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Résumé

Quinze caractères morphométriques et sept caractères méristiques furent étudiés sur 445 spécimens de touladis ou truites de lac (Cristivomer namaycush) en provenance de leur aire de répartition géographique. Les touladis du bassin hydrographique du Pacifique diffèrent particulièrement de celles des bassins hydrographiques de l'Arctique, de la Baie d'Hudson et de l'Atlantique. Ces différences sont remarquables quant à la longueur de la tête, la longueur pré-dorsale, le nombre de vertèbres et de branchiospines et quelques autres caractères morphologiques. Le degré de signification des résultats a été établi par l'utilisation de méthodes statistiques.

Les similarités et les différences observées parmi les touladis des principaux bassins hydrographiques océaniques et les différentes populations de touladis habitant ces différents bassins suggèrent, que ce poisson a survécu la dernière glaciation en Alaska et peut-être aussi dans d'autres régions nordiques, ainsi que dans certains refuges plus au Sud.

Les différences morphologiques significatives entre C. namaycush namaycush et C. namaycush siscowet du lac Supérieur ainsi que les informations déjà compilées sur les différents aspects de leur biologie supportent leurs positions sous-spécifiques.

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INTRODUCTION

The Lake trout (Cristivomer namaycush) is a distinctly North American salmonoid species. It is distributed all over northern North America, from the islands of the Canadian Archipelago south to the upper Mississippi valley, in the Great Lakes basin, and from British Columbia and Alaska east to Labrador. It is absent from the island of Newfoundland. West of the continental divide it is present in the upper Fraser System but absent from the Columbia River System. It is also absent from the Pacific Drainages north of Cook Inlet (Fig. I).

An interesting point in the lake trout distribution is its absence from Siberia. Almost all the other North American fresh-water fish which are distributed in the far north of western Canada and Alaska have been able to cross the Bering Strait into Siberia.

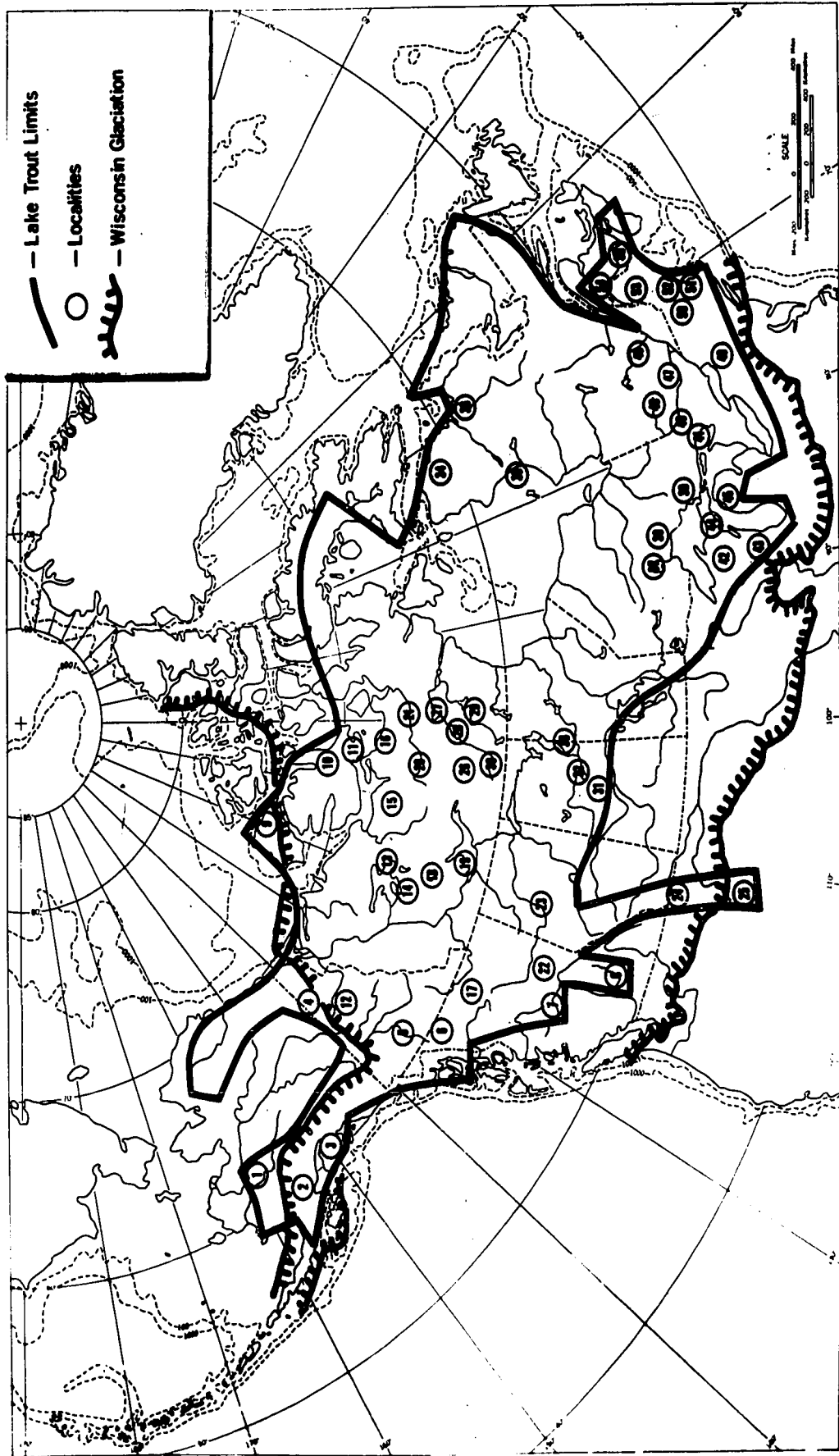
Lake trout are lake-dwelling fish and are usually found in deep lakes with sufficiently oxygenated waters (Eddy and Surber, 1947). They usually spawn in lakes, but river and stream spawning populations have been reported by some authors (Loftus, 1958; Seguin and Roussel, MS, 1967).

Although the lake trout is essentially a freshwater fish, it has been reported in salt and brackish waters (Dunbar and Hildebrand, 1952; Walters, 1953, and 1955).

The generic name of this species has undergone several changes since Walbaum (1794) designated the species as Salmo namaycush. After the generic name Salvelinus had been generally accepted for the chars, the lake trout was called Salvelinus namaycush by most American ich-

Fig. 1. Limits of endemic lake trout distribution based on the localities considered and also after Lindsey (1964). The glacial limits show only the last or Wisconsin Glaciation. The solid circles show the localities of the lake trout fossils. For the description of localities see Appendix I.

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thyologists for some time. In 1878 the generic name Cristivomer was established by Gill and Jordan for the species. Since then the generic status of Cristivomer had been commonly accepted and only since the appearance of an article by Morton and Miller (1954) has the name, Cristivomer, been frequently synonymized with Salvelinus. However, later authors i.e. Vladykov (1954 and 1963), Waters (1960), Rounsefell (1962) and Qadri (1964) have considered Cristivomer as a distinct genus from Salvelinus on the basis of serology, physiology, morphology, and distribution.

The Lake trout has long been considered a monotypic species and no serious attempt has been made to determine its intraspecific variations over its range. Scanty information is, however, available regarding intraspecific differences in lake trout. Martin (1940) compared two populations of lake trout, one from the North West Territories and the other from southern Ontario. He found that the heads and head parts of the northern lake trout were smaller than the southern lake trout, and attributed these morphological differences to variation in temperature.

Tsuyuki et al (1966) found differences in the blood proteins between the Cayuga Lake and Lake Superior lake trout. Others (Eschmeyer, 1957, 1965; Loftus, 1958) recognized different forms of lake trout in Lake Superior.

Conflicting theories have been put forth, in the past, to explain the postglacial dispersal of lake trout. Radforth (1944) believed that the lake trout survived the last glaciation in a northern refuge in Alaska. Walters (1955) and McPhail (1963) suggested that the lake trout

resided in the Mississippi valley during the last glaciation. Wynne-Edwards (1947) believed in a southern refuge for lake trout; although in 1952 he suggested the possibility of a northern refuge in the Yukon River basin.

Recently, Lindsey (1964) has discussed the lake trout's post-glacial dispersal and has suggested that the lake trout survived the last glaciation in several refuges in the south as well as the north.

The occurrence of several forms of lake trout (lean, siscowet, halfbreed, humper) in Lake Superior has been of considerable interest to taxonomists during the past few years. Eschmeyer (1957) designated all these forms, including several river-spawning forms described by Loftus (1958), as subpopulations. The existence of these subpopulations is revealed by differences in spawning localities and dates; size at first maturity (Eschmeyer, 1957) as well as some morphological and color differences.

Two of these subpopulations are given subspecific status - the "lean" lake trout, Salvelinus n. namaycush, and siscowet or "fat" lake trout, Salvelinus n. siscowet (Hubbs and Lagler, 1958). The siscowet occurs in deeper water (50-100 fathoms) of Lake Superior, while the lean lake trout are usually caught in shallower water. However, the bathymetric distribution of these two subpopulations overlaps broadly (Eschmeyer, 1955).

There has been a great deal of disagreement on the taxonomic status of the siscowet. Agassiz (1850) described the siscowet as a distinct species (Salvelinus siscowet). Jordan and Gilbert (1883) gave subspecific status to this form of lake trout. Later, Jordan

and Evermann (1911) retained the subspecific status of siscowet but remarked that it does not differ from the lean lake trout in any "technical respects", and that it is connected with the latter by a form of lake trout locally known as the "half breed". Since Jordan and Evermann's monograph (1911), most authors have recognized the subspecific status of the siscowet (Eddy and Surber, 1947; Hubbs and Lagler, 1958; Thurston, 1962; Eschmeyer and Phillips, 1965; Crawford, 1966). Slastenenko (1958), however, has given the siscowet specific status. Eschmeyer and Phillips (1965) thought that there were genetic differences between lean lake trout and siscowet on the basis of fat content.

Intrapopulation variation of lake trout has also been reported in Waterton Lakes, Alberta by Guerrier and Schultz (1957). The lake trout caught at depths of 100 meters were darker in color, had different feeding habits, matured at a smaller size and had slower growth rates. Such specimens were also caught, occasionally, in shallower water (3-30 meters) along with the typical lake trout.

In the present thesis attempts are made to explain:

- a) the intraspecific morphological variations over the distributional range of the lake trout;
- b) the postglacial dispersal and glacial refuges of lake trout;
- c) the morphological variations among the Lake Superior subpopulations of lake trout.

MATERIALS AND METHODS

Materials

A total of 445 specimens of lake trout, representing 66 localities in Alaska, Canada, and the northern United States, were examined for 15 morphometric and 7 meristic characters. The localities are shown in Fig. 1 and listed in Appendix I. The localities of Lake Superior subpopulations are shown in Appendix II.

The specimens were obtained from Quebec Department of Fish and Game; Quebec Wildlife Service, Ontario Department of Lands and Forests; National Museum of Canada; Royal Ontario Museum; Alberta Department of Lands and Forests; Institute of Fisheries, University of British Columbia; Museum of Zoology, University of Michigan; U.S. Fish and Wildlife Service; and other private sources.

Methods

Measurements of Body Parts: All the measurements were taken on the left side of the fish and recorded in millimeters using needle-point dividers. The measurements follow those of Vladykov (1954) and Hubbs and Lagler (1958). Fig. 2 shows the measurements considered in this study.

Fork Length. The distance from the tip of the snout to the fork of the tail fin.

Predorsal Length. The distance from the tip of the snout to the origin of the dorsal fin.

Ventral-anal length. The distance from the origin of the ventral fin to the origin of the anal fin.

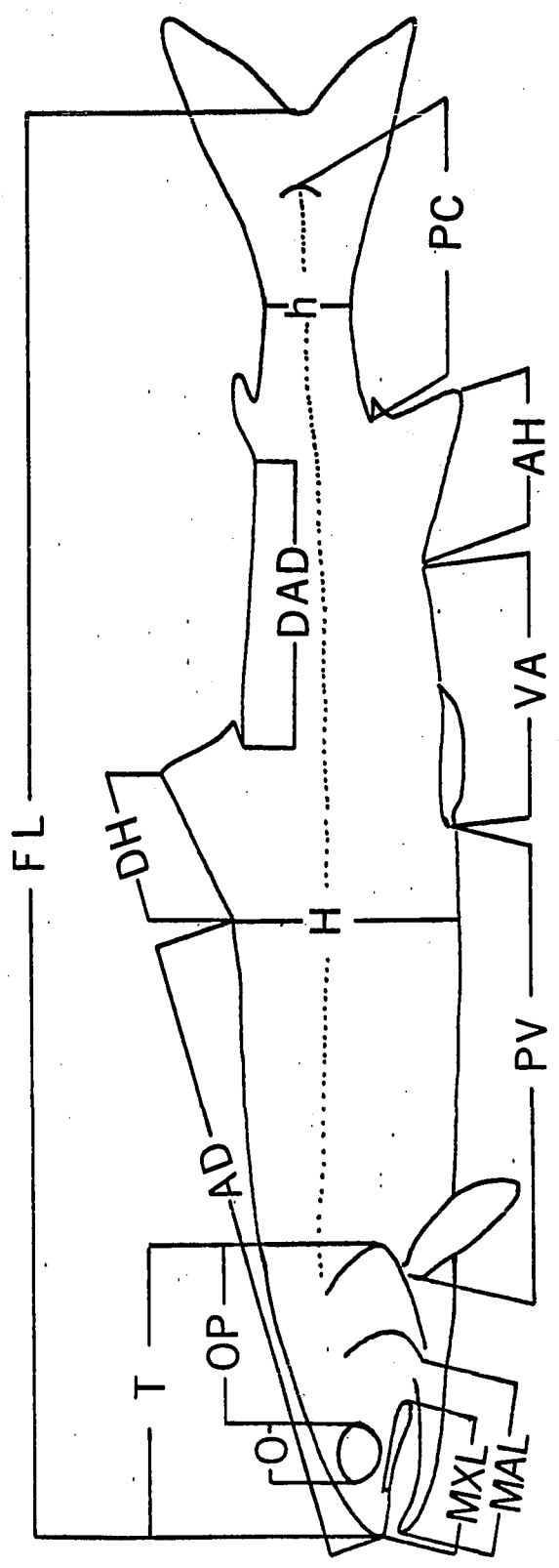


Fig. 2. Scheme of measurements considered. Interorbital width not shown. Fork length (FL), predorsal length (AD), ventral-anal length (VA), length of caudal peduncle (PC), dorsal-adipose length (DAD), depth of caudal peduncle (h), body depth (H), pectoral-ventral length (PV), height of dorsal fin (DH), height of anal fin (AH), head length (T), diameter of eyeball (O), postorbital length of head (OP), length of upper jaw (MXL), length of lower jaw (MAL).

Length of caudal peduncle. The oblique distance from the insertion of the anal fin to the end of the vertebral column. The end of the vertebral column was felt by caudal flexure.

Dorsal-adipose length. The distance from the insertion of the dorsal fin to the origin of the adipose fin.

Depth of caudal peduncle. The minimum depth of the caudal peduncle.

Body Depth. The vertical dimension at the origin of the dorsal fin.

Pectoral-ventral length. The distance from the origin of the pectoral fin to the origin of the ventral fin.

Height of dorsal and anal fins. From the origin of the fin to the tip of its anterior lobe.

Head length. The distance from the tip of the snout to the most distant point on the opercle, excluding the opercular membrane.

Diameter of eye-ball. The horizontal diameter of the eye-ball measured by inserting the prongs of the divider into the orbit.

Interorbital width. Minimum interorbital space. The dividers were not squeezed to exclude the thickness of the flesh (not shown in Fig. 2).

Postorbital length of Head. The greatest distance between the posterior margin of the orbit and the posterior opercular margin, excluding the opercular membrane.

Length of upper jaw. The distance between the anterior-most point of the premaxillary to the posterior-most point of the maxillary (excluding the maxillary membrane).

Length of lower jaw. The distance between the tip of the lower jaw and the posterior mandibular joint.

Meristic Characters: Two methods were used to study the meristic characters.

(a) Alizarin Staining: Only fresh specimens were stained. The method described by Vladykov (1962) was used with a great deal of modification.

The thawed out specimens were immersed in hot water (60-80°C) in a covered dish for 10 to 30 minutes depending on the size of the specimen, larger specimens were kept in hotter water for longer periods of time as compared to smaller specimens. The muscles from the left side were then removed very carefully with a pair of coarse forceps. Special care was taken while removing muscles from the ribs, inter-neurals and epineurals. In case of doubt the muscles were left intact around the above mentioned bones and were removed after staining. The specimens were then transferred to a 1-2% KOH solution to which alizarin stain was added according to the intensity of staining required. The specimens were left in this solution for 15-30 minutes and then an equal volume of 5% formalin was added in order to give strength to the muscles supporting the skeleton. Usually the specimens were kept overnight in the final solution. The specimens were then washed in cold water for 2-3 hours. The vertebral column was cleaned with the help of tooth brush and scalpel.

(b) Radiography: The preserved specimens were radiographed by the author at the National Museum of Canada on a General Electric

Mobile 90-15 X-ray machine. Some radiographs were made by the staff of the Royal Ontario Museum. The author used extra fine grain Kodak Industrial Type M X-ray film and exposed all plates at 10 MA, 55 KVP for 30 seconds at 32 inches focal length. The Royal Ontario Museum staff used Ilford's Ilfex film and exposed at 50 MA, 40 KVP for $1\frac{1}{2}$ seconds at 30 inches focal length. Both combinations gave good results. Kodak Type M film gave good results for radiographing small fish. The radiographs were read with the help of a medical X-ray viewer.

The following meristic characters were counted.

Total number of vertebrae. In all counts the last three upturned caudal vertebrae were counted. The first vertebra had a well defined neural spine and therefore it was easily identified. Occasionally vertebral centra were fused; specimens with vertebral aberrations were not used for vertebral counts.

Interneurals. All single elements anterior to the dorsal pterigiophores were counted. The first interneural which is flat and plate-like (Qadri, 1964) was included in the counts.

Dorsal fin rays and anal fin rays. All branched and unbranched fin rays were counted.

Total number of gill rakers. The first left gill arch was removed from each specimen and all the gill rakers, developed and undeveloped (Qadri, 1964), were counted under a binocular microscope.

Branchiostegal rays. Any branchiostegal ray which could be felt within the branchiostegal membrane was included in the count.

For comparative purposes, the 66 localities were grouped in two fashions (Fig. 3). In the first case the localities within each primary ocean drainage (i.e. Pacific, Arctic, Hudson, and Atlantic) were lumped to see the inter drainage variations in lake trout populations. Secondly, within each drainage the localities were grouped into areas. The twenty areas so demarcated over the range of the species represent a secondary watershed or an area of geographical or geological importance.

Statistical Methods: For morphometric data the relative growth method of analyses, developed by Huxley (1932) was used. This method consists of plotting the logarithm of any dimension of a body part against the logarithm of a dimension of the whole body over a series of sizes of the animal. Such logarithmic plots almost invariably show a linear relationship. This linear relationship between the logarithms indicates that the rate of change of body form is generally constant over the greater part of the growth. These continuous changes in body form can be described by determining the value of the slope, b in the relative growth equation, $\log y = \log a + b \times \log x$. Where y (eg. any body part) is the dependent variable, x (eg. body length) the independent variable, b the regression coefficient of y on x , and a the y -intercept of the regression line. The computations for regression analyses were done according to Steel and Torrie (1960) after logarithmic transformation of the morphometric data. The significance of regression coefficients was tested by a t -test according to Steel and Torrie (1960) at 5% and 1% levels.

Several authors (Huxley, 1932; Wilder, 1940; Martin, 1949;

Fig. 3. The five primary ocean drainages in northern North America
and the twenty areas from which lake trout were compared.

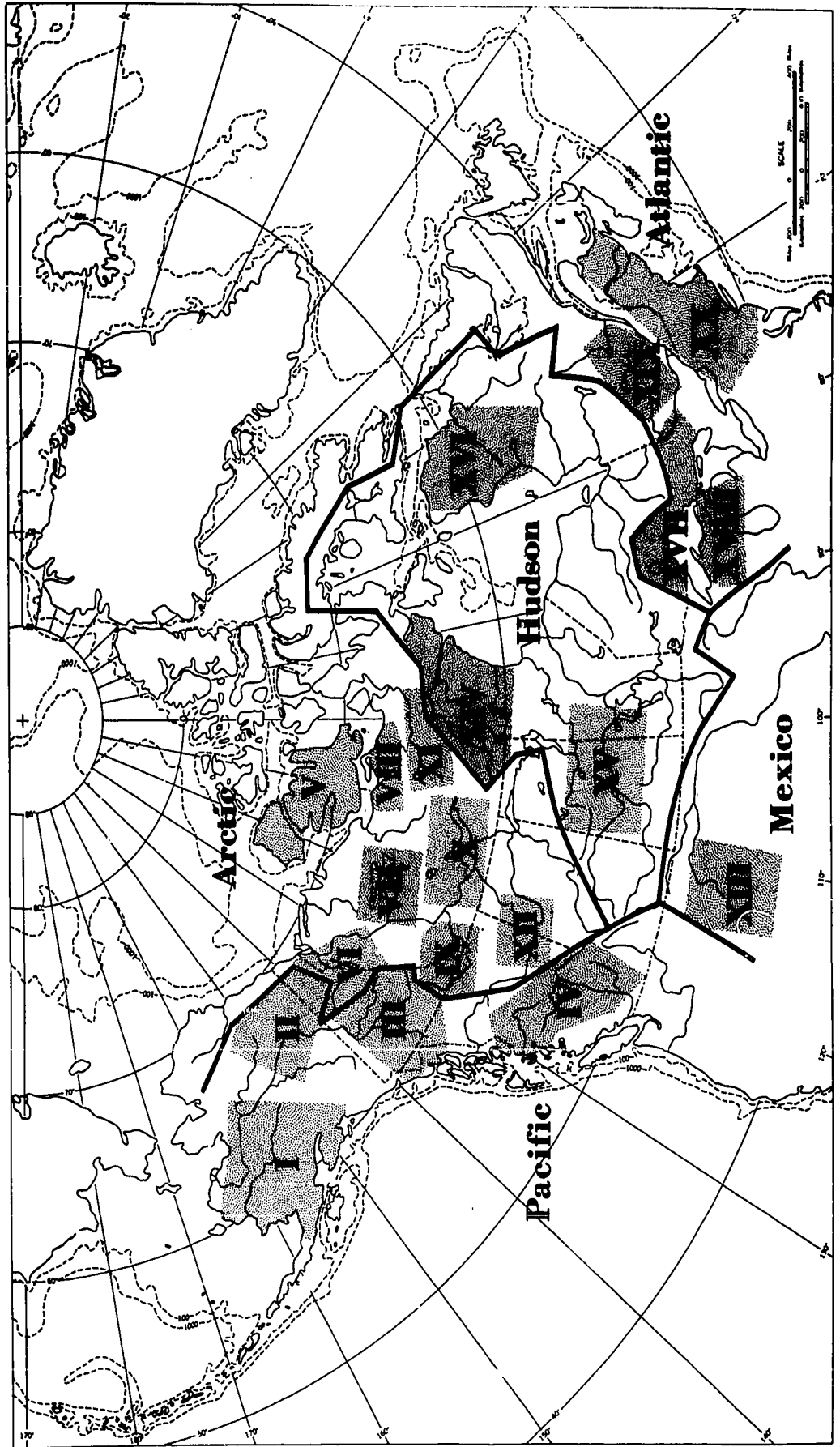


Fig. 1

Schaefer and Wilford, 1950; Godsil and Greenhood, 1951; Hart, 1952) have used linear regression analysis for the treatment of morphometric data. Other authors (Needham and Gard, 1959; Holt, 1960) have used body proportions for distinguishing intraspecific variations. The later method has received strong criticism from several authors (Schaefer and Walford, 1950; Lindsey, 1960).

For each meristic character, a one-way analysis of variance was performed and to test the significance of differences among the means the New Duncan's Multiple Range Test, with Kramer's modification was used (Steel and Torrie, 1960). Significance was tested at 5% level.

The computations were done on an IBM system 360 digital computer at the University of Ottawa Computing Centre.

RESULTS

I. DIVERSITY OF LAKE TROUT OVER ITS DISTRIBUTIONAL RANGE

Morphometric Studies

Interdrainage Comparison of Morphometric Characters

Head Measurements

The head length, interorbital width, postorbital length, upper jaw length, and lower jaw length were considered for interdrainage variation. Only significant differences are mentioned.

Head length. - The head length of both Pacific and Atlantic Drainage lake trout was longer than that of the Arctic and Hudson Drainage lake trout. The Arctic Drainage lake trout had longer head than the Hudson Drainage lake trout. (Tables I and III).

Interorbital width. - The interorbital width was greater in the Pacific Drainage lake trout than in the Arctic Drainage lake trout. The Atlantic and Hudson Drainage lake trout had greater interorbital width than the Arctic Drainage lake trout (Tables I and III).

Postorbital length. - The Pacific Drainage lake trout had longer postorbital length than the Arctic and Hudson Drainage lake trout; and the Atlantic Drainage lake trout had longer postorbital length than those of the Arctic Drainage (Tables I and III).

Upper jaw length. - The upper jaw was longer in the Pacific and Atlantic Drainage lake trout than in those from the Arctic and Hudson Drainage. The lake trout from the Arctic Drainage had longer upper jaws than those of the Hudson Drainage (Tables I and III).

Table I. Statistics describing the regressions of head parts on fork length of lake trout from various ocean drainages.

Character	Ocean Drainage	Fork Length mm	Regression Coefficient*	Standard error of Reg. Coefficient*	Constant*
Head Length	Pacific	237.0-531.0	1.179	0.053	-1.066
	Arctic	83.0-650.0	1.039	0.010	-0.712
	Hudson	176.0-580.0	0.985	0.018	-0.572
	Atlantic	169.0-679.0	1.094	0.019	-0.868
Inter-orbital Width	Pacific	237.0-531.0	1.189	0.046	-1.631
	Arctic	83.0-650.0	1.051	0.015	-1.291
	Hudson	176.0-580.0	1.113	0.024	-1.460
	Atlantic	169.0-679.0	1.135	0.021	-1.504
Post-orbital Length	Pacific	237.0-531.0	1.210	0.053	-1.382
	Arctic	83.0-650.0	1.087	0.010	-1.064
	Hudson	176.0-580.0	1.064	0.029	-1.001
	Atlantic	169.0-679.0	1.145	0.031	-1.224
Length of Upper Jaw	Pacific	237.0-531.0	1.323	0.073	-1.708
	Arctic	83.0-650.0	1.131	0.017	-1.232
	Hudson	176.0-580.0	1.066	0.026	-1.060
	Atlantic	169.0-679.0	1.203	0.023	-1.426
Length of Lower jaw	Pacific	237.0-531.0	1.286	0.063	-1.529
	Arctic	83.0-650.0	1.107	0.013	-1.083
	Hudson	176.0-580.0	1.048	0.021	-0.931
	Atlantic	169.0-679.0	1.168	0.021	-1.251

* Values in common logarithms

Lower jaw length. - The Pacific and Atlantic Drainage lake trout had longer lower jaws than that from the Arctic and Hudson Drainages trout (Tables I and III).

Body Measurements

Six body measurements, predorsal length, ventral-anal length, length of caudal peduncle, dorsal-adipose length, depth of caudal peduncle, and body depth were considered for interdrainage variations. No significant differences were observed in dorsal-adipose length and depth of caudal peduncle (Table III).

Predorsal length. - The Pacific Drainage lake trout had longer predorsal length than those from the Arctic, Hudson and Atlantic Drainages. This was the only measurement in which the Atlantic Drainage lake trout had a significantly lower value of regression coefficient than those of the Pacific Drainage. Both the Atlantic and Arctic Drainage lake trout had longer predorsal length than those of Hudson Drainage (Tables II and III).

Ventral-anal length. - The lake trout from the Hudson Drainage had significantly longer ventral-anal length than those of Atlantic Drainage (Tables II and III).

Length of caudal peduncle. - The lake trout from the Pacific Drainage had shorter caudal peduncle than those from Arctic and Hudson Drainages. The Atlantic Drainage lake trout also had shorter caudal peduncles than those from Arctic and Hudson Drainages (Tables II and III).

Body depth. - Body depth was deeper in the Atlantic Drainage lake trout than in Arctic Drainage lake trout (Tables II and III).

Table II. Statistics describing the regressions of body parts on fork length of lake trout from various ocean drainages.

Character	Ocean Drainage	Fork Length mm	Regression Coefficient*	Standard error of Reg Coefficient*	Constant*
Pre-dorsal Length	Pacific	237.0-531.0	1.169	0.031	-0.759
	Arctic	83.0-650.0	1.065	0.006	-0.486
	Hudson	176.0-580.0	1.011	0.011	-0.354
	Atlantic	169.0-679.0	1.080	0.014	-0.530
Ventral-anal Length	Pacific	237.0-531.0	1.026	0.054	-0.798
	Arctic	83.0-650.0	0.960	0.014	-0.619
	Hudson	176.0-580.0	0.993	0.020	-0.690
	Atlantic	169.0-679.0	0.926	0.019	-0.528
Length of Caudal Peduncle	Pacific	237.0-531.0	0.824	0.050	-0.384
	Arctic	83.0-650.0	0.962	0.010	-0.745
	Hudson	176.0-580.0	0.986	0.016	-0.796
	Atlantic	169.0-679.0	0.903	0.015	-0.597
Dorsal-adipose Length	Pacific	237.0-531.0	0.877	0.081	-0.395
	Arctic	83.0-650.0	0.975	0.012	-0.643
	Hudson	176.0-580.0	0.980	0.017	-0.659
	Atlantic	169.0-679.0	0.952	0.020	-0.566
Depth of Caudal Peduncle	Pacific	237.0-531.0	0.972	0.060	-1.057
	Arctic	83.0-650.0	0.934	0.013	-0.960
	Hudson	176.0-580.0	0.960	0.018	-1.020
	Atlantic	169.0-679.0	0.936	0.018	-0.978
Body Depth	Pacific	237.0-531.0	1.115	0.102	-0.998
	Arctic	83.0-650.0	1.023	0.019	-0.767
	Hudson	176.0-580.0	1.088	0.024	-0.938
	Atlantic	169.0-679.0	1.107	0.023	-0.974

*

Values in common logarithms

Table III. Significance of differences in morphometric characters among lake trout of various ocean drainages.

* Significant at 5% level
 ** Significant at 1% level
 D.F. Degrees of freedom

Character	Paci- Arc-		Paci- Hud-		Paci- Atlan-		Arc- Hud-		Arc- Atlan-		Hud- Atlan-	
	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t
Head Length	140	2.732**	74	3.772**	128	1.434	174	2.461*	228	-2.678**	162	-3.948**
Postorbital Length	139	2.465*	73	2.020*	127	0.698	172	0.905	226	-2.031*	160	-1.787
Interorbital Width	139	1.966*	74	1.245	127	0.851	173	-2.016*	226	-3.172**	161	-0.668
Length of Upper Jaw	136	2.265*	73	3.551**	124	1.647	169	1.816	220	-2.355*	157	-3.900**
Length of Lower Jaw	136	2.686**	73	3.918**	127	1.751	169	2.110*	223	-2.410*	160	-3.796**
Predorsal Length	139	3.642**	74	5.151**	131	2.069*	173	4.359**	230	-1.109	165	-3.497**
Ventral-anal Length	140	0.971	74	0.589	130	1.617	174	-1.151	230	1.391	164	2.287*
Length of caudal peduncle	138	-2.787**	74	-3.456**	132	-1.583	172	-1.127	230	3.223**	166	3.561**
Dorsal-adipose Length	140	-1.535	74	-1.708	130	-1.111	174	-0.194	230	1.002	164	0.974
Depth of caudal peduncle	140	0.591	73	0.240	131	0.600	173	-0.948	231	-0.102	164	0.835
Body depth	137	0.928	74	0.336	125	0.107	171	-1.632	222	-2.512**	159	-0.551

Interarea Comparison of Morphometric Characters

In order to interpret the morphometric variations among lake trout of different areas the head length, lengths of the upper and lower jaws, and predorsal length were considered.

Since all the areas did not have a sufficiently large sample size for the morphometric comparisons, only those areas which were represented by 15 or more fish were selected for comparisons. These areas are V, VII, and XII in the Arctic Drainage; XIV and XV in the Hudson Drainage; and areas XVIII, XIX, and XX in the Atlantic Drainage.

The lake trout of areas I, II, III, and IV in the Pacific Drainage did not show any significant differences in morphometric characters. The specimens from these areas were therefore grouped and then compared with the selected areas in other drainages. Table IV shows the number of characters in which each area differed significantly from the others. The results of the t-tests are given in appendix III-IV. The results of regression analysis are shown in Tables V and VI.

The significant differences in the morphometric characters among areas were ranked to determine the relationship among them. The ranking was done in the following fashion.

No significant difference

One significant difference

2-4 significant differences.

The ranked differences are shown in Fig. 4.

Comparison of Areas within Drainages

As the lake trout of the Pacific areas showed no significant differences, they were treated as one sample.

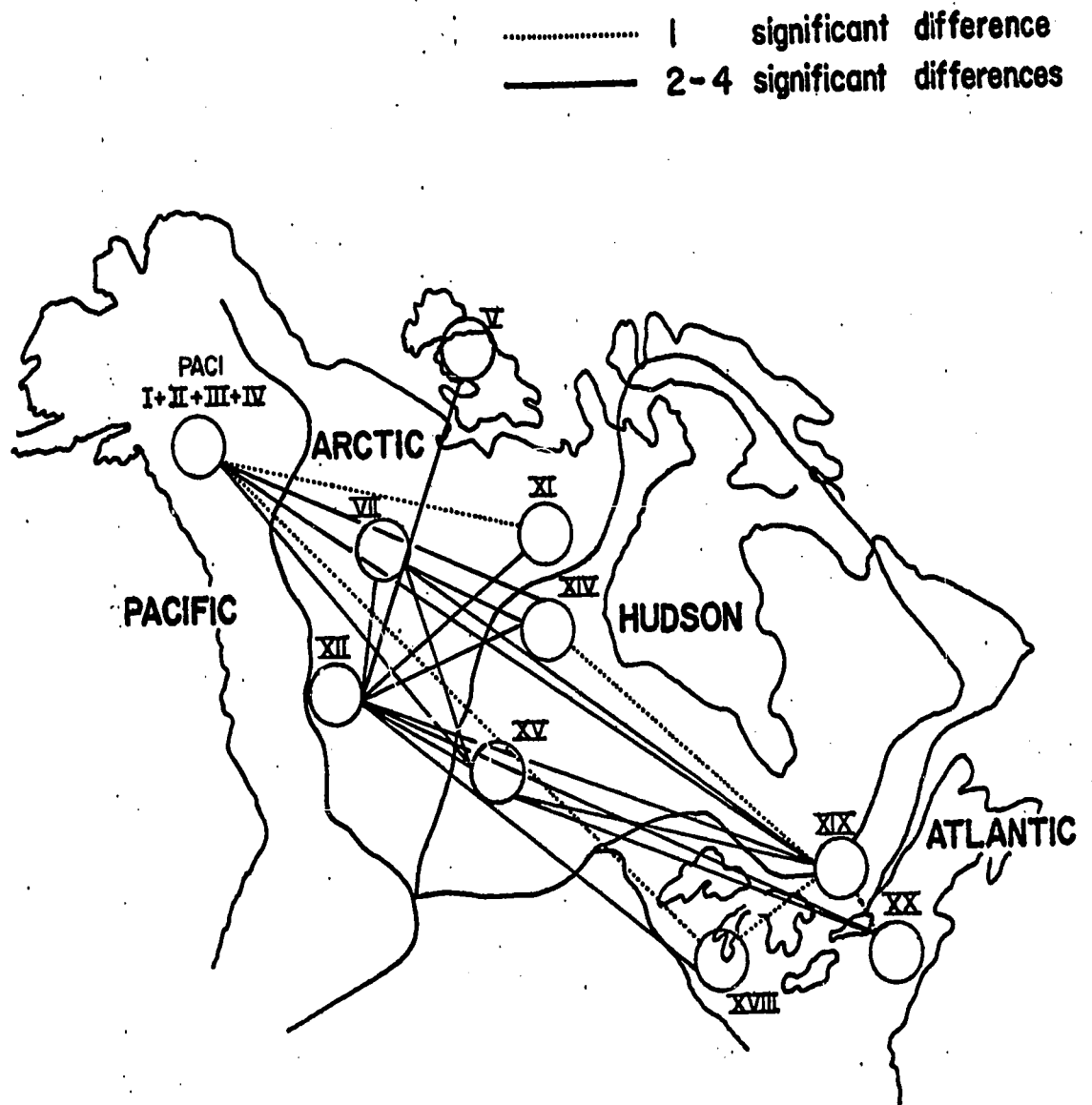


Fig. 4. Ranked morphometric differences among lake trout of Pacific Drainage (areas I + II + III + IV) and areas V, VII, XI, XII, XIV, XV, XVIII, XIX, and XX. Areas not joined by any line do not show any significant differences.

Arctic Ocean Drainage. - The lake trout of different areas in the Arctic Drainage showed the maximum number of significant differences among themselves. Area XII lake trout (Peace River System) differed significantly in having larger head, upper and lower jaws, and predorsal length from the lake trout of areas V (Canadian Archipelago), VII (Mackenzie River System), and XI (Back River System). Areas V, VII, and XI lake trout did not show any significant differences among themselves.

Hudson Bay Drainage. - No significant differences were observed among lake trout of areas XIV and XV of the Hudson Drainage.

Atlantic Ocean Drainage. - The lake trout of the Atlantic Drainage areas demonstrated some significant differences. The lake trout of area XIX (west of St. Lawrence River) had relatively smaller upper jaw than those of area XX (east of the St. Lawrence River). Area XIX lake trout also differed significantly from those of area XVIII (Wisconsin and Michigan) in having shorter predorsal length.

Comparison of Areas Between Drainages

The Pacific Drainage lake trout differed significantly from Arctic area VII lake trout in having longer predorsal length, and from area XI lake trout in having larger lower jaw. The Pacific lake trout did not show any significant differences from those of Arctic areas V and XII (Fig. 4).

The Pacific lake trout differed significantly from those of Hudson Drainage area XIV in having longer predorsal length, head, upper and lower jaws, and from area XV in having longer head, and upper and lower jaws.

Table V. Statistics describing the regressions of head length and length of upper jaw on fork length of lake trout from Pacific (I + II + III + IV); Arctic (V, VII, XI, and XII); Hudson (XIV, XV) and Atlantic (XVIII, XIX, and XX) Drainages.

Character	Areas	Fork Length mm	Regression Coefficient*	Standard error of Regression Coefficient*	Constant*		
Head Length	Pacific	I + II + III + IV	237.0-531.0	1.179	0.053	-1.066	
	Arctic	V	249.0-590.0	1.084	0.047	-0.848	
		VII	162.0-588.0	1.101	0.017	-0.872	
		XI	271.0-525.0	1.023	0.046	-0.679	
		XII	168.0-475.0	1.216	0.028	-1.112	
	Hudson	XIV	176.0-569.0	1.016	0.024	-0.649	
		XV	410.0-580.0	0.830	0.106	-0.158	
	Atlantic	XVIII	169.0-545.0	1.069	0.332	-0.783	
		XIX	218.0-586.0	1.052	0.014	-0.781	
		XX	211.0-679.0	1.095	0.037	-0.847	
	Length of Upper Jaw	Pacific	I + II + III + IV	237.0-531.0	1.323	0.073	-1.708
		Arctic	V	249.0-590.0	1.152	0.075	-1.316
			VII	162.0-588.0	1.221	0.028	-1.466
XI			271.0-525.0	1.160	0.093	-1.314	
XII			168.0-475.0	1.423	0.043	-1.914	
Hudson		XIV	176.0-569.0	1.079	0.037	-1.094	
		XV	410.0-580.0	0.917	0.144	-0.659	
Atlantic		XVIII	169.0-545.0	1.141	0.040	-1.251	
		XIX	218.0-586.0	1.171	0.018	-1.367	
		XX	211.0-679.0	1.217	0.052	-1.434	

* Values in common logarithms

Table VI. Statistics describing the regressions of lower jaw length and predorsal length on fork length of lake trout from Pacific (I + II + III + IV), Arctic (V, VII, XI, XII), Hudson (XIV, XV), and Atlantic (XVIII, XIX, XX) Drainages.

Character	Areas	Fork Length mm	Regression Coefficient*	Standard Error of Regression Coefficient**	Constant*		
Length of Lower Jaw	Paci- fic	I + II + III + IV	237.0-531.0	1.286	0.063	-1.529	
		Arctic	V	249.0-590.0	1.155	0.063	-1.231
			VII	162.0-588.0	1.174	0.024	-1.254
			XI	271.0-525.0	1.053	0.062	-0.948
	XII		168.0-475.0	1.334	0.036	-1.605	
	Hud- son Atlantic	XIV	176.0-569.0	1.082	0.029	-1.012	
		XV	410.0-580.0	0.895	0.123	-0.522	
		XVIII	169.0-545.0	1.160	0.037	-1.206	
			XIX	218.0-586.0	1.118	0.015	-1.142
			XX	211.0-679.0	1.194	0.044	-1.294
Pre-dorsal Length	Paci- fic	I + II + III + IV	237.0-531.0	1.169	0.031	-0.759	
		Arctic	V	249.0-590.0	1.087	0.033	-0.546
			VII	162.0-588.0	1.096	0.011	-0.561
			XI	271.0-525.0	1.091	0.023	-0.559
	XII		168.0-475.0	1.100	0.024	-0.570	
	Hud- son Atlantic	XIV	176.0-569.0	1.034	0.014	-0.408	
		XV	410.0-580.0	1.090	0.058	-0.571	
		XVIII	169.0-545.0	1.120	0.047	-0.628	
			XIX	218.0-586.0	1.042	0.012	-0.438
			XX	211.0-679.0	1.093	0.023	-0.559

* Values in logarithms

The Pacific lake trout differed significantly from those of area XVIII of Atlantic Drainage in having longer upper jaw and from those of area XIX in having longer predorsal length, head, and upper and lower jaws.

Of the four areas considered in the Arctic Drainage, only areas VII and XII showed significant differences from areas in the Hudson and Atlantic Drainages.

Area VII lake trout differed significantly from those of area XIV in having longer predorsal length, head, upper and lower jaws; and from XV in having longer head and upper jaw. Area VII lake trout also differed significantly from the lake trout of areas XIX of the Atlantic Drainage in having longer predorsal length, head, and upper jaw.

Area XII lake trout differed significantly from those of area XIV in having longer predorsal length, head, upper and lower jaws, and from area XV in having longer head, and upper and lower jaws.

Area XII lake trout also differed significantly from those of Atlantic areas XVIII, XIX, and XX in having longer head, upper and lower jaws.

The lake trout of area XIV of the Hudson Drainage differed significantly from the lake trout of area XIX of Atlantic Drainage in having shorter lower jaw.

The lake trout of area XV of Hudson Drainage differed significantly from lake trout of Atlantic area XIX in having shorter head, shorter upper and lower jaws, and from area XX in having shorter head and shorter upper jaw.

Meristic Studies

In the past several authors, especially Schmidt (1919), Hubbs (1926), Taning (1952), Seymour (1959) and Garside (1966) have commented

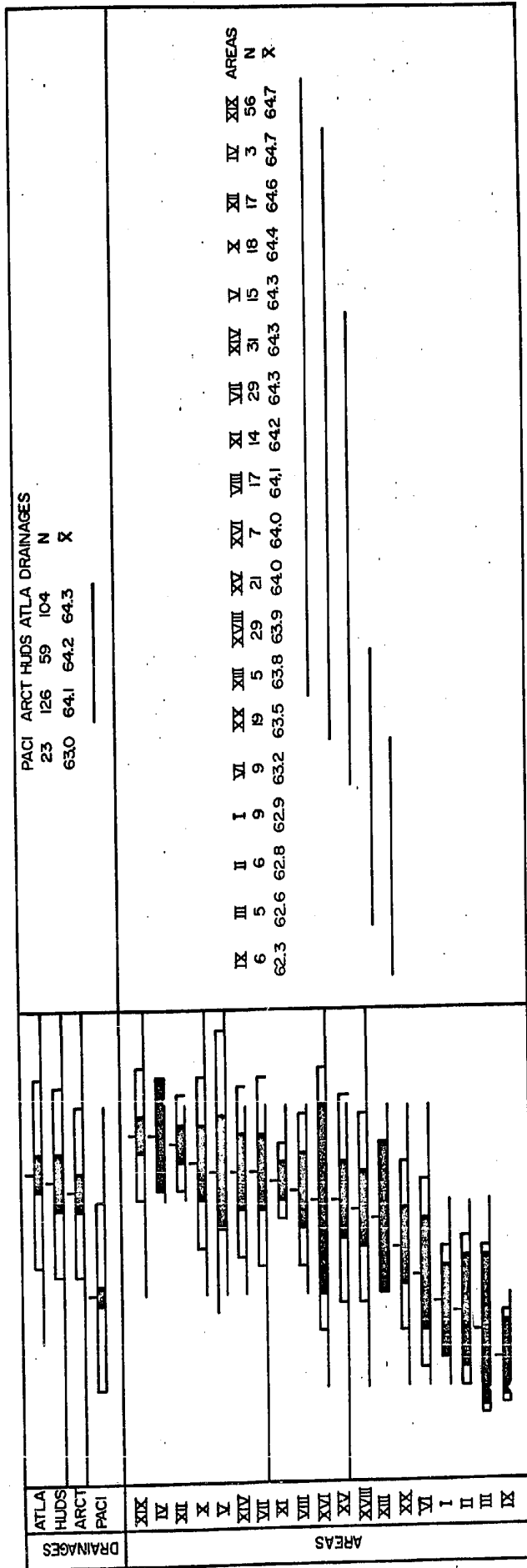


Fig. 5. Variations in the vertebral counts in lake trout from the four primary ocean drainages and from the areas* in each drainage. Horizontal bars show the range, the vertical bars show the means, the black rectangles show ± 2 standard errors of the mean, and open rectangles plus the black rectangles show ± 1 standard deviation of the mean.

On the right is shown the Duncan's Test to show the significant differences among means. Any two means underscored by the same line are not significantly different.

* No vertebral counts were available from area XVII.

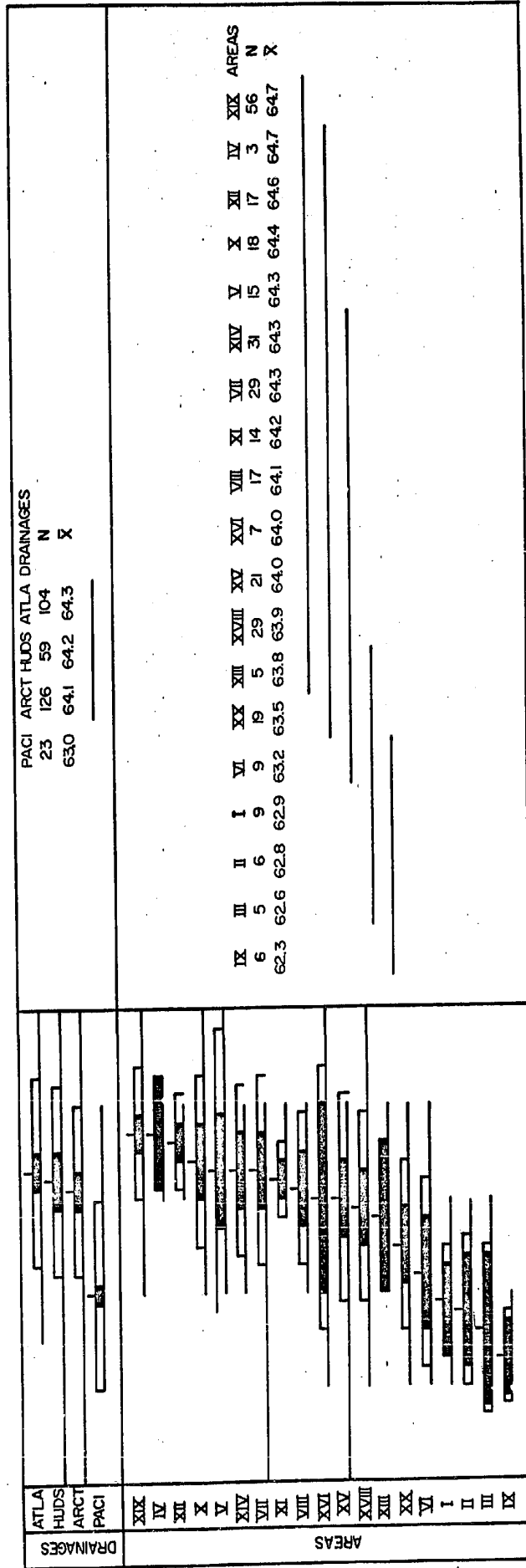


FIG. 5. Variability in the vertebral counts in lake trout from the four primary ocean drainages and from the areas* in each drainage. Horizontal bars show the range, the vertical bars show the means, the black rectangles show ± 2 standard errors of the mean, and open rectangles plus the black rectangles show ± 1 standard deviation of the mean.

On the right is shown the Duncan's Test to show the significant differences among means. Any two means underscored by the same line are not significantly different.

* No vertebral counts were available from area XVII.

on the influence of environmental factors on the number of meristic characters in fishes. However, a careful use of meristic characters has been extremely helpful in taxonomic studies (Vladykov, 1954; Bailey and Gosline, 1955; McPhail, 1961, 1963; Qadri, 1964, 1967; Martin and Sandercock, 1967).

Total Number of Vertebrae. - The mean number (63.0) of vertebrae in the Pacific Drainage lake trout differed significantly from those of the Arctic (64.1), Hudson (64.2), and Atlantic (64.3) Drainages. No statistical significance in the number of vertebrae was observed among the lake trout of the last three ocean drainages (Fig. 5).

The significant differences in vertebral counts among areas are summarized in Fig. 5. The mean number of vertebrae in the lake trout of areas I, II, and III in the Pacific Drainage were not significantly different from each other, nor from those of areas VI and IX in the Arctic Drainage, and area XX in the Atlantic Drainage. Area IV lake trout in the Pacific Drainage differed significantly from other areas in the same drainage.

For the lake trout, Vladykov (1954) mentioned a mean of 63.0 vertebrae; Norden (1961), 63.9; and Qadri (1964) 64.2; Slastenenko (1958) reported a range of 64-65 vertebrae.

Interneurons. - The mean number (18.4) of interneurons in the Pacific Drainage lake trout differed significantly from those of the Arctic (19.4), Hudson (19.2), and Atlantic (19.3) Drainages. No

significant difference was observed among the lake trout of the last three ocean drainages (Fig. 6).

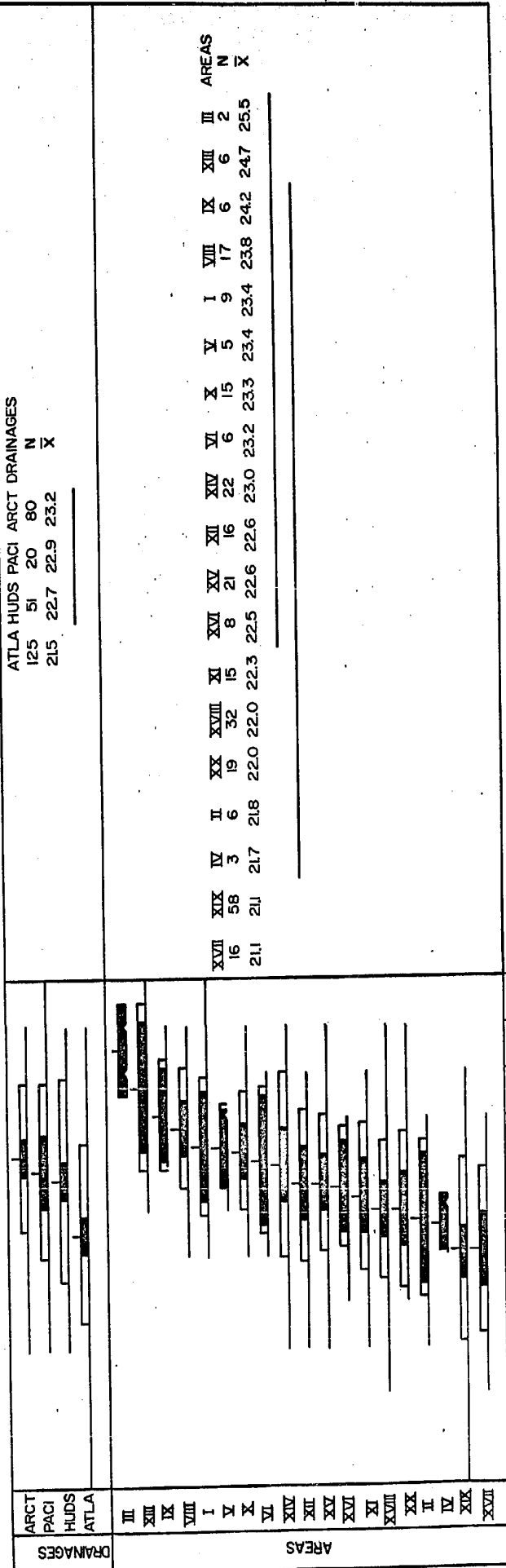
The significant differences among lake trout of different areas are summarized in Fig. 6. The mean numbers of interneurals in the lake trout of the Pacific Drainage areas, I, II, III, and IV did not differ from each other nor from area IX in the Arctic Drainage.

Dorsal Fin Rays. - The mean numbers (Pacific, 13.8; Arctic, 13.8; Hudson, 14.1; and Atlantic, 13.9) of dorsal fin rays did not differ significantly among lake trout of different ocean drainages.

Among lake trout of different areas, the mean number of dorsal fin rays did not show any definite geographic variational trend. However some significant differences were observed.

Eddy and Surber (1947) mentioned 11.0 dorsal fin rays for lake trout and Vladykov (1954) gave a mean of 11.1. These values do not conform with mine. My values are in close agreement with those of Qadri (1964) who gave a mean value of 13.9 dorsal fin rays. Undoubtedly Vladykov and Eddy and Surber had a different method of enumeration than mine. Vladykov counted these fin rays without the help of staining or radiographs and probably missed one or two very small anterior rays which are clearly visible in stained specimens and in radiographs.

Anal Fin Rays. - The mean numbers (Pacific, 13.0; Arctic, 13.2; Hudson, 13.4, and Atlantic, 13.0) of anal fin rays did not differ significantly among lake trout of different ocean drainages.



16 17 18 19 20 21 22 23 24 25 26 27

GILL RAKERS

Fig. 7. Variation in the gill raker counts in lake trout from the four primary ocean drainages and from the areas* in each drainage. Horizontal bars show the range, the vertical bars show the means, the black rectangles show ± 2 standard errors of the mean, and open rectangles plus the black rectangles show ± 1 standard deviation of the mean.

On the right is shown the Duncan's Test to show the significant differences among means. Any two means underscored by the same line are not significantly different.

* No gill raker counts were available from area VI.

Among lake trout of different areas, the mean number of anal fin rays did not show any definite variational trend. However, some significant differences were observed.

In lake trout, the mean values of 11.0, 10.8, and 13.8 of anal fin rays were given by Eddy and Surber (1947), Vladykov (1954), and Qadri (1964) respectively. My values are in agreement with those of Qadri (1964).

Total Number of Gill Rakers. - The mean number (21.5) of gill rakers in the Atlantic Drainage lake trout differed significantly from those of Hudson (22.7), Arctic (23.2), and Pacific (22.9) Drainage lake trout (Fig. 7).

Among lake trout of different areas, the mean values of the total number of gill rakers (Fig. 7) did not show the trend of variation seen in metameric characters i.e. vertebrae and interneurals.

Vladykov (1954) mentioned a mean of 20.2 gill rakers and Qadri (1964) gave a mean of 22.4 gill rakers. Martin and Sandercock (1967) gave mean values for the total number of gill rakers for the lake trout of three Algonquin Park lakes -- Lake Opeongo (21.06), Happy Isle (22.05), and Lake Louisa (22.26). All these values agree quite closely with those of my samples drawn from similar areas.

Branchiostegal Rays. - The mean values of branchiostegal rays in the lake trout of the Arctic and Hudson Drainages were not significantly different from each other while the mean values of Pacific and Atlantic lake trout were different from each other as well as from those of the Arctic and Hudson Drainage lake trout. Among lake trout of various areas, the mean values of branchiostegals rays did not show any definite trend of variation (Fig. 8).

Vladykov (1954) mentioned a mean value of 12.9 for lake trout and Qadri (1964) gave a mean value of 12.3. These values correspond with some of my values.

II- DIVERSITY OF LAKE TROUT IN LAKE SUPERIOR

Morphometric Studies

All of the 15 morphometric characters mentioned on page 6 were considered here. The summary of statistics describing the regressions of different head and body parts on fork length is shown in Tables VII, VIII, and IX. The results of the t-tests for the regression coefficients are summarized in Table X.

Postorbital length, ventral-anal length, dorsal-adipose length, pectoral-ventral length, height of the dorsal fin, and the height of the anal fin did not show any significant differences among the Lake Superior subpopulations.

Head Measurements

All the head measurements except the postorbital length showed significant differences among the four subpopulations.

Head length. - The head length of lean lake trout was longer than that of halfbreed and siscowet (Tables VII and X).

Diameter of eyeball. - The lean lake trout had larger eyeball diameter than that of the halfbreed; and the humper had larger eyeball diameter than either the halfbreed or siscowet (Tables IX and X).

Interorbital width. - The interorbital width was greater in lean lake trout than in halfbreeds and humpers. The siscowets also had greater interorbital width than humpers (Tables IX and X).

Length of upper jaw. - The lean lake trout had longer upper jaw than halfbreeds and siscowets (Tables IX and X).

Table VII. Statistics describing the regressions of body parts on fork length of various lake trout subpopulations from Lake Superior.

Character	Subpopulation	Fork Length mm	Regression Coefficient*	Standard error of Reg. Coefficient*	Constant*
Pre-dorsal Length	Lean	340.0-515.0	1.261	0.107	-1.012
	Halfbreed	308.0-518.0	1.011	0.035	-0.355
	Siscowet	331.0-775.0	1.105	0.054	-0.591
	Humper	212.0-455.0	1.063	0.033	-0.486
Ventral-anal Length	Lean	340.0-515.0	1.032	0.220	-0.818
	Halfbreed	308.0-518.0	1.148	0.078	-1.114
	Siscowet	331.0-775.0	1.046	0.073	-0.840
	Humper	212.0-455.0	1.029	0.055	-0.785
Length of Caudal Peduncle	Lean	340.0-515.0	1.584	0.218	-2.366
	Halfbreed	308.0-518.0	0.928	0.090	-0.693
	Siscowet	331.0-775.0	1.015	0.056	-0.907
	Humper	212.0-455.0	0.856	0.056	-0.502
Dorsal-adipose Length	Lean	340.0-515.0	1.148	0.213	-1.117
	Halfbreed	308.0-518.0	1.085	0.096	-0.920
	Siscowet	331.0-775.0	1.166	0.080	-1.140
	Humper	212.0-455.0	1.155	0.113	-1.092
Depth of Caudal Peduncle	Lean	340.0-515.0	1.080	0.145	-1.310
	Halfbreed	308.0-518.0	1.030	0.077	-1.210
	Siscowet	331.0-775.0	1.099	0.065	-1.350
	Humper	212.0-455.0	0.934	0.050	-0.935

*

Values in common logarithms

Table VIII. Statistics describing the regressions of body parts on fork length of various lake trout subpopulations from Lake Superior.

Character	Subpopulation	Fork Length mm	Regression Coefficient*	Standard Error of Regression Coefficient*	Constant*
Body Depth	Lean	340.0-515.0	1.569	0.179	-2.121
	Halfbreed	308.0-518.0	1.321	0.091	-1.463
	Siscowet	331.0-775.0	1.505	0.083	-1.936
	Humper	212.0-455.0	1.278	0.062	-1.345
Pectoral- ventral Length	Lean	340.0-515.0	0.855	0.215	-0.103
	Halfbreed	308.0-518.0	1.153	0.066	-0.871
	Siscowet	331.0-775.0	1.098	0.048	-0.719
	Humper	212.0-455.0	1.142	0.059	-0.850
Height of Dorsal Fin	Lean	340.0-515.0	0.631	0.193	-0.198
	Halfbreed	308.0-518.0	0.906	0.067	-0.510
	Siscowet	331.0-775.0	0.939	0.050	-0.627
	Humper	212.0-455.0	0.856	0.070	-0.397
Height of Anal Fin	Lean	340.0-515.0	0.860	0.156	-0.472
	Halfbreed	308.0-518.0	0.958	0.077	-0.729
	Siscowet	331.0-775.0	0.976	0.037	-0.786
	Humper	212.0-455.0	0.984	0.063	-0.807
Head Length	Lean	340.0-515.0	1.118	0.088	-0.944
	Halfbreed	308.0-518.0	0.908	0.040	-0.419
	Siscowet	331.0-775.0	0.917	0.030	-0.419
	Humper	212.0-455.0	0.961	0.038	-0.529

*
Values in common logarithms

Table IX. Statistics describing the regressions of body parts on fork length of various lake trout subpopulations from Lake Superior.

Character	Subpopulation	Fork Length	Regression Coefficient*	Standard Error of Regression Coefficient*	Constant*
Diameter of Eyeball	Lean	340.0-515.0	0.717	0.104	-0.659
	Halfbreed	308.0-518.0	0.451	0.064	0.035
	Siscowet	331.0-775.0	0.476	0.472	-0.015
	Humper	212.0-455.0	0.772	0.055	-0.793
Inter-orbital Width	Lean	340.0-515.0	1.354	0.128	-2.070
	Halfbreed	308.0-518.0	1.003	0.088	-1.161
	Siscowet	331.0-775.0	0.154	0.040	-1.541
	Humper	212.0-455.0	1.037	0.038	-1.242
Post-orbital Width	Lean	340.0-515.0	1.186	0.119	-1.337
	Halfbreed	308.0-518.0	1.016	0.064	-0.919
	Siscowet	331.0-775.0	0.964	0.033	-0.760
	Humper	212.0-455.0	1.011	0.045	-0.883
Length of Upper Jaw	Lean	340.0-515.0	1.397	0.141	-1.963
	Halfbreed	308.0-518.0	0.960	0.060	-0.848
	Siscowet	331.0-775.0	1.007	0.035	-0.940
	Humper	212.0-455.0	1.014	0.085	-0.959
Length of Lower Jaw	Lean	340.0-515.0	1.351	0.119	-1.762
	Halfbreed	308.0-518.0	0.969	0.050	-0.782
	Siscowet	331.0-775.0	0.997	0.035	-0.830
	Humper	212.0-455.0	1.018	0.047	-0.888

* Values in common logarithms

Length of lower jaw. - The lean lake trout had longer lower jaw than halfbreeds, siscowets, and humpers (Tables IX and X).

Body Measurements

The predorsal length, length of caudal peduncle, depth of caudal peduncle, and body depth showed significant differences in some comparisons.

Predorsal length. - Lean lake trout had longer predorsal length than the halfbreeds (Tables VII and X).

Length of caudal peduncle. - The lean lake trout had longer caudal peduncle than halfbreeds, siscowets, and humpers (Tables VII and X).

Depth of caudal peduncle. - The siscowets had deeper caudal peduncle than humpers (Tables VII and X).

Body depth. - The siscowets had deeper body than humpers (Tables VIII and X).

The lean lake trout differed significantly from halfbreeds, siscowets, and humpers in 7, 4, and 3 characters respectively (Table XI). The halfbreeds and siscowets do not differ from each other significantly but humpers differ from halfbreeds and siscowets in 1 and 4 characters respectively. The number of significant differences in morphometric characters tend to form three groups of lake trout in Lake Superior: (a) lean lake trout, (b) halfbreed and siscowet, and (c) humper.

Table X. Significance of differences in morphometric characters among various subpopulations of

Lake Superior.

* Significant at 5% level.

** Significant at 1% level.

Character	Lean x		Lean x		Lean x		Halfbreed x		Halfbreed x		Siscowet x	
	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t
Head Length	44	2.174*	45	2.152*	63	1.625	33	-0.161	51	-0.818	52	-0.883
Diameter of Eyeball	44	2.135*	44	1.930	63	-0.422	32	-0.282	51	-3.365**	51	-4.004**
Postorbital Length	44	1.244	45	1.872	63	1.419	33	0.718	51	0.059	52	-0.829
Interorbital Width	43	2.212*	44	1.522	62	2.664**	33	-1.604	51	-0.409	52	2.111*
Length of Upper Jaw	44	2.869**	45	2.851**	63	1.990	33	-0.648	51	-0.403	52	-0.078
Length of Lower Jaw	44	2.979**	45	2.939**	63	2.649*	33	-0.419	51	-0.609	52	-0.341
Predorsal Length	44	2.249*	45	1.144	62	1.957	33	-1.072	50	-0.947	51	0.682
Ventral-anal Length	39	0.517	40	-0.062	58	0.016	33	0.788	51	1.197	52	0.195
Length of caudal peduncle	43	2.804**	44	2.671*	61	3.772**	33	-0.772	50	0.681	51	2.010
Dorsal-adipose Length	34	0.271	35	-0.067	53	-0.021	33	-0.553	51	-0.378	52	0.081

cont'd ...

Table X. (cont'd)

Character	Lean x		Lean x		Lean x		Halfbreed x		Halfbreed x		Siscowet x		Siscowet x	
	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t	D.F.	t
Depth of caudal peduncle	44	0.297	45	-0.113	63	1.011	33	-0.578	51	1.030	52	2.036*		
Body depth	43	1.227	44	0.291	62	1.641	33	-1.242	51	0.372	52	2.231*		
Pectoral-ventral length	39	-1.401	40	-1.177	58	-1.431	33	0.602	51	0.109	52	-0.570		
Height of dorsal fin	44	-1.357	45	-1.627	63	-1.149	33	-0.350	51	0.436	52	0.952		
Height of anal fin	44	-0.562	45	-0.774	63	-0.747	33	-0.212	51	-0.237	52	-0.105		

An attempt was also made to determine the extent of variation in morphometric characters between the Lake Superior subpopulations and the lake trout of areas XVII, XVIII, XIX, and XX (Atlantic Drainage); areas VII and XII (Arctic Drainage); and area XIV (Hudson Drainage). See Fig. 3.

Four body measurements (predorsal length, length of caudal peduncle, depth of caudal peduncle, and body depth) and 4 head measurements (head length, interorbital width, and the length of both the upper and lower jaws) were considered. The "t" values of these comparisons are given in Appendix V-VIII.

The number of morphometric characters in which the Lake Superior subpopulations differed from the lake trout of the areas mentioned above are shown in Tables XI and XII.

As is apparent from the tables, the lean lake trout of Lake Superior differed from the lake trout of the Atlantic, Arctic, and Hudson areas. The siscowet and halfbreed as a group differed from the lake trout of these same areas in more characters than did the lean lake trout of Lake Superior.

It is interesting to note that the lean lake trout of Lake Superior differed significantly from the lake trout of all these areas in having deeper bodies and longer caudal peduncles. It appears that the lean lake trout of Lake Superior itself has diverged somewhat from the typical lake trout.

Meristic Studies

All of the 7 meristic characters mentioned on page 10 were considered.

Table XI. Significant differences in morphometric characters among lean, halfbreed, siscowet and humper of Lake Superior and lake trout of areas XVII, XVIII, XIX and XX.*

	Lean	Half- breed	Sisco- wet	Humper	XVII	XVIII	XIX	XX
Lean		1,2,5, 6,7,8	2,5,7, 8	2,6,8	2,	2,4	1,2,4, 6,8	2,4,
Half- breed			-	-	1,5,6, 7,	4,8	4,5,7, 8	5,7,8
Sisco- wet				3,4,6,	5,7,8	2,4,5, 7,8	2,3,4, 5,7,8	4,5,7, 8
Humper					5,6,	4,8	4,5,7, 8	5,8
XVII						4,	1,4,6,	-
XVIII							1,3,	-
XIX								3,8
XX								

*

1. Predorsal Length
2. Length of Caudal Peduncle
3. Depth of Caudal Peduncle
4. Body Depth
5. Head Length
6. Interorbital Width
7. Length of Upper Jaw
8. Length of Lower Jaw

Table XII. Significant differences in morphometric characters among lean, halfbreed, siscowet, and humper of Lake Superior and lake trout of areas VII, XII and XIV.*

	Lean	Half- breed	Sisco- wet	Humper	VII	XII	XIV
Lean		1,2,5, 6,7,8	2,5,7, 8	2,6,8	2,4	2,4	1,2,4
Half- breed			-	-	1,4,5, 7,8	5,7,8	4,5,
Siscowet				3,4,6,	4,5,7, 8	3,4,5, 7,8	3,4,5,
Humper					5,6,7, 8	5,6,7, 8	2,
VII						5,7,8	1,2,5, 7,8
XII							1,5,7, 8
XIV							

*

1. Predorsal Length
2. Length of Caudal Peduncle
3. Depth of Caudal Peduncle
4. Body Depth
5. Head Length
6. Interorbital Width
7. Length of Upper Jaw
8. Length of Lower Jaw

The total number of vertebrae, interneurals, ribs, and dorsal fin rays did not show any significant variation among the four subpopulations (Fig. 9).

Only the anal fin rays, gill rakers, and branchiostegal rays showed significant differences in some comparisons (Fig. 10).

Anal Fin Rays. - The halfbreeds had a significantly higher mean value of anal fin rays (14.4), than humpers (13.5) and leans (13.4).

Total Number of Gill Rakers. - Humpers had relatively high mean number of gill rakers (24.8), which differed significantly only from the mean value (23.0) in lean lake trout.

Branchiostegal Rays. - Humpers had a high mean number of branchiostegal rays (13.6) which differed significantly from the mean values in all the other subpopulations i.e. siscowet (12.8), halfbred (12.8), and lean (12.6).

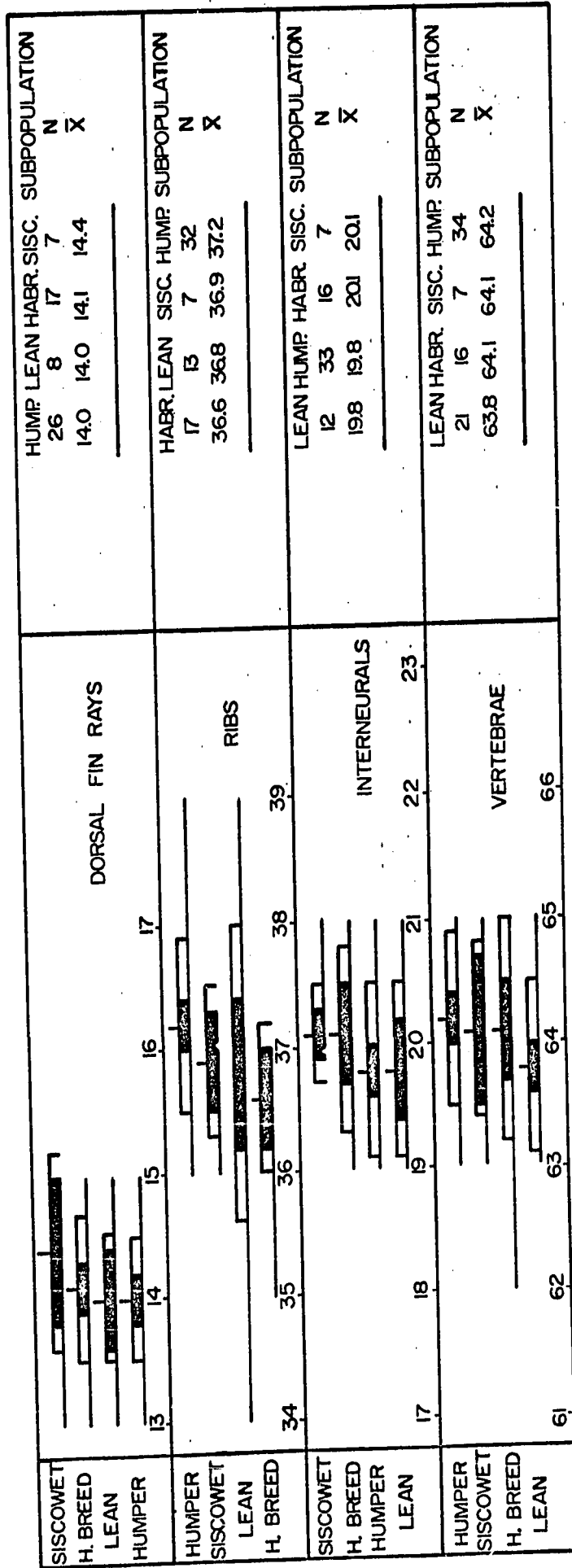


Fig. 9. Variation in the vertebral, interneural, rib, and dorsal fin ray counts in lean, siscowet, halfbreed (H. Breed, HBR), and humper (HUMP) lake trout from Lake Superior. Horizontal bars show the range, vertical bars show the means, black rectangles show ± 2 standard errors of the mean, and open rectangles plus the black rectangles show ± 1 standard deviation of the mean.

On the right is shown the Duncan's Test to show the significant differences among means. Any two means underscored by the same line are not significantly different.

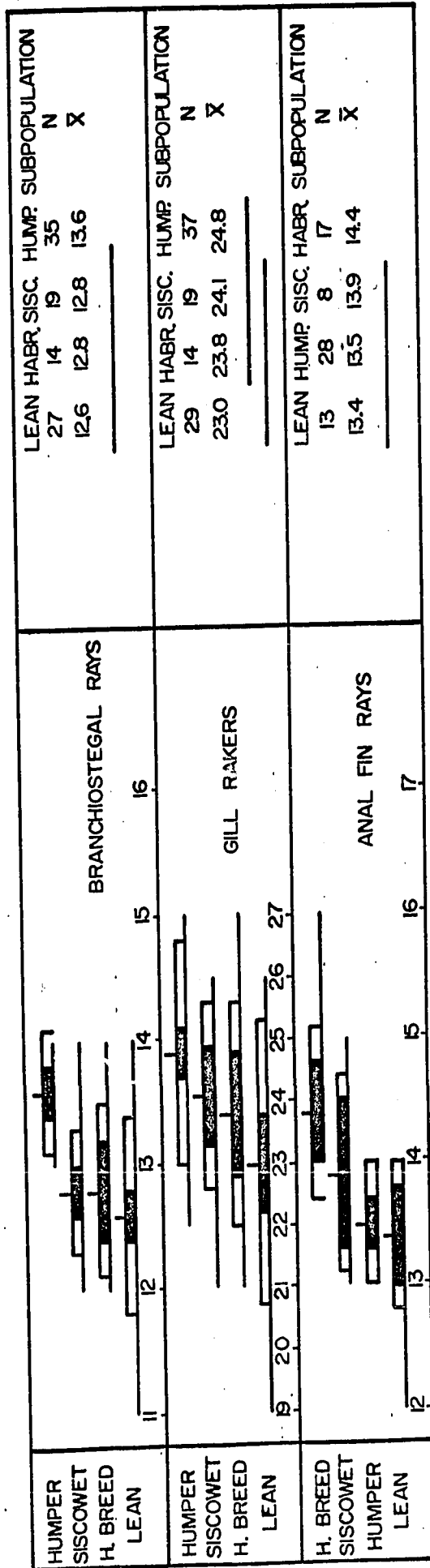


Fig. 10. Variation in the anal fin ray, gill raker, and branchiostegal ray counts in lean, siscowet (SISC), halfbreed (H. Breed, HABR), and humper (HUMP) lake trout from Lake Superior. Horizontal bars show the range, vertical bars show the means, black rectangles show ± 2 standard errors of the mean, and open rectangles plus the black rectangles show ± 1 standard deviation of the mean.

On the right is shown the Duncan's Test to show the significant differences among means. Any two means underscored by the same line are not significantly different.

DISCUSSION

The significant morphometric differences (Table III) among the lake trout of various ocean drainages i.e. Pacific, Arctic, Hudson, and Atlantic, indicated partially different gene pools of lake trout in these drainages.

The Pacific and Atlantic Drainage lake trout did not differ significantly from each other in any morphometric characters except predorsal length. On the other hand, the lake trout from each of these ocean drainages differed significantly from the Arctic and Hudson Drainage lake trout. Although the Pacific and Atlantic Drainage lake trout did not show significant differences from each other in morphometric characters, the values of regression coefficients were relatively lower in the Atlantic Drainage lake trout than in those of the Pacific Drainage (Tables I and II).

The interarea comparisons (Table IV and Fig. 4) of morphometric characters show that the Pacific Drainage lake trout do not differ significantly from area XX lake trout of the Atlantic Drainage. The Pacific Lake trout differ from areas XVIII and XIX lake trout (Atlantic) in 1 and 4 characters respectively. This suggests that most of the similarity of the Atlantic Drainage lake trout with the Pacific Drainage lake trout is contributed by area XX and area XVIII lake trout.

Deglaciation on the Atlantic Coast occurred earlier and more rapidly than in the upper Mississippi area and the Great Lakes basin (Newman and Fairbridge, 1960). According to these authors the initial ice retreat in the Long Island Sound area began about 30,000 B.P.

(before the present), and according to Hickox (1960) most of Nova Scotia was ice free by 10,000 B.P. It is suggested that the area XX lake trout originated and dispersed from a refuge on the Atlantic Coast, and invaded areas north west as well as south east of the St. Lawrence River. The deglaciation on the Atlantic Coast was followed by marine submergence (Flint, 1957) and the sea flooded the St. Lawrence lowlands forming the Champlain Sea. The Champlain Sea existed 1000 to 2000 years (Terasmae, 1959) and probably isolated populations of lake trout on both sides of St. Lawrence River. The lake trout of area XIX could due to isolation develop different characteristics from the populations in area XX.

Area XVIII lake trout seem to have originated from a refuge somewhere in the upper Mississippi valley. These lake trout do not differ significantly from those of areas XIV and XV in the Hudson Drainage nor from those of areas V, XI, and VII in the Arctic Drainage. Therefore, it is logical to say that the lake trout originating from the upper Mississippi refuge dispersed north into the present Hudson drainages, and some of the Arctic drainages. The lake trout originating from this refuge apparently shared their gene pool with those originating from the Atlantic refuge. This is suggested by the absence of significant morphometric differences between area XVIII and area XX lake trout. The sharing of populations of lake trout originating from the upper Mississippi and Atlantic refuges probably occurred through the tributaries of Ohio and Susquehanna rivers.

Radforth (1944) argued against a Mississippi refuge south of the ice sheet. Her objection was based upon the absence of suitable

habitats for lake trout in that area. However, Lindsey (1964) mentioned that in Wisconsin there are still natural lake trout populations close to the southern edge of glaciation. Some of the divides between Great Lakes and Mississippi basins in Wisconsin are low and swampy which is a less favourable route for lake trout dispersal. But we know that the topographical conditions of an area are not static; therefore these conditions may not have existed during the early stages of deglaciation. The presence of a fossil lake trout from Wisconsin close to the southern edge of glaciation within the present Mississippi Drainage (Fig. 1) leaves no doubt of lake trout having survived in a Mississippi refuge. This fossil was assigned to the interglacial period between the second and third Pleistocene glaciations by Hussakof (1916). However, recent radiocarbon dating techniques assign this fossil to the closing stages of the last or Wisconsin glaciation i.e. 12,500 to 16,000 B.P. (Lindsey, 1964). Gruchy (1968, in press) has recently described a second fossil lake trout from the Ottawa region. Its estimated age is $9,500 \pm 300$ years, suggesting that lake trout closely followed the northward retreat of the ice sheet.

It is important to note that the lake trout of the various areas in the Arctic Drainage (Fig. 4) showed a maximum number of significant differences among themselves. This suggests the invasion of these areas by the lake trout from various sources.

The Pacific Drainage lake trout differed significantly from those of most areas in the Arctic and Hudson Drainages except

those from areas V and XII in the Arctic Drainage (Appendix III-VI). The Pacific Drainage lake trout differed from areas VII and XI in only one character and therefore suggest close relationship with the Arctic drainage lake trout than from the lake trout of Hudson areas XIV and XV from which they differed in 4 and 3 characters respectively (Table VI and Fig. 4). It is suggested that the Pacific lake trout dispersed postglacially along the Canadian Arctic slope to the islands of the Canadian Archipelago (Area V), and possibly to the Back River Drainage (Area XI), where they mixed with the lake trout from the Mississippi refuge.

The lake trout of area XII (Peace River system) did not show any significant difference in morphometric characters from the Pacific Drainage lake trout, but differed strongly (in 3 characters) from the area XV (Hudson) lake trout. This suggests that the lake trout in the Peace River system had a different origin than those of the Churchill River system (area XV). The area XV lake trout, therefore, probably had their origin from the upper Mississippi refuge, which is substantiated by the fact that area XV lake trout did not differ from area XVIII lake trout significantly. On the other hand, area XII lake trout differ strongly (in 3 characters) from area XVIII lake trout, and this suggests that the lake trout in the Peace River system originated from an upper Missouri refuge. Natural populations of lake trout still occur in the upper Missouri River system (Henshall, 1907; Schultz, 1941; Vincent, 1963). The author examined some specimens from Montana and Wyoming but since the number of specimens was insufficient for sound morphometric studies, they were not included in the

analysis. Lindsey (1964) gave two explanations for the occurrence of natural populations of lake trout in Montana. Firstly, he suggested that the lakes in Montana with lake trout populations, lie immediately south of the Saskatchewan River basin and could have received lake trout from the Yukon River system through a temporary ice free corridor between the Cordilleran and Keewatin ice sheets. Secondly, he suggested that the populations of lake trout existed throughout the last glaciation in Montana and moved north with the retreating ice during deglaciation. I agree with this latter explanation and further suggest that the lake trout survived glaciation in an upper Missouri refuge in Montana and then dispersed north postglacially through the Peace, Fraser, Skeena, and Stikine River systems and shared gene pools with those lake trout which survived glaciation in a northern refuge in either Alaska or the Yukon valley. This is indicated by the absence of significant difference between the lake trout of Peace River system (area XII) and those of the Pacific Drainage.

The significant variations observed in meristic characters (Figs. 5 to 8) support the hypothesis that lake trout survived north, as well as south, of the ice sheet.

The meristic characters (vertebrae and interneurals) which are metameric in nature present similar pictures of variation (Figs. 5 and 6). The Pacific Drainage lake trout and the lake trout in areas which area at the boundary of the Pacific and Arctic Drainages show relatively lower mean values for these characters. The lake trout of areas VI, IX, and XII in the Arctic Drainage show similarities to those of Pacific areas. Areas VI, IX, and XII are in the Peel, Liard

and Peace River systems, respectively. These rivers, are within the Arctic drainage, yet they are very close to the Yukon and Fraser River systems in the Pacific Drainage. It is suggested that at some time since glaciation these rivers have shared headwaters with the Pacific rivers and that there has been some gene flow in lake trout populations from the Yukon River system to the Peel and Liard River system; and the Peace River system (area XII) to the Fraser River system (area IV). However, Wynne-Edwards (1947) suggested the Peel and Liard River systems as the possible dispersal routes for lake trout from the south into the Yukon.

The gill raker and branchiostegal counts do not present the same picture of variation as do the metameric counts. However, both gill raker and branchiostegal counts show higher mean values in the Pacific Drainage lake trout than in the Atlantic Drainage lake trout (Figs. 7 and 8).

The morphometric and meristic variations over the range of lake trout strongly suggest that the species survived the Wisconsin glaciation north as well as south of the ice sheet. The taxonomic treatment of the variations observed over the distributional range of the species will be risky at this stage.

Subspecies are conceived of as genetically distinct, taxonomically different, geographically separate populations belonging to the same species and therefore interbreeding freely at zones of contact (Mayr, 1942 and 1965). Subspecies has been generally recognized as a formal taxonomic category (International Commission of Zoological Nomenclature, 1948) and many subspecies have been named in various

groups of animals without serious consideration. Wilson and Brown (1953) apparently perturbed by the misuse of the subspecies category argued against the subspecies as a natural taxonomic category. Since the publication of Wilson and Brown's paper there has been a great deal of exchange in thought regarding the fate of the subspecies. Some (Gosline, 1954; Burt, 1954; Douth, 1955) favoured Wilson and Brown's ideas, while others (Edwards, 1954; Mayr, 1954; Parkes, 1955; Fox, 1955) wrote in support of subspecies as an obvious and natural taxonomic category. The present author believes in subspecies as a formal taxonomic category, but also suggests that a great care must be taken in assigning the trinomen to such populations.

The Pacific lake trout and the lake trout of Arctic areas adjacent to Pacific Drainage e.g. areas VI, IX, and XII seem to form a fairly homogeneous gene pool. This group of populations and the one of populations in the remainder of Arctic Drainage, as well as the Atlantic and Hudson Drainages may be behaving as subspecies with the zone of contact in the Arctic Drainage. However, I will not assign these groups of populations the status of subspecies until more information becomes available on different biological aspects i.e. ecology, reproductive behaviour, physiology of these populations.

The definition of subspecies given by Mayr (1942 and 1965) agrees with the situation existing between the siscowet and lean lake trout of Lake Superior. Siscowet is separated from the lean lake trout spatially in terms of depth. It occurs in deeper water (50-100 fathoms), while the lean lake trout occurs in shallower water. Recently, Crawford (1966) has worked out the average flotation pressures for the siscowet

and lean lake trout of Lake Superior. The average flotation pressure for siscowet was 6.3 atm. and for the lean lake trout 3.8 atm. With this, Crawford concluded that these fish could be neutrally buoyant at different depths. Eschmeyer (1954), discussing the reproduction of lake trout in southern Lake Superior, has pointed out that "the principal lake trout spawning grounds in United States waters of southern Lake Superior are widely distributed on rocky shoals, at depths of less than 20 fathoms", while most siscowets are caught at depths of 50 to 80 fathoms.

Morphologically, an adult siscowet could be distinguished from the lean lake trout by the relatively smaller and broader heads and deeper bodies (Table X). On the basis of the taxonomic, physiological and ecological differences pointed out above, the author thinks that the subspecific ranking of siscowet should be retained.

The sample of the halfbreed from Point aux Mines which the author examined showed trends of variation in morphometric characters similar to the siscowet. The absence of significant differences in the morphometric characters among siscowet and halfbreed indicate a close relationship with each other. Eddy and Surber (1947) suspected that the siscowet and lean hybridize in nature. The halfbreeds may, therefore, be the hybrids of siscowet and lean.

The humpers differ significantly from the leans as well as halfbreeds and siscowets in some morphological characters (Table X). Since not much is known about the biology of humpers in relation to other forms of lake trout in Lake Superior, their taxonomic ranking is not attempted.

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Appendix I. Lake trout samples from various ocean drainages and areas.

Drainage	Area No.	Locality No.	Locality	Location	Fork Length mm	No. of Specimens
Pacific	I	1	Aniak Lake, Alaska	62°N -160°W	237.0-443.0	9
		2	Kokhanok Lake, Alaska	59°24'N-154°10'W		
		3	Upper Trail Lake, Alaska	61°N -149°W		
II	4	Vaillant Lake, Yukon	66°13'N-140°13'W	322.0-531.0	6	
		III	5	Lake Laberge, Yukon	61°10'N-135°35'W	333.0-480.0
6	Atlin Lake, B.C.		59°N -133°W			
IV	7	Cunningham Lake, B.C.	54°N -124°W	273.0-481.5	3	
		8	Canim Lake, B.C.			51°N -120°W
Arctic	V	9	Banks Island, N.W.T.	74°03'N-119°43'W	249.0-590.0	16
		10	Zeta Lake, N.W.T.	71°00'N-106°38'W		
		11	Ferguson Lake, N.W.T. and	69°28'N-104°25'W		
			Greiner Lake, N.W.T.	69°07'N-105°10'W		
VI	12	Fairchild Lake, Yukon	64°58'N-133°43'W	83.0-180.0	10	
		VII	13	Great Bear Lake, N.W.T. and	66°14'N-117°50'W	162.0-588.0
Spark Plug Lake, N.W.T.	66°07'N-117°52'W					
Keller Lake, N.W.T.	63°55'N-121°25'W					
VIII	15	Kathawachaga Lake, N.W.T.	66°14'N-110°43'W	276.0-490.0	17	
		16	Ellice Lake, N.W.T.			68°02'N-103°28'W
IX	17	Simmons Lake, B.C.	59°N -129°W	252.0-348.0	6	
		X	18	Lac La Martre, N.W.T.	63°08'N-116°54'W	165.0-650.0
19	Great Slave Lake, N.W.T.			61°23'N-115°38'W		

Appendix I. cont'd.

Drainage	Area No.	Locality No.	Locality	Location	Fork Length mm	No. of Specimens
	XI	20	Beechy Lake, N.W.T.	65°12'N-106°28'W	271.0-525.0	15
		21	MacDougal Lake, N.W.T.	65°58'N-98°37'W		
	XII	22	Tachaeada Lake, B.C.	54°15'N-122°30'W	168.0-485.0	17
		23	Swan Lake, Alberta	55°00'N-117°49'W		
Mexico	XIII	24	St. Marys Glacier, Mont.	44°41'N-111°37'W	221.0-431.0	6
		25	Elk Lake, Montana and Heart Lake, Wyoming	44°25'N-110°50'W		
Hudson	XIV	26	Whitefish Lake, N.W.T.	62°36'N-106°43'W		
		27	Beverly Lake, N.W.T. and Aberdeen Lake, N.W.T.	64°36'N-100°38'W 64°27'N-99°00'W	176.0-569.0	35
		28	Dubawont Lake, N.W.T.	63°08'N-101°13'W		
		29	Angikuni Lake, N.W.T.	62°13'N-99°50'W		
		30	Wholdaia Lake, N.W.T.	60°43'N-104°10'W		
	XV	31	Lake Wasquesieu, Sask.	53°57'N-106°15'W	410-580.0	22
		32	Lac la Ronge, Sask.	55°0'N-105°0'W		
		33	Mackay Lake, Sask.	55°27'N-104°56'W		
	XVI	34	Museum Lake, Quebec	61°17'N-73°40'W	372.0-657.0	9
		35	Lakes on Braughton Isl., Quebec	57°23'N-76°48'W		
		36	Koksoak River, Quebec	58°0'N-68°0'W		
Atlantic		37	Lake Nipigon, Ont.	50°00'N-88°50'W		
		38	Long Lake, Ont.	49°50'N-87°00'W	295.0-571.0	18
	XVII	39	Rock Lake, Ont.	47°00'N-83°50'W		
		40	Lake Timagami, Ont.	47°00'N-80°05'W		
		41	Cache Lake, Ont. and Ragged Lake, Ont.	47°50'N-91°00'W 46°15'N-78°45'W		

Appendix I. cont'd.

Drainage Area No.	Locality No.	Locality	Location	Fork Length mm	No. of Specimens
XVIII	42	Trout Lake, Wisc.	46°05'N-89°40'W	169.0-545.0	32
	43	Crystal Lake, Wisc.	43°45'N-88°00'W		
	44	Pine Lake, Mich., Mountain Lake, Mich., Rush Lake, Mich. and First Pine Lake, Mich. Elk Lake, Mich. and Torch Lake, Mich.	46°53'N-87°52'W 46°51'N-87°55'W 46°54'N-87°55'W 46°51'N-87°51'W 45°50'N-85°25'W 45°00'N-85°00'W		
	45				
XIX	46	Lac aux Sangsues, Québec	46°30'N-77°57'W	218.0-586.0	58
	47	Dodds Lake, Québec	45°42'N-75°36'W		
	48	Saccacomie Lake, Québec and Normand Lake, Québec	46°29'N-73°14'W		
XX	49	Owasco Lake, N.Y.	43°00'N-76°50'W	211.0-679.0	19
	50	Stinson Lake, N.H.	43°50'N-71°45'W		
	51	Winnisquam Lake, N.H. and Squam Lake, N.H.	43°30'N-71°30'W 43°45'N-71°31'W		
	52	Lake Winnepesaukee, N.H.	43°30'N-71°20'W		
	53	Moosehead Lake, Maine	45°45'N-69°45'W		
	54	Baker Lake, N.B.	47°21'N-68°41'W		
	55	Chamkook Lake, N.B.	_____		

Appendix II. Subpopulations of lake trout in Lake Superior.

Sub-population	Locality	No. of Specimens	Fork Length mm
Lean	one mile west of McGuinness Point	15	422.0-558.0
Lean	Superior Shoal	15	340.0-462.0
Siscowet	Stannard Rock	18	331.0-775.0
Halfbreed	Point aux Mine Bank	18	308.0-518.0
Humper	Caribou Island, 60 miles northwest of Grand Marais, Michigan	18	324.0-455.0
Humper	Isle Royale, 3-4 miles east of Rock Harbor	19	212.0-442.0

Appendix VII. Significance of differences in regression coefficients of various body and head measurements, between "lean" lake trout of Lake Superior and lake trout from the other areas mentioned in Fig. 3

The degrees of freedom in each comparison are given in parentheses under each "t" value.

* Significant at 5% level.

** Significant at 1% level.

Character	Lean x VII	Lean x XII	Lean x XIV	Lean x XVII	Lean x XVIII	Lean x XIX	Lean x XX
Predorsal Length	1.785 (50)	1.549 (43)	2.468* (61)	1.384 (44)	0.882 (53)	2.572* (80)	1.613 (40)
Length of Caudal Peduncle	3.325** (50)	3.125** (42)	3.365** (60)	3.153** (43)	3.610** (52)	4.134** (79)	3.124** (40)
Depth of Caudal Peduncle	0.298 (51)	0.952 (43)	0.840 (60)	1.021 (43)	0.518 (53)	1.411 (80)	0.587 (41)
Body Depth	2.409* (49)	2.545* (42)	2.951** (60)	1.404 (38)	2.939** (52)	3.230** (77)	2.054* (40)
Head Length	0.180 (51)	1.038 (43)	-0.928 (61)	-0.104 (42)	0.421 (53)	0.804 (78)	0.219 (41)
Interorbital Width	1.320 (49)	1.496 (42)	1.485 (60)	0.001 (41)	-0.015 (52)	0.059 (76)	0.013 (40)
Length of Upper Jaw	1.184 (51)	-0.169 (43)	1.882 (60)	1.945 (42)	2.289* (51)	2.010* (76)	1.830 (41)
Length of Lower Jaw	1.391 (51)	0.133 (43)	1.977 (60)	2.455* (42)	2.056* (52)	2.812** (78)	2.152* (41)

Appendix VII. Significance of differences in regression coefficients of various body and head measurements, between "lean" lake trout of Lake Superior and lake trout from the other areas mentioned in Fig. 3

The degrees of freedom in each comparison are given in parentheses under each "t" value.

* Significant at 5% level.

** Significant at 1% level.

Character	Lean x VII	Lean x XII	Lean x XIV	Lean x XVII	Lean x XVIII	Lean x XIX	Lean x XX
Predorsal Length	1.785 (50)	1.549 (43)	2.468* (61)	1.384 (44)	0.882 (53)	2.572* (80)	1.613 (40)
Length of Caudal Peduncle	3.325** (50)	3.125** (42)	3.365** (60)	3.153** (43)	3.610** (52)	4.134** (79)	3.124** (40)
Depth of Caudal Peduncle	0.298 (51)	0.952 (43)	0.840 (60)	1.021 (43)	0.518 (53)	1.411 (80)	0.587 (41)
Body Depth	2.409* (49)	2.545* (42)	2.951** (60)	1.404 (38)	2.939** (52)	3.230** (77)	2.054* (40)
Head Length	0.180 (51)	1.038 (43)	-0.928 (61)	-0.104 (42)	0.421 (53)	0.804 (78)	0.219 (41)
Interorbital Width	1.320 (49)	1.496 (42)	1.485 (60)	0.001 (41)	-0.015 (52)	0.059 (76)	0.013 (40)
Length of Upper Jaw	1.184 (51)	-0.169 (43)	1.882 (60)	1.945 (42)	2.289* (51)	2.010* (76)	1.830 (41)
Length of Lower Jaw	1.391 (51)	0.133 (43)	1.977 (60)	2.455* (42)	2.056* (52)	2.812** (78)	2.152* (41)

Appendix VIII. Significance of differences, in regression coefficients of various body and head measurements, between "siscowet" of Lake Superior and lake trout from the other areas mentioned in Fig. 3. The degrees of freedom in each comparison are given in parentheses under each "t" value.

* Significant at 5% level
 ** Significant at 1% level

Character	Sisco- wet x VII	Sisco- wet x XII	Sisco- wet x XIV	Sisco- wet x XVII	Sisco- wet x XVIII	Sisco- wet x XIX	Sisco- wet x XX
Predorsal Length	0.192 (39)	0.079 (32)	1.625 (50)	-0.181 (33)	-0.197 (42)	1.635 (69)	0.199 (29)
Length of Caudal Peduncle	1.477 (40)	0.763 (32)	0.325 (50)	1.093 (33)	2.040* (42)	1.984* (69)	1.148 (30)
Depth of Caudal Peduncle	0.937 (40)	2.084* (32)	2.219* (49)	1.870 (32)	1.375 (42)	3.677** (69)	1.320 (30)
Body Depth	4.733** (39)	4.040** (32)	5.817** (50)	1.589 (28)	5.319** (42)	6.589** (67)	3.169** (30)
Head Length	-5.054** (40)	-7.065** (32)	-2.215* (50)	-3.248** (31)	-2.945** (42)	-4.331** (67)	-3.673** (30)
Interorbital Width	-0.518 (39)	-0.127 (32)	0.704 (50)	2.581* (31)	2.963** (42)	4.071** (66)	3.057** (30)
Length of Upper Jaw	-4.020** (40)	-7.240 (32)	-1.115 (49)	-0.236 (31)	0.276 (40)	-0.535 (65)	-0.582 (30)
Length of Lower Jaw	-3.687** (40)	-6.480** (32)	-1.580 (49)	0.993 (31)	0.091 (41)	1.111 (67)	-0.215 (30)

Appendix IX. Significance of differences, in regression coefficients of various body and head measurements, between "halfbreed" of Lake Superior and lake trout from the other areas mentioned in Fig. 3.

The degrees of freedom in each comparison are given in parentheses under each "t" value.

* Significant at 5% level
 ** Significant at 1% level

Character	Half- breed x VII	Half- breed x XII	Half- breed x XIV	Half- breed x XVII	Half- breed x XVIII	Half- breed x XIX	Half- breed x XX
Predorsal Length	-2.169* (38)	-1.851 (31)	-0.521 (49)	-2.264* (32)	-1.007 (41)	-0.730 (68)	-1.791 (28)
Length of Caudal Peduncle	0.081 (39)	-0.409 (31)	-0.832 (49)	0.010 (32)	0.465 (41)	0.159 (68)	-0.019 (29)
Depth of Caudal Peduncle	-0.005 (39)	1.042 (31)	0.797 (48)	1.069 (31)	0.300 (41)	1.680 (68)	0.420 (29)
Body Depth	2.025* (38)	1.946 (31)	2.536* (49)	0.352 (27)	2.494* (41)	2.777** (66)	1.339 (29)
Head Length	-3.435** (39)	-5.401** (31)	-1.499 (49)	-2.641* (30)	-2.015 (41)	-2.936** (66)	-2.860** (29)
Interorbital Width	-1.940 (38)	-1.729 (31)	-0.871 (49)	0.304 (30)	0.217 (41)	0.692 (65)	0.408 (29)
Length of Upper Jaw	-2.936** (39)	-5.399** (31)	-1.101 (48)	-0.975 (30)	-0.807 (39)	-1.217 (64)	-1.126 (29)
Length of Lower Jaw	-2.675* (39)	-5.039** (31)	-1.303 (48)	-0.114 (30)	-0.658 (40)	-0.294 (66)	-0.843 (29)

Appendix X. Significance of differences, in regression coefficients of various body and head measurements, between "humper" of Lake Superior and lake trout from the other areas mentioned in Fig. 3. The degrees of freedom in each comparison are given in parentheses under each "t" value.

* Significance at 5% level
 ** Significance at 1% level

Character	Humper x VII	Humper x XII	Humper x XIV	Humper x XVII	Humper x XVIII	Humper x XIX	Humper x XX
Predorsal Length	-0.988 (56)	-0.898 (49)	0.829 (67)	-1.203 (50)	-0.824 (59)	0.632 (86)	-0.705 (46)
Length of Caudal Peduncle	-0.934 (57)	-1.645 (49)	-2.442* (67)	-0.899 (50)	-0.368 (59)	-1.041 (86)	-1.011 (47)
Depth of Caudal Peduncle	-1.427 (58)	-0.244 (50)	-0.449 (67)	0.395 (50)	-1.052 (60)	0.862 (87)	-0.891 (48)
Body Depth	2.864** (57)	1.995 (50)	3.199** (68)	0.070 (46)	2.879** (60)	3.384** (85)	1.518 (48)
Head Length	-3.290** (58)	-5.311** (50)	-1.117 (68)	-2.549* (49)	-1.953* (60)	-2.417 (85)	-2.554* (48)
Interorbital Width	-2.808** (57)	-2.379* (50)	-0.994 (68)	-0.001 (49)	-0.210 (60)	-0.210 (60)	0.165 (48)
Length of Upper Jaw	-2.407* (58)	-4.146** (50)	-0.714 (67)	-0.428 (49)	-0.326 (58)	-0.784 (83)	-0.587 (48)
Length of Lower Jaw	-2.773** (58)	-5.209** (50)	-1.048 (67)	0.062 (49)	-0.803 (59)	-0.142 (85)	-1.038 (48)