

Postglacial Dispersal of Freshwater Fishes in the Québec Peninsula

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The possible postglacial dispersal of freshwater fishes in the Québec peninsula is described. We tested the hypothesis that fish dispersal was controlled more efficiently by movements of the earth crust and by morphological peculiarities of the peninsula than by upland divides presently found between river basins. Based on the actual distributions of 109 species of freshwater fishes, the presence and absence of these species was noted for each of 289 one-degree-square pixels of the peninsula. A geographical intermediate-linkage clustering was run with a spatial constraint, that is, only neighbouring pixels were allowed to cluster. Five main ichthyogeographic regions and 21 subregions were thus defined. The regional limits seem to be highly correlated with climatic, vegetational, and geomorphological limits or gradients. Knowing the fish species present in each subregion made it possible to deduce their pattern of postglacial dispersal, after computing a coefficient of dispersal direction between neighbouring subregions. The pattern of fish dispersal so derived assumes that the stenohaline species have crossed the centre of the peninsula. This can be explained by the isobasic movements since the end of the Wisconsin Ice Age, and also by a network of river headwater interconnections still extant today.

Cet article décrit la dispersion postglaciaire des poissons d'eau douce de la péninsule québécoise et tente de vérifier l'hypothèse selon laquelle la dispersion des poissons doit plus aux mouvements de l'écorce terrestre ainsi qu'à la géomorphologie particulière de ce territoire qu'aux limites d'altitude actuelles des différents bassins hydrographiques. Pour chacun des 289 pixels (ou : points d'image) d'un degré de côté qui couvrent la péninsule, la présence ou l'absence de 109 espèces de poissons d'eau douce fut notée à partir des cartes de répartition des espèces. Les pixels furent réunis en régions par groupement à liens intermédiaires avec une contrainte de contiguïté spatiale, ce qui signifie qu'on ne permettait qu'à des pixels voisins de se regrouper. Cinq régions ichthyogéographiques majeures, comprenant 21 sous-régions, furent ainsi définies. Les limites de ces régions semblent bien corrélées avec des limites ou des gradients climatiques, botaniques ou géomorphologiques. A partir des listes d'espèces présentes dans chaque sous-région, un coefficient de direction de la dispersion fut calculé entre sous-régions voisines pour déduire le schème général de la dispersion postglaciaire. Le schème ainsi trouvé suggère que plusieurs espèces sténohalines ont traversé la péninsule par son centre. Ceci peut s'expliquer par les mouvements des isobases depuis la fin de la glaciation du Wisconsin ainsi que par l'existence d'un réseau d'interconnexions entre les têtes des rivières. Ce réseau existe d'ailleurs toujours.

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The emerging field of quantitative biogeography has been reviewed by Crovello (1981), who discussed the 10 stages of biogeographic data analysis. This approach makes it possible to test various historical or ecological hypotheses regarding geographically distributed phenomena, using multidimensional data. The data sets may describe community composition, or the physical environment that the plants or animals live in. The various descriptors can be integrated through multidimensional analysis. This is more likely to bring answers to biogeographic problems than an analysis based on one descriptor at a time because of the interactions between ecological variables that are found in the real world. Examples of such studies have been reviewed by Peters (1971). Other methods have been used by Goodall (1974)

for plant distribution data, and by Bock and Root (1981) for landbirds.

The ichthyogeographic knowledge of northeastern North American fresh waters began (Legendre 1963) with the explorations by Jacques Cartier (Pouliot 1934), Samuel Champlain (Laverdière 1870), and the Jesuits (Thwaites 1896–1901), but until recently, comprehensive biogeographic data had been compiled, for large areas of Québec, mostly in unpublished manuscripts by V. C. Wynne-Edwards, L. R. Richardson, V. D. Vladykov, and G. Préfontaine (Legendre 1971), except for the maps in Scott and Crossman (1973). The postglacial dispersal of a few species in western Québec was described by Dadswell (1972, 1974). On the other hand, interest in classification of waters for stocking purposes was manifest in

governmental offices since 1944 (Prévost 1944) and has extended to ecologists (Legendre et al. 1980). Legendre (1971) reviewed the literature available on Québec fish biogeography and summarized the research needed in the future. The present paper follows in these footsteps.

Our objective was to describe and explain the dispersal of freshwater fishes in the Québec peninsula since the last glaciation. The Laurentide Ice Sheet retreated from the peninsula from approximately 14 000 to 5000 yr ago. Since then the fish species reinvaded the territory; we understand that stenohaline species came northward from United States refugia through the Great Lakes, the province of Ontario, and New England states via some or all of the temporary postglacial southern watershed interconnections such as those illustrated by Prest (1970), while euryhaline species arrived mostly from the Atlantic and Arctic seas. Our main hypothesis is that species dispersal was controlled more efficiently by movements of the earth crust and by morphological peculiarities of the peninsula than by mountain ranges and other altitudinal limits presently found between river basins. It is then obvious that we cannot follow the example of Legendre and Beauvais (1978) or Bailey and Smith (1981) who took the river watershed as the basic Operational Geographic Unit (OGU: Crovello 1981) of their numerical analyses.

Our biogeographic analysis proceeds in three steps: (1) The peninsula is divided into faunistically homogeneous regions, on the basis of present distribution maps of fish species, and according to an objective clustering criterion. It will be shown that the limits of these empirical regions do correspond to various types of natural barriers, gradients, or limits. (2) Patterns of species dispersal between these relatively homogeneous regions are sought, using a numerical approach based on the present fish distributions. (3) A physical mechanism is proposed, in terms of a network of presently extant river interconnections, to explain the dispersal pattern suggested by the dispersal analysis results for stenohaline and for euryhaline species.

Materials and Methods

Distribution maps for 109 species of freshwater fishes, covering the Québec peninsula, were published by Bergeron and Brousseau (1981), following the recommendations of Legendre (1971) about basic compilations that were necessary to initiate a synthesis of Québec ichthyogeography. Although admittedly incomplete, these maps assemble almost all of the fish census data presently available for Québec.

Since we did not wish to impose the pattern of river watersheds as an a priori assumption onto the ichthyogeographic data, the territory under study was divided instead into 289 pixels ("picture cells") of 1° of longitude by 1° of latitude, and the presence or absence of each fish species was recorded for each pixel in a 289 × 109 data matrix.

Clustering Procedure

The coefficient of Sørensen (1948) (see the first part of the formula for DD₂ in Table 1) was used to compute the similarity between all pairs of pixels on the basis of the fish presence-absence data, thus forming a 289 × 289 similarity matrix. Using this matrix, the pixels were clustered with a constraint of space contiguity, i.e. only neighbouring pixels were allowed to cluster, as proposed by several authors (Lefkovitch 1978, 1980;

Lebart 1978; Monestiez 1978). As a clustering procedure, single linkage was discarded because surfaces were sought, rather than elongated dendrites of first-clustering pixels extending through the territory. On the other hand, complete linkage was also discarded to allow smooth gradients to be present in the resulting zoogeographic regions. Instead, an intermediate solution was used, and the pixels were clustered by a proportional-link linkage clustering algorithm, modified for the space contiguity constraint already mentioned. The connectedness required for the fusion of two clusters was $Co = 50\%$. Details on the various methods of clustering available to ecologists can be found in Chapter 7 of Legendre and Legendre (1983).

The clustering program was designed to produce maps instead of the usual dendrograms. On each map (samples, Fig. 1), each contiguous cluster of pixels is represented by a different letter. A new map was produced for each level of similarity where clustering activity occurred.

Coefficient of Dispersal Direction

To determine the pattern of dispersal between the regions delineated by clustering, coefficients of dispersal direction were computed for all pairs of neighbouring regions, based on a comparison of their present fish faunas. The information to be compared for each pair of adjacent regions can be represented by the following 2 × 2 contingency table:

		x_2	
		+	-
x_1	+	a	b
	-	c	

where a is the number of common species, b is the number of species exclusive to region x_1 , and c is the number of species exclusive to region x_2 .

Assumption 1: The species did not arise by evolution in situ. They dispersed into the territory in relatively recent geological time. The assumption is tenable for the whole of the Québec peninsula, where the inlandis retreated between approximately 14 000 and 5000 yr ago (Andrews and Tyler 1977). It would make the forthcoming formulae useless, however, in areas where one could postulate local speciation among the fauna or flora under study. This could be the case with *Moxostoma hubbsi* (Legendre 1952, p. vi), which was stated to be endemic in Québec by Bailey and Smith (1981, p. 1555), an opinion to which we do not necessarily concur because postglacial times are seemingly too short for the production of a species presenting such elaborate anatomical differences in structures.

Assumption 2: Species dispersed in the past from regions of high to low species density, along present-day species gradients. Consequently, there are indications that a dominant flow of species dispersal occurred from a region x_1 to a region x_2 : (2.1) if a good number of the species are common (value a above) and (2.2) if b is substantially larger than c (or the opposite).

When either of these conditions is not fulfilled, it does not

mean that a flow of species has not occurred between x_1 and x_2 , but rather that there is no indication of that flow remaining in the present faunal distribution. Condition (2.1) simply states that unless two adjacent regions possess species in common, it would be difficult to think of these two faunas as deriving one from the other. Condition (2.2) creates the picture of a fauna "waiting at the border" to invade an adjacent region; this process must have taken place when species gradually invaded a recently deglaciated area, arriving simultaneously or in turn, from x_0 to x_1 , and then from x_1 to x_2 . This second part of the assumption is not as strong as the first part, since one can think of various situations where a present faunal pattern could have been produced by other dispersal mechanisms.

In a first example, let us consider the problem of extinction: suppose that a region x_1 contains two groups of faunal elements, a and c , which dispersed to a more northern region x_2 , after which the group of c species disappeared from x_1 . Region x_1 then contains only the a species, in common with x_2 , while x_2 also contains the c species, which would seem to indicate a dispersal pressure from x_2 to x_1 , while the true dispersal took place from x_1 to x_2 . Fortunately, in the territory under investigation, this situation seems unlikely to have happened in a significant number of cases, because the species that dispersed far into deglaciated territory should have possessed a wide ecological valence or tolerance.

Another case where assumption (2.2) would be untrue is found in special instances of the situation where two regions, x_0 and x_1 , have contributed to the formation of the fauna of their common neighbour x_2 . Let us take the most complex example and suppose for the sake of the argument that region x_0 contained $(a + b)$ faunal elements, which were all passed to region x_2 , and that x_1 contained $(a + c)$ faunal elements, all of which were passed to x_2 . A comparison would show that x_2 now contains c elements unknown in x_0 , while x_2 also possesses b elements unknown in x_1 , which would indicate a dispersal flow from x_2 to both x_0 and x_1 . Such an extreme situation may happen from time to time, giving a false indication of the dispersal direction. It is very unlikely, however, that this could occur in a large number of contiguous regions. Consequently, although any single set of species exclusive to a region does not give any certainty as to the direction of species dispersal, a general pattern of dispersal indicated by multiple region – pair comparisons over a wide area should be more reliable.

A coefficient of dispersal direction, with several variants of increasing complexity, can be designed as follows:

(1) Basic form: $a(b - c)$. The two quantities obtained independently from assumptions (2.1) and (2.2) are multiplied. If one wishes to visualize a species flow from region x_1 to x_2 by an arrow, then $(b - c)$ gives both the length and direction of the arrow (actually, the sign gives the direction), while a would give its width. If either one of these dispersal components is zero, then the arrow has a null surface area, which means that no migration occurred between x_1 and x_2 .

(2) To make the coefficients comparable for pairs of faunas of different richness, each term should be standardized by dividing it by the richness of the fauna. This first usable form of the coefficient of dispersal direction will be called DD_1 and its formula is

$$DD_1 = \frac{a}{(a + b + c)} \frac{(b - c)}{(a + b + c)}$$

which can be thought of as the probability of passing from region x_1 to region x_2 , for each species.

(3) The first part of DD_1 , $a/(a + b + c)$, can easily be recognized as Jaccard's (1901) coefficient of community. Following Sørensen (1948), many workers prefer to give double weight to the common species in this assessment of similarity, which would result in a new form for the coefficient of dispersal direction:

$$DD_2 = \frac{2a}{(2a + b + c)} \frac{(b - c)}{(a + b + c)}$$

The first part of this formula is Sørensen's coefficient.

(4) These two basic forms, DD_1 and DD_2 , can be applied to all the species of the data set, with the possibility that some species distribution maps, whose contours have been drawn freehand, might generate some mathematical noise by giving a species presence in a region only because the shaded portion of this species' distribution map touches one pixel of the region in question. To avoid this problem, the same pair of equations can be applied only to species present, for example, in 25%, in 50%, or in 75% of the cells of each region. Computing them for these three subsets of species, and also for all species present, gives rise to eight ways of calculating the binary form of the dispersal direction coefficient. They are divided into those giving single weight (DD_1 form) and those giving double weight (DD_2 form) to the common species (Table 1).

(5) Instead of relying on presence-absence data, it might be more interesting to base the measure of dispersal direction on quantitative data. In our study, the quantitative data of interest are not the abundance of each species in the various regions, which would measure the species' success in the various potential niches available, but rather the fraction of each region's surface occupied by each species, taken as an indirect measure of the availability of both dispersion routes and suitable niches. The proportion of each region's pixels in which each species is found is presented in Table 2. These data can be assembled in two quantitative forms of the coefficient of dispersal direction: a form giving single weight to common species (DD_3 in Table 1) and a form giving them double weight (DD_4 in Table 1). The first part of DD_4 is Steinhaus' coefficient of similarity, also shown in Table 1, which is used to measure the resemblance between regions' faunas. If presence-absence data are used instead of quantitative data, Steinhaus' measure becomes Sørensen's coefficient of similarity (Legendre and Legendre 1983).

An example for the computation of these coefficients is given in Table 3. W is the sum of the minimum frequency for all species, this minimum being defined for each species as its frequency in the region where it is the rarest. A and B are the sums of the frequencies of all species in each of the two regions. From Table 3, it is easy to compute DD_3 , Steinhaus' coefficient (S), and DD_4 for the comparison of regions 11 and 12:

$$DD_3 = \frac{W(A - B)}{(A + B - W)^2} = \frac{0.84(0.88 - 4.42)}{(0.88 + 4.42 - 0.84)^2} = -0.1495$$

$$S = \frac{2W}{(A + B)} = \frac{2 \times 0.84}{(0.88 + 4.42)} = 0.3170$$

$$DD_4 = S \times \frac{(A - B)}{(A + B - W)} = 0.3170 \times \frac{(0.88 - 4.42)}{(0.88 + 4.42 - 0.84)} = -0.2516$$

TABLE 1. The four different forms of the coefficient of dispersal direction (DD) used in this study. DD₁ and DD₂ are computed for all species of a region, or only for those species present in at least 25, 50, or 75% of the pixels of the region. Steinhaus' coefficient of similarity (*S*), used to compare regions, is included.

	Common species: single weight	Common species: double weight
Presence-absence	$DD_1 = \frac{a(b-c)}{(a+b+c)^2}$	$DD_2 = \frac{2a}{(2a+b+c)} \frac{(b-c)}{(a+b+c)}$
Quantitative	$DD_3 = \frac{W(A-B)}{(A+B-W)^2}$	$DD_4 = \frac{2W}{(A+B)} \frac{(A-B)}{(A+B-W)}$
Quantitative similarity		$S = \frac{2W}{(A+B)}$

DD₃ and DD₄ show differences of scale, these two coefficients being largely monotonic. Finally, it can easily be shown that if presence-absence data are used instead of region frequency data, DD₃ becomes DD₁ and DD₄ becomes DD₂.

The binary forms of the coefficient open the way to a test of asymmetry of the 2 × 2 contingency table; this test is also known as the McNemar test. To test the null hypothesis that there is no asymmetry between two adjacent regions ($H_0: b = c$), we can compute the test statistic

$$\chi^2 = \frac{(b-c)^2}{(b+c)}$$

which is distributed as χ^2 with one degree of freedom. The log-linear form equivalent to this test is

$$X^2 = 2[b \ln b + c \ln c - (b+c) \ln ((b+c)/2)]$$

(Sokal and Rohlf 1981), which should be preferred to the first formula in the case of small values of *b* and *c*, as in the present study. In the formula, we replace $x \ln x$ by 0 when $x = 0$, since

$$\lim_{x \rightarrow 0} x \ln x = 0.$$

We will use it as a two-tailed test of significance of the difference between *b* and *c*, setting the probability of a type I error at $\alpha = 0.05$. If a specific hypothesis of dispersal was being tested (i.e. if the direction of an arrow was specified by the hypothesis and we wished to test if this arrow had a significant "length"), the test would be one-tailed.

Results and Discussion

Definition of Homogeneous Ichthyogeographic Regions

The dendrogram in Fig. 2 was drawn from the series of maps produced by the agglomerative clustering program (samples, Fig. 1). To limit the number of subregions, 21 clusters of contiguous pixels were picked out. No subregion was formed from less than three pixels. Also shown in Fig. 2 is the similarity level where each subregion aggregated at least 75% of its final number of pixels. On this dendrogram, the similarity levels of 0.50 and 0.70 were arbitrarily chosen to draw the map of regions (Fig. 3). Five clusters are well isolated at the 0.50 similarity level and define five main ichthyogeographic regions, blown apart in Fig. 3. The clusters isolated at the 0.70 similarity level represent main subregions, separated by full lines, while the clusters joining each other above the 0.70 similarity level represent minor regional components which are separated by

broken lines. Clustering the pixels after removing the seven introduced species (I in Table 2) produced almost exactly the same dendrogram (Fig. 2), with only a few pixels being passed in three cases to adjacent minor subregions (those separated by broken lines in Fig. 3). In each major region, the subregions are numbered in a consecutive manner: region 1 (map 11 and 12): northern tundra; region 2 (map 21–23): east coast; region 3 (map 31–33): northwestern Gulf and estuary of St. Lawrence River; region 4 (map 41–43): upper St. Lawrence and Ottawa Valley (Champlain Sea area); region 5 (map 51–60): centre of the peninsula.

Since the limits of these ichthyogeographic regions do not correspond to the four major hydrographic watersheds of the peninsula (Hudson Bay, Ungava Bay, Atlantic Ocean, St. Lawrence River), the next question a biogeographer may ask is whether this partition of the territory makes sense, that is, do the dividing lines correspond to natural barriers, gradients, or limits? Notwithstanding the fact that a correlation does not imply a causality, this question was answered by looking at various physical or biological phenomena that were likely to influence the dispersal of fish species. Some of them, selected among other equally suggestive limits available in literature, are plotted in Fig. 4 and discussed hereafter.

Climatic gradients

(a) Region 1 (11 and 12) is separated from region 5 by the 16°C average maximum temperature in July (Wilson 1971). (b) This same climatic line corresponds to the northern portion of the division between subregions 21 and 53–54, while the southern portion of this same division corresponds to the isoline of lakes freezing over by November 20 (Wilson 1971). (c) Subregions 22 and 23 are separated from both 21 and 53 by the isoline of 810 mm annual precipitation (SEBJ 1978). (d) This same isoline also fits very well with the northern limit of subregion 55. (e) The dividing line between subregions 57–59 and 58–60 is close to the isoline of lake freeze-over by November 10 (Wilson 1971). (f) The growing season is shorter than 70 d above the northern limit of subregion 12 (Wilson 1971), which indicates severe climatic conditions. (g) Finally, the divisions between subregions 42, 31, and 32, as one goes down the St. Lawrence River, correspond very well to isolines of maximum summer temperatures (July and August; Houde 1978).

Geographic barriers

(a) Subregion 32 is bounded north of the St. Lawrence by a line of waterfalls, which prevent many euryhaline species from

TABLE 2. Fish distribution data from the maps of Bergeron and Brousseau (1981), divided into the subregions of Fig. 3 (head of the columns). Data represent the percentage of presence of each species in the various pixels composing each region. Codes: S = stenohaline; E = euryhaline; I = introduced.

No. and species ^a	Code	11	12	21	22	23	31	32	33	41	42	43	51	52	53	54	55	56	57	58	59	60
Petromyzontidae																						
1- <i>Ichthyomyzon fossor</i>	S	—	—	—	—	—	—	—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
2- <i>Ichthyomyzon unicuspis</i>	S	—	—	—	—	—	—	—	—	8	43	—	—	—	—	—	—	—	—	—	—	—
3- <i>Lampetra appendix</i>	S	—	—	—	—	—	—	—	—	—	71	—	—	—	—	—	—	—	—	—	—	—
4- <i>Petromyzon marinus</i>	E	—	—	—	26	57	86	100	100	—	57	33	—	—	—	—	3	—	—	—	—	—
Anguillidae																						
5- <i>Anguilla rostrata</i>	E	—	—	—	84	—	100	100	100	75	100	100	—	—	2	—	—	—	—	—	—	6
Acipenseridae																						
6- <i>Acipenser fulvescens</i>	S	—	—	—	—	—	43	—	—	100	100	—	—	—	—	—	—	100	100	100	100	89
7- <i>Acipenser oxyrinchus</i>	E	—	—	—	89	—	86	91	100	—	43	—	—	—	3	—	—	—	—	—	—	—
Amiidae																						
8- <i>Amia calva</i>	S	—	—	—	—	—	—	—	—	8	86	—	—	—	—	—	—	—	—	—	—	—
Lepisosteidae																						
9- <i>Lepisosteus osseus</i>	S	—	—	—	—	—	14	—	—	58	71	—	—	—	—	—	—	—	—	—	—	—
Hiodontidae																						
10- <i>Hiodon alosoides</i>	S	—	—	—	—	—	—	—	—	33	—	—	—	—	—	—	—	—	—	100	—	—
11- <i>Hiodon tergisus</i>	S	—	—	—	—	—	14	—	—	100	57	—	—	—	—	—	—	—	—	78	—	—
Clupeidae																						
12- <i>Alosa pseudoharengus</i>	E	—	—	—	—	—	86	91	100	—	57	—	—	—	—	—	—	—	—	—	—	—
13- <i>Alosa sapidissima</i>	E	—	—	—	—	—	71	91	100	—	57	—	—	—	—	—	—	—	—	—	—	—
14- <i>Dorosoma cepedianum</i>	S	—	—	—	—	—	57	—	—	—	57	33	—	—	—	—	—	—	—	—	—	—
Salmonidae																						
15- <i>Coregonus artedii</i>	S	4	—	—	—	—	57	—	—	100	71	100	33	91	58	—	69	100	100	100	100	100
16- <i>Coregonus clupeaformis</i>	S	—	74	19	16	71	100	82	—	100	100	100	100	91	98	100	100	100	100	100	100	100
17- <i>Coregonus nipigon</i>	S	—	—	—	—	—	—	—	—	—	—	—	—	55	—	—	—	100	100	89	—	—
20- <i>Oncorhynchus kisutch</i>	I	—	—	—	—	—	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
21- <i>Oncorhynchus nerka</i>	I	—	—	—	—	—	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
23- <i>Prosopium cylindraceum</i>	S	4	42	38	26	100	71	9	—	42	57	33	100	64	100	100	100	80	20	—	100	89
24- <i>Salmo clarki</i>	I	—	—	—	—	—	—	—	—	—	43	—	—	—	—	—	—	—	—	—	—	—
25- <i>Salmo gairdneri</i>	I	—	—	—	—	—	14	18	43	17	100	33	—	—	—	—	—	—	—	—	—	—
26- <i>Salmo salar</i>	E	4	—	—	—	—	100	100	100	17	71	67	17	—	71	100	52	—	—	—	—	17
27- <i>Salmo trutta</i>	I	—	—	—	—	—	—	—	—	17	100	100	—	—	—	—	—	—	—	—	—	—
28- <i>Salvelinus fontinalis</i>	S	—	100	100	100	100	86	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
29- <i>Salvelinus namaycush</i>	S	60	100	63	16	14	100	55	14	83	100	100	100	91	100	100	100	100	—	11	100	94
30- <i>Salvelinus salvelinus</i>	E	100	100	100	100	100	86	91	29	17	43	—	100	82	55	100	7	—	20	—	—	28
Osmeridae																						
32- <i>Osmerus mordax</i>	E	—	—	—	32	57	100	100	100	58	100	100	—	—	—	—	24	—	—	—	—	50
Umbridae																						
33- <i>Umbra limi</i>	S	—	—	—	—	—	14	—	—	50	100	33	—	—	—	—	—	—	—	—	—	—
Esocidae																						
34- <i>Esox a. americanus</i>	S	—	—	—	—	—	—	—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
35- <i>Esox a. vermiculatus</i>	S	—	—	—	—	—	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
36- <i>Esox lucius</i>	S	20	89	—	95	100	71	73	—	100	100	100	100	100	100	100	100	100	100	100	100	100
37- <i>Esox masquinongy</i>	S	—	—	—	—	—	—	—	—	75	100	33	—	—	—	—	—	—	—	—	—	—
38- <i>Esox niger</i>	S	—	—	—	—	—	—	—	—	—	29	33	—	—	—	—	—	—	—	—	—	—

TABLE 2. (Continued)

No. and species ^a	Code	11	12	21	22	23	31	32	33	41	42	43	51	52	53	54	55	56	57	58	59	60
Ictaluridae																						
39- <i>Ictalurus natalis</i>	S	—	—	—	—	—	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
40- <i>Ictalurus nebulosus</i>	S	—	—	—	—	—	14	—	—	50	100	100	—	—	—	—	—	—	—	—	—	—
41- <i>Ictalurus punctatus</i>	S	—	—	—	—	—	—	—	—	42	86	—	—	—	—	—	—	—	—	—	—	—
42- <i>Noturus flavus</i>	S	—	—	—	—	—	—	—	—	—	71	—	—	—	—	—	—	—	—	—	—	—
43- <i>Noturus gyrinus</i>	S	—	—	—	—	—	—	—	—	8	57	—	—	—	—	—	—	—	—	—	—	—
44- <i>Noturus insignis</i>	S	—	—	—	—	—	—	—	—	8	—	—	—	—	—	—	—	—	—	—	—	—
Catostomidae																						
45- <i>Carpiodes cyprinus</i>	S	—	—	—	—	—	—	—	—	—	57	—	—	—	—	—	—	—	—	—	—	—
46- <i>Catostomus catostomus</i>	S	—	5	100	21	29	100	82	—	100	100	100	100	100	100	100	100	100	100	100	100	100
47- <i>Catostomus commersoni</i>	S	—	—	—	—	29	86	64	—	100	100	100	17	100	98	100	100	100	100	100	100	100
48- <i>Moxostoma anisurum</i>	S	—	—	—	—	—	—	—	—	8	86	33	—	—	—	—	—	—	—	—	—	—
49- <i>Moxostoma carinatum</i>	S	—	—	—	—	—	—	—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
50- <i>Moxostoma hubbsi</i>	S	—	—	—	—	—	—	—	—	—	43	—	—	—	—	—	—	—	—	—	—	—
51- <i>Moxostoma macrolepidotum</i>	S	—	—	—	—	—	—	—	—	50	100	—	—	9	—	—	—	20	—	11	—	—
52- <i>Moxostoma valenciennesi</i>	S	—	—	—	—	—	—	—	—	25	86	—	—	—	—	—	—	—	—	—	—	—
Cyprinidae																						
53- <i>Carassius auratus</i>	I	—	—	—	—	—	—	—	—	—	29	33	—	—	—	—	—	—	—	—	—	—
56- <i>Couesius plumbeus</i>	S	—	—	—	26	86	71	100	14	100	86	67	100	—	98	33	100	40	40	100	80	100
57- <i>Cyprinus carpio</i>	I	—	—	—	—	—	29	—	—	8	86	—	—	—	—	—	—	—	—	—	—	—
58- <i>Exoglossum maxillingua</i>	S	—	—	—	—	—	14	—	—	8	71	33	—	—	—	—	—	—	—	—	—	—
59- <i>Hybognathus hankinsoni</i>	S	—	—	—	—	—	—	—	—	83	86	—	—	—	—	—	—	—	—	—	—	—
60- <i>Hybognathus nuchalis</i>	S	—	—	—	—	—	—	—	—	17	86	33	—	—	—	—	—	—	—	—	—	—
61- <i>Notemigonus crysoleucas</i>	S	—	—	—	—	—	100	18	—	100	100	100	—	—	—	—	7	—	—	11	17	
62- <i>Notropis atherinoides</i>	S	—	—	—	—	—	—	—	—	100	100	—	—	—	—	—	—	40	—	11	11	
63- <i>Notropis bifrenatus</i>	S	—	—	—	—	—	—	—	—	—	57	—	—	—	—	—	—	—	—	—	—	—
64- <i>Notropis cornutus</i>	S	—	—	—	—	—	43	18	—	100	100	100	—	—	—	—	—	—	—	—	33	
65- <i>Notropis heterodon</i>	S	—	—	—	—	—	—	—	—	8	43	—	—	—	—	—	—	—	—	—	—	—
66- <i>Notropis heterolepis</i>	S	—	—	—	—	—	29	—	—	100	100	33	—	—	—	—	—	—	—	—	—	—
67- <i>Notropis hudsonius</i>	S	—	—	—	—	—	—	—	—	83	100	—	—	—	—	—	—	60	20	11	—	6
68- <i>Notropis rubellus</i>	S	—	—	—	—	—	—	—	—	42	100	33	—	—	—	—	—	—	—	—	—	—
69- <i>Notropis spilopterus</i>	S	—	—	—	—	—	—	—	—	8	86	—	—	—	—	—	—	—	—	—	—	—
70- <i>Notropis stramineus</i>	S	—	—	—	—	—	—	—	—	—	86	33	—	—	—	—	—	—	—	—	—	—
71- <i>Notropis volucellus</i>	S	—	—	—	—	—	—	—	—	83	100	—	—	—	—	—	—	—	—	—	—	—
72- <i>Pimephales notatus</i>	S	—	—	—	—	—	—	—	—	50	100	33	—	—	—	—	—	—	—	—	—	—
73- <i>Pimephales promelas</i>	S	—	—	—	—	—	—	—	—	100	100	100	—	—	—	—	—	—	—	—	—	—
74- <i>Rhinichthys atratulus</i>	S	—	—	—	—	—	57	18	—	8	86	100	—	—	—	—	—	—	—	—	—	22
75- <i>Rhinichthys cataractae</i>	S	—	—	—	—	71	100	45	—	100	100	100	17	100	92	67	100	100	100	100	100	100
76- <i>Semotilus atromaculatus</i>	S	—	—	—	—	—	100	27	—	83	100	100	—	—	—	—	7	—	—	22	94	
77- <i>Semotilus corporalis</i>	S	—	—	—	—	—	71	—	—	100	100	100	—	—	—	—	7	40	100	100	60	100
78- <i>Semotilus margarita</i>	S	—	—	—	—	—	100	73	—	100	100	100	—	—	9	—	100	20	40	100	80	100
Gadidae																						
79- <i>Lota lota</i>	S	—	—	—	—	—	100	18	—	100	100	100	50	100	91	67	100	100	100	100	100	100
80- <i>Microgadus tomcod</i>	E	—	—	—	100	—	86	100	100	—	29	—	—	—	3	—	—	—	—	—	—	11

TABLE 2. (Concluded)

No. and species ^a	Code	11	12	21	22	23	31	32	33	41	42	43	51	52	53	54	55	56	57	58	59	60
Gasterosteidae																						
81- <i>Apeltes quadracus</i>	E	—	—	—	—	—	43	100	100	—	14	33	—	—	—	—	3	—	—	—	—	—
82- <i>Culaea inconstans</i>	S	—	—	—	—	—	86	—	—	100	100	100	—	—	—	—	—	20	100	100	40	100
83- <i>Gasterosteus aculeatus</i>	E	100	84	100	100	86	100	100	100	42	71	33	17	91	62	67	14	100	100	33	—	44
84- <i>Gasterosteus wheatlandi</i>	E	—	—	—	5	—	57	27	57	—	—	—	—	—	—	—	—	—	—	—	—	—
85- <i>Pungitius pungitius</i>	E	100	100	100	100	100	100	100	100	100	86	33	100	100	100	100	100	100	100	100	100	100
Cyprinodontidae																						
86- <i>Fundulus diaphanus</i>	S	—	—	—	—	—	57	18	29	8	86	33	—	—	—	—	—	—	—	—	—	—
87- <i>Fundulus heteroclitus</i>	E	—	—	—	—	—	—	—	57	—	—	—	—	—	—	—	—	—	—	—	—	—
Percopsidae																						
88- <i>Percopsis omiscomaycus</i>	S	—	—	—	—	—	29	—	—	100	100	33	—	—	—	—	—	80	80	100	—	100
Atherinidae																						
89- <i>Labidesthes sicculus</i>	S	—	—	—	—	—	—	—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
Percichthyidae																						
90- <i>Morone americana</i>	E	—	—	—	—	—	—	—	—	—	71	—	—	—	—	—	—	—	—	—	—	—
91- <i>Morone chrysops</i>	S	—	—	—	—	—	—	—	—	—	57	—	—	—	—	—	—	—	—	—	—	—
92- <i>Morone saxatilis</i>	E	—	—	—	—	—	86	45	57	—	57	33	—	—	—	—	—	—	—	—	—	—
Centrarchidae																						
93- <i>Ambloplites rupestris</i>	S	—	—	—	—	—	—	—	—	92	100	67	—	—	—	—	—	—	—	—	—	—
94- <i>Lepomis gibbosus</i>	S	—	—	—	—	—	—	—	—	83	100	67	—	—	—	—	—	—	—	—	—	—
95- <i>Lepomis macrochirus</i>	S	—	—	—	—	—	—	—	—	—	43	—	—	—	—	—	—	—	—	—	—	—
96- <i>Lepomis megalotis</i>	S	—	—	—	—	—	—	—	—	8	43	—	—	—	—	—	—	—	—	—	—	—
97- <i>Micropterus dolomieu</i>	S	—	—	—	—	—	14	—	—	75	100	100	—	—	—	—	—	—	—	—	—	6
98- <i>Micropterus salmoides</i>	S	—	—	—	—	—	—	—	—	50	100	—	—	—	—	—	—	—	—	—	—	—
99- <i>Pomoxis nigromaculatus</i>	S	—	—	—	—	—	—	—	—	8	71	—	—	—	—	—	—	—	—	—	—	—
Percidae																						
100- <i>Ammocrypta pellucida</i>	S	—	—	—	—	—	—	—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
101- <i>Etheostoma caeruleum</i>	S	—	—	—	—	—	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
102- <i>Etheostoma exile</i>	S	—	—	—	—	—	—	—	—	100	86	33	—	—	—	—	—	—	—	—	—	11
103- <i>Etheostoma flabellare</i>	S	—	—	—	—	—	—	—	—	25	100	33	—	—	—	—	—	—	—	—	—	—
104- <i>Etheostoma nigrum</i>	S	—	—	—	—	—	29	—	—	42	100	67	—	—	—	—	—	—	—	—	—	—
105- <i>Etheostoma olivaceum</i>	S	—	—	—	—	—	—	—	—	—	57	33	—	—	—	—	—	—	—	—	—	—
106- <i>Percina fluviatilis</i>	S	—	—	—	—	—	100	9	—	100	100	100	—	—	—	—	—	100	100	100	40	100
107- <i>Percina caprodes</i>	S	—	—	—	—	—	57	9	—	100	100	33	—	—	2	—	7	60	—	44	—	44
108- <i>Percina copelandi</i>	S	—	—	—	—	—	—	—	—	—	86	—	—	—	—	—	—	—	—	—	—	—
109- <i>Stizostedion canadense</i>	S	—	—	—	—	—	—	—	—	75	86	—	—	—	—	—	—	—	60	100	—	—
110- <i>Stizostedion vitreum</i>	S	—	—	—	—	—	—	—	—	100	100	100	—	36	2	—	10	100	100	100	100	94
Sciaenidae																						
111- <i>Aplodinotus grunniens</i>	S	—	—	—	—	—	—	—	—	67	86	—	—	—	—	—	—	—	—	—	—	—
Cottidae																						
112- <i>Cottus bairdi</i>	S	—	16	6	11	—	29	—	—	100	86	33	83	100	88	—	7	100	100	100	100	94
113- <i>Cottus cognatus</i>	S	—	16	—	11	29	86	64	—	100	100	100	—	100	98	—	100	100	100	100	100	100
114- <i>Cottus ricei</i>	S	—	—	—	—	—	29	—	—	92	43	67	—	—	—	—	3	—	—	33	—	94
115- <i>Myoxocephalus quadricornis</i>	E	4	21	19	—	—	—	—	—	8	—	—	—	9	3	—	—	20	20	—	—	—

^aSpecies of the Québec ichthyofauna whose distribution is not given in Bergeron and Brousseau (1981): 18-*Hucho hucho* (extinct); 19-*Oncorhynchus gorbuscha* (extinct); 22-*Oncorhynchus tshawytscha*; 31-*Thymallus arcticus* (extinct); 54-*Chrosomus eos*; 55-*Chrosomus neogaeus*.

TABLE 3. Data for the computation of coefficients DD_3 , DD_4 , as well as Steinhaus' similarity. Comparison of subregions 11 and 12: data from Table 2. The body of the table shows the relative frequencies of the nine stenohaline species present in these two ichthyogeographic subregions.

Region	Species code									Sum for x_{11} A	Sum for x_{12} B	Sum of minima W
	15	16	23	28	29	36	46	112	113			
x_{11}	0.04	0	0.04	0	0.60	0.20	0	0	0	0.88		
x_{12}	0	0.74	0.42	1	1	0.89	0.05	0.16	0.16		4.42	
Minimum	0	0	0.04	0	0.60	0.20	0	0	0			0.84

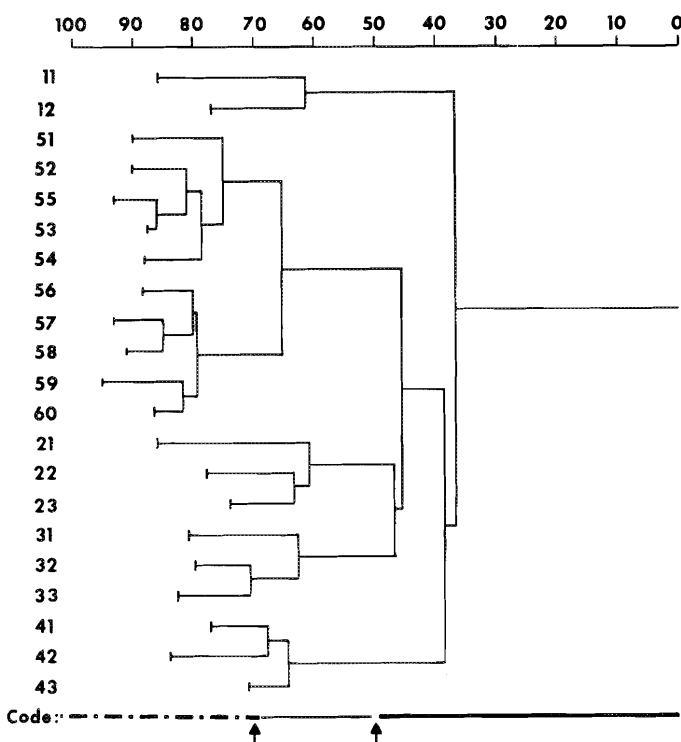


FIG. 2. Dendrogram of pixel clustering into ichthyogeographic regions. The arm corresponding to each region is shown only from the similarity level where 75% of its pixels are clustered. The division code for Fig. 3 is shown below the dendrogram.

going upriver. In small rivers, the falls actually lie to the south of this line, closer to the Gulf coast. Larger rivers are located in much wider and deeper valleys dug out by glaciers, so that the waterfalls are farther inland, usually north of 51°N . (b) On the other hand, the two highest mountain chains of the Québec peninsula (Otish, Torngat, Fig. 4) seem to have had little effect on the present distribution pattern of the fish species. They may, however, have had an influence on the dispersal routes, as will be discussed later.

Geomorphological limits

(a) Subregions 41, 42, and 43 are related to one another hydrologically and climatologically, and also because they share the effects of postglacial outlets of Lake Huron and the Champlain Sea postglacial transgression (Anonymous 1970) (not drawn in Fig. 4). This transgression left most of the lowlands of region 4 covered with marine sediments. (b) The line separating subregions 52, 56, and 57 on the one hand from 53 and 59 on the other corresponds to the limit of the surface deposits left by the Tyrrell Sea marine transgression (Anonymous 1970). Indeed, one of the isobase maps published by

Andrews and Tyler (1977) shows that after the retreat of the ice margin, the northern limit of James Bay had, 6000 yr B.P., an altitude about 150 m lower than present, thus allowing the extension of this marine transgression. The marine sediments create in these subregions chemical (ions) and physical (turbidity) water conditions very different from those occurring in the Laurentide Shield plateau area (53, 55, 59), conditions that have in turn a strong influence on the composition of the fish community, as previously discussed (Legendre and Beauvais 1978; Legendre et al. 1980).

Vegetation

Subregions 51 and 53 are separated by the Arctic tree line (trees are still found, however, along Leaf River, which runs across subregion 51). Subregion 51 is then mostly a tundra habitat, yet somewhat warmer than the tundra subregions 11 and 12.

Thus, the ichthyogeographic regions delineated by the clustering procedure seem to hold, being apparently related to factors that could have influenced fish dispersal. The enumeration of potentially explanatory factors above also suggests that it would be interesting to test the species concerned (Table 2) for these same factors, under laboratory conditions.

Postglacial Dispersal Pattern

As already delineated, the ichthyogeographic regions appear to have a relative, internal homogeneity. On that basis, a definition of the pattern of fish postglacial dispersal may be attempted, using the various forms of the coefficient of dispersal direction described under Materials and Methods. It should be remembered that, given two adjacent fish faunas, a single value of this coefficient does not guarantee that dispersal did occur as described by this coefficient value; it merely indicates a possibility that the events occurred in this way. The overall picture produced by combining many values of this coefficient may, however, be considered as a stronger reconstruction of the postglacial dispersal history.

For each pair of adjacent subregions, 10 versions of the coefficient of dispersal direction were computed, as explained under Materials and Methods (the qualitative forms DD_1 and DD_2 for the species present in at least 1, 25, 50, and 75% of each region, respectively, and then the quantitative forms DD_3 and DD_4). In all but three cases, there was no contradiction of sign (the sign gives the direction of the dispersal arrow) between the 10 versions, for the coefficients that were retained as significant (see Fig. 5 and 7 and the following discussion).

To plot maps, it is necessary to select one version of the coefficient that best represents all the others. This selection was made on the basis of matrix correlations (also known as cophenetic correlations), computed with Pearson's r linear correlation and with Spearman's r rank-order correlation

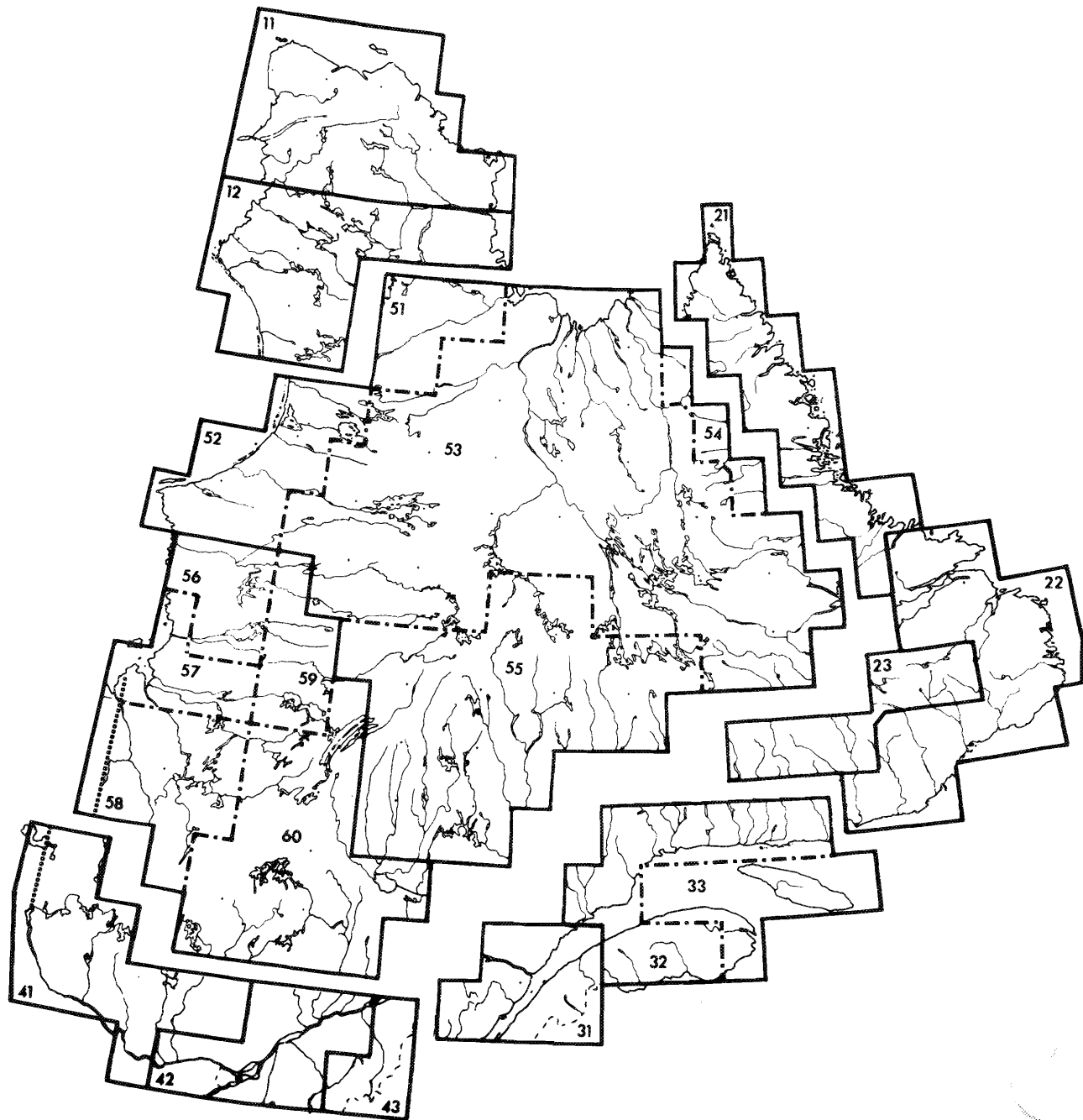


FIG. 3. Map of ichthyogeographic regions (breaks) and subregions of the Québec peninsula. Hierarchy of divisions: break > full lines > broken lines. The similarity levels corresponding to these division codes can be found on Fig. 2.

coefficients, between all pairs of versions of the coefficient DD. Details on this method can be found in Sokal and Rohlf (1962) and in Legendre and Legendre (1983). In all cases, the correlation between the version giving single weight and that giving double weight to the common species is very high. On the other hand, the quantitative versions (DD₃ and DD₄) rank first in their ability to represent all the other versions of the coefficient, followed by the binary versions computed on the species present in 50% of the cells, followed closely in turn by the binary versions computed on the species present in 25% of the cells. The two more extreme versions (frequency larger than or equal to 75% and larger than 0%) are far less efficient in rendering the variations of all the other versions. Among the quantitative versions of the coefficient, DD₄ is preferred

because it is easier to compare with Steinhaus' coefficient of similarity between regions, both giving double weight to the common species.

The test of significance of the direction, developed at the end of the Materials and Methods section, can be applied only to data in binary form. Using again the matrix correlation approach, we found that the binary versions of the coefficient that most closely resemble the quantitative versions (higher Pearson and Spearman correlations) were those computed from the species present in at least 50% of the cells, followed very closely by the versions computed from the species present in at least 25% of the cells. Thus, the test of asymmetry was applied to 2 × 2 contingency tables made, on the one hand, of the species present in at least 50% of the cells of each region and, on

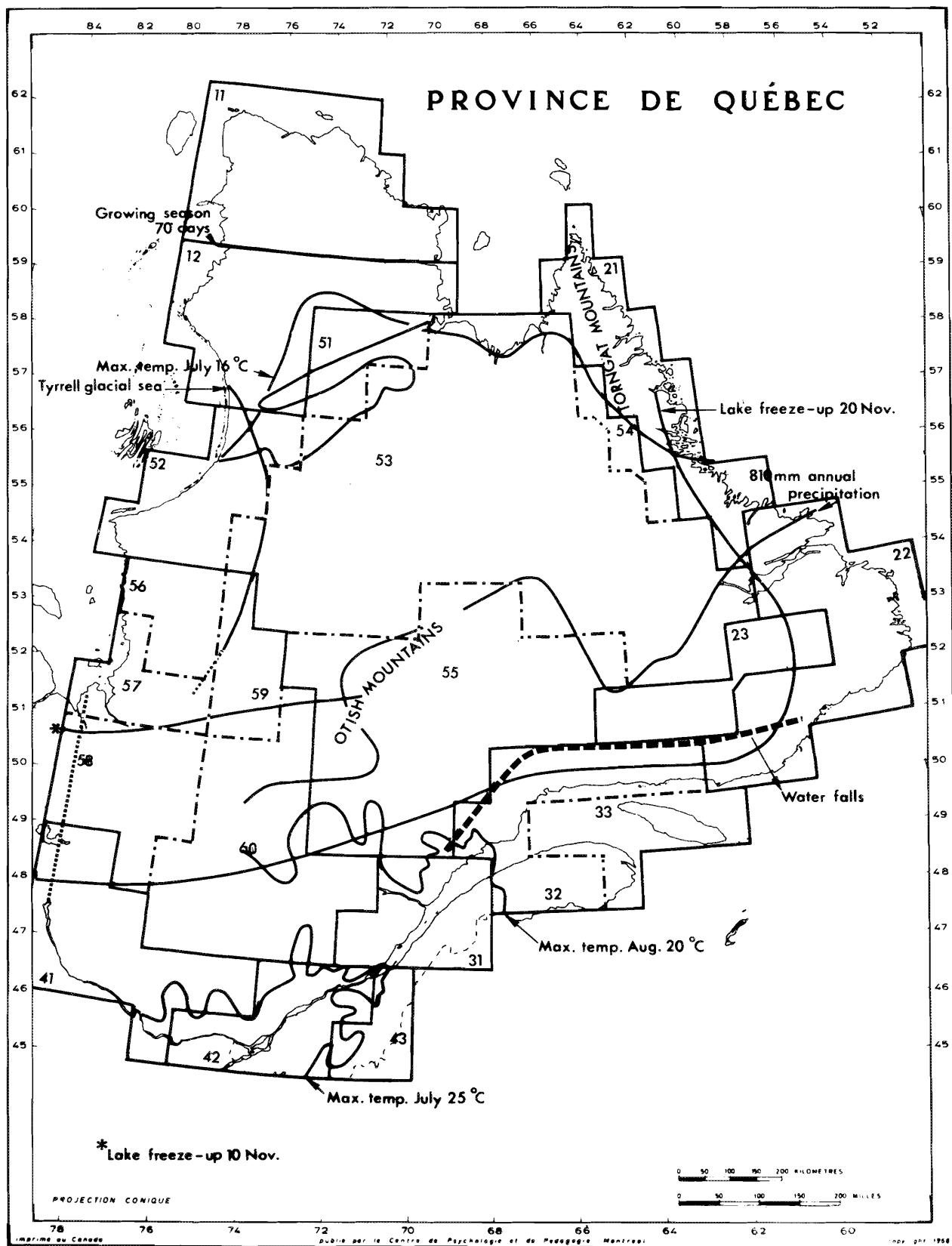


FIG. 4. Various types of natural barriers, gradients, or limits drawn on the map of the 21 ichthyogeographic subregions. See explanations in the text. The heavy broken line shows the general location of a line of waterfalls bounding subregion 32 north of the St. Lawrence.

the other, of the species present in at least 25% of the cells of each region. The log-linear form of the test was used. When the null hypothesis (H_0 : no asymmetry) could be rejected, at the 5% confidence level, on either one of these two contingency tables, an arrow was drawn with the direction and length provided by the DD_4 version of the coefficient of dispersal direction.

Stenohaline species (here understood as confined to fresh water) and euryhaline species (seagoing, or indifferent) were treated as two separate files for these computations, since they were likely to have acceded to the territory by different dispersal routes. The recently introduced species (code I, Table 2) were not considered in this part of the study. The results are presented in map form in Fig. 5 and 7. The actual values of the coefficients, together with Steinhaus' coefficient of similarity between adjacent regions, are listed in Table 4.

In most instances, nonsignificant asymmetry (Table 4) corresponds to high values of Steinhaus' similarity coefficient, although this is not always the case. For instance, the stenohaline species do not show any asymmetry between subregions 53 and 55 because the two faunas are very similar to one another ($S = 0.90$), having possibly been formed by the same dispersal movement. On the other hand, subregions 21 and 22 do not show asymmetry although their faunal similarity is rather weak ($S = 0.57$), indicating that they have few stenohaline species in common. Over all subregions, the value of Pearson's r correlation between Steinhaus' similarity and the absolute value of DD_4 is -0.53 for the stenohaline species and -0.69 for the euryhaline species, showing that these two measures are not completely correlated and thus may be expected to carry complementary information.

Figure 5 may be interpreted as follows, keeping in mind that there is only one arrow drawn (at the most pictorially convenient place) between any two adjacent subregions.

(a) The glacial history tells us that the stenohaline species are likely to have reinvaded the peninsula from the southern and western refugia, mainly through routes (double-tailed arrows) provided by connections such as those illustrated on Prest's (1970) maps, whose map numbers are used in discussing connections.

South connections, tributaries to the southshore

St. Lawrence River:

(1) Map 16e: 12 800 – 12 700 yr B.P.; toward Bay of Fundy, St. John River – headwaters of Chaudière River, via a marginal glacial lake in Québec, southeast of Québec city (outflow traced on map of Anonymous 1970).

(2) Map 16e: 12 800 – 12 700 yr B.P.; Connecticut – St. François river connection, via marginal glacial Lake Sherbrooke.

(3) Maps 16f, 16g, 16h: 12 500 – 12 000 yr B.P.; Hudson – Richelieu – St. François river connections, via marginal glacial Lake Vermont, in various Fort Ann stages.

Southwest connections, Great Lakes to the main

St. Lawrence River:

(4) Maps 16a to 16j: 14 000 – 11 500 yr B.P.; and map 16x: 6000 yr B.P.; Mississippi River and tributaries – Great Lakes connections.

(5) Maps 16b, 16c: 13 600 – 13 200 yr B.P.; Susquehanna River – marginal glacial Finger Lakes (Newberry Lake), later tributaries to Lake Ontario.

West connection, Great Lakes to the Ottawa River:

(6) Maps 16k to 16x: 11 200 – 6000 yr B.P.; Lake Huron

TABLE 4. Measures of fish postglacial dispersal (using the quantitative form DD_4 of the coefficient) and of similarity (Steinhaus' coefficient) between neighbouring subregions. NS: McNemar's test of significance shows that the asymmetry in the corresponding 2×2 contingency table is not significant.

Region pair	Stenohaline species		Euryhaline species	
	DD_4	Steinhaus' coefficient	DD_4	Steinhaus' coefficient
11–12	-0.2516	0.3169	NS	0.9399
12–51	-0.3176	0.6353	NS	0.8046
12–52	-0.3290	0.5160	NS	0.9372
21–22	NS	0.5733	-0.2914	0.6923
21–53	-0.3070	0.4166	NS	0.8108
21–54	-0.3320	0.5350	NS	0.9337
22–23	-0.3124	0.6508	0.2142	0.7173
22–32	-0.2715	0.4511	-0.2958	0.7376
22–53	-0.3053	0.4125	0.3381	0.5706
23–32	NS	0.6414	-0.3343	0.5654
23–53	-0.3313	0.6744	NS	0.7206
23–55	-0.3386	0.6415	0.3349	0.5686
31–32	0.3193	0.5565	NS	0.9212
31–42	-0.3298	0.4942	NS	0.7692
31–43	-0.2272	0.7338	0.3397	0.5353
31–55	0.2387	0.6823	0.2426	0.2929
31–60	-0.0494	0.7792	0.2782	0.3546
32–33	0.2295	0.2825	NS	0.9258
32–55	-0.2229	0.7089	0.2361	0.2826
41–42	-0.2488	0.7576	-0.3078	0.5010
41–58	0.2836	0.6517	NS	0.5926
41–60	0.3040	0.6760	NS	0.8058
42–43	0.3238	0.6452	0.3106	0.6421
42–60	0.3121	0.4961	0.2994	0.4337
51–53	-0.2275	0.8401	NS	0.7097
52–53	NS	0.8683	NS	0.7583
52–56	-0.2856	0.7736	NS	0.7971
53–54	0.2446	0.8217	NS	0.8651
53–55	NS	0.8998	NS	0.6870
53–59	-0.2237	0.8281	0.3338	0.5019
55–59	-0.1748	0.8360	NS	0.6591
55–60	-0.3028	0.7240	NS	0.7037
56–57	NS	0.8586	NS	0.9565
56–59	NS	0.8415	NS	0.6250
57–58	-0.1703	0.8704	NS	0.7143
57–59	NS	0.8090	NS	0.5882
58–60	NS	0.8293	NS	0.6857
59–60	-0.2131	0.8306	-0.3424	0.5625

(various glacial stages) – Lake Nipissing (various glacial stages) – Ottawa River; connections up to the marginal glacial stages of Lakes Barlow and Ojibway–Barlow, one vestige of which is Lake Témiscamingue at the head of the Ottawa River.

West connection, Great Lakes to south James Bay tributaries:

(7) Map 16p: 9500 yr B.P.; Lake Superior (glacial Minong–Houghton transition) – marginal glacial stage of Lake Ojibway–Barlow, one vestige of which is Lake Abitibi, tributary to James Bay.

(b) On the south shore of the St. Lawrence River, the dispersal coefficient shows the species progressing to the Eastern Townships (43) and to the tip of the Gaspé peninsula (33).

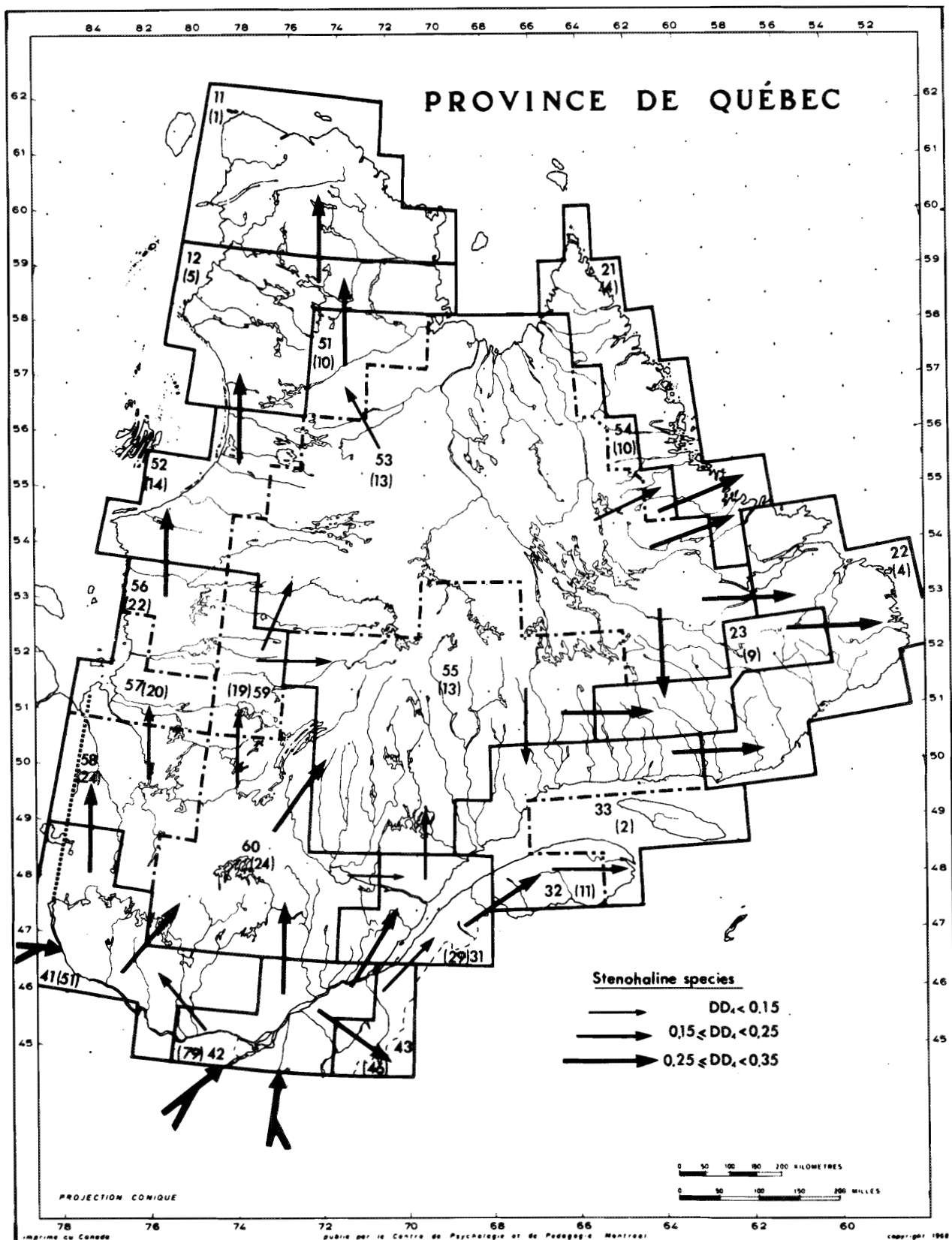


FIG. 5. Postglacial dispersal of the stenohaline species, as computed in this study. The arrows represent the direction and magnitude of the coefficient of dispersal direction (DD_4) for pairs of adjacent subregions. The numbers in parentheses, accompanying subregion identifications, are the numbers of species present in at least 25% of this region's pixels. The double-tailed arrows represent hypothesized incoming routes from inland (or sea: Fig. 7) glacial refugia.

(c) A dispersal movement northward is clear from the DD₄ arrows, from subregions 41 and 42 in the south to subregions 12 and 11 at the northern end of the peninsula. It must have been helped, up to the 52nd parallel, by the formation of glacial Lake Ojibway-Barlow, along the margin of the ice sheet receding towards Hudson Bay (Fig. 6).

(d) The DD₄ arrows also show the species progressing towards the centre of the peninsula, subregions 52 and 53 ($S = 0.87$) and 53–55 ($S = 0.90$) being so similar to one another that they are likely to have been formed by the same dispersal process.

(e) Finally, the dispersion coefficient arrows show the stenohaline species reaching the east coast regions from the centre of the peninsula, and coming down into rivers of the St. Lawrence north shore (which is now inaccessible to stenohaline species from the south, the St. Lawrence estuary containing sea water in subregions 33, 32, and 31). This whole dispersal process can be summarized as in Fig. 6. Mechanisms allowing the species to cross the centre of the peninsula are suggested in the next section on dispersal routes.

As for the low altitude areas of subregions 31 and 32, where a great similarity in stenohaline fish faunas is found on either side of the St. Lawrence, two complementary explanations may be proposed: (a) Toward the final stages of the ice melting, sufficiently large amounts of fresh water may have formed a partly unmixed layer above the sea water, near the shores, to allow the stenohaline species to progress down river along the shores and reach many of the St. Lawrence lower river and gulf tributaries. Such a layer exists now in the Saguenay Fjord (Drainville 1968). (b) The lowlands of the St. Lawrence Valley form a climatic gradient (Fig. 4), from colder (east) to warmer (west), so that both shores of subregion 32 present the same habitat, at least for the climatic component. The same is true for subregions 31 and 42. These two phenomena acting together are a possible explanation for the presence of the same stenohaline fish faunas on opposite shores of this seawater mass.

The number of species present in at least 25% of each region's pixels show an impoverishment of the fish fauna as the dispersal took place, northward and eastward (Fig. 5). This phenomenon can be accounted for by one of the following explanations: (1) either the dispersal process is not completed, and more species will eventually reach the northern and eastern regions, or (2) the species advance has been stopped by climatic or water condition limits that they cannot cross. Only experiments under controlled laboratory conditions, or experimental transplants in nature, could enable us to decide between these two hypotheses in each particular case. The correlations illustrated in Fig. 4 between regional boundaries and various types of potentially limiting factors indicate, however, that the limiting condition hypothesis must contain some truth.

The small number of stenohaline species that are now found in the seaside areas (less than 70% in subregions 11, 12, 21, 22, 31, 32, 33, 53) may also be partly the result of competition. Indeed, some stenohaline species may have failed to invade certain areas because euryhaline species had already occupied the available niches. Experimental transplants in nature could help to answer this question.

The map for the euryhaline species (Fig. 7) does not contain as many DD₄ arrows as Fig. 5 because the small number of euryhaline species present, often widely scattered, caused many arrows to be nonsignificant. The mechanism of entrance is here very different, since most euryhaline species must have reached

the coastal regions from the sea and from the Gulf of St. Lawrence, as indicated by the double-tailed arrows. It is remarkable that no DD₄ arrow is significant between the pairs of subregions 33–32 ($S = 0.93$) 32–31 ($S = 0.92$) and 31–42 ($S = 0.77$), the euryhaline species having supposedly had equal access to these territories via the St. Lawrence estuary. Dispersal coefficient arrows lead, however, to all the inland territories adjacent to the southern and eastern coastal subregions, suggesting that the euryhaline species went up many of the coastal rivers.

Subregion 55 is among the poorest in euryhaline species, the dispersal arrows that reach it being partly an indication of dispersal potential. This potential is inhibited to a large extent by the series of steep waterfalls that cut off the lower from the upper basins of many St. Lawrence north shore rivers, shown by the heavy broken line in Fig. 4. Only two euryhaline species are present in 50–100% of the pixels of subregion 55: the ninespine stickleback, *Pungitius pungitius*, whose distribution extends to the whole peninsula, and the freshwater salmon, *Salmo salar*, whose range covers the eastern half of the peninsula, limited by a line running south roughly from the west coast of Ungava Bay to the Lake St. John area and the upper course of the St. Lawrence River. This species may have reached the inland territories through various routes: by rivers of subregions 22, 32, or 31, or, during the Champlain Sea episode (when Lakes Ontario and Champlain were colonized by *S. salar*), straight northward from subregion 31 to the centre and the east of region 5 (map: 51–60) where it is now found dispersed throughout. From there (according to V.L.'s hypothesis), descendants of this inland freshwater population went down to Ungava Bay as a new endemic searun population, now confined to the bay (i.e. not joining the regular Atlantic migrants on the Greenland feeding grounds), in accord with the three considerations that follow.

In the sea, the searun Atlantic salmon *S. salar* is not known to appear along the northernmost 100-km strip of the coast of Labrador (north from Ramah to Cape Chidley), nor along the Ungava Bay side of that Cape. Neither does it reach the extreme northern headland of Québec from Leaf River along the Hudson Strait to Wolstenholme, nor has it ever been found in Hudson Bay waters. The two mentions in Bergeron and Brousseau (1982, p. 49) for the Hudson Bay are freshwater *S. salar*. In our opinion, the searun seems unable to inhabit the local waters of Arctic origin, as appears to be also the case of the western waters of Davis Strait and Baffin Bay, where there are no salmon (Carter 1979, map).

In Ungava Bay, the Atlantic salmon forms a population apparently confined to the voluminous affluents of the bay tributaries, with no connection to the Atlantic migrant population. No Greenland-tagged salmon have ever been returned from Ungava Bay tributaries.

Salmon from these rivers possess a recognizable morphological trait, ecophysiologically tied to the Arctic climate of the area, i.e. scales showing 5–11 river years in the parr stage. No salmon above 7 river years appear to have been reported from Atlantic migrants in Greenland waters (Lear 1976). Consequently, we hypothesize that this species reached Ungava Bay through the inland routes described in the following section. Very peculiar behavioural traits, observed in 1979–81 on the Ungava Bay salmon population and recently reported by Robitaille et al. (1982), may support the idea that we are facing a new local searun population, born of a freshwater population.

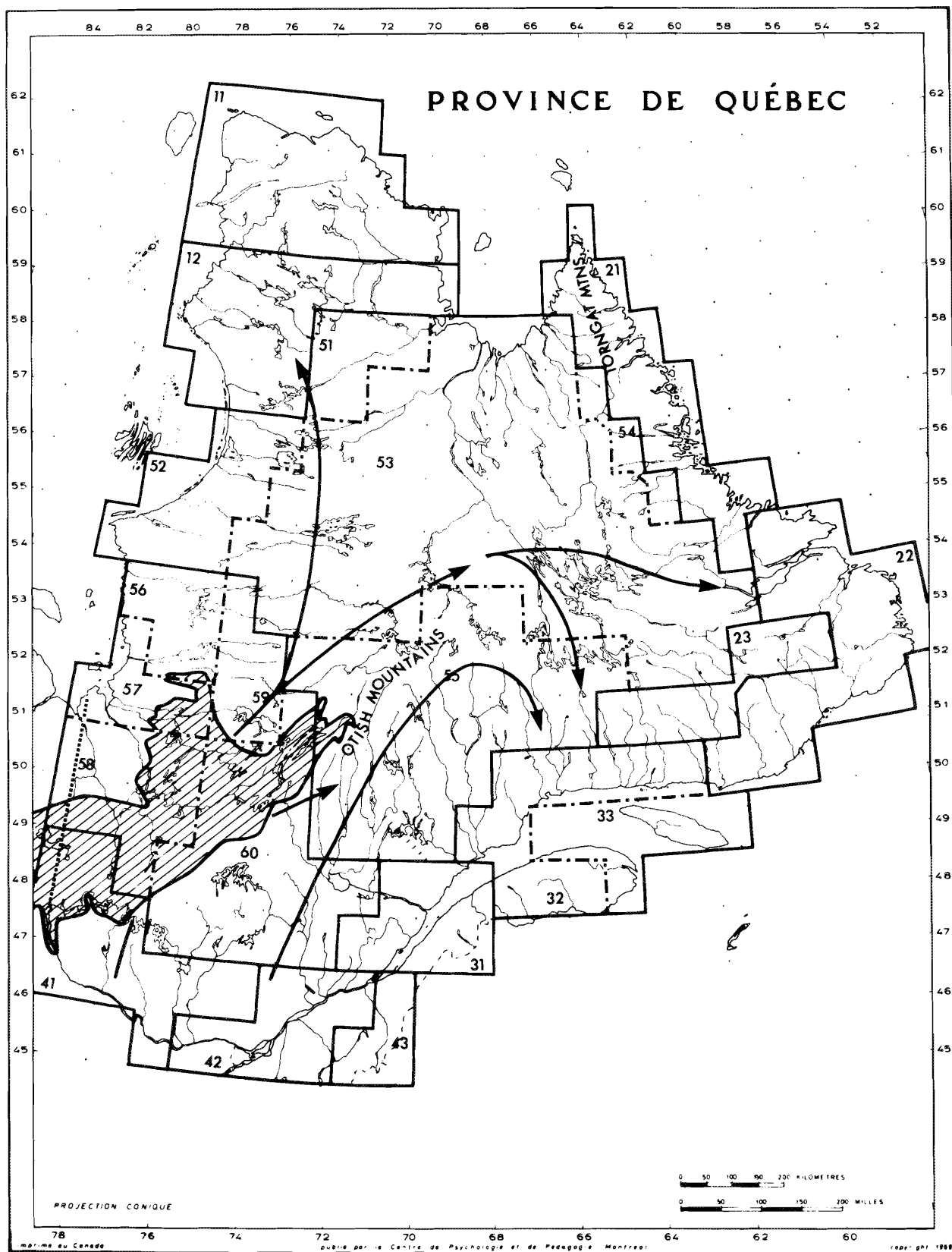


FIG. 6. Summary of the stenohaline species dispersal, detailed in Fig. 5. Hatched area: maximum extension of the Ojibway-Barlow glacial lake (Anonymous 1970).

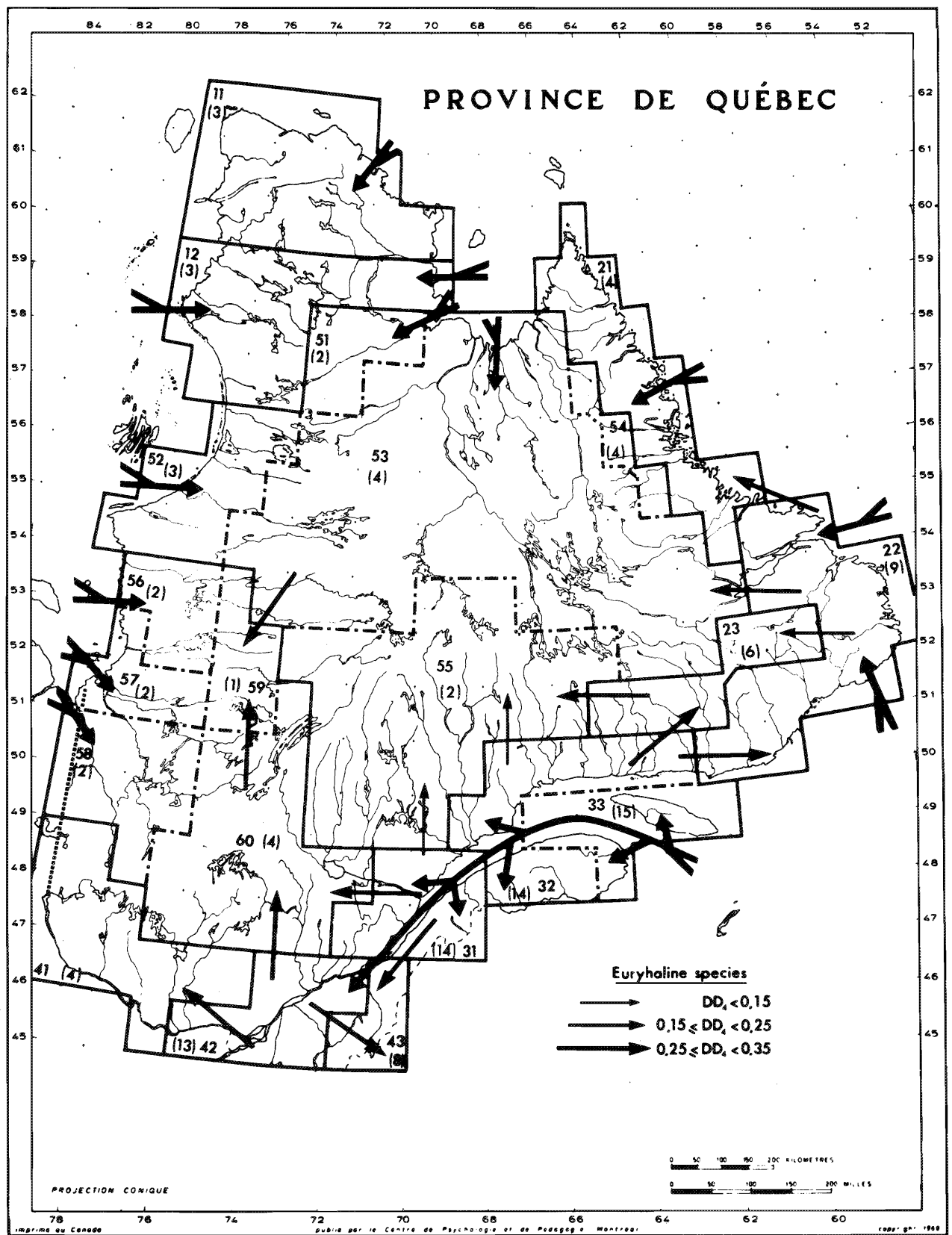


FIG. 7. Postglacial dispersal of the euryhaline species, as computed in this study. See Fig. 5 for details.

The computed dispersal patterns illustrated in Fig. 5 and 7 presuppose the existence of physical mechanisms allowing the fish species to reach and cross the centre of the peninsula. Two non-mutually exclusive types of mechanisms can be suggested.

On the one hand, when the glacier disappeared from Québec about 6000 yr ago, the whole peninsula was tilted westward, with the northern tip of James Bay lower than at present by about 150 m, as shown on the isobase maps published by Andrews and Tyler (1977). Consequently, many river segments now flowing towards Ungava Bay or the Atlantic may have flowed westward, along the slope that existed then. We hypothesize that a dynamic process of gradually shifting river interconnections took place as the peninsula rose back to its present isobasic position.

On the other hand, a vast and unusual network of interconnections at the headwaters of the major rivers still exists, and radiates from the centre of the peninsula towards its edges (Fig. 8). These connections are mostly permanent but a few are seasonal. Their existence will not be a surprise to those who have had an opportunity to fly at low altitude over central Québec, since the area where the ice sheet melted is often a gigantic network of lake interconnections, a phenomenon that is not obvious on the blank map we used to draw the figures here.

Interconnected Rivers in the Americas

Watershed interconnections are known occasionally in the literature. The existence of Québec river connections is obvious in a few cases from the names of lakes on published maps, such as Summit Lake and lac à Deux Décharges, their waters flowing toward opposite watersheds. In other cases, indications are found in reports of the explorers of the last century. Many other connections were found by a careful examination of topographic maps, followed by checks on aerial photographs or, in doubtful cases, in the field. Direct evidence of river interconnections in the Gulf of St. Lawrence North Shore area was also obtained through correspondence with M. Jean-Marie Brassard (Research Service of the Ministère du Loisir, de la Chasse et de la Pêche du Québec), who was interested in the question and "had been there" himself by canoe. Our quest for river interconnections began as the result of a chain of haphazard encounters with published reports. Our interest was triggered because interconnected rivers, on the one hand, are relatively rare aspects in geography and, on the other, are utterly unsuspected by the public, except for scattered regional specialists who may know about them. For example, a university lecturer in geography said a few years ago to his class that a lake could only discharge its waters through one outlet. This flat statement was quite credible to his students, since liquid water in natural masses has essentially one level, not several. This simplistic view of nature must be rectified.

Only about half of the citations on interconnected rivers that we encountered in the literature are reported here. Natural interconnections only are considered, to the exclusion of man-made ones. We will now try to show that interconnected rivers are rare events in the Americas. This will help to emphasize the exceptional configuration found in the Québec peninsula, which is the basis for one of the two mechanisms suggested above to explain the crossing of the centre of the peninsula by stenohaline fish species.

In the Rocky Mountains of the United States, along the continental divide, there is the Two-Ocean Pass in Wyoming, where each of at least two streams forks on the near-level, alpine

meadow ground of the pass, outflowing branches from each reunite from the opposite ends of the pass. These branches flow toward the Pacific Ocean via the Snake and Columbia rivers, on the one hand, and toward the Atlantic Ocean via the Yellowstone, Missouri, and Mississippi rivers, on the other. "It is certain that there has been, and usually is, a free waterway through Two-Ocean Pass of such a character as to permit fishes to pass easily and readily from the Snake River over to the Yellowstone — or in the opposite direction," said ichthyologist Evermann (1893) after visiting the area on 17 August 1891. For the eastern side of the continent, the same author recalled another author's citation, "in the highlands of Maine, where a rivulet discharges a portion of its waters into the Atlantic and the remainder into the St. Lawrence"; unfortunately, we did not succeed in retracing this on our maps. Then, "Two-ocean Pond in Yellowstone Park.... During the flood seasons, it discharges on the eastern rim into the Gulf of Mexico, and from the western edge into the Pacific ocean" (Redway 1890). In the same way, Talcott (1894) reported on Portage Lake, discharging both in Rivière du Loup in Québec, and in the north and south branches of the West Branch of Penobscot River in Maine. Thompson (1842, Part III, p. 67) reported on a pond with two outlets, located in northern Vermont, south of the Québec border.

In South America, in southern Venezuela, Territorio de Amazonas, the upper Orinoco River suddenly divides into two branches. Its main stream continues flowing west, then north and northeast toward its gigantic delta on the Atlantic Ocean south of the Island of Trinidad, while a large branch turning abruptly southward, the Casiquiare River, connects via the Rio Negro with the Amazon River in Brazil to flow toward the Atlantic. This interconnection of two great streams, perhaps the first known of its kind, appeared on a 1738 map by Father Antonio Caulin, in a geographical description of the Orinoco watershed (Caulin 1779 (1958), p. 296). To satisfy his curiosity, Alfred Russel Wallace went to see the place of the connection in 1851, also providing a map of these rivers, and he rather unkindly stated that, 50 yr before, Alexander Humboldt had not reached that far (Wallace 1889 (1972)). The diverging branches are indicated by arrows in the *National Geographic Atlas of the World* (National Geographic Society 1970, p. 74, 76). This explains directly how these two great streams, so far apart according to usual notions, have in part the same fish fauna, such as the great "electric eel" *Electrophorus electricus* (Berg 1947, p. 444). As at the Two-Ocean Pass in the United States, there is, according to a recent map of Ecuador, and sitting also just on the continental divide in the Andes 40 km directly east from Quito, a lake with two discharges. One flows west, finally joining the Rio Esmeraldas, a tributary of the Pacific Ocean, while the other, flowing east, connects via the Río Marañón with the Amazon (Anonymous 1974). In Brazil, a connection exists between the Amazon (via the Tocantins River discharging near Belém, just south of the equator and south of the vast Amazon delta) and the Rio San Francisco, a tributary of the Atlantic, at about 10°15'S, some 300 km south of the city of Recife. The two rivers have at least three species of Cichlidae in common (Haseman 1912, two maps tracing stream connections, also rejecting some other previously cited connections for South America).

Several examples exist in Canada. In northern Saskatchewan, Lake Wollaston has two northern outlets (National Geographic Society 1970, p. 56, 63), one leading west toward Lake Athabasca, flowing to the Mackenzie River (a tributary of the Arctic Ocean, at the western end of Mackenzie District in the

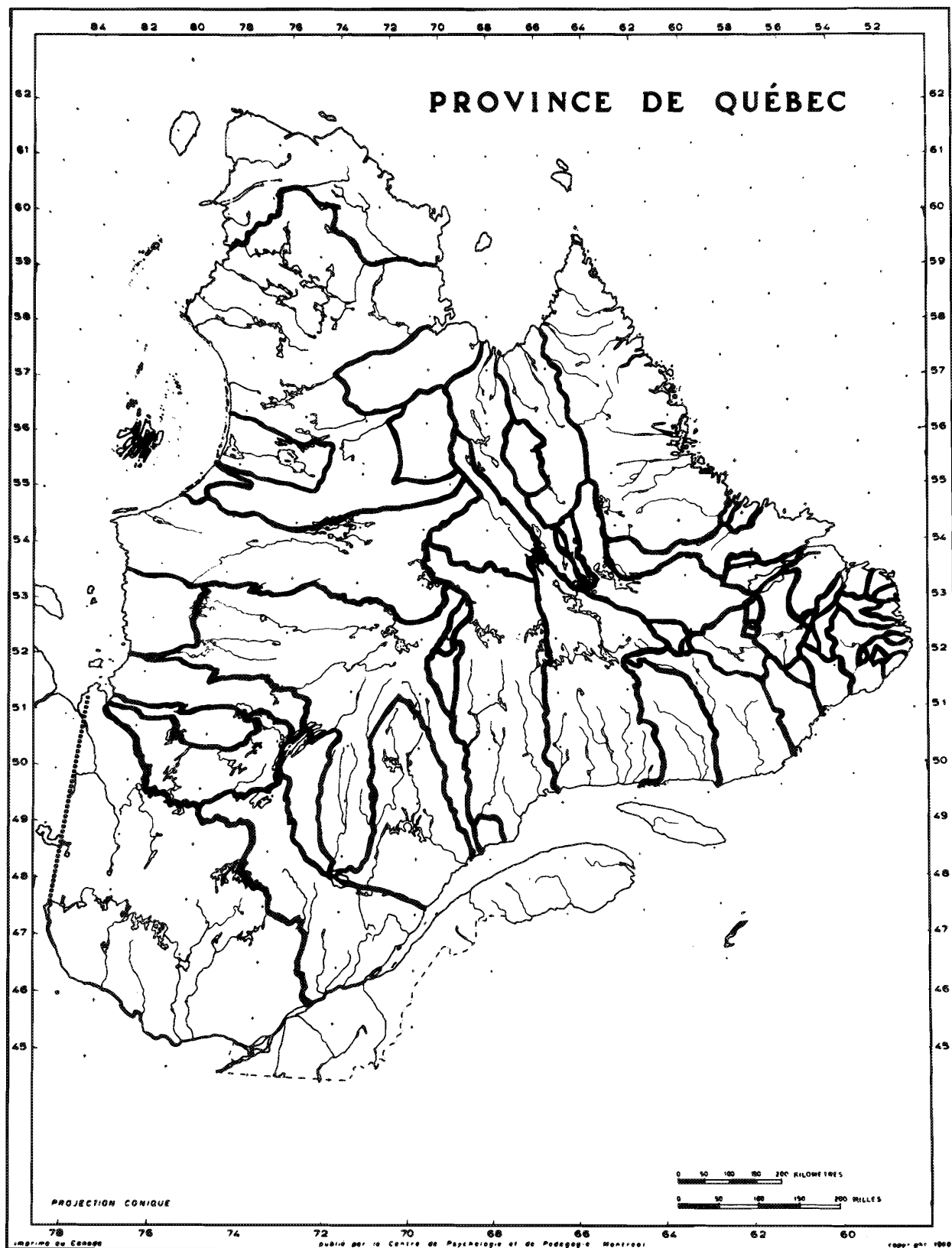


FIG. 8. Present network of river interconnections in the Québec peninsula.

Northwest Territories), and the other outlet flowing east and then south to the Churchill River, a tributary of Hudson Bay, on its west coast in northeastern Manitoba. E. A. Preble explained the presence of the grayling *Thymallus arcticus* in the lower Churchill River, tributary to Hudson Bay, by a direct water connection with Athabasca Lake (cited in Chambers 1914, p. 296). In the Canadian Rocky Mountains, at the Athabasca Pass, a small two-outlet lake sitting again on the continental divide was discovered 17 October 1824 by the Hudson's Bay Company governor, George Simpson (cited in MacKay 1966, p. 186–189). It discharges east into the Athabasca River and west into the Columbia River. The latter historian added: "Today the line separating British Columbia from Alberta divides this tiny lake." The lake is found as described on two old maps (Sproat 1873; Anonymous 1900); in Anonymous (1900, p. 6), the lake name is the one given by Simpson: Committee's Punch Bowl. As a consequence, Lake Athabasca, in northern Alberta and Saskatchewan, has a present-day continuous connection with four watersheds outflowing at near right angle directions: one direction south and west, to the Pacific Ocean, via the Athabasca and Columbia rivers; another one south, to the Gulf of Mexico via the Two-Ocean Pass and Columbia River connection with the Mississippi; another north, to the Arctic Ocean via the Mackenzie River; and the last one east, to Hudson Bay via the Churchill River. Thus, common fish species, or sister species, eventually evolved within these watersheds after the deglaciation, such as seen today among the Coregoninae (*Prosopium cylindraceum* and *P. williamsoni*) and the Catostomidae (*Catostomus commersoni* and *C. macrocheilus*), may become readily explained distributional patterns. Finally, there may be yet another two-ocean connection in the Canadian Rockies, in the vicinity of Kicking Horse Pass. Along highway 93 in Alberta, between Banff and Jasper, there is a stream that forks into two branches. One of them reportedly ends up in the Atlantic and the other in the Pacific. This was related to us by Jeanne and Thérèse Legendre, sisters of the second author, who heard it in 1977 from a Brewster Company bus driver and tourist guide.

In central Ontario, the Muskoka River offers two peculiarities (Canadian federal maps 31D, 31E and 41H, scale 1:250 000). First, about 5 km west of Lake Muskoka, this river bifurcates, both branches (Moon and Muskoka) flowing toward Georgian Bay. Farther downstream, the Muskoka River flows into Go Home Lake, which has two outlets (Go Home and Muskoka), both flowing again toward Georgian Bay (P. Ross, Université de Montréal, pers. comm.). Since all three courses flow toward Georgian Bay (Lake Huron), this hydrological curiosity would not be expected to have much impact on fish distributions. Such is not the case with a lake, located on the heights of the Laurentide Peneplain in eastern Ontario: Lake Timagami connects through a maze of lakes and rivers, as shown on maps, north and then east with Lake Témiscamingue located between the provinces of Ontario and Québec, a headwater of the Ottawa River (which is a large tributary of the St. Lawrence). Lake Timagami also connects to the south with Lake Nipissing, which flows to Lake Huron via Rivière des Français (Canadian federal maps, scale 1:250 000, here given in a succession so as to follow the course of the waters: 31M, 41P, 41I, 31L; maps not repeated in the References). On map 41P/1, scale 1:50 000, the northern connection of Lake Timagami with the Ottawa River is found just south of the line between Canton Township in Nipissing District to the south and Medina Township in Timiskaming District to the north. Confirmation of this geo-

graphical water arrangement is found in the literature (Chénier 1937, p. 51).

On the Atlantic side of Canada, "from some marshy lakes on the isthmus which connects Nova Scotia with the mainland the river Missiquash flows to the Bay of Fundy; a small stream, sometimes dry in summer, also flows northward from the same lake to the Baie Verte [on the Gulf of St. Lawrence side of the isthmus]" (G. 1891). This hydrologic situation may explain how some of the smaller fish species, more or less indifferent to water salinities, are found on either side of the isthmus. They may have often crossed it directly from the Atlantic – Bay of Fundy side to the Gulf of St. Lawrence side. The distributional maps of some of these species found to occupy waters of the isthmus (Livingstone 1953) suggest that such crossover fish species may be those, for example, of the families Petromyzontidae (*Petromyzon marinus*), Clupeidae (*Alosa pseudoharengus*), Salmonidae (*Salvelinus fontinalis*), Osmeridae (*Osmerus mordax*), Anguillidae (*Anguilla rostrata*), Cyprinodontidae (*Fundulus diaphanus* and perhaps *F. heteroclitus*), Gadidae (*Microgadus tomcod*), Percichthyidae (*Morone americana*, and perhaps also *M. saxatilis*), and Gasterosteidae (all three so-called marine species, *Apeltes quadracus*, *Gasterosteus aculeatus*, *Pungitius pungitius*).

Freshets and their effect on fish migrations are a universally ignored mechanism. This may be tied to their year-to-year variability and to their usually short duration. During these brief periods, however, the volumes of water exchanged between watersheds are often considerable, so much so that large communities of fishes may be passively transported. Under northern North American climatic conditions, freshets may occur at any time of the year, for example, during autumn rains and spring heavy snow thaws, and after heavy local summer rainfalls. Even though occasional, their erratic recurrence during decades or centuries has undoubtedly acted in the past as an efficient intermediary (in time) mechanism in passive migration or transportation of fishes. Ichthyogeographers seem to have forgotten them. Such temporary interconnections between watersheds were heavily cited in the past throughout North America; some examples follow. First, there was the case of repeated seasonal "modern" (i.e. postglacial) connections between southern Lake Michigan and the Mississippi River, as related by the second discoverer of the Mississippi, La Salle (1682 (1879), p. 166). Weld (1807, Vol. I, p. 69, 330) documented a seasonal, northern Green Bay connection with the Mississippi. In northwestern New York, Wright (1918, p. 544) mentioned a connection between the Susquehanna River and Lake Ontario via Lake Cayuga, among the Finger Lakes. In northwestern Canada, as elsewhere, a river that normally functions as a lake outlet will not reverse and flow into the lake. There is, however, the exception of a river playing both roles alternatively according to whether it is in the freshet season or in some other time of the year. This occurs because of a local converging set of geographical conditions at the west end of Lake Athabasca. Two large rivers converge, the Athabasca from the south and the Peace from the west, with a rather large lake, Lake Clair, acting as a stabilizer between them in much the same way as do stabilizing basins erected alongside man-made canals for navigation. On 22 September 1808, a fur trader with the Northwest Company wrote: "...with a number of persons, in several canoes, I left Fort Chippewyan [at the west end of Lake Athabasca]; and, after coming two miles in Athabaska Lake, we entered a small river [small in terms of the country], which is about thirty six miles long [one of several local outlets of the big

lake], and which now [in September] runs out of that Lake into Peace river; but, when this river [the small one] is high, it discharges itself into the Lake [Athabasca]" (Harmon 1911, p. 140). Concerning streams that flow into the St. Lawrence, from its Québec north shore, an early nineteenth century army engineer had this to say after an exploration party set out to open the country to colonization: "These lakes discharge themselves by innumerable shallow streams, into the St. Maurice [tributary of the St. Lawrence just below Lake St. Pierre, or St. Peter] and aux Lievres [tributary of the Ottawa River] Rivers...; in one or two instances the streams swell into large and rapid rivers and discharge [westward] into the Ottawa and [eastward] Lake St. Peter in a direct course" (Ingall 1831, p. 14). At the beginning of the present century, several large parties supported by business and the Québec government explored the territory for extensions of railways to James Bay, and one of their land surveyors wrote: "The Height of Land between the St. Lawrence and James Bay waters is scarcely perceptible, the waters interlock and some of the lakes discharge both ways during freshets" (O'Sullivan 1903, p. 23). An accompanying map showed the permanent connection between the headwaters of the St. Maurice River (the previously cited tributary to the St. Lawrence) and Nottaway River, tributary to the southeastern end of James Bay, following precisely the same line as the southeast-northwest one shown at the extreme lefthand side of Fig. 8. The interconnection is a two-discharge lake, shown on present-day maps.

In Québec, such direct interconnections between rivers were never mentioned in the approximately 500 accounts of travels and explorations since the discovery of the country by Europeans, written by, or for, *coureurs de bois*, voyageurs, furriers, missionaries, businessmen, and soldiers. Such mentions appear only after the first quarter of the last century with the advent of naturalists attached to exploration parties, sent out to establish the possibilities of opening the then backcountry to colonization. To our knowledge acquired from these readings, the first documented connection, found in 1828, is the well-known three-discharge Lake Kénogami (Baddeley 1829, p. 117; Ballantyne 1851, map), 3 km wide on the average, 27 km long, and 102 m deep. This glacially formed fjord, about 15 km south of and parallel to the upper Saguenay River, has one natural outlet (la Belle-Rivière) westward to Lake St. Jean (St. John), and two parallel eastern outlets, Rivière des Sables and Rivière Chicoutimi, flowing northward toward the Saguenay River. Another Québec river interconnection was reported in 1859 by Ferland (1859, p. 111) between River St. Augustin, a North Shore tributary of the lower Gulf of St. Lawrence, and Kenamou River which falls into Baie des Esquimaux (Hamilton Inlet).

The Québec exploratory reports of the Canadian geologist A. P. Low were the initial incentive to our inventory when V. L. came upon them some 30 yr ago. Low criss-crossed the land from Hudson Bay to the Atlantic and from Ungava Bay to the St. Lawrence, toward the end of the last century. He wrote about Summit Lake, which has two outlets, one going to Ungava Bay via the Kaniapiskau and Koksoak rivers, and the southern one being a tributary of Manicouagan River that empties into the Gulf of St. Lawrence. He added: "This is not an uncommon case with lakes situated along the watershed in the northern region underlain by Laurentian rocks....Lake Kaniapiskau has *three* discharges" (our italics) (Low 1897, p. 107L). The following citation, with bracketed references, shows that tracing back old geographical autochthonous names of maps would be in itself

quite a story if detailed: "The Great Whale river...is divided [upstream] into two almost equal branches...the Abchigamich [then the Indian name of the presently named Great Whale River, later extended to its course above the fork] and Coast branches of the river.... This stream [the Abchigamich], according to the Indians [Low was not there himself to check], takes its rise in a large lake of the same name [now called Lake Bienville, 110 km long east-west] situated about 100 miles [160 km] farther inland. A striking peculiarity of this lake is that it has *several* outlets and being situated directly on the height of land, it drains eastward by a tributary of the Koksoak river which empties into Ungava bay, while its westward flowing outlets form the head waters of the Abchigamich [Great Whale] river and also of the Little Whale river [both tributaries to the eastern shore of Hudson Bay]. Such lakes with *double* outlets are not uncommon in Labrador, but it rarely happens that *three* rivers take their rise in the same lake" (our italics) (Low 1903, p. 35D-37D). In former atlases, Lake Bienville had its Indian name corrupted otherwise, such as "Apickacumish" (Walling 1875, maps p. 15, 99, 103) and "Apiskigamish" (Rand McNally & Company 1938, map p. 17). There is a correction to make in Low's last citation. It seems he probably misunderstood his Indian counsels, as he gives Lake Bienville (Abchigamich) as a tributary of Koksoak River, which it is not. There is in fact a continuous connection between them, but it is through a set of four lakes (Lenouiller, Novereau, Decoigne, and Jacquemont) all at the same altitude and higher by some 30 m than both Lake Bienville and the Koksoak River (map 23M). It is these small lakes that discharge toward either watershed and that are thus the headwaters. On the other hand, we never succeeded in finding a connection between Lake Bienville and the Little Whale River, so that it looks as if there are only two present-day interconnections with Lake Bienville, i.e. that of the Great Whale and that of the Koksoak. Another hypothesis may be formulated, however: the Little Whale River connection with Lake Bienville may have been extant when Low talked with the Indians, and it may have drained out since then, due to the action of one or several occurrences such as (1) the considerable isostatic rebound of the Hudson Bay side of Québec, which may have broken the water connection (140 m rebound in the past 6000 yr, according to Andrews and Tyler (1977, fig. 6), i.e. about 230 cm/100 yr), (2) a possible filling up of headwater lakes by aquatic plants, turning the water bodies into more or less dried-up bogs, and (3) the less abundant rainfalls since the end of the "Little Ice Age," which started in the fifteenth century and terminated around 1890. If this hypothesis is correct, it would make it a case of a connection disappearing in historical times.

One way or the other, it was Low's provocative words, "three discharges," "two outlets," "this is not an uncommon case," etc., that launched 10 yr ago our overall examination of the Québec maps available, with the purpose of possibly locating other multiple-outlet lakes that he had not named or otherwise indicated. The result is Fig. 8. At the present state of our research, and apart from the freshwater part of the main St. Lawrence River, 41 rivers are seen to be interconnected today via 68 headwaters. This is a hitherto unheard of (if not intolerable!) situation. To cite only a few examples of explanations of the present distribution of some freshwater fish species, this incomparable, extensive, and multiple-connection network of rivers may be considered as a simple mechanism explaining how fishes, starting from Upper St. Lawrence waters, came, through centuries or millenia, across the Québec penin-

sula and reached eastward to the Hamilton Inlet (*Catostomus catostomus*, *C. commersoni*, *Rhinichthys cataractae*, *Couesius plumbeus*, *Lota lota*; Backus 1957) and to the lower reaches of the southern tributaries of Ungava Bay (Bergeron and Brousseau 1981), and even to the very northern extremity of the mainland close to Hudson Strait (*Salvelinus namaycush*, *Esox lucius*, *C. catostomus*; Bergeron and Brousseau 1981).

To our knowledge from the literature, there is no other reported instance of connections as extensive as the network discovered and described here. By analogy with the blood capillary networks of anatomy, we call it the *rete mirabile* (admirable network) of Québec rivers.

The postglacial dispersal patterns of fishes in the Québec peninsula can then be explained on the one hand by the isobasic movements of the peninsula since the end of the Wisconsin Ice Age, and on the other by the very elaborate network of river interconnections still extant today. In this way, dispersal routes were available for most fish species to reach all parts of the peninsula.

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