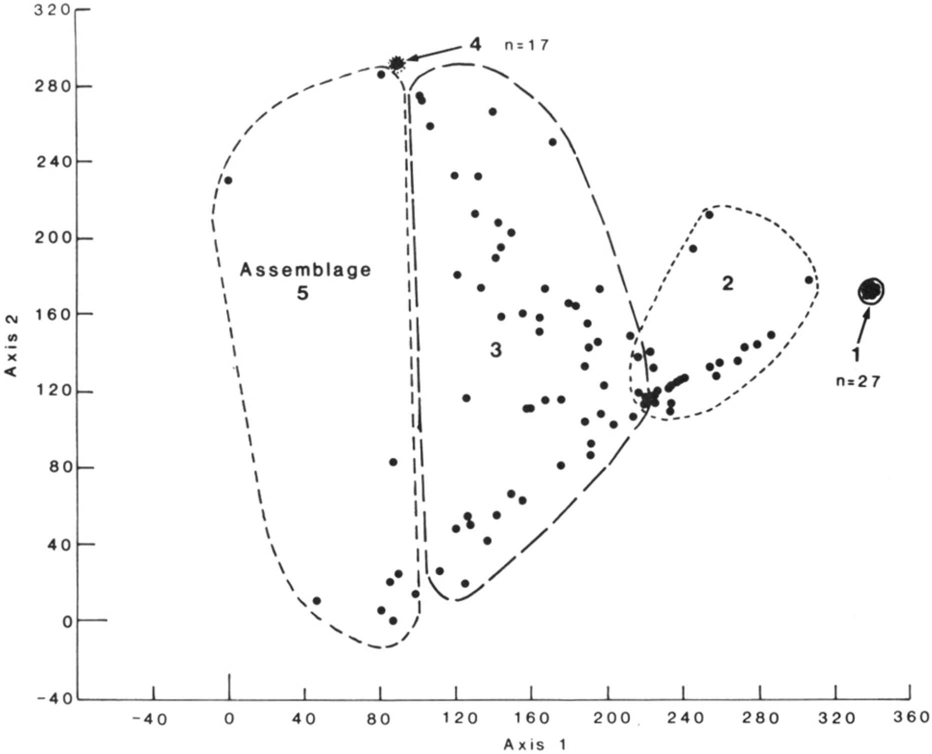


Fig 1 Each lake surveyed is positioned, according to the fish species present, on a grid of the first two ordination axes, as determined by detrended correspondence analysis. Axis calibrations are ordination scores.

We have also plotted the position of the lakes on a grid of the first two ordination axes, which combined account for 80% of the total variance (Fig 1). Assemblages 1 (brook trout only) and 4 (yellow perch only) form distinct clusters. Assemblages 3 and 5, however, become broadly smeared along axis 2, indicating considerable heterogeneity along the axis. Thus most of the variance accounted for by axis 2 is associated with assemblages 3 and 5. Lakes of assemblages 3 and 5 with low scores on axis 2 are dominated by a white perch-chain pickerel association. High scores along axis 2 in assemblages 3 and 5 are associated with either yellow perch or smallmouth bass. Variance accounted for by axes 3 and 4 (not shown in this paper) are mainly associated with separating fallfish from brown bullhead (axis 3) and smallmouth bass from yellow perch (axis 4). We may summarize the results of the detrended correspondence analysis by saying that two lake clusters with assemblages of low species richness (brook trout only and yellow perch only) are defined. Another large cluster of lakes is characterized by a highly species-rich assemblage of which white sucker, brown bullhead, fallfish and yellow perch are most numerous. Other common species in this assemblage are *Lepomis gibbosus* (pumpkinseed sunfish), *Notemigo-*

*rus crysoleucas* (golden shiner) and chain pickerel. The golden shiner is probably much more common in this assemblage than is indicated by our data. Brook trout occur occasionally in assemblage 3.

Assemblage 2, intermediate between assemblages 1 and 3, is characterized by the presence of brook trout and white sucker - other common species of assemblage 3 occurring infrequently. Lake chub are probably more common in lakes with assemblage 2 than our data indicate.

Assemblage 5 may represent one end of the gradient of assemblage 3 with white perch, chain pickerel and smallmouth bass frequently co-occurring. At the other extreme, assemblage 3 grades into assemblage 2 - the white sucker, brook trout assemblage.

One can also ordinate the fish species, instead of the lakes, on the same ordination axes in the DECORANA program (Fig 2). Comparing Figs 1 and 2, we can see that brook trout and yellow perch occupy the positions of lake assemblages 1 and 4, respectively on the grid of ordination axes 1 and 2. White suckers, *Salmo salar* (landlocked salmon) and *Couesius plumbeus* (lake chub) occupy the region of assemblage 2. The region of assemblage 3 is occupied by brown bullhead, fallfish, pumpkinseeds and golden shiners; chain pickerel, white perch and smallmouth bass

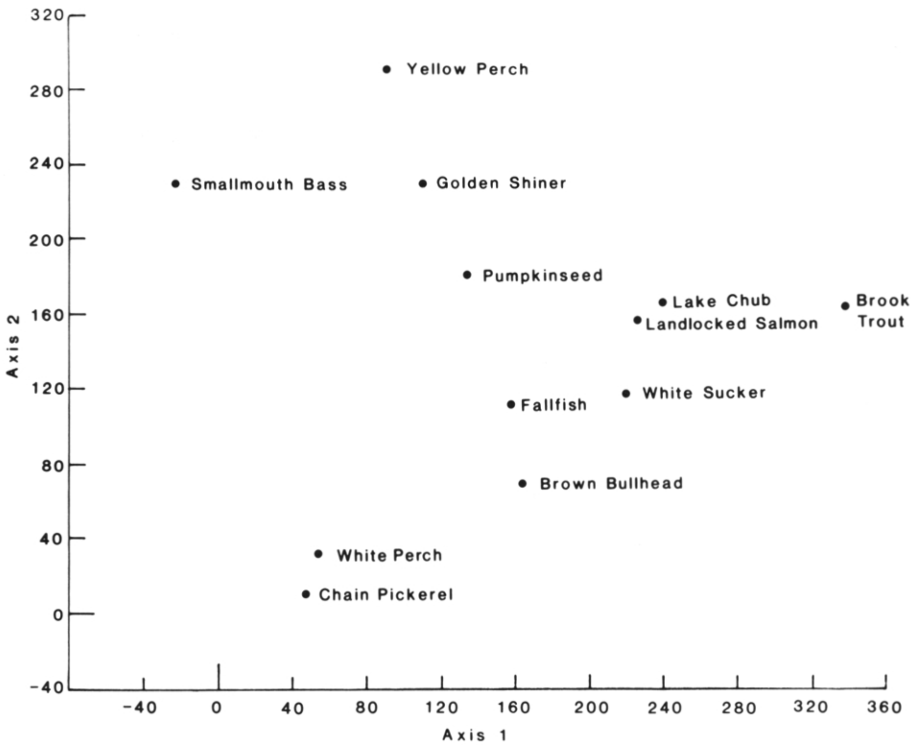


Fig 2 The location of each of the fish species used in the detrended correspondence analysis are arrayed in relation to the first two ordination axes (the same axes on which lakes are arrayed in Fig 1).

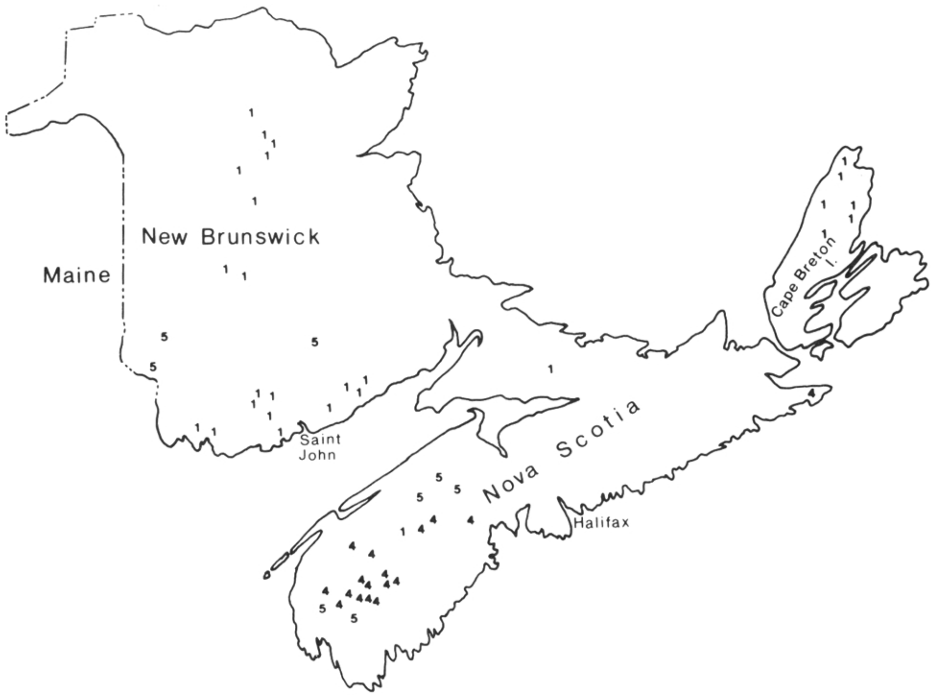


Fig 3 Geographic location of lakes containing fish assemblages 1, 4 and 5.

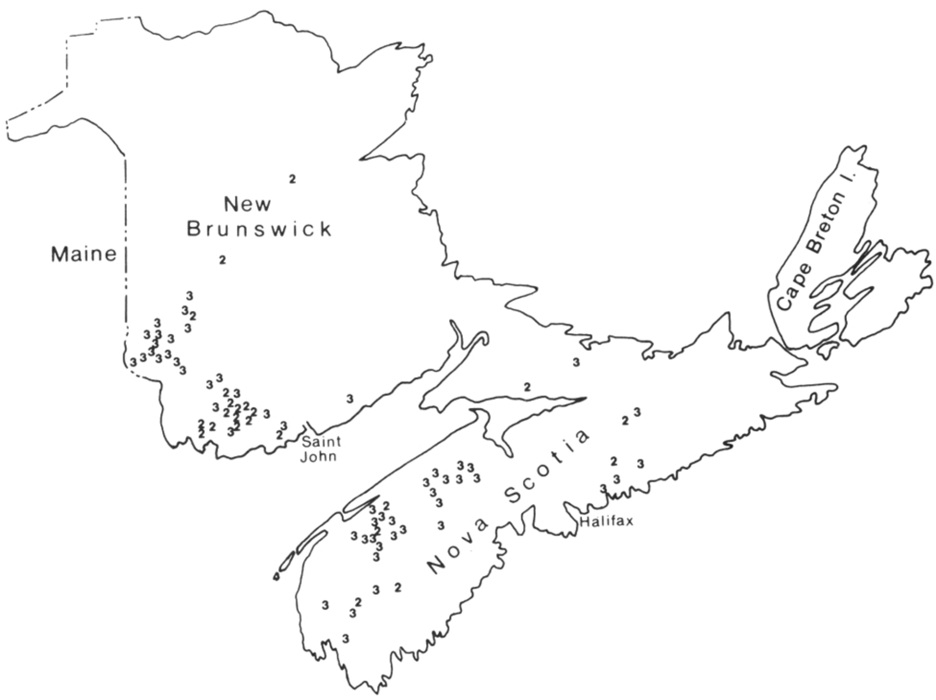


Fig 4 Geographic locations of lakes containing fish assemblages 2 and 3.

occupy the space of assemblage 5. The smallmouth bass lakes are widely separated from chain pickerel and white perch on axis 2; however, they were netted from only a small number of lakes.

*Geographical location of various assemblages.* Surveys were not performed uniformly throughout New Brunswick (N.B.) and Nova Scotia (N.S.). Southwestern N.B. and southwestern N.S. were surveyed most intensively, with fewer lakes surveyed in north-central N.B., eastern N.S. and Cape Breton Island (Figs 3, 4). Nevertheless, within the constraints of the surveying biases, the various species assemblages occupied different geographic locations. Assemblage 1 (brook trout only, Fig 3) was the only assemblage encountered in Cape Breton island. It was also the most numerous assemblage in north-central N.B. (8 of 10 lakes) and in the lakes sampled in southern N.B. to the east of Saint John (4 of 5 lakes). On the other hand, the assemblage was encountered only once (of 51 lakes) in southwestern Nova Scotia, and in only one of 10 lakes in eastern Nova Scotia.

Lakes with assemblage 4 (yellow perch only) were encountered only in southwestern N.S. (16 of 51 lakes) and eastern N.S. (1 of 10).

Lakes containing assemblages 2, 3 and 5 all had similar geographic distributions (again emphasizing that they are really segments of a continuum), being the predominant assemblages encountered in southwestern N.B., southwestern N.S. and eastern N.S. Lakes with assemblage 3 were most numerous: 22 of 45 lakes in southwestern N.B. 24 of 51 lakes in southwestern N.S., and 5 of 10 lakes in eastern N.S. Lakes containing assemblage 2 constituted 11 of 45 lakes in southwestern N.B., and were particularly frequent in coastal drainages to the west of Saint John (Fig 4). Assemblage 2 was in 4 of 51 lakes sampled in southwestern N.S., and 3 of 10 in eastern N.S.

Lakes with assemblage 5 were encountered least frequently - in 2 of 45 lakes in southwestern N.B., and 5 of 51 in southwestern N.S. One very acidic lake in southern N.B., from which only chain pickerel were collected, also fell into this assemblage.

*Correlation of the various assemblages with lake physico-chemical parameters.* When a discriminant function analysis was performed to determine significant correlations of the various fish assemblages with lake physico-chemical parameters, pH and lake area were the significant parameters in determining occurrence of the various fish assemblages (Table I). The concentration of chloride and DOC were of marginal significance. The first two discriminant functions accounted for 95% of the variance (Table II), with function 1 being primarily related to lake area and function 2 to pH. Thus assemblage 1 (brook trout only) was characteristic in lakes of less surface area than the other assemblages. The assemblages with greatest numbers of species, 3 and 5, tended to be found in lakes of greater surface area. Assemblage 4, on the other hand, was found in lakes characterized by low pH (mean of 4.6), whereas the mean pH of lakes yielding the other assemblages was over 5.6 (Table III). In Fig 1, we can envisage that axis 1 represents lakes of decreasing surface area as one moves along the axis from left to right. Brook trout tend to be found in the smallest lakes while smallmouth bass, chain pickerel and white perch tended to be found more frequently in lakes of largest surface area.

Although axis 2 is strongly influenced by pH, lakes associated with assemblages 1, 2, 3 and 5 have similar mean pH levels, and are centered at about the middle of axis 2. Only assemblage 4 is polarized at the low pH end of the axis.

Several other environmental parameters were significant in discriminant functions 3 and 4, but accounted for very little of the total variance. The significance of the concentration of chloride is probably geographical - N.B. lakes had lower mean $Cl^-$ concentrations than N.S. lakes. Thus, assemblages 1 and 2 had a greater bias of N.B. lakes, consequently lower mean $Cl^-$ (Table III). Dissolved organic carbon (DOC) contributes to acidity of unbuffered waters (e.g. Kerekes *et al.*, 1986). The significance of DOC in discriminant function 4 is in part attributable to the higher mean DOC concentrations in lakes of assemblage 4. Excluding these acidic lakes, there is a trend of increasing mean DOC concentration with increasing mean lake area. The coefficient for depth was also significant in discriminant function 4 due to the shallower mean depths for lakes of assemblage 4. Lake depths recorded for this survey are based on a single sounding in each lake. More complete morphometry data on these lakes would be required to warrant further comment.

*Prediction of fish assemblage from lake physico-chemical parameters.* On the basis of the first two discriminant functions, assemblage membership for the various lakes was correctly predicted in 50% of the cases (Table IV). Prediction scores were highest

**Table I** Wilks' Lambda (U-statistic) test for significant differences among assemblage means for the 7 environmental parameters utilized in the discriminant function analysis.

| Parameter | $\lambda$ | F ratio (4,114 df) | Significance |
|---|---|---|---|
| $Depth^{1/2}$ | 0.956 | 1.299 | 0.275 |
| pH | 0.740 | 10.03 | 0.000* |
| Log $(K^{+}+1)$ | 0.976 | 0.705 | 0.590 |
| $Cl^{-}$ | 0.934 | 2.029 | 0.095 |
| $SO_4^{2-}$ | 0.958 | 1.236 | 0.300 |
| log (DOC+1) | 0.931 | 2.119 | 0.083 |
| log area | 0.712 | 11.50 | 0.000* |

* Statistically significant.

**Table II** Discriminant analysis of lake fish assemblage.

| Discriminant function | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Percent of variance | 55.5 | 39.1 | 3.2 | 2.0 |
| Cumulative percent | 55.5 | 94.6 | 97.8 | 99.8 |
| Significance | 0.000 | 0.001 | 0.833 | 0.696 |
| Variables and standardized discriminant function coefficients. | | | | |
| Log area | .893 | -.193 | .278 | -.109 |
| pH | .515 | .909 | -.430 | .370 |
| log (DOC+1) | .373 | -.232 | -.134 | .128 |
| $Cl^{-}$ | .282 | -.086 | -.452 | .609 |
| log $(K^{+}+1)$ | -.332 | -.148 | .226 | .174 |
| $Depth^{1/2}$ | .101 | .078 | -.067 | -.658 |
| $SO_4^{2-}$ | .015 | .087 | .916 | .209 |
| Pooled within-group correlations between discriminating variables and canonical discriminant functions. *: statistically significant ($p < .01$). | | | | |
| Log area | .851* | -.203 | .180 | -.264 |
| pH | .240 | .925* | -.074 | .171 |
| $SO_4^{2-}$ | -.48 | .213 | .836* | .350 |
| $Depth^{1/2}$ | .144 | .263 | -.057 | -.650* |
| $Cl^{-}$ | .130 | .383 | .272 | .494* |
| log (DOC+1) | .198 | -.363 | -.086 | .437* |
| log $(K^{+}+1)$ | .026 | .246 | .062 | .285* |

for lakes containing assemblages 1 and 4 (62.5% and 80% correct prediction, respectively), which is reasonable since these assemblages were the most distinctive; lakes with assemblage 1 having small surface area, and those with assemblage 4 being acidic. Prediction scores for lakes with assemblages 3 and 5 were low, being no greater than could be accounted for by chance (50%). The low predictability reflects the similarity of these assemblages. If they are combined, the percentage of correct predictions for the combined lakes is 63. Thirty percent of the lakes containing assemblages 2 were predicted to contain assemblage 1, and may represent some of the smaller lakes with the brook trout-white sucker assemblage.

**Table III** Means of various enviornmental parameters for the fish assemblages in 119 lakes.

| Assemblage | Depth (m) | Area (ha) | pH | $K^+$ | $Cl^-$ | $SO_4^{2-}$ mg $L^{-1}$ | DOC | Number |
|---|---|---|---|---|---|---|---|---|
| 1 | 3.2 | 22.5 | 5.67 | 0.28 | 2.63 | 3.94 | 4.9 | 24 |
| 2 | 4.0 | 55.5 | 5.84 | 0.28 | 2.46 | 3.92 | 5.0 | 23 |
| 3 | 3.7 | 90.4 | 5.94 | 0.28 | 3.06 | 3.93 | 5.8 | 50 |
| 4 | 2.8 | 70.7 | 4.60 | 0.24 | 3.99 | 3.69 | 7.0 | 15 |
| 5 | 3.8 | 92.3 | 5.66 | 0.26 | 3.54 | 3.40 | 6.2 | 7 |

26 cases excluded from analyses.

15 had missing or out-of-range group codes (no fish caught).

11 had at least one missing discriminating variable (usually depth).

*Missed species.* Seventeen lakes in N.S. and 21 in N.B. included in this work have been the subject of previous surveys (Alexander *et al.*, 1986; Prov. of N.B. Dept. Natural Resources, unpubl. surveys). The species obtained in our survey are compared to those previously reported in Table V. In the first column of Table V, the percentage of 38 lakes in which each of the species considered was found is presented. For example, brook trout were sampled from 27 of 38 lakes, or 71%. Our survey, on the other hand, collected brook trout from 17 of the 38 lakes (45%, column 2). The third column of Table V shows the number of the remaining lakes in our survey (90-includes "fishless" lakes) which yielded brook trout - 51 (57%). If we assume that 71% is the percentage of all lakes surveyed which really contained brook trout; then an additional 13 of the remaining 90 lakes should also contain brook trout. Therefore, the total number of lakes which contained missed brook trout populations is estimated to be 23-10 of the 38 lakes surveyed more than once plus an estimated 13 of the 90 lakes which were only surveyed once. These estimated missed species totals are given in column 4 of Table V. The final column gives the estimated

**Table IV** Predicted assemblage membership based upon discriminant functions 1 and 2. Underlines show correct predictions. Overall correct percentage was 50.4%. Percentage in parentheses.

| Assemblage | 1 | 2 | 3 | 4 | 5 | Number |
|---|---|---|---|---|---|---|
| 1 | *15(62.5)* | 5(20.8) | 1( 4.2) | 1( 4.2) | 2( 8.3) | 24(20.2) |
| 2 | 7(30.4) | *10(43.5)* | 2( 8.7) | 1( 4.3) | 3(13.0) | 23(19.3) |
| 3 | 5(10.0) | 6(12.0) | *20(40.0)* | 8(16.0) | 11(22.0) | 50(42.0) |
| 4 | 1( 6.7) | 1( 6.7) | 1( 6.7) | *12(80.0)* | 0(0) | 15(12.6) |
| 5 | 1(14.3) | 0(0) | 2(28.6) | 1(14.3) | *3(42.9)* | 7( 5.9) |

**Table V** Estimation of fish species missed by our survey. Comparison of presence-absence data with data from other surveys for 38 of the 128 lakes surveyed (first two columns). Estimated numbers of lakes where a particular species may have been missed was derived by subtracting the percentage of lakes with species present in our survey (e.g. 45% for brook trout) from the percentage with species present in all surveys (71% for brook trout); and assuming that the species should have been present in the same additional percentage of the remaining 90 lakes (e.g. 26% for brook trout). Figures in parentheses are percentages.

| Species | Lakes with species present, all surveys | Lakes with species present, our survey | No. of remaining lakes with species in our survey | Est. no. of lakes where species missed | Est. total no. of lakes with species (sum of previous three columns) |
|---|---|---|---|---|---|
| *Salvelinus fontinalis* | 27 (71) | 17 (45) | 51 (57) | 23 | 91 |
| *Catostomus commerconi* | 28 (74) | 22 (58) | 50 (56) | 16 | 88 |
| *Perca flavescens* | 17 (45) | 15 (39) | 50 (56) | 5 | 70 |
| *Ictalurus nebulosus* | 17 (45) | 15 (39) | 32 (36) | 8 | 55 |
| *Couesius plumbeus* | 15 (39) | 3 (8) | 7 (7.8) | 28 | 38 |
| *Notemigorus crysoleucas* | 8 (21) | 1 (3) | 7 (7.8) | 16 | 24 |
| *Semotilus corporalis* | 7 (18) | 5 (13) | 14 (16) | 4 | 23 |
| *Morone americanus* | 4 (10) | 3 (8) | 15 (17) | 2 | 20 |
| *Lepomis gibbosus* | 4 (1) | 1 (3) | 6 (6.7) | 6 | 13 |
| *Micropterus dolomieui* | 3 (8) | 2 (5) | 5 (5.6) | 3 | 10 |
| *Esox niger* | 1 (3) | 0 (0) | 5 (5.6) | 3 | 8 |
| *Salmo salar* | 3 (8) | 1 (3) | 0 (0) | 4 | 5 |

total number of lakes (of 128) containing each species. It is apparent that some species were sampled quite reliably, for example, yellow perch were netted from 65 of the lakes, and were estimated to be missed only in an additional 5 lakes. Golden shiners and lake chub, on the other hand, were probably sampled very inefficiently. We estimate that we missed golden shiners in 16 lakes, and sampled them only from 8.

Did the missed species affect the designation of the various assemblages? Of the 38 lakes surveyed more than once, 21 were in assemblage 3 — the diverse assemblage. Additional species would not alter their classification unless possibly they were white perch or smallmouth bass (conversion to assemblage 5). As we stated above, white perch were netted very efficiently and smallmouth bass were infrequent in these headwater lakes. Therefore, it would seem that the presence of additional species would not alter many lakes assigned to assemblage 3. Six lakes surveyed more than once were lakes we found to contain brook trout only (assemblage 1). Of these 6 lakes, 3 yielded white suckers in the other surveys, which would shift them to assemblage 2. Our ordination results indicate that lakes containing assemblage 2 resembled those containing assemblage 1 in physico-chemical parameters, averaging a slightly larger surface area.

Four of the 38 lakes were found to be yellow perch-only lakes (assemblage 4) in our survey. Of these four, only one was found to contain additional species (brook trout and white perch) in other surveys. Considering the low mean pH of lakes in this category, it is probable that many of them contain no other species used in this analysis (Harvey, 1980; Smith *et al.*, 1986; Haines *et al.*, 1986).

Four of the 38 lakes yielded no fish in our survey. One of them yielded yellow perch in other surveys, indicating that it should be in lakes designated as containing assemblage 4. One other was found to contain white sucker, brook trout and lake chub, indicating that in reality it contained assemblage 2. It is probable that some of our "fishless" lakes contained either assemblages 1, 2 or 4. It seems unlikely that many of them would contain assemblages 3 or 5, as at least some of the species would have been caught.

We conclude that inclusion of missed species would not change the basic assemblages elucidated by the ordination techniques used here. The relative numbers of lakes containing the various assemblages would probably have changed - primarily due to transfer of some brook trout-only lakes (assemblage 1) to those containing white sucker and brook trout (assemblage 2).

*"Fishless" lakes.* Seventeen lakes in the survey yielded no fish when gill-netted. However, two of them had been found to contain fish by other surveys (see above section). In addition, one lake had contained brook trout and pumpkinseeds in a study some 40-years-ago (Smith, 1952). The percentage of lakes yielding no fish was about 8% for lakes with pH $>$4.5 (Fig 5), but rose to 33% for lakes with pH$\leq$4.5. Fishless lakes at these lowest pH levels had a larger mean lake area (Table VI), because three of the five lakes had areas of 70-150 ha. In contrast, lakes in the higher pH categories were consistently small, all with areas less than 30 ha. Although of smaller surface area the "fishless" lakes of higher pH had greater average maximum depth than the most acidic ones. The highly acidic lakes also had high average DOC.

## Discussion

Five fish assemblages were identified from the ordination analysis: brook trout; brook trout-white sucker; multi-species, with white sucker, brown bullhead, and yellow perch the most frequent components; yellow perch; and another diverse assemblage with greater emphasis on white perch, chain pickerel and smallmouth bass. Lake area was the single most important variable separating these assemblages, with brook trout lakes averaging the smallest in area. With increasing lake size, the assemblage present progressed from brook trout-white sucker, to the multi-species assemblages with assemblage 5 (emphasizing white perch and smallmouth bass) inhabiting the lakes of greatest area.

The trend of increasing species richness with increasing lake area has been observed previously (Johnson *et al.*, 1977; Eadie and Keast, 1984; Rahel, 1984; Haines *et al.*, 1986; Kelso *et al.*, 1986; Matuszek and Beggs, 1988). The explanation may lie in the immigration-extinction theory of MacArthur and Wilson (1967) or in the fact that lakes with more surface area are liable to have a greater diversity of habitats, and can thus support more diverse fish populations. The fact that the group of lakes with least surface area (brook trout lakes) are no shallower than the other lake groups may be indicative of lesser littoral areas in these lakes, a factor in limiting species diversity.

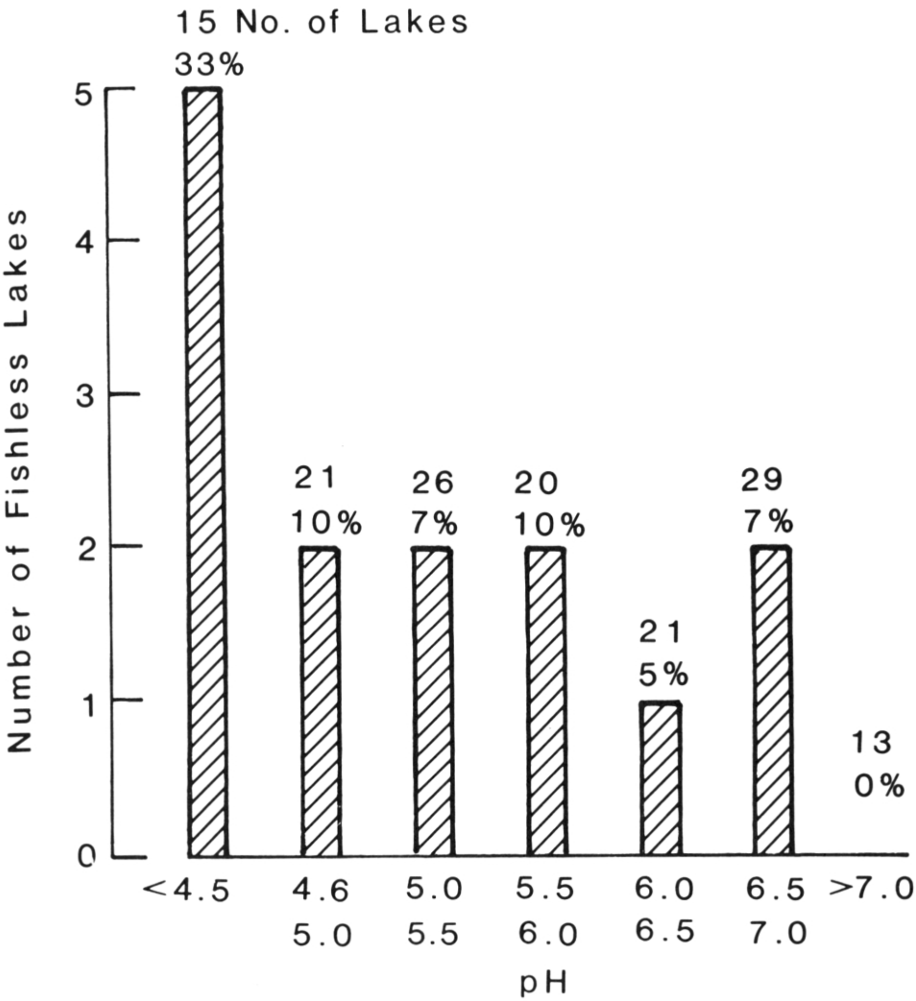


Fig 5 Numbers of sampled lakes which yielded no fish for seven pH categories. Upper number above the bar is the total number of lakes in the category. The lower number is the percentage of the lakes in the category which yielded no fish.

**Table VI** Means of physico-chemical parameters of lakes yielding no fish.

| *pH class of lakes* | Area (ha) | Depth (m) | $K^+$ | $Cl^-$ | pH | $SO_4^{2-}$ mg $L^{-1}$ | DOC | Number |
|---|---|---|---|---|---|---|---|---|
| $\leq$ 4.5 | 73 | 2.5 | .24 | 3.5 | 4.43 | 4.1 | 9.7 | 5 |
| 4.6 $<$ 5.5 | 20 | 4.3 | .20 | 3.0 | 5.01 | 3.4 | 3.4 | 4 |
| $>$ 5.5 | 21 | 4.9 | .20 | 2.4 | 6.29 | 4.1 | 4.7 | 5 |

Haines *et al.* (1986) found their "depauperate" lakes to be in this category. Brook trout may not require extensive littoral areas for successful reproduction or may be superior competitors in homogenous habitats. Alexander *et al.* (1986) also found brook trout presence to be correlated negatively with most other species - probably due to the brook trout-only lakes in their data base. Many of the brook trout lakes, however, probably contained the ninespine stickleback as well, a species too small to be caught in our gill-nets.

Lake area is a factor determining the morphoedaphic index (*sensu* Ryder, 1965) of lakes, which is correlated with lake productivity. Consequently, it may be inferred -other factors being equal - that the brook trout lakes are probably the least productive of lakes. This concept is consistent with the usual eutrophication sequence where the salmonid community of low diversity is supplemented by percid, then cyprinid communities as eutrophication proceeds. Higher morphoedaphic indices have been correlated with high rates of eutrophication (Kelso *et al.*, 1986).

The white sucker-brook trout assemblage (assemblage 2) inhabits lakes of slightly greater mean area than the brook trout lakes. Otherwise, the other physico-chemical parameters are very similar for these two lake types. Although insufficient temperature records for the lakes were available to permit its inclusion as a parameter in the discriminant function analysis, lakes containing assemblages 1 and 2 may have cooler temperature regimes. Brook trout and lake chub, other members of assemblage 2, are considered "cool water" species (e.g. Greeley, 1931).

The diverse species assemblage (assemblage 3) occupies headwater lakes of greater area and forms a continuum with assemblage 5 in the larger lakes. Study of larger numbers of lakes with more thorough sampling might reveal patterns within this assemblage which cannot be seen with the present data. This assemblage is probably also common in higher order lakes of the Maritime region. The "centrachid" and "cyprinid" assemblages of Haines *et al.* (1986) were not distinguishable in our lake data. Assemblage 3 might have broken down further had we used additional sampling methods which collected small species efficiently.

The yellow perch-only lakes are similar in physico-chemical characteristics to those containing assemblage 3, but are more acidic and tend to have higher levels of DOC. Higher DOC is often correlated with a lower pH in poorly buffered waters (Kerekes *et al.*, 1986). Consequently, these lakes are probably receiving more organic acidity than lakes in the other assemblages. In addition to natural organic acidity, there is evidence that pH reduction in waters of low alkalinity occurs through atmospheric transport of acidity to these waters (Kerekes *et al.*, 1986) - particularly in seasons of high discharge. Fish populations in lakes which are initially naturally more acidic would seem to be at greater risk from anthropogenic acidification. Smith *et al.* (1986) found that the minimum pH tolerated by most species was 4.7-4.8, with the yellow perch tolerating pH levels to 4.4. Rahel (1984) found a yellow perch-*Umbra* assemblage to be associated with the acid Wisconsin lakes. *Umbra* does not occur in the Maritime provinces, nor does it attain a size to allow it to be caught by standard gill-nets. Rahel (1984) also found a "cyprinid" assemblage indicative of lakes with low oxygen partial pressures under ice cover. Some of the "fishless" lakes of N.B. may be so due to low winter oxygen values.

Lakes containing assemblage 5 were of greatest surface area, and may not be qualitatively different in reality from those with assemblage 3. Some of these lakes, were not headwater lakes. Categorizing lakes on the basis of smallmouth bass presence-absence is questionable, as its distribution is determined mainly through recent introductions by humans.

In summary, three factors - lake area, lake acidity, and geographic locality appear primarily responsible for determining species composition of Maritime lakes. High lake acidity seems to be correlated with low species richness and presence of a yellow perch assemblage. Lakes of small surface area are frequently inhabited only by brook trout. This study suggests that 10-15% of the headwater lakes surveyed are too acidic for the survival of any potential sport fish species other than yellow perch. Most of these lakes occur in southwestern N.S. Watt *et al.* (1983) have made a case for lowered pH in rivers of southwestern N.S. over the last 30-40 years. This conclusion was based primarily upon the former presence of salmon runs in rivers which are now too acidic to permit salmon survival. The conclusion is supported by some (admittedly scanty) pH measurements of 30 years ago. If rivers of this area are now more acidic, it would seem reasonable to suppose that lakes of the area are more acidic as well, since lakes and rivers form linked drainage systems. If this hypothesis is correct, then populations of brook trout, white suckers, brown bullhead and several other species frequently associated with assemblage 3 may well have been lost. The data presented here indicate that 20-25% of headwater lakes in southwestern N.S. are too acidic for larger species other than yellow perch.

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**Appendix 1** The lakes surveyed are shown in sequence as ordered along axis 1 of the detrended correspondence analysis (accounting for 48% of the variance). Various species used in the analysis are arrayed horizontally. Lake numbers listed in column at the far right matched those in Peterson et al. (1986) so that fish species can be matched to water chemistry if desired. Numbers prefaced with a 1 are New Brunswick lakes (e.g. 1-66), those with a 2 are Nova Scotia lakes. The letters in the column second from the right represent results of a hierarchial cluster analysis of the fish species data (Twinspan; Hill, 1979b). Lakes with the same letter were clustered together. Horizontal dotted lines indicate designated assemblages. Legend for the fish species abbreviations are: BT (brook trout), LC (lake chub), LLS (landlocked salmon), WS (white sucker), BB (brown bullhead), FF (fallfish), PS (pumpkinseed), GS (golden shiner), YP (yellow perch), WP (white perch), CP (chain pickerel), SmB (smallmouth bass). Numbers for the various species are relative abundances, as explained in the text.

| Fish species | | | | | | | | | | | | | Lake |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BT | LC | LLS | WS | BB | FF | PS | GS | YP | WP | CP | SmB | Cluster | no. |
| Assemblage 1 | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | A | 1-66 |
| 1 | | | | | | | | | | | | A | 2-42 |
| 1 | | | | | | | | | | | | A | 1-7 |
| 2 | | | | | | | | | | | | A | 1-54 |
| 2 | | | | | | | | | | | | A | 1-51 |
| 2 | | | | | | | | | | | | A | 1-25 |
| 2 | | | | | | | | | | | | A | 1-24 |
| 1 | | | | | | | | | | | | A | 1-6 |
| 2 | | | | | | | | | | | | A | 1-10 |
| 4 | | | | | | | | | | | | A | 2-75 |
| 4 | | | | | | | | | | | | A | 2-74 |
| 4 | | | | | | | | | | | | A | 2-73 |
| 3 | | | | | | | | | | | | A | 2-76 |
| 4 | | | | | | | | | | | | A | 2-72 |
| 3 | | | | | | | | | | | | A | 1-69 |
| 2 | | | | | | | | | | | | A | 1-1 |
| 3 | | | | | | | | | | | | A | 1-67 |
| 3 | | | | | | | | | | | | A | 1-65 |
| 1 | | | | | | | | | | | | A | 1-4 |
| 4 | | | | | | | | | | | | A | 2-71 |
| 4 | | | | | | | | | | | | A | 1-63 |
| 4 | | | | | | | | | | | | A | 2-57 |
| 4 | | | | | | | | | | | | A | 1-59 |
| 4 | | | | | | | | | | | | A | 1-58 |
| 4 | | | | | | | | | | | | A | 1-57 |
| 4 | | | | | | | | | | | | A | 1-60 |
| Assemblage 2 | | | | | | | | | | | | | |
| 2 | | | 2 | | | | | | | | | A | 1-27 |
| 3 | | | 3 | | | | | | | | | A | 1-33 |
| 1 | | | 1 | | | | | | | | | B | 1-16 |
| 1 | 1 | | | 1 | | | | | | | | C | 1-18 |
| 4 | | | 3 | 2 | | | | | | | | C | 1-21 |
| 2 | | | 2 | | | | | 1 | | | | B | 2-3 |
| 1 | | | 1 | | | | | | | | | B | 1-15 |
| 1 | | | 1 | | | | | | | | | B | 1-2 |
| 2 | | | 1 | 1 | | | | 1 | | | | C | 2-6 |
| 1 | | | 2 | | | | | | | | | B | 1-26 |
| 1 | | | 3 | | | | | | | | | B | 1-13 |

**Appendix 1** (cont'd)

| | | | | | Fish species | | | | | | | | Lake |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BT | LC | LLS | WS | BB | FF | PS | GS | YP | WP | CP | SmB | Cluster | no. |
| 3 | | | 4 | | 1 | | | | | | | B | 1-12 |
| 1 | | | 4 | | | | | | | | | B | 2-66 |
| 1 | | | 1 | 1 | 1 | | | | | | | B | 1-56 |
| 1 | | | | 2 | | | | | | | | C | 1-17 |
| 1 | | | 3 | | | | | | | | | B | 2-61 |
| 1 | | | 3 | | | | | | | | | B | 2-59 |
| 1 | | | 2 | 1 | | | | | | | | B | 2-62 |
| 1 | 3 | | 4 | | | | | 1 | | | | C | 1-62 |
| 1 | | | 4 | | | | | | | | | B | 1-29 |
| | | | | | | Assemblage 3 | | | | | | | |
| 1 | | | 2 | | | | | 1 | | | | C | 1-55 |
| 1 | | | 2 | | 1 | | 1 | 1 | | | | C | 1-53 |
| 2 | 1 | 1 | 3 | 2 | 1 | | | | | | | C | 1-45 |
| | | | 2 | 1 | | | | 1 | | | | C | 2-39 |
| 1 | | | 2 | 1 | | | | | | | | B | 1-14 |
| 1 | | | 2 | | | | | 1 | | | | C | 2-11 |
| | | | 4 | 2 | | | | | | | | C | 1-40 |
| | | | 1 | 2 | | | | 1 | | | | C | 2-30 |
| 1 | | | 2 | | 1 | | | 2 | | | | C | 1-31 |
| | | | 3 | 2 | | | | 1 | | | | C | 2-2 |
| | | 1 | 2 | | 1 | | 2 | 1 | | | | C | 1-19 |
| | | | 1 | 1 | | | | | | | | C | 2-5 |
| | | | 2 | | | | | 1 | | | | D | 1-3 |
| | | | 2 | 1 | | | | 1 | | | | C | 2-48 |
| 1 | | | 2 | | | | | | 1 | | | B | 2-63 |
| | | | 3 | 2 | 1 | 1 | | | | | | C | 1-46 |
| 1 | | | 3 | 2 | | | | 2 | | | | C | 2-10 |
| 1 | | | 2 | 1 | 2 | 1 | | 2 | | | | C | 1-48 |
| 1 | | | 4 | 2 | | | | 3 | | | | C | 2-60 |
| | | | 2 | 2 | | | | 1 | | | | C | 2-7 |
| | 1 | | 1 | 2 | | | | | | | | C | 2-40 |
| 1 | | | | | | | | 1 | | | | E | 2-35 |
| 1 | | | | | | | | 1 | | | | E | 2-36 |
| | | | 4 | 1 | 2 | 2 | 1 | 4 | | | | C | 1-34 |
| | 1 | | 1 | 1 | 3 | | | 1 | | | | C | 1-50 |
| | | | 4 | 2 | 2 | 1 | | 3 | | | 1 | C | 1-36 |
| | | | 3 | 1 | 2 | 1 | 1 | 2 | | | | C | 1-37 |
| | | | | | 1 | | | | | | | F | 1-68 |
| | | | | | 1 | | | | | | | F | 1-5 |
| | | | 1 | 1 | | 1 | | 1 | | | | C | 1-22 |
| | 1 | | 3 | | | | | | | | | C | 1-30 |
| | | | | 4 | | | | | 1 | | | C | 2-56 |
| | | | 2 | | | | | 1 | 2 | | | G | 1-32 |
| | | | 2 | 1 | | | | 2 | | | | C | 2-8 |
| | 1 | | 1 | 2 | | | | 2 | | | | C | 2-9 |
| | | | 2 | 2 | | | 1 | 2 | | | | C | 2-22 |

**Appendix 1** (cont'd)

| | | | | | Fish species | | | | | | | | Lake |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BT | LC | LLS | WS | BB | FF | PS | GS | YP | WP | CP | SmB | Cluster | no. |
| | | | 3 | 1 | | | | 4 | | | | C | 2-51 |
| 1 | | | | 3 | | | | 1 | 2 | | | C | 2-33 |
| | | | 2 | 2 | | | 1 | 2 | | | | C | 2-47 |
| 1 | | | | | | | | 1 | | | | E | 2-32 |
| | | | 3 | | | | | | 3 | | | G | 1-43 |
| | | | 1 | 3 | | | | 3 | | | | C | 2-38 |
| | | | 1 | | | | | 1 | | | | D | 2-49 |
| | | | 3 | 2 | | | 3 | 4 | | | | C | 2-58 |
| | | | 2 | 1 | 1 | | | | 1 | 2 | | G | 1-44 |
| | | | 3 | 1 | 1 | | | 1 | 3 | 2 | | G | 1-39 |
| | 1 | | 1 | | | | | | 1 | | 1 | G | 1-47 |
| 1 | | | | | | | | 2 | | | | B | 2-65 |
| | | | 1 | | 1 | | | 1 | | 1 | 1 | D | 1-38 |
| | | | 2 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | | G | 1-42 |
| | | | 2 | 2 | | | | 4 | | | | C | 2-50 |
| | | | 4 | 1 | | | | 1 | 4 | | | G | 2-4 |
| | | | 1 | 1 | | | | 4 | | | | C | 2-43 |
| | | | 1 | | | | | 2 | | | | D | 2-15 |
| | | | 1 | | | | | 2 | | | | D | 2-13 |
| | | | 2 | 2 | 1 | | 1 | | 4 | | | G | 2-23 |
| | | | | | | Assemblage 4 | | | | | | | |
| | | | | | | | | 1 | | | | H | 2-68 |
| | | | | | | | | 3 | | | | D | 2-14 |
| | | | | | | | | 1 | | | | H | 2-54 |
| | | | | | | | | 2 | | | | D | 2-27 |
| | | | | | | | | 1 | | | | H | 2-53 |
| | | | | | | | | 1 | | | | H | 2-45 |
| | | | | | | | | 2 | | | | D | 2-25 |
| | | | | | | | | 2 | | | | D | 2-19 |
| | | | | | | | | 1 | | | | H | 2-44 |
| | | | | | | | | 1 | | | | H | 2-37 |
| | | | | | | | | 1 | | | | H | 2-31 |
| | | | | | | | | 1 | | | | H | 2-29 |
| | | | | | | | | 1 | | | | H | 2-28 |
| | | | | | | | | 1 | | | | H | 2-24 |
| | | | | | | | | 1 | | | | H | 2-21 |
| | | | | | | | | 1 | | | | H | 2-17 |
| | | | | | | | | 1 | | | | H | 2-12 |
| | | | | | | Assemblage 5 | | | | | | | |
| | | | 2 | 2 | | | | 2 | 4 | | | C | 2-52 |
| 1 | | | 3 | 1 | | | | 1 | 4 | | | G | 2-41 |
| | | | 1 | 1 | | | | 2 | 3 | | | G | 2-55 |
| | | | 2 | 2 | | | | | 4 | | 2 | G | 1-41 |
| | | | | | | | | 4 | | | 3 | D | 1-49 |
| 1 | | | 1 | 1 | | | | 1 | 4 | | | G | 2-34 |
| | | | | | | | | | | 2 | | F | 1-64 |
| | | | 1 | | | | | 1 | | | 4 | D | 2-46 |