Brook Trout (*Salvelinus fontinalis*) Population Structure in Acidified Lac Tantaré, Quebec

Jean-Jacques Frenette and Julian J. Dodson

Département de biologie, Université Laval, Cité Universitaire, Ste-Foy (Qué.) G1K 7P4

Frenette, J.-J., and J. J. Dodson. 1984. Brook trout (*Salvelinus fontinalis*) population structure in acidified Lac Tantaré, Quebec. Can. J. Fish. Aquat. Sci. 41: 865–877.

To present evidence of acid-induced stress, we studied the population structure and distribution of brook trout (*Salvelinus fontinalis*) in acidified Lac Tantaré, Quebec. Trout greater than 21 cm (FL) represented only 16.2 and 10% of the population sampled in 1979 and 1980, respectively. Survival rates of trout from 1979 to 1980 indicated higher survival among individuals >25 cm, mortality occurring primarily among fish of 13–25 cm. The marked decline in numbers of fish occurring at 21 cm coincided with the size at which 50% of the female trout population reached sexual maturity, suggesting that postspawning mortality contributes to the high mortality observed among these fish. Comparisons of population and individual growth rates revealed that smaller fish of age-classes 1 to 5 suffer higher mortality than do the larger individuals of these age-classes, implicating mortality agents other than those related to spawning. We provide evidence to support the hypothesis that the most probable cause of mortality is size-related differential exposure to toxic stress whereby small brook trout (<25 cm) are found in lake areas (brooks) exhibiting the most potentially toxic combination of pH and aluminum, thus enhancing the exposure of the most susceptible part of the population to toxic stress. Large brook trout (⩾25 cm) are found in the "safest" lake areas (springs), thus diminishing the exposure of the least susceptible part of the population to toxic stress and enhancing survival. Female trout exhibit delayed sexual maturity relative to other Quebec populations, attaining 50% maturity at age 3 and a length of 21–24 cm such that the major part of the population's reproductive effort is provided by those fish representing only 15% of the population in 1979 and 1980. During the October spawning season, 20% of potential spawners exhibited retarded oogenesis. These reductions in reproductive effort and changes in spawning site selection provide evidence in support of the hypothesis that recruitment failure may be occurring in the Tantaré brook trout population.

La structure de population et la distribution de la truite mouchetée (*Salvelinus fontinalis*) dans un lac acide, le lac Tantaré, sont décrites afin de mettre en évidence un stress occasionné par l'acidité en dynamique de population. Les truites dont la taille dépasse 21 cm (LF), représentent seulement 16.2 et 10 % de la population échantillonnée en 1979 et 1980 respectivement. Les taux de survie des truites de 1979 à 1980 indiquent une survie plus élevée chez les individus > 25 cm, la mortalité frappant surtout les poissons mesurant de 13–25 cm. Le déclin rapide des poissons se produit à 21 cm en longueur et coincide avec la taille à laquelle 50 % de la population des truites femelles atteint la maturité sexuelle, ce qui suggère une mortalité post-frai pouvant contribuer à la mortalité élevée observée parmis ces poissons. La comparaison des taux de croissance individuels et de la population révèle une mortalité plus élevée chez les petits poissons parmi les classes d'âge 1 à 5, que chez les gros individus de ces classes d'âge, ce qui implique d'autres agents de mortalité que ceux reliés au frai. L'exposition différentielle au stress acide faisant intervenir la taille s'avère l'hypothèse la plus probable pour expliquer la mortalité. En effet les petites truites mouchetées (< 25 cm) se retrouvent dans les régions lacustres (ruisseaux) où l'on retrouve la combinaison potentielle de pH et d'aluminium la plus toxique, ce qui a pour effet d'augmenter l'exposition de la partie la plus susceptible de la population au stress toxique. Les grosses truites mouchetées (⩾ 25 cm) se retrouvent dans les régions lacustres les plus "sûres" (sources) ce qui diminue l'exposition de la partie la moins susceptible de la population au stress toxique et augmente la survie. Par rapport à d'autres populations du Québec, les femelles présentent une maturité sexuelle retardée; celles-ci atteignent 50 % de maturité à 3 ans et une longueur de 21–24 cm de telle sorte que l'effort reproductif de la majeure partie de la population repose sur ces poissons, lesquels représentent seulement 15 % de la population en 1979 et 1980. Lors de la période de frai d'octobre, 20 % des géniteurs potentiels présentent une oogénèse retardée. Ces réductions de l'effort reproductif ainsi que les changements dans la sélection des sites de frai viennent appuyer l'hypothèse selon laquelle un échec du recrutement peut se produire au sein de la population de truite mouchetée de Tantaré.

Received June 1, 1983
Accepted February 3, 1984

Reçu le 1 juin 1983
Accepté le 3 février 1984

The impact of acidification in freshwater lakes and rivers has been a subject of major concern in many countries of the world (Drablos and Tollan 1980). A large number of Quebec lakes are presently undergoing acidification due to acid precipitation (Bobée et al. 1982). The loss of fish populations associated with an increase in hydrogen ion and toxic metal concentrations is attributed principally to reproductive failure as opposed to mortality of adult fish (Haines 1981;

Spry et al. 1981). Numerous effects occur in populations prior to extinction including reduction in population size, altered age structures, increased, decreased, or unaltered growth, size-selective mortality among older or younger fish, and failure of recruitment of new age-classes into the population (Harvey 1982). These population responses vary with species and location. The brook trout (*Salvelinus fontinalis*), an important freshwater game fish in eastern Canada, has poorly documented population responses to acidification. Moreover, observations of the effects of lake acidification on fish behavior, activity, maturation, and spawning are particularly lacking in the literature (Harvey 1982).

The purpose of our study was to determine over a 2-yr period the population structure of brook trout living in an unexploited acidified lake and to look for evidence of acid-induced stress. Our objectives were to document size distribution, growth, mortality, maturity, and the distribution of fish in relation to hydrogen ion and aluminum concentrations, those toxic factors most frequently associated with acid stress in fish.

Materials and Methods

Lac Tantaré and its Chemical Characteristics

Lac Tantaré (altitude 457 m) is a head-water Laurentide Highlands lake located in the Tantaré ecological reserve (47°04′N, 71°32′W) north of Quebec City. Limnological and paleolimnological evidence for the long-range atmospheric transport of acid pollutants and heavy metals into Lac Tantaré was discussed by Ouellet and Jones (1983) who concluded that Lac Tantaré began to be acidified no later than about 1950. In 1979 and 1980, pH varied between 4.64 and 6.06 among the various locations and sampling periods, while conductivity (25°C) ranged from 14 to 25 μS. Transparency was high, varying between 7.5 and 12.8 m throughout the season. Dissolved oxygen concentrations ranged from 7.9 to 11.8 mg/L in the 0.5- to 2-m depth zone, saturation remaining above 90% throughout the period of study.

The Tantaré ecological rserve was created in 1978. No fish exploitation has occurred since 1977. Prior to 1977, the lake was privately owned and only light exploitation was permitted. The native brook trout population is the only fish species present in the lake.

A van Dorn water sampler was used to collect water at a depth of 2 m from stations A, B, C, D, and E (Fig. 1). Water was slowly transferred into polyethylene bottles rinsed with lake water for pH determination, with acid for aluminum determinations, and into DOB bottles for dissolved oxygen measurements. Stations F, G, and H (brooks, Fig. 1) were sampled 15 cm from the bottom with prerinsed polyethylene and DOB bottles.

Temperature was measured directly with a Hydrolab thermistor. PH was measured in the field using a Sargent-Welch model PBX portable pH meter standardized at pH 7.0 and 4.0 before each series of readings. PH measurements were also made in the laboratory within 4 h of sampling using a Fisher expanded scale pH meter. Dissolved oxygen values were obtained using Winkler's standard method. Conductivity determinations were provided by G. H. Jones, I.N.R.S.-eau, Quebec. Aluminum concentrations were determined by atomic absorption spectrophotometry (Guimont and Pichette 1979).

Fish Sampling

Trap nets, seines, and gill nets were used to capture fish. Positions of the sampling stations are given in Fig. 1. Stations were grouped into three regions: littoral zone, defined as the 0- to 2-m depth zone in all basins; springs, several small areas (0.09–2 m^2) located in the 2- to 3-m depth zone where groundwater seeped from the bottom; and brooks, small inlets (approximately 2 m in width) flowing from the surrounding hills. Capture methods and sampling frequency for each station are summarized in Table 1. Due to the extreme clarity of the water, the presence or absence of fish in the brooks and springs was easily noted by direct visual observation. No brook trout were observed in these zones prior to the end of June and thus, seining was initiated only at the beginning of July.

Fish collections were made primarily with Pennsylvania-type trap nets constructed of 32-mm ABS tubing and 6-mm-mesh nylon netting. Leaders were 30 m long and the wings were 18 m long. Trap nets were set in 1.5–2.0 m of water, the leader placed perpendicular to the shore. All trap nets were sampled daily from June 7 to July 31 in 1979 and from May 15 to July 3 in 1980 and every 2 d until September 1 twice weekly thereafter until the end of October in both years. A 5-mm-mesh nylon bag seine was used to sample the brooks, and a 5-mm-mesh purse seine 20 m long and 4 m deep was employed in the springs. Experimental gill nets of five different mesh sizes (2.5, 3.8, 5.1, 6.4, and 7.6 cm) were used to obtain additional samples for the analysis of otoliths, gonads, stomach contents, etc., and only sparingly because of the limited number of killed specimens permitted in the ecological reserve.

All fish captured by trap netting or seining were released following sampling. We anaesthetized all fish by immersion in a solution of methylpentynol. Fork length was measured to the nearest millimetre. Trout greater than 13 cm were marked with individually numbered spaghetti dart tags. Prior to release, fish were transferred to a bath of malachite green for 15–30 s followed by a recovery period in a lake water tank. Fish were considered fully recovered when swimming actively in an upright position.

Analysis

Size, age, survival, and distribution of fish — The length–frequency distribution of brook trout was calculated by 3-cm length intervals for fish captured in June at stations 1, 2, and 3. This coincides with the period when fish were distributed throughout the littoral zone and trap net catches were most representative of the population. Recapture and multiple recapture rates during this period were also calculated by size-class ($<$21 and $\geqslant$21 cm) to assess any possible gear-induced bias in length–frequency distribution.

A total of 241 scales (1979–80) and 168 otoliths (1980), among which 115 scales and otoliths were from the same fish, were used for age determination of brook trout. Scales were removed from the left side of the fish between the end of the dorsal fin and lateral line and mounted between acetate sheets (Power 1964). The acetate sheets were immersed in a 2% KOH solution for 4–6 h to eliminate the excessive quantity of mucus present on the scales and to clarify the annuli. Otoliths were sanded and immersed in methyl salicylate oil for several hours prior to reading. Age was determined from two independant readings for each specimen using scales and/or otoliths. In case of disagreement between the first two readings, a third reading was made to determine the age. Two independent readers were

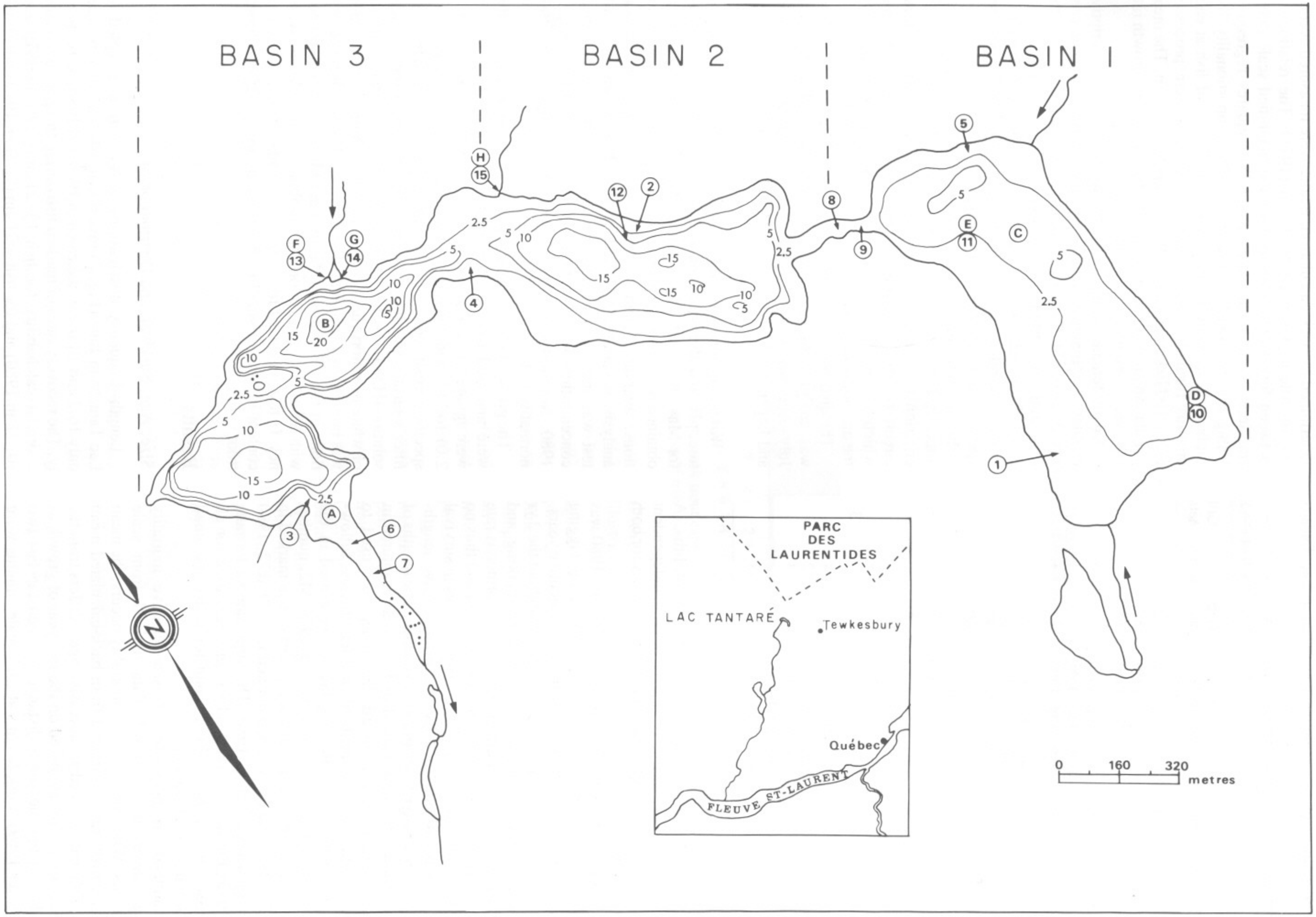


FIG. 1. Bathymetry and position of sampling stations in Lac Tantaré for 1979 and 1980. Depths contours in metres.

TABLE 1. Summary of fish sampling undertaken at Lac Tantaré, 1979–80.

				Sampling frequency		
Basin	Region	Station	Sampling date	Trap nets	Seines	Gill nets
I	Littoral 1	1	June–Oct. 1979	82		
			May–Oct. 1980	82		
		9	May–Oct. 1980	68		
	Springs	10	July–Aug. 1979		3	
			Aug.–Oct. 1980		1	1
		11	July–Aug. 1980		1	3
II–III	Littoral 2	2	June–Oct. 1979	82		
			May–Oct. 1980	81		
		3	June–Oct. 1979	77		
			May–Oct. 1980	80		
		4	July–Oct. 1979	60		
		5	Aug.–Oct. 1979	31		
		6	Sept.–Oct. 1979	8		
		7	May–Oct. 1980	37		
		8	May–Oct. 1980	73		
		12	July–Aug. 1980			3
	Brooks	13	Aug. 1979		4	
			Aug. 1980		2	
		14	July–Aug. 1980		3	
		15	Aug. 1979		4	
			Aug. 1980		3	

used for scale examinations and one reader for otoliths. A subsample of the otoliths was read by a second independent reader. Readings were in agreement in 70% of all cases for both scales and otoliths.

The survival rate of brook trout between 1979 and 1980 was calculated using Ricker's method (1975) based on tagging experiments done at the start of fishing in two consecutive years. Although marking and recapturing occurred throughout the 2 yr of our study, Ricker's method was used as marking and capturing were carried out at the same time at a continuous rate and all recaptured fish were released as new marks and thus no mortality resulted from fishing. To identify changes in survival rate with length, we classified fish according to five length-classes in two successive years of their existence. The lengths of fish from each length-class marked in 1979 and recaptured in 1980 were averaged and standard deviations were used to determine the range of increments of each length-class following 1 yr of growth. The following factors were used in the calculations: M1, number of fish marked in 1979; M2, number of fish marked in 1980; R11, 1979 recaptures of fish marked in 1979; R12, 1980 recaptures of fish marked in 1979; R22, 1980 recaptures of fish marked in 1980. The large sample formula (Ricker 1975) for survival rate and variance was used for all length-classes except the $\geq$35 cm group for which the small sample formula was employed.

We examined the possibility of size-selective mortality within age-classes using growth data derived from scale measurements. When size-selective mortality occurs, the mean population growth rate, estimated from back-calculated mean lengths of fish that survived at successive ages, differs from the true individual growth rate based on the last year of growth as calculated from the measured distance between the last two annuli (Ricker 1969). Fork lengths at each scale annulus were determined by back-calculation. Scales were measured according to criteria described by Tesch (1971). The relationship between fork length (millimetres) and magnified scale radius (millimetres) was calculated using least-squares regression. Using this relationship, Fraser's (1916) proportionality formula, and the scale measurements, the length of fish at each annulus formation was calculated. All data were processed using the Nickerson et al. (1980) computer program. The mean population growth rate (GX) and the true individual growth rate (G) were computed according to Ricker (1975).

Ninety females sampled in 1980 were used for a descriptive evaluation of maturity stages. Complete ovaries were preserved in Gilson's fluid (Bagenal 1978). Eggs were liberated from the ovarian tissue, sorted using sieves of 1, 2, 3, 4, and 5 mm, and counted. Maturity was defined using the criteria of Henderson (1963), all individuals containing eggs >1 mm being potential spawners during the current season.

Brook trout in Quebec lakes do not necessarily spawn annually (Vladykov 1956; Power 1966). There is no simple criterion to identify the age and length at maturity in these circumstances. Therefore, the smallest age and length group in which 50% of the fish were maturing to spawn was adopted as the age and size at maturity (Morin et al. 1982).

The distribution of small (<25 cm) and large ($\geq$25 cm) trout was analyzed by region for the periods of May–June and July–August 1980 using a contingency table analysis (Legendre and Legendre 1979).

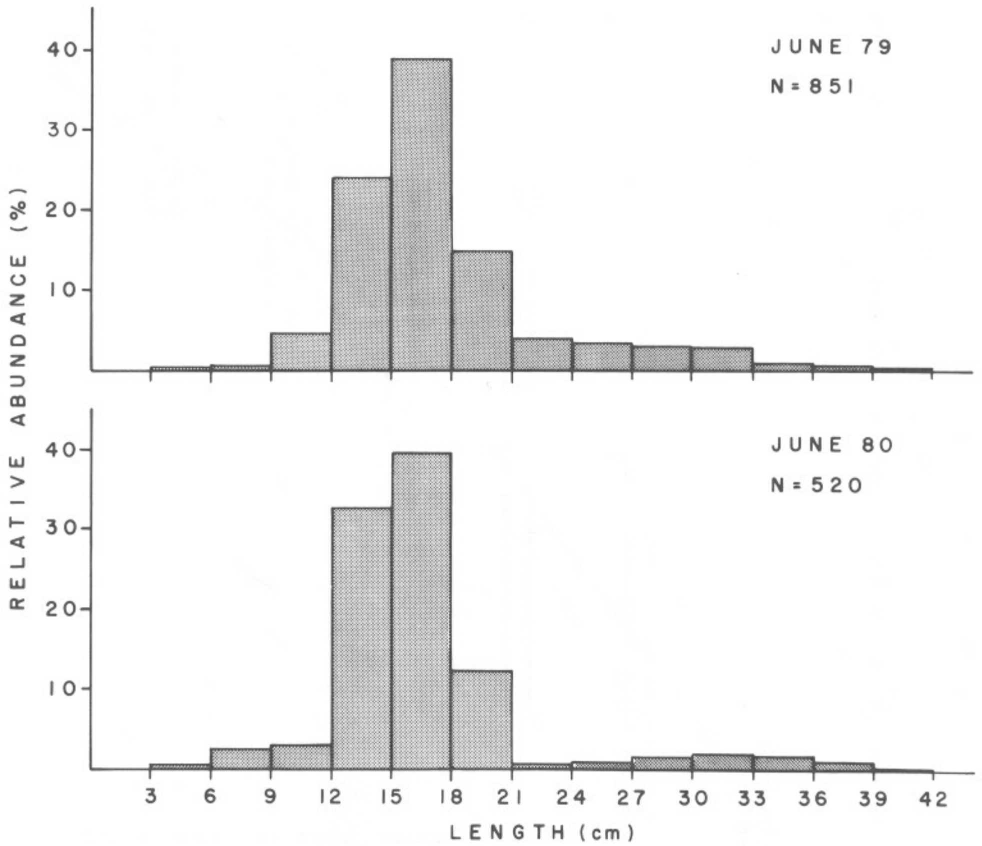
Water characteristics and aluminum in fish gills — Temperature, pH, and aluminum concentrations in water were averaged for May–June and July–August 1980. Mean pH values were obtained by converting pH measures to hydrogen ion concentrations, averaging, and converting back to pH. A one-way analysis of variance followed by a Student–Newman– Keuls test was used to compare temperature, pH, and aluminum concentrations in water of the four regions during July–August 1980. Normality was verified using a Kolmogorov–Smirnov normality test.

The gills of 19 brook trout, sampled at stations 8 and 9 in July, were analyzed for tissue concentrations of aluminum. Gills were agitated in an acid solution (5 mL of 0.01 N, HNO_3, pH = 2.0) for 1 h and filtered with a polycarbonate membrane of specific porosity equal to 1 μm. Rinsed gills were taken from the filter's surface and digested in a weak nitric and perchloric acid solution (HNO_3–$HClO_4$). This was heated until the appearance of white perchloric acid smoke, and the volume of the solution was brought to 10 mL with dilute HNO_3. Aluminum concentrations in the solution and the original filtrate were determined with an atomic absorption spectrophotometer. A Mann-Whitney U test was used to compare the ranks of total aluminum content in gills of small (<25 cm) and large ($\geq$25 cm) brook trout.

Results

Size, Age, Survival, and Distribution of Fish

Length–frequency distributions of brook trout sampled in Lac Tantaré in June (Fig. 2) reveal that fish >21 cm represent only 16.2 and 10.0% of the catch in 1979 and 1980, respectively. The recovery rates of marked fish during this period indicate a similar catchability for fish 13–21 cm (7.9% in 1979 and 10.7% in 1980) and for fish $\geq$21 cm (7.2% in 1979 and 12.5%



reduce

FIG. 2. Length–frequency distributions of brook trout captured in Lac Tantaré during June 1979 and June 1980 at stations 1, 2, and 3. N = number of fish sampled.

in 1980). In addition, bias due to fish repeatedly recaptured in trap nets during this period is negligible, representing only 0.2 and 1.5% of the catch in 1979 and 1980, respectively. Catches of fish <13 cm indicate an increase in abundance from June (97 in 1979 and 71 in 1980) to July (871 in 1979 and 284 in 1980), suggesting a low catchability for fish of this length group in June.

Growth curves obtained from back-calculated and observed mean fork length-at-age (Fig. 3) demonstrate a fairly constant increase in size to age 4. Thereafter, growth rate declines. Maximum age observed was 7+.

Survival rates of brook trout for 1979–80 (Table 2) indicate a higher survival rate for individuals ≥25 cm in length. Thus, mortality occurred primarily among fish measuring 13–25 cm, which represented 76 and 83% of the tagged population in 1979 and 1980, respectively. Brook trout measuring 13–25 cm correspond approximately to fish of 2 and 3 yr of age (Fig. 3). The ratio of the number of recaptured fish to marked fish for the entire 1979 season (R11/M1, Table 2) and for the entire 1980 season (R22/M2, Table 2) demonstrates a greater recovery success for those groups exhibiting the poorest survival. This observation supports the conclusion that R12/M1 (Table 2) reflects true survival and that increased mortality among fish measuring <25 cm is not an artifact related to poor recovery success of these fish.

The higher population growth rate (GX) relative to individual growth rate (G) (Table 3) indicates a negative selective mortality within a year-class, the smaller fish of a year-class dying at a higher frequency than the larger. This tendency is not demonstrable for the 6-yr-old age-class. Age 7 was disregarded, as only one fish was available. The difference between GX and G (expressed in length) of survivors at successive ages (1–5) is illustrated in Fig. 4.

Female trout sampled in 1980 attained sexual maturity at an age of 3 yr and a length of 21 cm (Fig. 5). The secondary growth phase of eggs (exceeding 1 mm in diameter) started at the end of June and continued through October (Fig. 6). However, samples obtained during the October spawning season revealed an intermediate group (Fig. 6) representing 20% of the sampled fish, suggesting a retardation of egg development among potential spawners.

Brook trout of all sizes were present solely in the two littoral regions and were absent from brooks and springs during the period May–June 1980 (Fig. 7). Contingency table analysis of trout distribution in the littoral zone revealed that large fish (≥25 cm) are significantly more abundant in the littoral zone of basin 1 ($P < 0.05$, a posteriori) and significantly less abundant in the littoral zone of basin 2 ($P < 0.05$, a posteriori) when compared with all other fish ($X^2 = 31.9$, $P < 0.001$).

Trout distribution was quite different during the July–August 1980 period (Fig. 7). Brooks were more frequented by small fish (<25 cm), whereas large fish (≥25 cm) frequented the springs ($G^2 = 562.3$, $P < 0.001$). Both size groups were equally distributed throughout the two littoral zones ($P < 0.05$, a posteriori).

Water Characteristics and Aluminum in Fish Gills

Littoral zones and brooks are characterized by similar temperatures during the months of May and June (Table 4). Brooks, however, are more acid than the littoral zones. For July–August 1980, temperature, pH, and aluminum values are

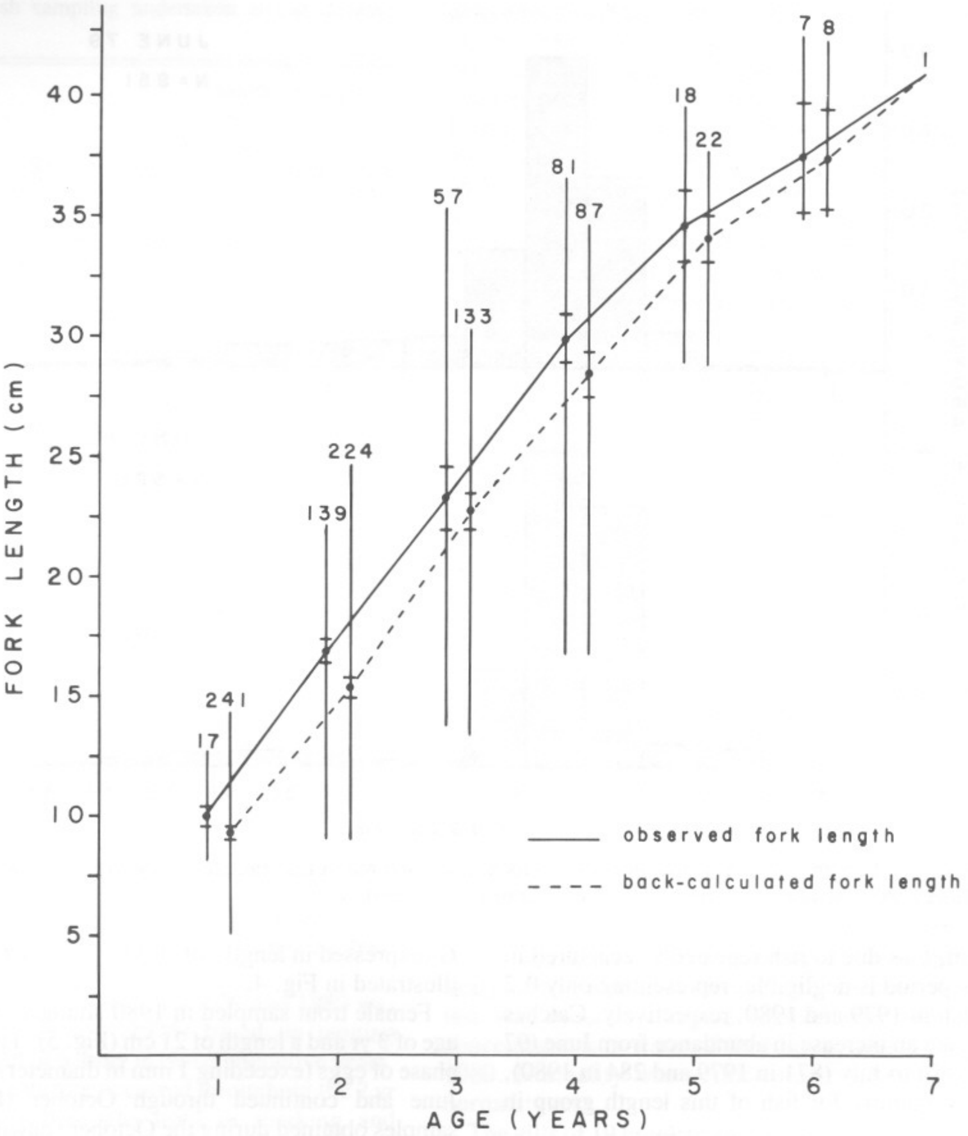


FIG. 3. Mean size at age of brook trout calculated from observed fork lengths and back-calculated fork lengths. Points are means, vertical lines are ranges, and horizontal lines are 95% confidence limits. Numerals indicate number of measurements.

significantly different among the four regions ($P < 0.01$). Temperature is significantly higher ($P < 0.05$) in the littoral zones than in the brooks and springs, the springs being the coldest. pH values are significantly different ($P < 0.05$) for each of the regions, being lowest in the brooks and highest in the springs with the littoral zones exhibiting intermediate values. Aluminum concentrations were significantly higher ($P < 0.05$) in the brooks than in the littoral zones or springs.

Total aluminum analysis on fish gills reveals a mean concentration of 120.4 μg/g dry wt (range = 41–500) among 14 individuals <25 cm and 67.4 μg/g dry wt (range 50–78) among 5 individuals ⩾25 cm in length. No significant differences in aluminum concentrations exist between small (<25 cm) and large (⩾25 cm) fish ($P > 0.05$).

Discussion

Population Structure

The analysis of the Lac Tantaré brook trout population structure revealed that mortality occurs primarily among fish measuring 13–25 cm, survival rate being greatest among older and larger fish. The presence of older age-classes (up to 7+) comparable with those found in native brook trout populations in general (5+ to 8+, Scott and Crossman 1973) supports the conclusion that mortality does not occur primarily among older and larger fish. An alternative hypothesis is that the observed population structure and calculated survival rate could have resulted from differences in size-related catchability. However, the similar June recovery rates for marked fish measuring 13–21 cm and ⩾21 cm suggest that catchability is similar for all fish >13 cm. Furthermore, the negligible multiple recapture rates in June did not bias the length–frequency distribution. We conclude that the length–frequency histograms for June (Fig. 2) are a true representation of the population structure of Lac Tantaré brook trout >13 cm.

In July and August, brook trout are no longer distributed throughout the littoral zone, with larger brook trout (⩾25 cm) being concentrated in springs and smaller brook trout (13–25 cm) being concentrated in brooks (Fig. 7). As a result, trap

TABLE 2. Survival rate of brook trout in Lac Tantaré between 1979 and 1980 (see text for explanation of symbols).

	Length group in 1979 (expected length group in 1980 in parentheses) (cm)				
	13.0–19.9 (20.0–27.9)	20.0–24.9 (25.0–29.9)	25.0–29.9 (29.0–32.9)	30.0–34.9 (33.0–35.9)	≥35.0 ≥36.0
M1	1008	170	186	109	34
M2	501	154	156	107	45
R11	210	20	14	4	4
R12	49	9	27	8	2
R22	132	43	26	24	4
R11/M1	0.208	0.118	0.075	0.037	0.118
R22/M2	0.263	0.279	0.167	0.224	0.089
R12/M1	0.049	0.053	0.145	0.073	0.059
Survival rate	0.185	0.190	0.871	0.327	0.529
SE	0.029	0.066	0.020	0.126	0.442

realise

✓

TABLE 3. Computation of growth rates for Lac Tantaré brook trout, 1979–80.

	Population growth			Mean individual growth		
Age interval	Length interval (mm)	Difference of natural logarithms	Instantaneous growth rate *GX*	Length interval (mm)	Difference of natural logarithms	Instantaneous growth rate *G*
1–2	72.6–140.5	0.660	1.929	89.9–140.5	0.446	1.304
2–3	140.5–214.9	0.425	1.242	160.7–214.9	0.291	0.851
3–4	214.9–280.8	0.267	0.780	233.3–280.8	0.185	0.541
4–5	280.8–341.5	0.196	0.573	303.3–341.5	0.119	0.348
5–6	341.5–372.9	0.088	0.257	341.6–372.9	0.088	0.257

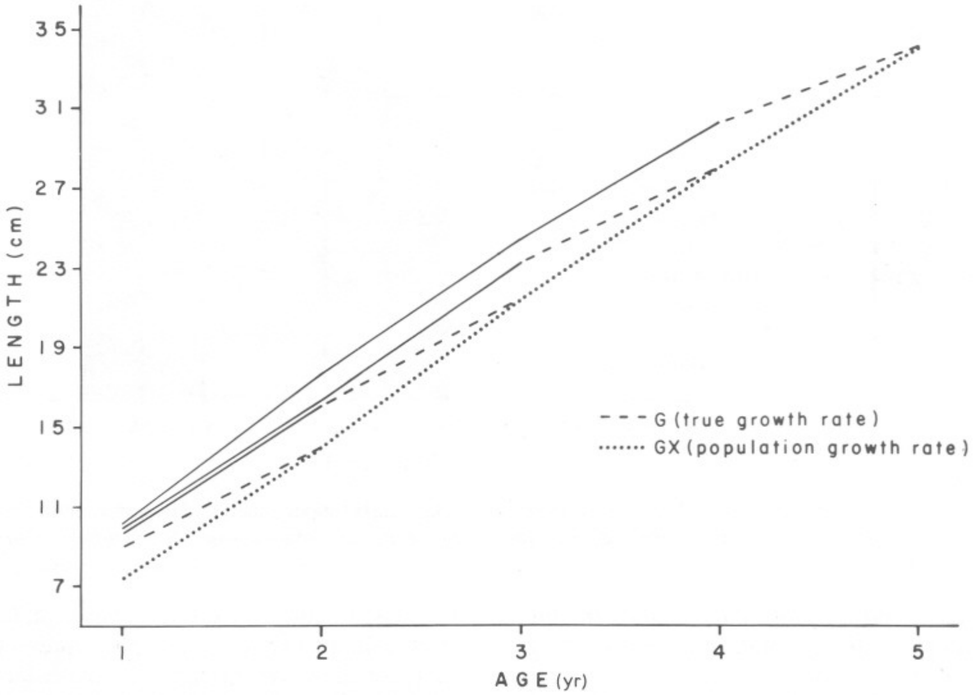


FIG. 4. Growth rate of Lac Tantaré brook trout. Broken lines indicate individual growth rate (*G*), which represents the increase in length of fish of a given age-class during their last year of growth. Dotted line indicates population growth rate (*GX*), which represents the increase in length of the population from one age-class to another. Solid lines indicate the increase in length of fish preceding the last year of growth.

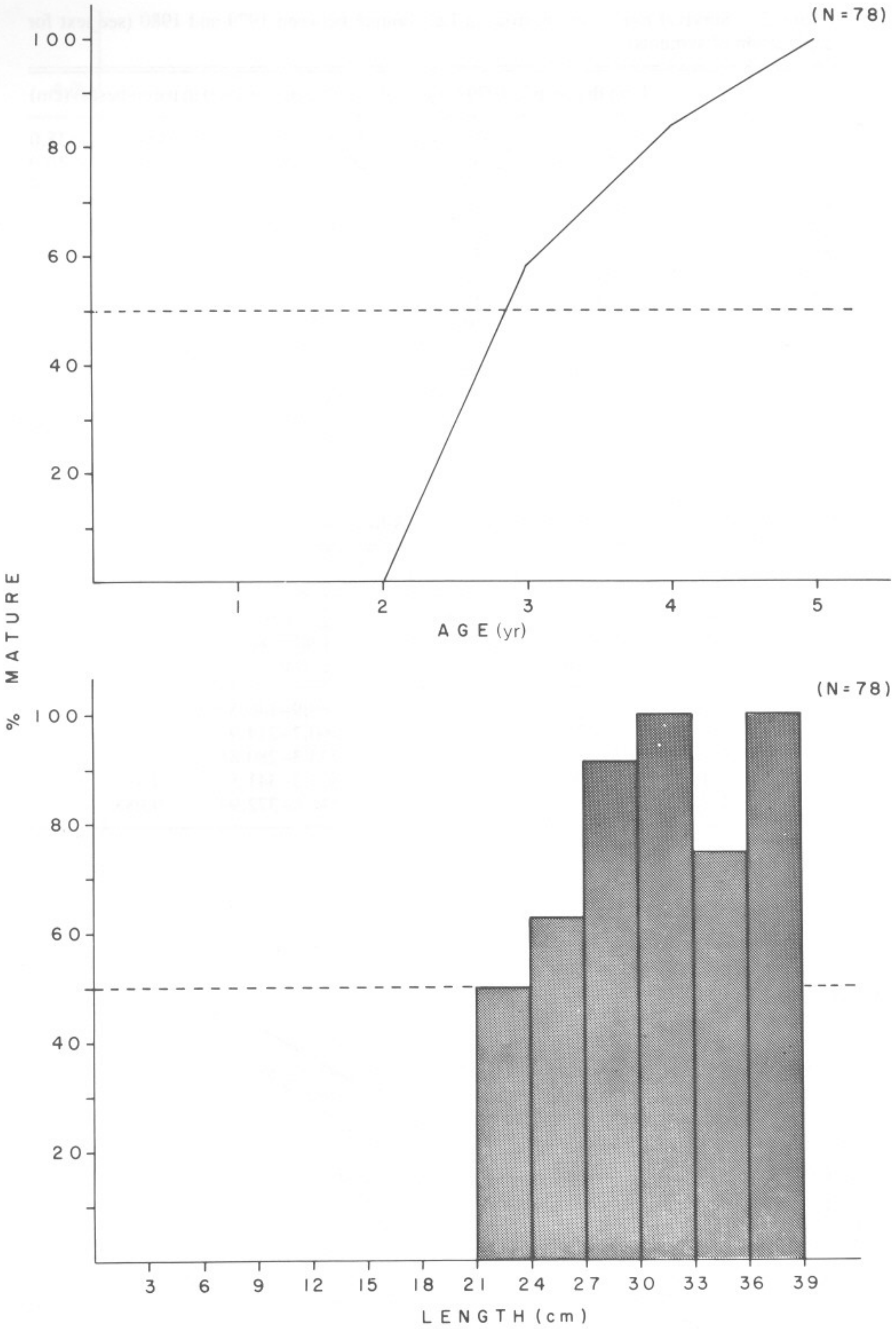


FIG. 5. Percent mature females of brook trout in each age-class (upper panel) and in each length-class (lower panel), Lac Tantaré, in 1980. Broken lines indicate the 50% mature level. N = number of fish analyzed.

net catches are no longer representative of population structure. Total seasonal catches of brook trout of different length-classes using all fishing gear do not provide an unbiased representation of population structure, as the effort of seining in springs and brooks is not equivalent to the effort of trap netting in littoral zones (Table 1). Recapture rates calculated for the 1979 and 1980 fishing seasons (Table 2) decline with increasing size, reflecting the relatively low fishing effort in the springs (Table 1). Thus, frequency histograms based on total seasonal catches of all fishing gear would bias the representation of population structure. However, mortality estimates based on total seasonal catches will not be affected by this bias, as the 1980 fishing effort to recapture fish tagged in 1979 and in 1980 is identical within each length group. As a result, R12/M1 divided by R22/M2 (survival rate, Table 2) is a valid estimate of survival rate.

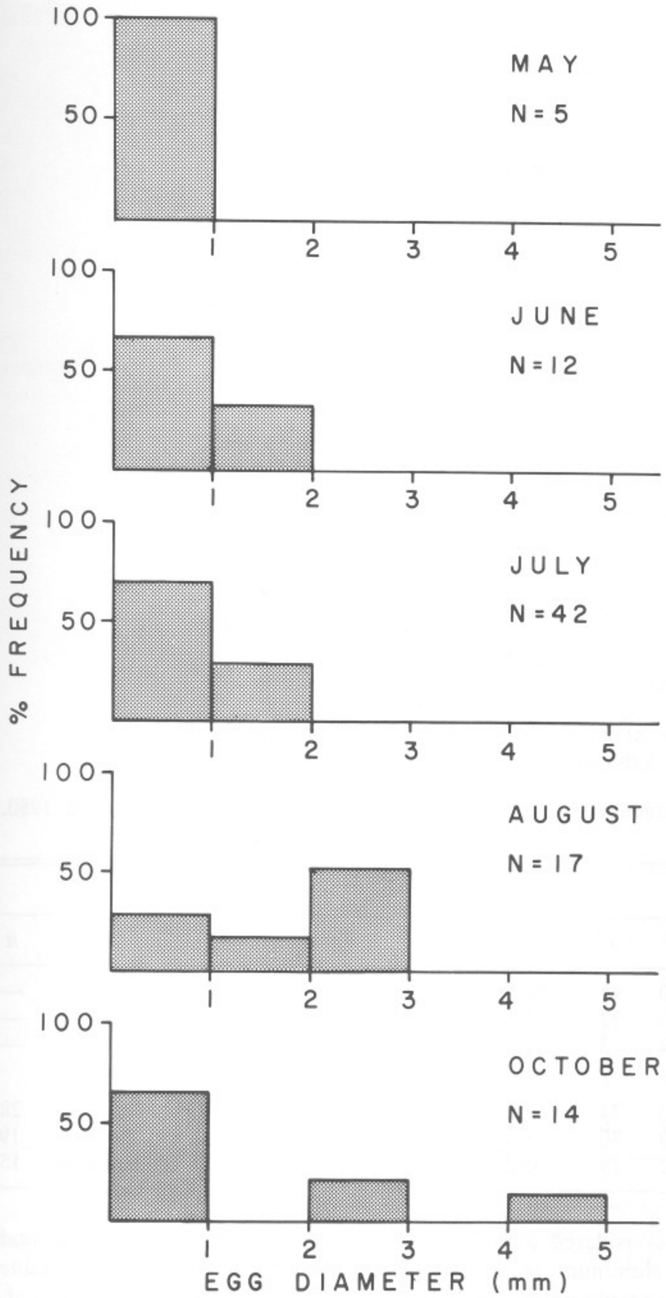


FIG. 6. Frequency distribution of egg diameter for female brook trout sampled in Lac Tantaré during 1980. *N* = number of fish examined.

Brook trout <13 cm were not tagged and no survival estimates are available for this group. It is unlikely that the apparent scarcity of fish <13 cm in June is entirely due to recruitment failure. Their increased abundance in July suggests that the catchability of these fish changes with time. No conclusion can be made concerning mortality among brook trout <13 cm or recruitment of young-of-the-year fish.

The higher mortality rates experienced by fish in the 13–25 cm length group, relative to larger fish, could have resulted from three factors: (1) predation, (2) postspawning mortality, or (3) greater susceptibility of small fish to the toxic effects of acidification in combination with the greater exposure of small brook trout to these toxic factors.

The population structure does not appear to be the result of predation as the main factor responsible for mortality. In Lac Tantaré, the larger brook trout were the only fish to be considered as potential predators. However, cannibalism was observed in only 5% of the stomachs sampled among the >30 cm segment of the population. In addition, this length-class constitutes a very low percentage of the population (Fig. 2). Other potential predators observed at Lac Tantaré included great blue herons (*Ardea herodias*), ospreys (*Pandion haliaetus*), belted king fishers (*Ceryle alcyon*), common loons (*Gavia immer*), and common mergansers (*Mergus merganser*). Although the extent of mortality caused by such predation is unknown, it seems unlikely that predation by the very low numbers of these predators present could alone be responsible for the pattern of mortality observed among Lac Tantaré brook trout.

The rapid decline in the numbers of fish indicated in the frequency distribution (Fig. 2) occurs at approximately the size at which 50% of the female trout population reaches sexual maturity, suggesting that postspawning mortality may be a major cause of the decline. Loss of older fish has been reported for a population of white suckers (*Catostomus commersoni*) in the acidified George Lake, Ontario, where eight age-classes disappeared in 12 yr (Harvey 1982). Poor survivorship was observed after fish reached the age of maturation. Rosseland et al. (1980) reported that the absence of older European perch (*Perca fluviatilis*) and brown trout (*Salmo trutta*) in three acid lakes may have resulted from additional stress due to spawning. Therefore, the possibility exists that postspawning mortality related to acid stress may have contributed to the observed mortality among the 13–25 cm group. However, we know of no physiological evidence in support of this hypothesis.

The pattern of mortality observed among the Lac Tantaré brook trout population may result from the greater susceptibility of small fish to the toxic effects of acidification in combination with the greater exposure of small brook trout to these toxic factors. The following discussion provides evidence in support of this hypothesis.

Chemical Influences on Population Structure

The physiological effects of low pH on fish have been identified as disturbances in acid–base regulation, ionoregulation, and oxygen uptake and transfer (Fromm 1980; Spry et al. 1981). Gill damage is recognized as the primary mode of acid toxicity in fish (Leivestad 1982). Elevated metal concentrations associated with acidified lakes (Beamish 1974, 1976; Scheider et al. 1979) have also been identified as important toxicity factors in acid-stressed fish. Aluminum concentration appears to be very important in determining survival of fish in acid waters. The toxic effect of aluminum in brook trout in combination with pH has been recognized (Cronan and Schofield 1979; Baker and Schofield 1980; Schofield and Trojnar 1980). Brook trout exposed to aluminum concentrations of 0.2 mg/L at pH 5 exhibited gill hyperplasia and mucus secretion (Schofield and Trojnar 1980). Brown trout exposed to aluminum concentrations of 0.15 mg/L at pH 5 exhibited a loss of blood ions and clogging of the gills with mucus (Leivestad et al. 1980; Muniz and Leivestad 1980). Gills clogged with mucus were also observed in brook trout and brown trout exposed to aluminum concentrations of 450 μg/L at pH 5 (Rosseland et al. 1980). Fishkills were reported in Sweden when aluminum concentrations found in the gills of cisco (*Coregonus albua*) ranged from 40 to 47 mg/kg (wet wt) as compared with 5–6 mg/kg (wet wt) in the gills of reference cisco (Grahn 1980). Death was attributed to suffocation by clogging of the gills.

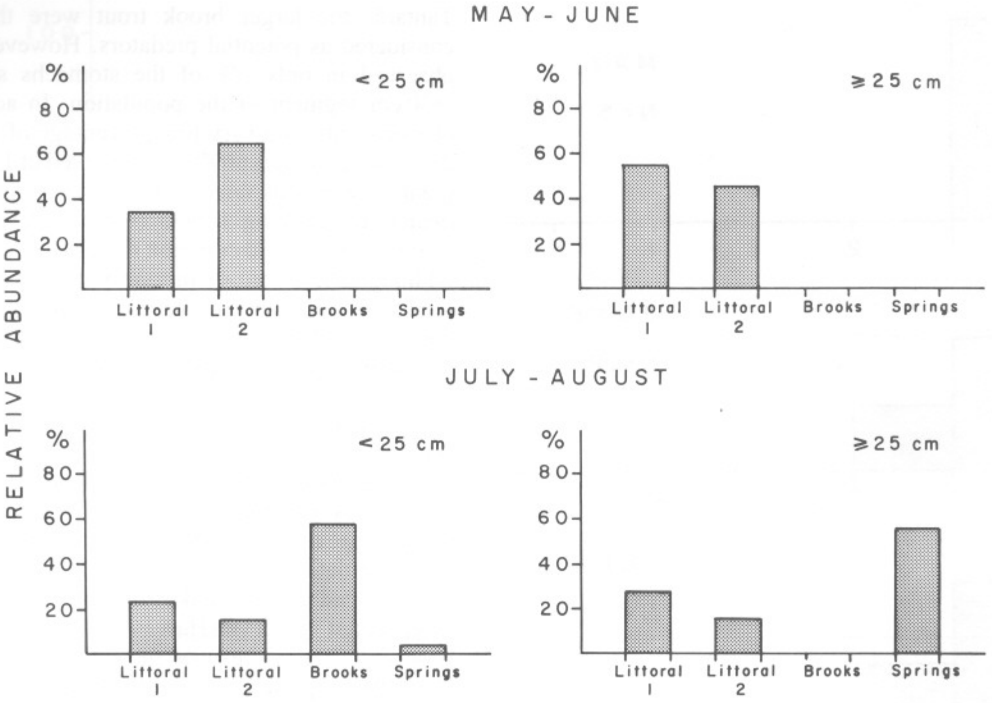


FIG. 7. Relative abundance (percentage of total catch) of small (<25 cm) and large (≥25 cm) brook trout in the four sampling regions of Lac Tantaré during the May–June and July–August period of 1980.

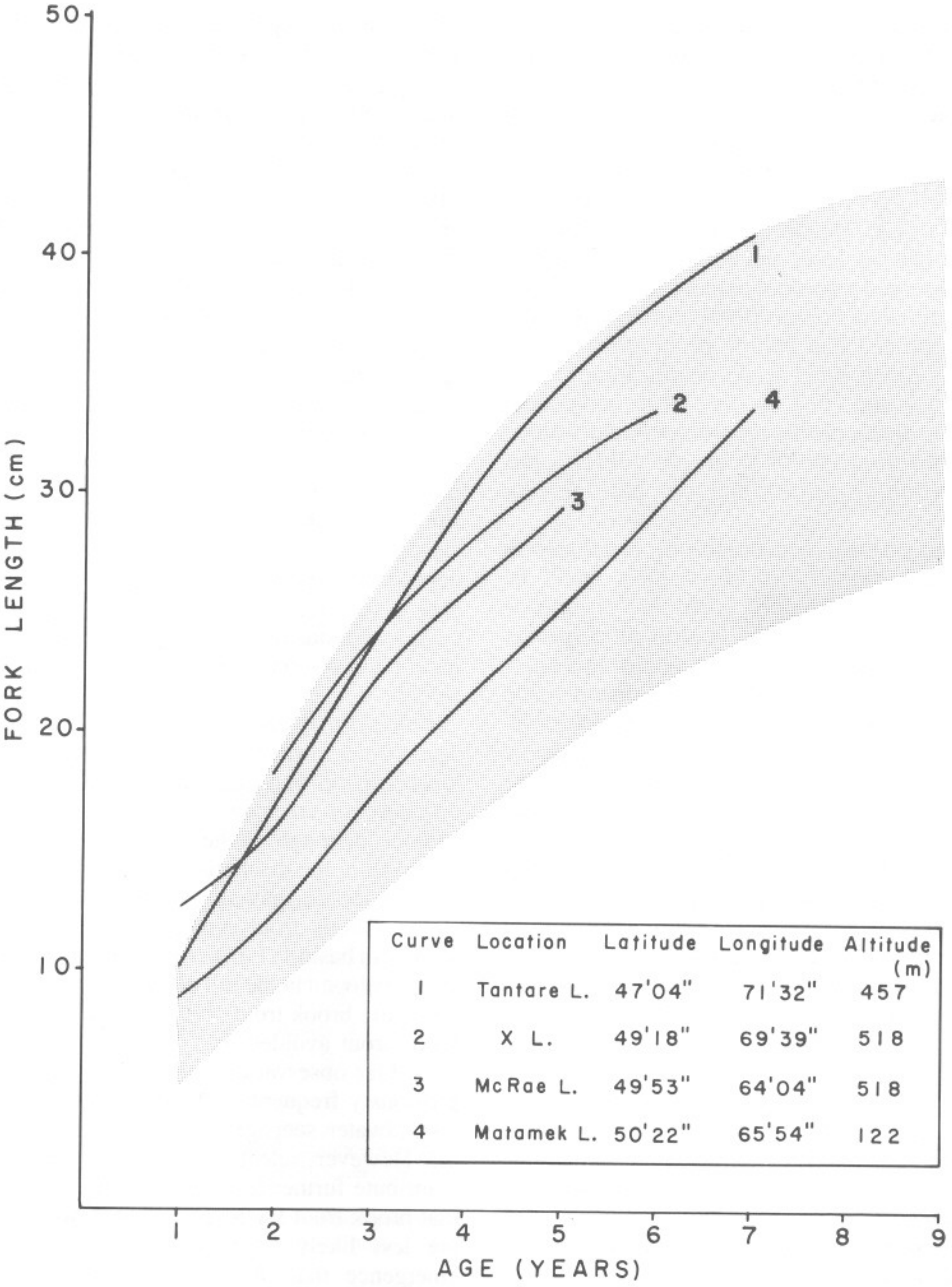
TABLE 4. Mean ($\bar{m}$), range (r), and number of observations (n) of temperature (°C), pH, and Al (mg/L) by sampling zone, Lac Tantaré, 1980. Dash indicates no data.

	Littoral 1			Littoral 2			Brooks			Springs		
May–June	$\bar{m}$	r	n	$\bar{m}$	r	n	$\bar{m}$	r	n	$\bar{m}$	r	n
Temperature	15.0	8.5–21.5	47	15.2	7.2–21.0	97	14.5	14.0–15.0	2	—	—	—
pH	5.47	5.26–5.65	19	5.33	5.02–5.50	37	4.68	4.64–4.72	2	—	—	—
Al	0.08	0.08–0.08	2	0.19	0.14–0.24	3	—	—	—	—	—	—
July–Aug.												
Temperature	20.9	17.5–24.5	38	20.3	18.0–23.0	74	16.0	11.5–20.5	39	12.9	7.0–21.0	28
pH	5.56	5.23–5.86	15	5.39	4.97–5.69	30	5.07	4.65–5.41	28	5.82	5.50–6.06	19
Al	0.05	0.02–0.09	9	0.11	0.04–0.22	19	0.27	0.12–0.60	14	0.10	0.02–0.24	15

The toxicity of aluminum varies with pH and the presence of complexing agents (Driscoll et al. 1980; Baker and Schofield 1980). Baker (1982) reviewed this aspect of toxicity and reported that survival of brook trout and white sucker fry was most correlated with inorganic aluminum concentrations. She argued that organically complexed aluminum may be a significant aluminum form in many acid waters, and yet, aluminum complexed with organic ligands does not appear to be toxic. Thus, measurements of total aluminum may substantially overestimate the potential toxicity of these waters to fish.

Since total aluminum concentrations were determined at Lac Tantaré, it is not possible to quantify the toxic inorganic fraction of aluminum present in these waters. However, the pH values (5.82) observed in the springs make it highly probable that most of the inorganic aluminum precipitates, since its solubility is very low at pH >5.5 (Driscoll 1980, cited in Baker 1982). Although springs appear to be "safe" areas with regard to aluminum toxicity, the detrimental impact of the water quality present in the brooks is not as easy to assess. pH in the brooks (5.07) is low enough to assure the solubility of inorganic aluminum. Therefore, the only way that the brooks can be considered as safe a the springs is to assume that the total aluminum present is composed of 100% nonexchangeable organic aluminum. This appears unlikely, as Campbell et al. (1984) found that total aluminum in water sampled in the inlet of Basin 1 in Lac Tantaré was composed of 55% exchangeable inorganic aluminum. As we do not have similar measurements for streams sampled in the present study, we cannot quantify their degree of toxicity. We assume similar values as those revealed by Campbell et al. (1984) and propose that the brooks are potentially more toxic to brook trout than are the springs.

Small brook trout sampled in the littoral zone of Lac Tantaré exhibited the highest individual concentrations of aluminum in gills and a mean concentration almost double that exhibited by large trout. Although the great variability in aluminum concentrations observed among small brook trout prevents any demonstration of statistically significant differences between large and small fish, these observations support the proposition that small trout are exposed to potentially more toxic situations than are large trout. However, as no data are presently available concerning the nature, concentration, and toxicity of aluminum in the gills of adult brook trout, we cannot assess the level of



Curve	Location	Latitude	Longitude	Altitude (m)
1	Tantare L.	47'04"	71'32"	457
2	X L.	49'18"	69'39"	518
3	McRae L.	49'53"	64'04"	518
4	Matamek L.	50'22"	65'54"	122

FIG. 8. Growth of native brook trout. The hatched band indicates the range of observed growth of native brook trout stocks from a variety of regions and different freshwater habitats (after Power 1980). Curves indicate growth of brook trout from several Quebec lakes. Data sources: curve 1, this study; curve 2, Saunders and Power (1970); curves 3 and 4, Carscadden (1970). All curves were fitted by eye to mean fork length data.

toxicity associated with the concentrations of total aluminum measured in Lac Tantaré brook trout.

Increased size appears to confer a resistance advantage to fish exposed to acid conditions. The number of secondary lamellae per millimetre of filament in fish gills decreases with increasing fish size (Muir 1969). Robinson et al. (1976) concluded that detrimental ion fluxes or impeded gas exchange at the gill surface should occur less rapidly in larger fish, which have relatively smaller gill surface areas, on a weight equivalent basis, than do smaller fish. Survival times of 92-g brook trout were 35% greater than 2-g trout at low pH values (Robinson et al. 1976). Under low pH conditions, 25-cm brook trout had longer survival times than 17-cm trout (Swarts et al. 1978).

Age, being correlated with size, is also found to be directly related to fish survival in acid water. Kwain (1975) found 18-mo rainbow trout (*Salmo gairdneri*) to be more resistant to acidity than 4-mo-old fingerlings, and during the course of 1 yr, resistance times increased for rainbow trout in low-pH waters. Adults of brook trout (Menendez 1976) and fathead minnows (*Pimephales promelas*) (Mount 1973) were found to be the most resistant of all life stages to reduced pH.

If increased size confers an advantage to brook trout exposed to acid stress, we would expect improved survival among faster growing fish. This would increase the rate at which relative gill surface area was decreased and also permit the occupation and defense of less stressful habitats. The selective mortality observed among slower growing Lac Tantaré brook trout of ages 1–5 supports the hypothesis that slow-growing fish experience increased mortality.

As the growth rate of Lac Tantaré brook trout prior to acidification of the lake is unknown, it is impossible to determine whether the growth rate observed in 1979–80 represents an increase in growth in response to acidification. However, the growth of Lac Tantaré brook trout is better than that observed in other Quebec lakes and is situated at the upper limit of the range of observed growth of native freshwater brook trout populations described by Power (1980) (Fig. 8). Ryan and Harvey (1980) demonstrated that yellow perch (*Perca flavescens*) of age groups 1–3 responded to lake acidification with an increased rate of growth and cited six articles demonstrating increased growth rates of nonpiscivorous fish in acid waters, including young rainbow trout, brook trout, bluegill (*Lepomis macrochirus*), roach (*Rutilus rutilus*), and rock bass (*Ambloplites rupestris*).

Harvey (1982) discussed the hypothesis that the better growth observed in some acid-stressed fish populations could be attributed to an increase in food supply, where this resource is limiting, as a result of diminished intra- and/or inter-specific competition as populations decline. Arguing against this interpretation is Brett's (1979) hypothesis that "the prime demand for food is imposed by the maintenance requirement of the fish, with a further demand dictated by the potential growth capacity (influenced by growth hormone)." Brett argued that these interlocking requirements set the limits of voluntary food intake and hence growth rate. Therefore, the relation between increased food availability and increased growth rate cannot be readily assumed. An alternative hypothesis for the apparent changes in growth rate is that selective mortality among slow-growing fish results in greater mean lengths at age among survivors, thus inflating growth rates. The mechanisms responsible for what appears to be improved growth of fish under acidic conditions must be the subject of further ecological and physiological studies.

In conclusion to this part of the discussion, we propose that although postspawning mortality may contribute to the high mortality observed among the 13–25 cm length group, the observation of negative selective mortality among immature as well as mature fish (ages 1+ to 5+) implicates other sources of mortality. We hypothesize that the most probable cause of this mortality is size-related differential exposure to toxic stress. In July and August, small brook trout (<25 cm) are found in lake areas (brooks) exhibiting the most potentially toxic combination of pH and aluminum, thus enhancing the exposure of the most susceptible part of the population to toxic stress. Large brook trout (⩾25 cm), on the other hand, are found in the "safest" lake areas (springs), thus diminishing the exposure of the least susceptible part of the population to toxic stress and enhancing survival. We propose that greater survival among the larger individuals of ages 1+ to 5+ may be related to the increased resistance to the toxic effects of acidification apparently afforded by increased size combined with the occupation of more favorable habitats (springs).

The failure of recruitment of new age-classes into fish populations has been identified as one of the most striking effects of acidification (Harvey 1982). Although no younger age-classes are missing from the Lac Tantaré population, recruitment failure appears likely, as the age and length at maturity of female brook trout is delayed compared with other Quebec lakes. Lac Tantaré brook trout attain 50% maturity at 21–24 cm in length and age 3+ whereas Carscadden (1970) observed sexual maturity at age 1+ for female brook trout of Lake MacRae in Quebec, with 95% of female fish maturing at age 3+ at a mean fork length of 222 mm. Similarly, 96% of female brook trout were mature in Matamek Lake at age 3+ and a fork length of 17 cm (Saunders and Power 1970). Vladykov (1956) found that brook trout of Laurentide Park, Quebec, can spawn at 13 cm fork length. As a result of this delay, the major part of the Lac Tantaré population's reproductive effort occurs among fish >21 cm in length, that segment representing only 15% of the population in 1979 and 1980.

Possible recruitment failure is also indicated by the apparent retarded maturation of the eggs of potential spawners sampled during the spawning season. This would have the effect of further reducing the reproductive effort of the population. Ruby et al.'s (1977) observation that low pH reduced the ability of flagfish (*Jordanella floridae*) oocytes to form mature eggs suggests that low pH may be responsible for the delay. Low pH also appears to impair oogenesis by interfering with yolk deposition (Peterson et al. 1982). In the absence of historical data concerning maturation in the Lac Tantaré population, we cannot demonstrate conclusively that the apparent retarded maturation observed in Lac Tantaré brook trout is caused by acidification.

Low pH may also disrupt spawning behavior in brook trout. The former owners of Lac Tantaré (H. Ross, Ecotan Ltée, Quebec City, pers. comm.) observed that many hundreds of brook trout were spawning preferentially at the discharge (Fig. 1) some 20 yr ago. In the fall of 1979, several hundred fish were observed in the discharge for 3 consecutive days only. No fish were observed spawning at the discharge in the fall of 1980. Rather, brook trout spawned preferentially in the vicinity of springs in basin 1. Furthermore, new springs (station 11, Fig. 1) that developed in the fall of 1980 were immediately occupied by spawning brook trout. Johnson and Webster (1977) found that brook trout avoided water of pH <5.0 in selecting spawning sites. Our observations suggest that fish may have abandoned previously frequented stream spawning sites in favor of new groundwater seepage spawning sites characterized by higher pH. However, selection of such spawning sites may ultimately contribute further to recruitment failure. Trojnar (1977) noted that brook trout fry incubated at lower but sublethal pH levels are less likely to experience acid-induced mortality upon emergence than those incubated in spring upwellings. In conclusion, we hypothesize that although the extent of mortality among young-of-the-year fish cannot be quantified due to problems of catchability, recruitment failure due to acid stress may contribute to the low relative abundance of brook trout <13 cm in length.

Acknowledgments

We thank Louis Bernatchez, Lucie Lebeuf, Luc Major, and Nicole Perreault for valuable field assistance, Dr G. H. Jones, I.N.R.S.-eau, Quebec, for providing the aluminum analyses and conductivity data, and Roger Miville-Deschesnes for his assistance during the computer analysis. This project was funded by a grant from Mr Harry Ross, Centre de Recherche Ecotan Inc. Additional funding was provided by a grant from NSERC to J.J.D.

References

BAGENAL, T. B. 1978. Aspects of fish fecundity, p. 75–101. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. John Wiley & Sons, New York and Toronto. 520 p.

Baker, J. P. 1982. Effects on fish of metals associated with acidification, p. 165–176. *In* R. Johnson [ed.] Acid rain/fisheries. Northeastern Division, American Fisheries Society, Bethesda, MD. 357 p.

Baker, J., and C. Schofield. 1980. Aluminum toxicity to fish as related to acid precipitation and Adirondack surface water quality, p. 292–293. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Sur nedbors virkning pa skog og fisk (SNSF Project), Oslo, Norway. 383 p.

Beamish, R. J. 1974. Loss of fish populations from unexploited remote lakes in Ontario, Canada, as a consequence of atmospheric fallout of acid. Water Res. 8: 85–95.

1976. Acidification of lakes in Canada by acid precipitation and the resulting effects on fishes. Water Air Soil Pollut. 6: 501–514.

Bobée, B., Y. Grimard, M. Lachance, and A. Tessier. 1980. Nature et étendue de l'acidification des lacs du Québec. Institut national de la recherche scientifique, Centre de l'eau, Université du Québec, Sainte-Foy (Qué.). Rapp. Sci. No. 140: 275 p.

Brett, J. R. 1979. Environmental factors and growth, p. 599–677. *In* W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. 8. Bioenergetics and growth. Academic Press, New York, NY. 786 p.

Campbell, P. G. C., M. Bisson, R. Bougie, A. Tessier, and J.-P. Villeneuve. 1984. Speciation of aluminum in acidic freshwaters. Anal. Chem. (In press)

Carscadden, J. E. 1970. Ecology of brook trout (*Salvelinus fontinalis*) in two lakes in the upper Matamek river system, Québec. M.Sc. thesis, University of Waterloo, Waterloo, Ont. 67 p.

Cronan, C. S., and C. L. Schofield. 1979. Aluminum leaching response to acid precipitation: effects on high elevation watersheds in the northeast. Science (Wash., DC), 204: 304–306.

Drablos, D., and A. Tollan [ed.] 1980. Ecological impact of acid precipitation. Sur nedbors virkning pa skog og fisk (SNSF Project), Oslo, Norway. 383 p.

Driscoll, C. Jr., J. P. Baker, J. J. Bisogni, Jr., and C. L. Schofield. 1980. Aluminum speciation and its effect on fish in dilute acidified waters. Nature (Lond.) 284: 161–163.

Fraser, C. M. 1916. Growth of the spring salmon. Trans. Pac. Fish. Soc. Seattle 1915: 29–39.

Fromm, P. O. 1980. A review of some physiological and toxicological responses of freshwater fish to acid stress. Environ. Biol. Fish 5(1): 79–93.

Grahn, O. 1980. Fish kill in two moderately acid lakes due to high aluminum concentration, p. 310–311. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Sur nedbors virking pa skog og fisk (SNSF Project), Oslo, Norway. 383 p.

Guimont, J., and M. Pichette. 1979. Méthodes de dosage d'éléments en trace dans les sédiments, les roches et les eaux. Ministère des richesses naturelles du Québec, Québec (Qué.). Rapp. No. A.C. 5: 1–76.

Haines, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

Harvey, H. H. 1982. Population responses of fishes in acidified waters, p. 227–242. *In* R. Johnson [ed.] Acid rain/fisheries. Northeastern Division, American Fisheries Society, Bethesda, MD. 357 p.

Henderson, N. E. 1963. Influence of light and temperature on the reproductive cycle of the eastern brook trout, *Salvelinus fontinalis* (Mitchill). J. Fish. Res. Board Can. 20: 859–897.

Johnson, D. W., and D. A. Webster. 1977. Avoidance of low pH in selection of spawning sites by brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 34: 2215–2218.

Kwain, W. 1975. Effects of temperature on development and survival of rainbow trout, *Salmo gairdneri*, in acid waters. J. Fish. Res. Board Can. 32: 493–497.

Legendre, L., and P. Legendre. 1979. Ecologie numérique. Vol. 1. Masson, Paris, and Les Presses de l'université du Québec. 197 p.

Leivestad, H. 1982. Physiological effects of acid stress on fish, p. 157–164. *In* R. Johnson [ed.] Acid rain/fisheries. Northeastern Division, American Fisheries Society, Bethesda, MD. 357 p.

Leivestad, H., I. P. Muniz, and B. O. Rosseland. 1980. Acid stress in trout from a dilute mountain stream, p. 318–319. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Sur nedbors virkning pa skog og fisk (SNSF Project), Oslo, Norway. 383 p.

Menendez, R. 1976. Chronic effects of reduced pH on brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 118–123.

Morin, R., J. J. Dodson, and G. Power. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), and round whitefish (*Prosopium cylindraceum*) populations of eastern James–Hudson Bay. Can. J. Fish. Aquat. Sci. 39: 958–967.

Mount, D. I. 1973. Chronic effect of low pH on fathead minnow survival, growth and reproduction. Water Res. 7: 987–993.

Muir, B. S. 1969. Gill dimensions as a function of fish size. J. Fish. Res. Board Can. 26: 165–170.

Muniz, I. P., and H. Leivestad. 1980. Toxic effects of aluminum on the brown trout *Salmo trutta*, p. 320–321. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Sur nedbors virkning pa skog og fisk (SNSF Project), Oslo, Norway. 383 p.

Nickerson, S., D. M. Ryan, G. Somerton, and J. Wright. 1980. A computer program for processing fish age and growth data. Can. Tech. Rep. Fish. Aquat. Sci. 964: IV + 20 p.

Ouellet, M., and H. G. Jones. 1983. Paleolimnological evidence for the long-range atmospheric transport of acidic pollutants and heavy metals into the province of Québec, eastern Canada. Can. J. Earth Sci. 20: 23–36.

Peterson, R. H., P. G. Daye, G. L. Lacroix, and E. T. Garside. 1982. Reproduction in fish experiencing acid and metal stress, p. 177–196. *In* R. Johnson [ed.] Acid rain/fisheries. Northeastern Division, American Fisheries Society, Bethesda, MD. 357 p.

Power, G. 1964. A technique for preparing scale smears. Trans. Am. Fish. Soc. 93: 201–202.

1966. Observations on the speckled trout (*Salvelinus fontinalis*) in Ungava. Nat. Can. 93: 187–198.

1980. The brook charr, *Salvelinus fontinalis*, p. 141–203. *In* E. K. Balon [ed.] Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague.

Ricker, W. E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26: 479–541.

1975. Computation and interpretation of biological statistics of fish populations. Bull. 191, Department of the Environment, Fisheries and Marine Service, Ottawa, Ont. 382 p.

Robinson, G. D., W. A. Dunson, J. E. Wright, and G. E. Mamolito. 1976. Differences in low pH tolerance among strains of brook trout (*Salvelinus fontinalis*) J. Fish Biol. 8: 5–17.

Rosseland, B. O., I. Sevaldrud, D. Svalastog, and I. P. Muniz. 1980. Studies on freshwater fish populations: effects of acidification on reproduction, population structure, growth and food selection, p. 336–337. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Sur nedbors virking pa skog og fisk (SNSF Project), Oslo, Norway. 383 p.

Ruby, S. M., J. Aczel, and G. R. Craig. 1977. The effects of depressed pH on oogenesis in flagfish *Jordanella floridae*. Water Res. 11: 757–762.

Ryan, P. M., and H. H. Harvey. 1980. Growth responses of yellow perch, *Perca flavescens* (Mitchill), to lake acidification in the La Cloche Mountain Lakes of Ontario. Environ. Biol. Fishes 5: 97–108.

Saunders, L. H., and G. Power. 1970. Population ecology of the brook trout, *Salvelinus fontinalis*, in Matamek Lake, Québec. J. Fish. Res. Board Can. 27: 413–424.

Scheider, W., D. Jeffries, and D. Dillon. 1979. Effects of acidic precipitation on Precambrian freshwaters in Southern Ontario. J. Great Lakes Res. 5: 45–51.

Schofield, C. L., and J. Trojnar. 1980. Aluminum toxicity to fish in acidified waters, p. 341–366. *In* T. Toribara, M. Miller, and P. Morrow [ed.] Polluted rain. Plenum Press, New York, NY. (Cited in Haines 1981)

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184: 966 p.

Spry, D. J., C. M. Wood, and P. V. Hodson. 1981. The effects of environmental acid on freshwater fish with particular reference to the soft water lakes in Ontario and the modifying effects of heavy metals. A literature review. Can. Tech. Rep. Fish. Aquat. Sci. 999: 145 p.

Swarts, F. A., W. A. Dunson, and J. E. Wright. 1978. Genetic and environmental factors involved in increased resistance of brook trout to sulfuric acid solutions and mine acid polluted waters. Trans. Am. Fish. Soc. 107: 651–677.

Tesch, F. W. 1971. Age and growth, p. 93–120. *In* W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. 2nd ed. I.B.P. Handb. No. 3. Blackwell Scientific Publications, Oxford.

Trojnar, J. R. 1977. Egg hatchability and tolerance of brook trout (*Salvelinus fontinalis*) fry at low pH. J. Fish. Res. Board Can. 34: 574–579.

Vladykov, V. D. 1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. J. Fish. Res. Board Can. 13: 799–841.