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Niches and fish associations in lakes of northwestern Quebec

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Abstract

Fishing data from 378 sites, from lakes in northwestern Quebec, were compared to environmental descriptors through contingency table analyses and partial correlation coefficients, in order to establish the distributions and the niches of the main fish species in those lakes. A probabilistic measure of species co-occurrence, followed by complete linkage clustering, made it possible to describe five associations of species, four of which are amenable to ecological interpretation. Finally, measures of evenness (equitability) of the frequency distribution of species at the various sites show a gradient between the low land area nearer James Bay, where biological productivity is high, and the inland plateaus which represent a more stable and less productive environment.

Introduction

Extensive hydroelectric projects, carried out by the Society of Energy of James Bay (SEBJ), are in the process of modifying, in an important manner, the physiognomy of northwestern Quebec. This territory of 410,000 sq km (Fig. 1) covers the area of land which, on the Quebec side, belongs (or will belong following construction activities) to the drainage basin of James Bay (Laverdiere 1969). James Bay forms the southern extremity of Hudson Bay on the Hudson Sea. In particular, a wide diversity of plans will affect the lakes of this region, plans which will integrate them in a hydroelectric network or which will make them accessible for recreational purposes.

Important data have been collected for this territory since 1973 in order to define the ecology particular to this region. Along with other data, an appreciable quantity of information is now available on the fishes of this territory and the environment in which they live. This information has already been collated by Magnin (1977) in the form of distributional maps for the different species of this territory. The present study attempts more to determine which ecological factors explain the distribution of each of 29 fish species captured since 1973 by the sampling gear of the SEBJ in the lakes of northwestern Quebec, in order to provide planners with a data synthesis which will serve them in the development and management of the territory. It is based on the data available from the SEBJ as well as the Society for the Development of James Bay (SDBJ): data from fish catches, physico-chemical data from the lakes, descriptions of the environment, drawn from the ecological map of the territory. This study is particularly concerned with describing the niches of different species as well as the associations that form between them. Certain geological factors controlling their distribution will also be studied. The regularity of species distributions serves in the end, as much as synthetic biotic parameters, to show the principal biogeographic gradient in this territory.

The present work attempts, then, to use ecological inventory data collected for diverse reasons but different from those of this study, to illuminate the ecology of fishes of this territory. Although it may always be more interesting to analyze the data after all possible data have been collected, the ecologist must not forget the fact that the problems involving development of the territory must frequently be resolved rapidly, that it is necessary for the planner to have recourse to data already accumulated in general ecological data banks which have been placed on file in the course of previous years' study or studies elsewhere in N. America or Europe. It is time to develop methods for analyzing these data banks, lest ecologists be excluded from participating in planning decisions, whereas it is possible for him to use the important fraction of these data, collected at great expense, in a multivariate analysis, without even having to compromise their quality. The present article hopes then to be a contribution to the methods of jointly analysing data drawn from disparate data files.

Materials

Betwenn 1973 and 1976, a large number of lake stations have been sampled by the SEBJ team, in different hydrographic basins of northwestern Quebec. The basins considered in this paper are presented in Table I and Figure 2. For 378 lake stations, one finds, in the data banks of the SEBJ, data on the fish captured by various gear along with the time and duration of the fishing effort. For these 378 stations (totaling 299 lakes), the data files also furnished a description of the physical environment, shown in the first part of Table II, which also includes the percentage of lakes for which various measurements are available. All these parameters, except lake surface area, have been measured at each station and hence are not necessarily representative of the entire lake. When mean depth and maximum depth measurements differ between stations from the same lake, the largest values were subsequently used for all stations from that lake.

The study site has been thoroughly inventoried, since 1973, by the team of ecologists from the Section of Regional Ecological Studies of Environment Canada (SEER). The territory has been divided into about 40,000 territorial units or "ecological cells," each cell composed of the intersection of a terrestrial and aquatic ecosystem (Legendre and Gagnon 1977), in such a way that each cell corresponds to the descriptors of its terrestrial ecosystem and its aquatic ecosystem (Table II, lower portion). These data are assembled in the data bank of the SDBJ which has permitted us to withdraw from it a data file containing ecological cells corresponding to the lake stations of the present study. The ecological cell which corresponds to each lake station had been determined from the geographic coordinates of the station.

All environmental data had been collected in a single data file, in which the 378 lake stations were described by 24 parameters (the 21 parameters in Table II and the three in Table IV). Table III presents thee codes utilized in defining parameters 9 to 21, in order to be able to explicitly describe the niches of different species in Tables V through VIII.

For most of the 299 lakes, there only exists results from a single sampling effort in the data bank of the SEBJ. Only 25 of these lakes have been sampled at more than one station, while Lake Sakami has the greatest number (10) of sampling stations. On the other hand, some stations have been studied in detail, with one having been sampled 50 times during the period under study.

Most of the following results have been obtained from a data file on the occurrence of 29 fish species, where one will find the French and Latin names in the section of results entitled "Species Associations." This data file has been assembled with regard only to the species collected at a station, without regard to the number of individuals caught, the gear or number of sampling times. Sixteen species have been captured at more than 15 lake stations. At stations where more than one collection was made, the same species were regularly collected, leading us to believe that the data file, collected as it was, was nevertheless worthy of analysis.

The data file on fish species abundance was not assembled as easily. In fact about forty different types of fishing gear have been used by the SEBJ between 1973 and 1976, ranging from entanglement nets to fishing poles. To establish the relative abundance of different species in the different lakes of the territory, it was first necessary to select one of these sampling gear. The experimental multifilament gill net with mesh size (stretched) ranging from 2.5 to 10.2 cm was chosen, since it was used most frequently (about 40% of the collections) and it provided, by far, the greatest number of captures for the majority of the species, and in the greatest number of stations. This net, 1.8 m tall, was composed of 6 nets, each 30 m long, attached end to end. It was set at the lake bottom, most of the time starting at the shoreline. The data file of species abundances was produced from 238 stations and 14 species, using only those species captured at least twice with this net. The data consist of the fish catch, standardized as the number of specimens which would have been caught if the net had been set for 24 hours ($R = 24n/h$ where n is the number of individuals captured and h the number of hours the net was set. In the case of replicate sampling at a station the mean catch per unit effort (CPU) was used for each species.)

A study of the abundance data (Beavais and Legendre 1977) has already shown that the CPU of the gill net was not a linear function of fishing time. This phenomenon seems to be due to several factors such as (1)the principal species studied may be highly territorial so that when the net is first set, it captures the individuals with nearby territories, and hence no new individuals remain to be caught during the remaining net set; (2)furthermore, it is probable that the first individuals caught, especially if they are large, quickly render the net inoperable by wrapping themselves up in it. The result is that abundance data calculated such as described above, is of very limited value. It will only be used in the following analysis to calculate the evenness of species distributions.

Methods

Study of Species Diversity

The species diversity of a community is a synthetic biological parameter which may show a relationship with other community properties as well as with the various environmental factors to which each community is exposed. Species diversity, as well as its components, may be measured by numerous methods. These methods have been reviewed by Pielou (1969), Hendrickson and Ehrlich (1971), Hurlbert (1971) and more recently by Legendre and Legendre (1978b).

Diversity may be measured by Shannon's formula (1948):

$$H = -\sum p_i \log p_i$$

where the p_i's are the relative frequencies or probabilities of different species encountered in the samples. This measure of diversity is not influenced by the number of sampling efforts nor the duration of a net set, since it is calculated using the relative frequency of the different species. It varies however as a function of the number of species, a parameter most subject to error in the data file of species abundances, since the file only contains data from the experimental multifilament gill-netting. The net poortly sampled the smallest species as well as long, narrow-bodied species like the burbot. This problem is less important in the data file containing presence/absence data, since gill net catches there account for only about 40% of the species collected. Consequenctly, it seemed more appropriate to compare the species composition from various stations using a statistic which is independent of the number of species.

As first suggested by Margalef (1958), Lloyd and Ghelardi proposed in 1964 a measure of the equitability (evenness) of species distributions which only takes into account the form of the species abundance curve, thus eliminating the effect of the number of species. This measure lies between 0 and 1 and is calculated from the formula:

$$R = H/H(max) = H/\log n$$

where H(max) = log n represents the maximum diversity which would occur if each of the n species were equally abundant. This measure, better adapted for the use of relative abundance data, has been used as the basis for comparing samples in order to discover the principle gradients in the set of lakes under study.

Study of Species Distributions and Niche Characteristics

The niche concept used in the present study is that of the fundamental niche proposed by Hutchinson (1957). This is defined as a hypercube, where the niche of a species consists of the distribution of individuals in a multidimensional space representing various environmental factors.

The method of analysis we chose makes this definition operational. It consists of determining, for each environmental factor included in the niche definition, the interval or subset of environmental conditions which "favor" the presence of a species. The presence or absence of each species is compared with each environmental factor in a contingency table. The rows of these rectangular tables correspond to the various subdivisions of the environmental factor, and they have two columns, one for the presence and one for the absence of a species. Each cell of the table corresponds then to one description (observation) for the variable "presence/absence", and to one description (observation) for the niche variable. One can then record the number of samples which have positive values for these two observations. A particular category of a habitat factor is said to favor a species if it occurs there more often than if its distribution were random. The method of analyzing contingency tables in terms of conditional probabilites is given in more detail in Legendre and Legendre (1978b), along with other statistics one may calculate from contingency tables.

As an additional means of analyzing the data, we calculated non-parametric partial correlations between species presence/absence and each environmental factor. The partial correlations permit the discovery of any relationship between two variables (here the presence of a species and some environmental factor), by removing the influence that other variables might have on this correlation. Kendall's non-prametric correlation coefficient allows one to measure the relationships between two variables which are ordinal but not necessarily metric or linearly realted. These coefficients may also be combined in calculating partial correlations, but unfortunately they cannot be tested for statistical significance (Kendall 1948). Ten continuous variables, divided into ordered classes, have been included in this calculation and compared with the presence or absence of each species.

The Study of Species Associations

Different concepts of species associations have appeared in the literature. Several of these have been reviewed by Southwood (1966) in the framework of studies on insect, and by Legendre and Legendre (1978a) in relation to phytoplankton. Since the most reliable data of the present study are those on the presence/absence of species, a concept of association based on the co-occurrence of species, rather than their correlation or some other quantitative measure of dependence, seemed appropriate.

The method used, due to Krylov (1968) consisted of first determining, for each species pair the probability of association by using chi-squared values obtained from 2x2 contingency tables consisting of presence/absence data for all stations. The calculation of chi-squared values included a correction for continuity and the associated probabilities were evaluated using one degree of freedom. Since we were only interested in positive associations, Krylov recommends assigning a probability of independence equal to 1 for any two species for which the expected frequency of co-occurrence is larger than or equal to the observed frequency of co-occurrence. The probabilities obtained have values between 0 and 1, and they approach 0 when two species are closely associated, so that the threshold of significance (eq. p less or equal to .05) may be used as the limit which defines an association between two species. Below this value (or any other that may be chosen) the species are considered linked in a significant fashion and the complement of the above probability may be used as a measure of species association ($s = 1-p$, $0 \leq s \leq 1$).

The probabilities of co-occurrence, thus calculated, may be assembled in a nxn matrix (n = the number of species being considered). Krylov recommends a method of clustering related species by using a given minimum similarity value (e.g. $s \geq .95$). Independent groups with at least three species, interrelated at the chosen probability level, may then be defined as species associations using the following rules: (1)between two possible divisions of the species, one chooses the division which results in groups containing the largest number of species possible; (2)between several non-independent groups which contain the same number of species, one chooses the partition which maximizes the number of independent groups; (3)if the preceeding criteria do not resolve the choice between one or the other of two species, one includes in the group, the one which has the lowest affinity with the other species groups. The first two criteria are due to Fager (1957) while the third was suggested by Krylov (1968). After having identified by this method groups of related species, one may finally associate the remaining species with one or more of these groups (see Venrick 1971, for a reference on the ordination program by Fager). These "satellite" species are not associated with every member of a species group, and may be satellites for several groups. Species associations described by this method give the best account of the complexity of the organization of biological communities.

In the present study, the method of Fager-Krylov-Venrick described above produced, using $s = 1-p \geq 0.95$, too many equivalent groups of species to be able to choose among them. A similarity of $s \geq 0.989$ was chosen, which produced interpretable species groups. Species groups thus obtained have been represented by plotting the species along the first two principal coordinate axes (Gower 1966) calculated from the similarity matrix as recommended by Legendre (1976) (see Figure 3 in the results section).

Results and Discussion

Diversity

The measures of the evenness of fish species distribution at different stations in the lakes, were compared to the environmental factors listed in Table 2 by a contingency table. This analysis reveals the following relationships.

Whereas in the west, diversity is low, it becomes higher and higher as one proceeds towards the eastern section of the territory, or with higher elevations or with increased water transparency (there are, however, also lakes with low diversity in the eastern plateau). According to Legendre's interpretation (1973), this indicates that in the eastern plateau region, there are lakes of lower biological productivity and which consequently, are a more stable environment than the more productive lakes situated in zones of marine invasion.

The different nature of lakes of the plateau versus lowland may be essentially explained by the geology of northwestern Quebec. In fact, following the retreat of the Scheffer glacial icecap, 7,000 to 8,000 years ago, the flooding of James Bay (sea of Tyrrell) caused by the depression of the earth under the weight of the ice, would have reached areas today that are at altitudes of 240 to 270 meters (Lee 1960). This zone of marine invasion, as well as an area affected by the extension of glacial lake Barlow-Ojibouai in the southern portion of the territory, constitute what would be called the lowland region as opposed to the plateau (which was not affected by the Tyrrell Sea and little affected by Lake Barlow-Ojibouai).

The lowland region is thus characterized by clay deposits and little geographic relief; as Laverdiere has described it (1969:238): "marine sedimentation having caused the levelling of the lowland terrain." Lakes here are shallow, stream and riparian habitats are very abundant and, as a consequence of marine and glacial lake invasions, lie upon clay soils covered with organic sediments, marine or littoral. One would expect then, to find there lakes with turbid water (a result of the suspension of bottom materials), warm and with high conductivity. The plateau region, on the other hand, is characterized by a more hilly relief (with very little stream and riparian habitat) and by soil covered with fluvial-glacial sediments. Lakes there frequently have clearer water, lower conductivity and are colder than lowland lakes.

Distributions

The extent of species' distributions in lakes of the territory was established by analyzing the contingency table containing presence/absence data and the environmental deescriptors, latitude and longitude (Table 4). The list of species follow the order of associations (see page 151); within associations the order is that of the capture frequency. From this table, as well as from the species' distribution maps from Beavais and Legendre (1977) which space constraints prevent reproducing here, one may characterize the distribution of various species in relation to geographic and biogeographic landmarks present in Figure 1. These distributions are briefly discussed below. We will want to further discuss these distributions in relation to species associations.

1. Species with a wide distribution, but which most characterize the plateau: lake whitefish, long-nosed sucker, lake trout, round whitefish.

2. Species characteristic of the lowland region:

2.1 Species occurring throughout the territory, but most characteristic of the lowland: northern pike, white sucker, walleye, burbot.

2.2 Species limited to the western portion of the territory:

2.2.1 Species present from north to south: toullibee, lake sturgeon (both were captured at less than 15 stations).

2.2.2 Species found north of the Eastmain River: lake cisco (also found in the Mistassini region), yellow perch. The following species, captured at less than 15 stations, would belong to this group: troutperch, spot tail shiner, emrald shiner, 5-spined stickleback, pearl dace and the longnose dace.

2.2.3 Species captured at less than 15 stations, which are limited to the boreal zone (50 degree parallel) in the southwest of the territory: mooneye, golden eye, sauger.

3. Certain species, because of their shape or size, would only be caught using seines, minnow traps, trammel nets or fish toxicants. But these methods were only used at stations in the Grande River basin as well as at lake Caniapiscau (with the exception of seines which were also used in the Eastmain and Nichicun regions). Since the species ennumerated here were captured at only these stations, there is a good chance that they may occur at other stations but our sampling was not adequate to collect them. These species are the lake chub, 9-spined stickleback, mottled sculpin and 3-spined stickleback. The slimy sculpin and the fouille-roche would be included in this group.

4. Other species.

4.1 The brook trout was only found in lakes in the northern portion of the territory, (north of the 53rd parallel) except for Lake Mistassini, Lake Village (9 m secchi depth) and on other lakes in the region of the Eastmain River. It is found, however, in rivers that lie in the south. This could be attributed to the fact that at the time of the last glaciation, the brook trout found refuge in the Atlantic and not in the Mississippi region, as that was the case for most of the species of northwest Quebec, and during post-glacial colonization, it penetrated into this region using a northern route through Hudson Bay (Power 1975:114). The natural barriers to colonization as well as the greater competition from other fishes in southern lakes would explain the absence of brook trout from lakes situated south of the 53rd degree of latitude.

4.2 The land locked Atlantic salmon is only found in our study area in the region of Lake Caniapiscau, which still belongs (temporarily) to the drainage basin of Ungava Bay, in the northeastern part of Quebec. It was only captured in 6 stations during the present study.

Niches

Tables 5 through 7 present the ecological niches of 16 fish species captured from at least 15 stations. It was judged best not to make niche generalizations for the other species. These species will, however, be mentioned when describing the species associations.

The niche is described using the 21 variables enumerated in Table 2. The first eight variables are quantitative while the rest are recorded using the codes described in Table 3. However, even the first group of variables was divided into classes for the analysis of niches using a contingency table, so that it is the limit of these classes and not the raw data itself which defines the niches.

Tables 5 through 8 indicate the environmental parameters which "favor" the presence of certain species associations. These tables divide the species according to the associations described in the following section.

Table 9 completes the niche descriptions by revealing, through partial correlations, which are the environmental parameters favoring the presence of a species once the effects of correlated parameters have been removed. This table shows the importance of latitude, altitude, lake surface area, water transparency and specific conductance in separating out species into the first two associations.

Dissolved oxygen measurements (taken 1 meter below the surface) could have been excluded from these calculations since the lakes in this territory do not generally have oxygen deficiencies. As dissolved oxygen is expressed in mg/liter and not percentage saturation, partial correlations in this table indicate then, in an inverse manner, the influence of water temperature once other factors such as geographic position have been eliminated. Thus, for the lake trout and brook trout, a negative correlation with oxygen would indicate that at comparable geographic positions, there is a greater chance of finding these salmonids in warmer water, which, at saturation, contain less dissolved oxygen. On the other hand, longitude is supplanted in importance by transparency and specific conductance, which better indicate the division of the territory into a lowland and a plateau region. The sign of the partial correlations for altitude will be explained in the following section. Finally, lake depth by itself seems to be of little importance: the species studied here are more influenced by surface area, transparency and specific conductance which are themselves related to lake depth.

The niche descriptions will be discussed further in the next section in the general framework of an ecological explanation of species associations.

Species Associations

Five species associations are formed at the level of similarity $s = 1-p \geq 0.989$, when one includes the 29 fish species in the calculations. These associations are shown in Figure 3 in the reduced space of the first two principle coordinate axis calculated from the matrix of species similarities. If one only includes the 16 species present at 15 or more lake stations, one finds at $s \geq 0.99$, the same lake whitefish and northern pike species associations as before; the brook trout association loses one species (the slimy sculpin which was caught at only 8 stations) and the lake trout and troutperch associations disappear since all their species (except the troutperch) are removed from the calculations. The three resulting associations are those described in Tables 5 through 7. The lake whitefish and northern pike associations are particularly interesting, not only because they were already formed at similarity levels of 0.999 and 0.995 respectively, but also because the species composing them are present at a large number of stations (16 to 70%).

Lake whitefish association (Table 5)

Lake whitefish	_Coregonus clupeaformis_
Longnose sucker	_Catostomus catostomus_
Lake trout	_Salvelinus namaycush_
Round whitefish	_Prosopium cylindraceum_

Lake chub *Couesis plumbeus*

Even though these species are present throughout the study area, they are most abundant in the northern plateau section (altitude above 250 m, east of 75 degrees W and north of 54 degrees N). This association characterizes large, clear lakes (secchi depth 2 to 9 m) having a low conductivity (less than 10μs) as shown by the partial correlations of Table 9. These lakes are slightly acidic, with shorelines that slope gently and inlet/outlet streams present. This association largely occurs in an area with undulating relief having a thick layer of glacial till where stream and riparian habitats are rare.

The negative correlation in Table 9 between species occurrence and altitude indicates that, when one controls for all other factors, including geographic position, these species have a greater chancee of having reached downstream rather than upstream lakes in their post-glacial dispersal. Some of these species occur more abundantly in deep lakes (lake whitefish, white sucker); the lake chub prefers shallower lakes.

Satellite species: Atlantic salmon (*Salmo salar*) (connected to the round whitefish by s = 0.9992) and the burbot (*Lota lota*) (connected to the longnose sucker by s = 0.9999) and to the slimy sculpin by the same s value in the brook trout association). The Atlantic salmon shares the ecological characteristics of the other species in this association, but it was only caught at six stations in Lake Caniapiscau, at the extreme eastern edge of the territory. The burbot is more abundant and widely distributed in this region, its abundance was probably underestimated by the gill nets. Its niches include that of the species discussed above, but it is most abundant where the specific conductance is elevated by intrusion of marine waters.

Northern pike association (Table 6)

Northern pike	*Esox lucius*
White sucker	*Catostomus commersoni*
Walleye	*Stizostedion vitreum*
Cisco	*Coregonus artedii*
Yellow perch	*Perca fluviatilis*

This association is characteristic of the western lowlands (at an altitude near 300 m). The distribution of these species characterizes the zone of marine invasion (75 to 80 degrees W). The northern pike, white sucker and walleye also occur further east, but are much less abundant there. The frequency of capture of these species increases as one approaches James Bay. Lakes having this association are smaller than those with the lake whitefish association:

transparency is less (secchi depth = 0 to 2 m) and the specific conductance is greater (10 to 50 µs) as shown by the partial correlations of Table 9. The pH is neutral and shoreline slopes are moderate. These lakes are situated in mountainous areas with thick organic sediments. The rivers contain organic sediments or rocks and sediments of glaciolacustrine origin. River and riparian habitats are more abundant than for the lake whitefish association.

The positive partial correlation with altitude (Table 9) indicates that the species in question are more often found in upstream lakes than in lakes situated near James Bay.

The northern pike prefers shallower lakes than the white sucker or walleye. Also, lakes which favor the presence of the northern pike and white sucker have larger rivers associated with them than lakes favoring the other three species.

Brook trout association (Table 7)

Brook trout	<u>Salvelinus fontinalis</u>
9-spined stickleback	<u>Pungitius pungitius</u>
Mottled sculpin	<u>Cottus bairdi</u>
3-spined stickleback	<u>Gasterosteus aculeatus</u>
Slimy sculpin	<u>Cottus cognatus</u>

This association includes four small-bodied species (the two sticklebacks and two sculpins) which were only captured where seines, minnow traps, fish poisons or electroshocking were used. These gear were only used on lakes in the Grande River Valley, consequently this limits where we found these species. Since such gear were rarely used in the upstream portion of the Grande River basin, an artificial separation was created (Fig. 3) between the brook trout and the other four species. The likely occurrence of the latter went undetected in ten localities where habitat conditions were favorable.

It was not surprising to find the brook trout associated with the four small species since it is a well known predator of them (Scott and Crossman 1974). Table 7 indicates that the species in this association have several components of their niche in common. They are most abundant in lakes situated in mountainous areas or hilly regions with a thick glacial till, where rivers and riparian habitats are rare. These lakes are 2.5 sq. km or larger and their rivers, overlying till, do not exhibit much meandering. This summary is limited by the small proportion of stations effectively sampled for small species and would merit revision after a more extensive study is done.

<u>Satellite species</u>: burbot, <u>Lota lota</u>, (linked to the

slimy sculpin by s = 0.9999 and linked to the white sucker in the northern pike association by the same value) as well as three other small species captured at fewer than 15 stations and whose association might be due to chance: the brook stickleback (Culea inconstans) the pearl dace (Semotilus margarita) and the longnose dace (Rhynichtys cataractae). The association of burbot with this group might also be due to chance since it is established through the slimy sculpin, a species not abundant in the data set we have employed. However, examination of species association at s greater than or equal to 0.95 show that the burbot could be placed with either the brook trout or lake whitefish association. This says then, that the association of the burbot with brook trout must reflect common habitat preferences, and this is observed in comparing Tables 7 and 8. It should be noted that both species are predators of sculpins and sticklebacks (Scott and Crossman 1974).

Toullibee association

Toullibee	Coregonus nipigon
Lake sturgeon	Acipenser fulvescens
Goldeye	Hiodon alosoides
Mooneye	Hiodon tergisius
Walleye	Stizostedion canadense

Except for the toullibee and lake sturgeon, these species are confined to the lower limit of the territory. It is not, therefore, necessary to search for the reason of their association solely in habitat characteristics, but also in the fact that they are all at the northern limit of their distributions and are not very abundant. All were captured at fewer than fifteen stations.

Examination of environmental data (not reproduced here because of few samples) shows that this association inhabits waters similar to the northern pike association since, according to the available data, the majority of these species prefer turbid smaller lakes with neutral pH and having a conductivity which is high for this region (10 to 40 μs). These lakes are situated in a landscape where rivers and riparian habitats are abundant. It is distinguished from the northern pike association by being more typical of areas having a thick layer of fluvial or glacio-lacustrine sediments, such as occurs in the southern portion of the study area, in the zone of invasion by glacial lake Barlow-Ojibouai.

Troutperch association (Table 8)

Troutperch	Percopsis omiscomaycus
Spottail shiner	Notropis hudsonius
Emerald shiner	Notropis atherinoides

Although these species would have been caught with the seine or multifilament experimental gill net, which had been used extensively throughout the territory, these three species only occurred in a limited portion of the west-central region, at sites G2, G3, SK and EM (see Figure 2). Moreover, the two cyprinids were only captured at 7 and 1 stations respectively, thus limiting any description of the environmental correlates of this association.

If one accepts that these three species were really limited to this region, one could describe their niche as close to that of the northern pike association (data not reeproduced here): a region with thick organic sediment deposits, hilly or mountainous relief, rivers and riparian habitats more abundant than on the plateau, lakes with steep banks and a low transparency.

A better sampling of these smaller species would permit an assessment of the value of this association.

Satellite species: the longnose dace, Rhynichtys cataractae captured at only one station.

Conclusions

1) The regularity of species distribution patterns is lowest in the western portion of the territory, but one finds it becomes more and more predictable with increasing altitude, which indicates for those lakes lower biological productivity and a stabler environment.

2) The two fish associations most evident from this study are the lake whitefish association (which includes the longnose sucker, lake trout, round whitefish and lake chub) and the northern pike association (which includes the white sucker, walleye, cisco and yellow perch). When one examines the distribution of the species in the northern pike association, one perceives that the probability of capturing the five species, as one moves away from the bay and reaches an altitude of 250 m or more, is less than their mean capture probability for the whole territory (the perch disappears completely). This altitude (250 m) corresponds precisely to the limit of the post-glacial marine invasion. On the other hand, the species of the lake whitefish association increases in abundance (although the increase is irregular for the lake whitefish and lake chub) starting at about 350 m. One can say then that the northern pike association characterizes the portion of the territory which was subject to marine invasion, having lakes with turbid and warm waters, with high conductivity and hence high biological productivity, whereas the lake whitefish association characterizes the plateau of the north and east of the region, further from the bay, where

one finds cold clear water lakes, with low conductivity and hence low biological productivity.

3) A group of small species were only found in certain hydrographic basins in the center of the territory, possibly because of insufficient sampling with minnow traps, seines, fish toxicants and gill nets. The association analysis groups these species with the brook trout, which uses them as forage. The brook trout is itself essentially limited to lakes north of 53 degrees, possibly because of its post-glacial dispersal mechanism. The burbot utilizes these same species as prey and might be associated with them, but the analysis shows that it might also be attached to the lake whitefish association.

4) A group of rare species are at the northern limit of their distribution. They are the lake trout, toullibee, lake sturgeon, mooneye, goldeneye and sauger. These species are for the most part limited to the southern portion of the study site, where they occur in the same type of lakes as the northern pike. These lakes are formed in depressions formed in lacustrine deposits.

5) The other species were captured at too few stations to draw conclusions about their distribution. The land-locked Atlantic salmon, rare in the study area, is known to be limited to lakes with a high transparency and low conductivity in the Lake Caniapiscau region, probably because its post-glacial dispersion was from the Atlantic refuge, via the bay of Ungava, whereas most of the other species came from the Mississippi refuge via the great glacial lakes (Power 1975).

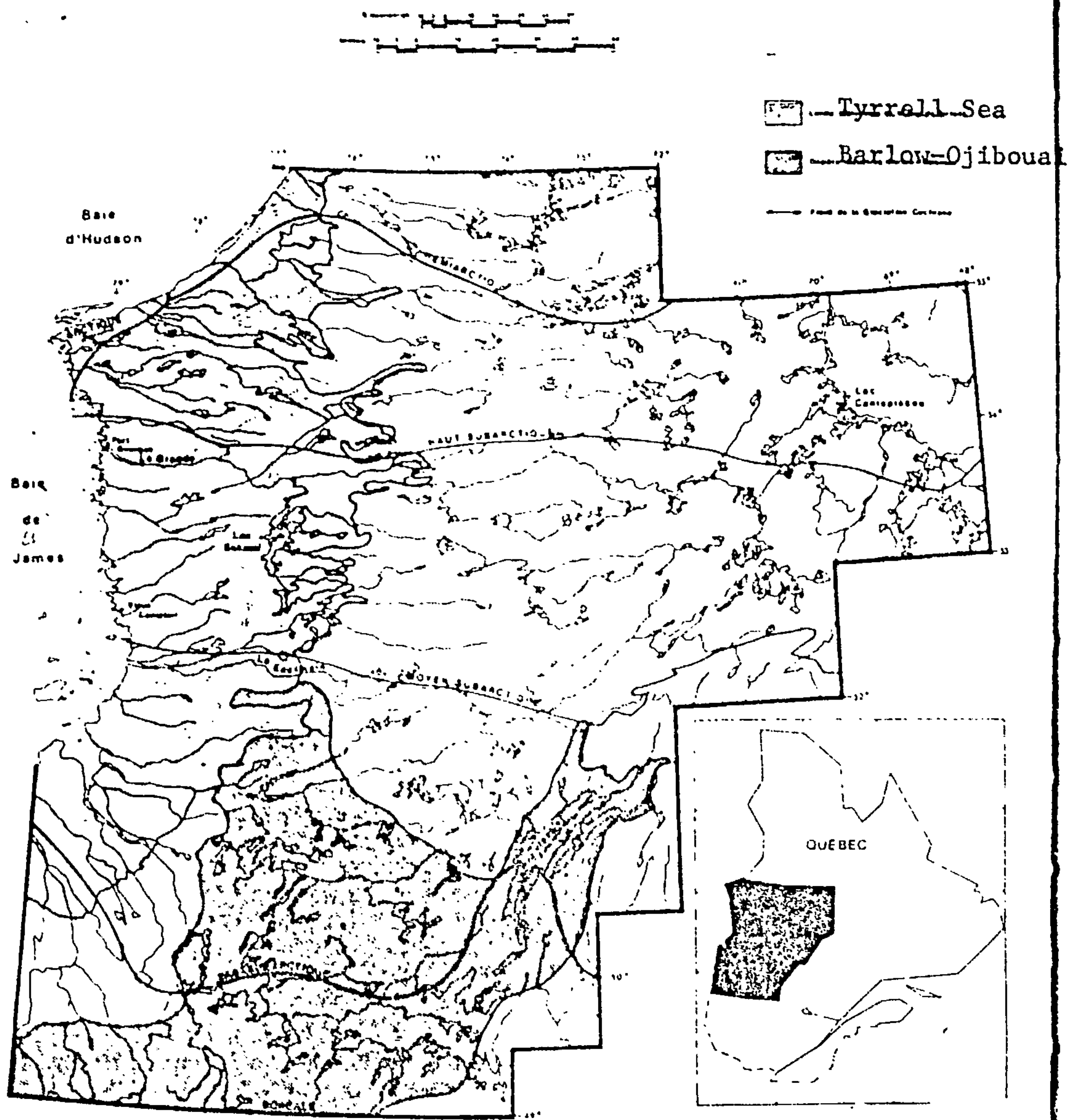

Fig. 1. Map of the study area showing bioclamatic zones (Zarnovican et al. 1976) and post-glacial limits of the Tyrtell Sea and Lake Barlow-Ojibouai.

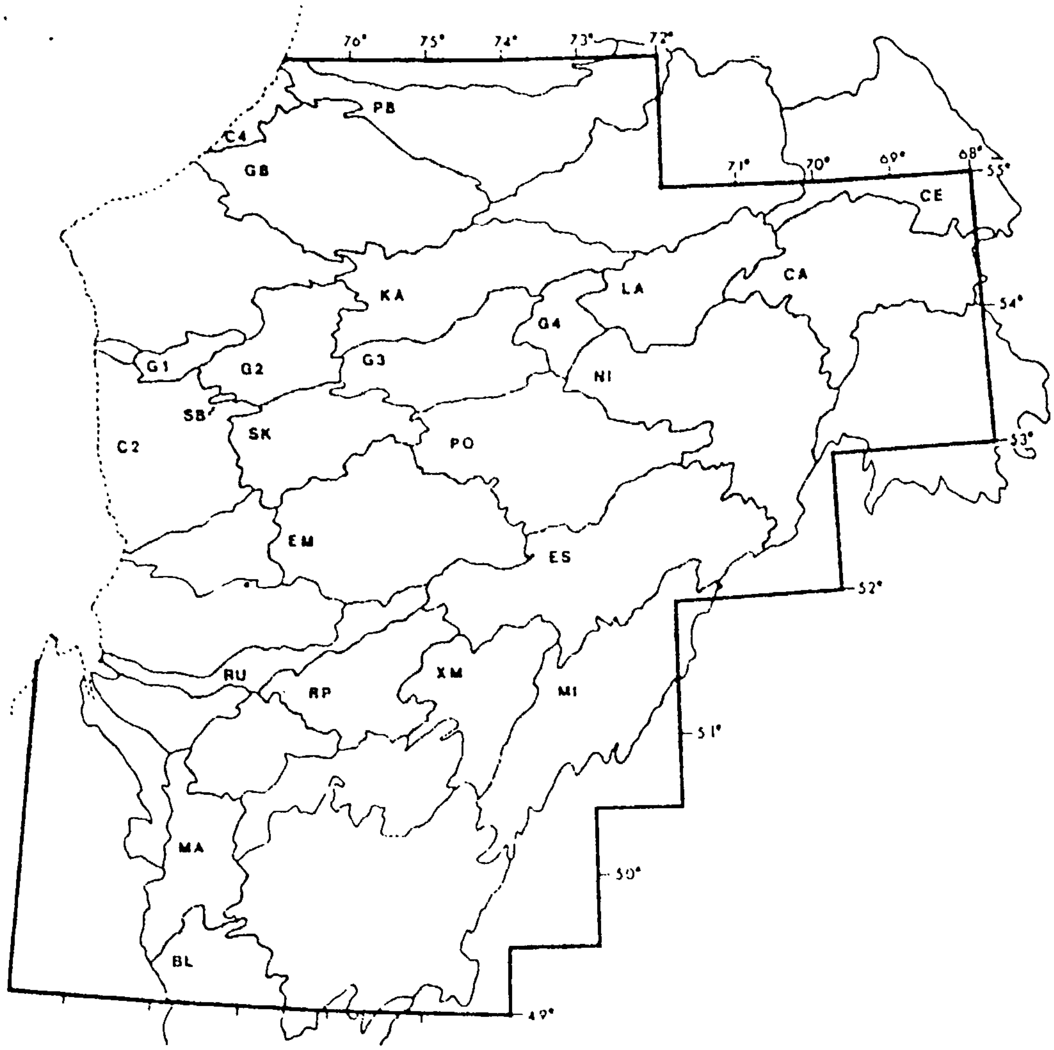

Fig. 2. Map of northeaster Quebec showing the hydrographic basins identified by their codes (see Table 1).

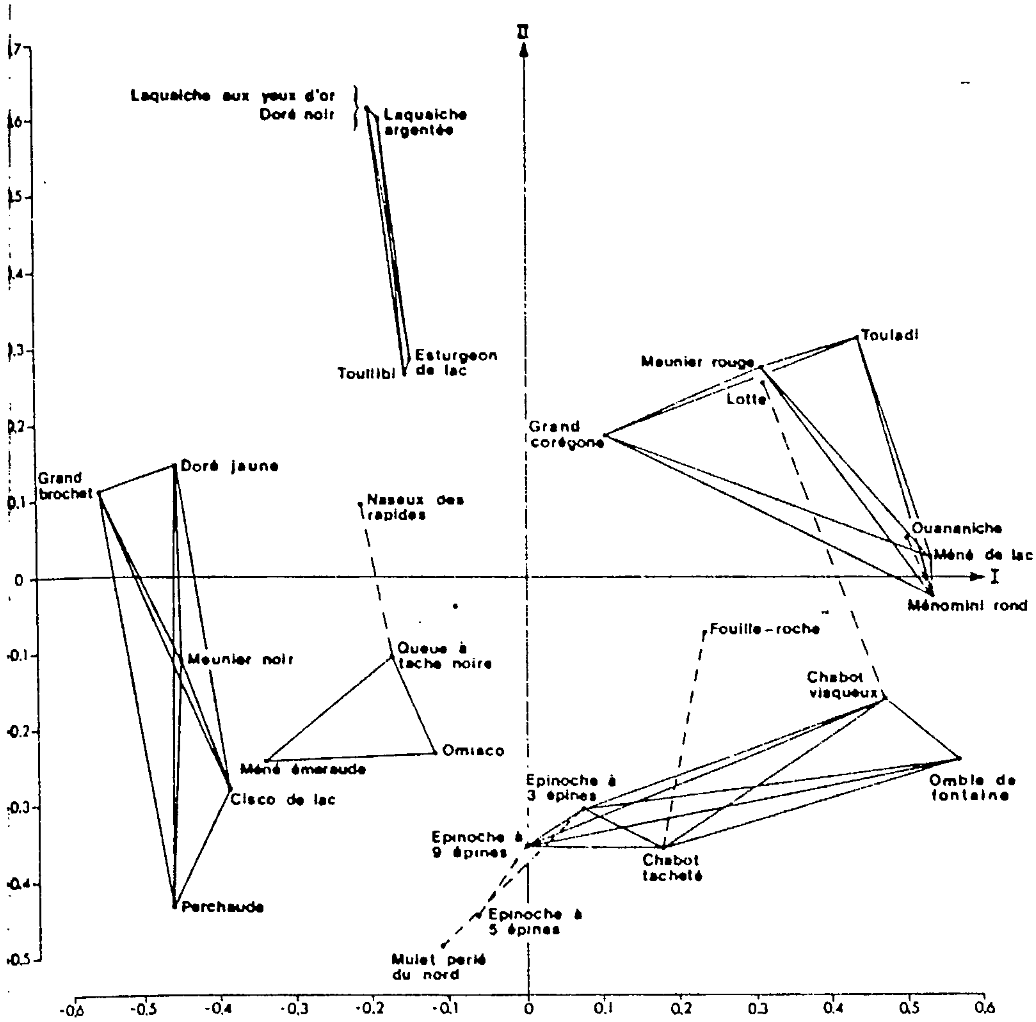

Figure 3. Graphical representation of fish species associations on the first two principle coordinate axis, which account for 55% of the sum of squares between species. Solid lines unite species associated at the level of S = 1-p .989. Dotted lines show sattelite species.

French/English names

aquaiche aux yeux d'or/goldeye
ore noir/Sauger
aquaiche argentee/mooneye
sturgeon de lac/lake sturgeon
oulibi/Toulibee

ore jaune/Walleye
rand brochet/northern pike
eunier noir.white sucker
isco de lac/Cisco
erchaude/Yellow perch

ene emeraude/Emerald shiner
nisco/Troutperch
ueue a tache noir/Spottail shiner
aseux des rapides/Longnose dace

Touladi/Lake trout
Meuneir rouge/Longnose sucker
Lotte/Burbot
Grand coregone/Lake whitefish
Ouananiche/Atlantci salmon
Mene de lac/Lake chub
Menomini round/Round whitefish

Fouille-roche/
Chabot visqueux/Slimy sculpin
Omble de fontaine/Brook trout
Chabot tachete/Mottled sculpin
Epinoche a 3 epines/3-spined stickleback
Epinoche a 9 epines/9-spined stickleback
Epinoche a 5 epines/5-spined stickleback
Mulet perle du nord/Pearl dace

Table 1

Regions where lakes have been sampled for fishes by the SEBJ during 1973-1976.

Code for hydrographic basin	Basin name	Number of stations sampled
BL	Rivière Bell	1
CA	Lac Caniapiscau	54
CE	Canyon Eaton	1
C2	Nouveau-Comptoir	23
C4	Manitounuk	1
EM	Rivière Eastmain (embouchure)	26
ES	Rivière Eastmain (tête)	3
GB	Grande Rivière de la Baleine	3
G1	Réservoir LG1	1
G2	Réservoir LG2	88
G3	Réservoir LG3	60
G4	Réservoir LG4	23
KA	Rivière Kanaaupscow	3
LA	Rivière Laforge	14
MA	Lac Matagami	6
MI	Lac Mistassini	11
NI	Lac Nichicun	3
PB	Petite Rivière de la Baleine	1
PO	Rivière de Pontois	4
RP	Rupert-La Marte	3
RU	Rivière Rupert (embouchure)	2
SB	Secteur de base (Lac Nathalie)	29
SK	Lac Sakami	15

Table 2

Descriptors of the physical environment (top portion) and the ecological systems (bottom portion) drawn from the data banks of the SEBJ and the SDBJ, respectively. These descriptors are detailed in Table 3.

Descriptors	Percentage of stations for which the information was available.
Mercator coordinates	100
1) Altitude (m)	100
2) Mean Depth (m)	67
3) Maximum depth (m)	67
4) Lake area (km^2)	67
5) Water transparency (Secchi: m)	51
6) Conductivity (μS)	50
7) pH	49
8) Dissolved oxygen measures at 1 m below the surface (mg/l)	41
9) Relief	95
10) Depth of movable materials (till)	95
11 and 12) Nature of the geologic material of the system (dominant and sub-dominant)	95
13) Category of Aquatic Ecosystem	95
14) Abundance of rivers	95
15) Abundance of riparian habitats	87
16) Drainage system	85
17) River channel	85
18) Gradient of the basin	85
19) River gradient or current	85
20 and 21) Nature of the geological material of the rivers (dominant and sub-dominant)	85

Table 3

Explaination of the descriptors 9 through 21 listed in Table 2.

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9) Relief
- F = flat
- U = undulatory
- R = hilly
- H = foothills
- M = mountainous

10) Depth of movable materials (dom & subdom)
- 1) thick
- 2) thick & thin
- 3) thick & even
- 4) thin & thick
- 5) thin
- 6) thin & even
- 7) even & thick
- 8) even & thin
- 9) even

11,12,20,21) Geologic material
- 0 = bedrock in places
- 1 = till
- 2 = fluvial-glacial sediments
- 3 = sediments of delta origin
- 4 = fluvial or glacial-lacustrine sed
- 5 = marine or littoral sediments
- 6 = littoral sediments
- 7 = organic sediments
- 8 = erosion deposits
- 9 = wind-blown deposits

13) Category of Aquatic Ecosystem
- A- less than 5% water
- B- 5-15% water
- C- more than 15% water
- F- 2.5 km^2 lakes 5 km^2
- GG- 5 km^2 lakes 10 km^2
- N- 10 km2 lakes 25 km^2
- R- lakes 25 km^2
- I- shoreline of a large river

14,15) Abundance of rivers & riparian habitats
- 1 = absent or rare
- 2 = few
- 3 = moderate
- 4 = abundant

16) Drainage system
- 1 = open, upland
- 2 = open, some upland
- 3 = open, swampy
- 4 = restrained, upland
- 5 = restrained, some upland
- 6 = restrained, swampy
- 7 = closed, upland
- 8 = closed, some upland
- 9 = closed, swampy

17) River channel
- 1 = regular
- 2 = meandering
- 3 = very meandering
- 4 =

18) Gradient of basin
- 1 = mild
- 2 = moderate
- 3 = abrupt

19) River gradient (dominant & subdominant)
- 1) mild
- 2) mild, moderate
- 3) mild, abrupt
- 4) moderate, mild
- 5) moderate
- 6) moderate, abrupt
- 7) abrupt, mild
- 8) abrupt, moderate
- 9) abrupt

Table 4

)istribution of 16 fish species captured at 15 or more stations. Only Geographic :ptors which 'favor' the presence of a species are listed. See Table 1 for region . Species are divided into the various associations discussed in the text.

Species	Regions	Longitude	Latitude
'hitefish	CA,G3,LA,SK	69-71, 74-77ơ	54-55
sucker	CA,LA,MI,SB,SK	69-75	54-55
:rout	CA,G3,G4,LA,MI	68-75	54-56
whitefish	CA	68-75	54-56
:hub	CA,G3	68-72	54-55
ern pike	C2,G2,G3,G4,SB,SK	75-80	53-54
iosed sucker	EM,G2,G3,SB,SK	75-79	51.5-54
/e	C2,EM,G2,G3,SB,SK	75-78	49-53.5
	EM,G2,G3,SB	75-80	52-54
ɹ perch	G2,SB	76-78	52-54
trout	G2,G3	72-76	53-56
ied stickleback	-	76-78	52.5-54
ed sculpin	-	76-78	-
ied stickleback	-	76-78	53-54.5
›erch	-	74-78	52-54
:	-	77-79	53-53.5

Table 4

Distribution of 16 fish species captured at 15 or more stations. Only Geographic descriptors which 'favor' the presence of a species are listed. See Table 1 for region codes. Species are divided into the various associations discussed in the text.

Species	Regions	Longitude	Latitude
Lake whitefish	CA,G3,LA,SK	69-71, 74-77	54-55
White sucker	CA,LA,MI,SB,SK	69-75	54-55
Lake trout	CA,G3,G4,LA,MI	68-75	54-56
Round whitefish	CA	68-75	54-56
Lake chub	CA,G3	68-72	54-55
Northern pike	C2,G2,G3,G4,SB,SK	75-80	53-54
Long-nosed sucker	EM,G2,G3,SB,SK	75-79	51.5-54
Walleye	C2,EM,G2,G3,SB,SK	75-78	49-53.5
Cisco	EM,G2,G3,SB	75-80	52-54
Yellow perch	G2,SB	76-78	52-54
Brook trout	G2,G3	72-76	53-56
9-spined stickleback	-	76-78	52.5-54
mottled sculpin	-	76-78	-
3-spined stickleback	-	76-78	53-54.5
Troutperch	-	74-78	52-54
burbot	-	77-79	53-53.5

Table 5

The niche of species from the L. whitefish association. The first two lines represent the percentage of stations at which the species was captured and the three species most closely associated with it, in decreasing order of association ($S \geq 0.99$). Only descriptors which 'favor' the presence of a species in at least 10 stations are listed. Descriptors 1-8 are given in the appropriate units, descriptors 9-21 are coded as explained in table 3.

	Lake whitefish Coregonus clupeafor.	Longnose sucker C. catostomus	Lake trout S. namaycush	Round Whitefish P. cylindraceum	Lake chub C. plumbeus
% of stations	70%	41%	38%	16%	16%
Associated species	Longnose sucker Lake trout Round whitefish	lake trout Lake whitefish Lake chub	Longnose sucker Round whitefish Lake chub	Lake trout Longnose sucker Lake chub	Lake trout Longnose sucker Round whitefish
1). Altitude (m)	200-500	350-550	300-550	350-550	250 -300& 500-550
2) Mean depth (m)	45-60	15-60	-	-	0-15
3) Maximum depth (m)	90-120	30-120	-	-	0-30
4) Lake area (km^2)	10-100	10-100	10-100	-	-
5) Transparency (m)	0-1, 3-9	2-5	2-9	2-7	2-3
6) Conductivity (μS)	0-20, 30-40	0-10	0-10	0-10	0-10
7) pH	6-7	6-6.5	5-6.5	5-6.5	5-6.5
8) Dissoved O_2 (mg/l)	7-8, 9-10	9-10	7-8	8-12	7-8
9) Relief	U,H	U,H	U	-	U
10) Till depth	1,2,4	1,4	1,2,4	1,4	1
11) Dominant material	1,2	1	1,2	1	1
12) Sub-dominant mat.	1,2,8	1,8	1,2	1	1
13) Cat. Aqua. Ecosy.	F,G,N,R	F,G,N,R	C,F,N,R	C,R	C,F,R
14) Rivers	1	1	1	1	1
15) Riparian Habitat	1	1	1	1	1,2
16) Drainage	1,2	1	1,2	1	2
17) River Bed	1	0,1,2	3	2	2
18) Gradient of the basin	1	1,3	1	1	1
19) River current	1,4,5,8	1,5	1,2	-	1,2,4
20) River Materials (dom)	1,2	0,1	1	1	1
21) River materials (sub-dom)	1,2,4	1,4	1,4	1,4	1,4

Table 6

The niche of species from the northern pike association. The first two lines represent the percentage of stations at which the species was captured and the three species most closely associated with it, in decreasing order of association ($S \geq 0.99$). Only descriptors which 'favor' the presence of a species in at least 10 stations are listed. Descriptors 1-8 are given in the appropriate units, descriptors 9-21 are coded as explained in table 3.

	Northern pike Esox lucius	White sucker C. commersoni	Walleye S. vitreum	Cisco Coregonis artedi	Yellow perch P. flavescens
% of stations	63%	58%	42%	28%	16%
Associated species	White sucker Yellow perch Cisco	Northern pike Walleye Yellow perch	Cisco White sucker Northern pike	Walleye Yellow perch Spottail shiner	Cisco White sucker Northern pike
1). Altitude (m)	0-300	100-300	100-300	0-250	100-200
2) Mean depth (m)	0-15	15-60	-	-	-
3) Maximum depth (m)	0-30	30-120	30-60	-	-
4) Lake area (km^2)	0-10	10-30	-	0-10	0-10
5) Transparency (m)	0-3	0-2	0-2	0-2	0-2
6) Conductivity (μS)	20-40	10-50	10-40	20-80	10-30
7) pH	7-7.5	5.5-6, 6.5-7.5	6.5-7.5	6.5-7	6.5-7
8) Dissoved O_2 (mg/l)	6-10	7-8, 9-10	-	8-9	8-12
9) Relief	R,H	R	R	R	R
10) Till depth	1-3	1,4,7	2,7	7	7
11) Dominant material	2,5,7	5,7	5,7	7	7
12) Sub-dominant mat.	2,6,7	7	7,8	7	7
13) Cat. Aqua. Ecosy.	B,C,G	B,F,G,N,R	F,G,R	B,F,G	B
14) Rivers	2,3	2,3,4	2,3	2,3	2,3
15) Riparian Habitat	2,3	2,3,4	3	2	3
16) Drainage	2	1,2	1,2	5	5
17) River Bed	1,2	1,2	3	2,3	3
18) Gradient of the basin	2	2	2,3	2	2
19) River current	2,5	4,5	2,5	2	2
20) River Materials (dom)	0,2,4,7	0,4,7	0,4,7	0,4	4
21) River materials (sub-dom)	0,4,7	0,7	0,4,7	0,4	7

Table 7

The niche of species from the brook trout association. The first two lines represent the percentage of stations at which the species was captured and the three species most closely associated with it, in decreasing order of association ($S \geq 0.99$). Only descriptors which 'favor' the presence of a species in at least 10 stations are listed. Descriptors 1-8 are given in the appropriate units, descriptors 9-21 are coded as explained in table 3.

	Brook trout S. fontinalis	9-spined stickleback P. pungitius	Mottled sculpin Cottus bairdi	3-spined stickleback G. aculeatus
% of stations	19%	7%	5%	5%
Associated species	Round whitefish 3-spined stick lake trout	3-spined stick. mottled sculpin Troutperch	slimy sculpin 3-spined stick. 9-spined stick.	9-spined stick. mottled sculpin slimy sculpin
1). Altitude (m)	350-400	100-250	100-200	100-200
2) Mean depth (m)	0-15	-	-	-
3) Maximum depth (m)	-	-	-	-
4) Lake area (km^2)	-	-	-	-
5) Transparency (m)	3-9	-	-	-
6) Conductivity (μS)	0-30	-	-	-
7) pH	6.5-7.5	-	-	-
8) Dissoved O_2 (mg/l)	-	-	-	-
9) Relief	R,H,M	R	U,R	R
10) Till depth	-	1	1	1
11) Dominant material	1	1	1	1
12) Sub-dominant mat.	1	7	7	7
13) Cat. Aqua. Ecosy.	F,G,N	N,R	N,R	-
14) Rivers	1,2	2	1,2	1,2
15) Riparian Habitat	1,2	2	-	1,2
16) Drainage	1	-	1,2	-
17) River Bed	1,2	2	1,2	2
18) Gradient of the basin	1	2	-	2
19) River current	4	2	2	-
20) River Materials (dom)	1	-	-	-
21) River materials (sub-dom)	1,7	1	1	-

Table 8

The niche of species from the troutperch & burbot association. The first two lines represent the percentage of stations at which the species was captured and the three species most closely associated with it, in decreasing order of association ($S \geq 0.99$). Only descriptors which 'favor' the presence of a species in at least 10 stations are listed. Descriptors 1-8 are given in the appropriate units, descriptors 9-21 are coded as explained in table 3.

	Troutperch P. omiscomaycus	Burbot Lota lota			
% of stations	4%	11%			
Associated species	Spottail shiner 9-spined stick.	Longnose sucker Slimy sculpin mottled sculpin			
1). Altitude (m)	150-250	100-400			
2) Mean depth (m)	-	-			
3) Maximum depth (m)	-	30-120			
4) Lake area (km^2)	-	-			
5) Transparency (m)	-	3-5			
6) Conductivity (μS)	-	20-50			
7) pH	-	6.5-7.5			
8) Dissoved O_2 (mg/l)	-	-			
9) Relief	R	R			
10) Till depth	1	4,7			
11) Dominant material	-	1			
12) Sub-dominant mat.	7	7			
13) Cat. Aqua. Ecosy.	-	R			
14) Rivers	2	2,3,4			
15) Riparian Habitat	2,3	2,3			
16) Drainage	-	1			
17) River Bed	2	3			
18) Gradient of the basin	-	2,3			
19) River current	1,2	5,6,7			
20) River Materials (dom)	-	0			
21) River materials (sub-dom)	-	1			

Table 9

Partial correlations between species presence and 10 environmental descriptors (using Kendall's r). Correlations less than 0.07 are not shown, values greater than 0.15 are noted with an asterisk*. The 16 species are those which were captured from at least 15 stations, as in the preceeding tables.

	Longitude	Latitude	Altitude	Mean depth	Max. depth	Lake area	Transpar.	Conduc.	pH	Dissolved oxygen
Lake whitefish	-.14	.17*	-.17*	-	-	-.16*	-	-	-	-.08
Longnose sucker	-	.28*	-.10	-.13	.12	-.19*	.19*	-.07	-.08	-
Lake trout	-.12	.48*	-.20*	-	-	-	.27*	-.20*	-	-.17*
Round whitefish	-	.21*	-	-	-	-	.11	-	-	-
Lake chub	-	.17*	-.08	-	-	-	.07	-.11	-	-
Northern pike	-	-.18*	-	-	-	-	-	-	-	-
White sucker	-	-.23*	.09	-	-	-	-.20*	.08	-.08	.07
Walleye	-.09	-.22*	.08	-	-	-.16*	-.13	-	-	-
Cisco	-.07	-.20*	-	-	-	-.13	-.09	.16*	-	-
Yellow perch	-	-.21*	-	-	-	-	-	.14	-	-
Brook trout	-	.09	-	-.09	.07	-.12	-	-	-	-.12
9-spined stickl.	-	-.10	-	-	-	-	-	-	-	-
Mottled sculpin	-	-	-	-	-	-	-	-	-	-
3-spined stickl.	-	-	-	-	-	-	-	-	-	-
Troutperch	-	-.07	-	-	-	-	-	-	-	-
Burbot	-	-	-	-.11	.12	-	-	-	-	-