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RELATIONSHIPS AMONG NORTH AMERICAN SALMONIDAE

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ABSTRACT

The strengths of the relationships among species and genera of North American Salmonidae are assessed from published data on hybridization, coloration, and other attributes. The genus *Salmo* shows the greatest intrageneric variation. Phylogenetically, *Salmo gairdneri* is as close to the species of *Oncorhynchus* as to *Salmo salar;* and *Salmo trutta*, at the other extreme, is about midway between *S. salar* and the species of *Salvelinus*. The genus *Salvelinus* is a closely knit group. Of its species, *Salvelinus marstoni* shows the closest affiliation with *Salmo.*

Published data are scanty for several species and the methods of taking and recording data vary so widely that comparison of data taken by different investigators is hazardous.

RELATIONSHIPS AMONG NORTH AMERICAN SALMONIDAE

By George A. Rounsefell, *Fishery Research Biologist*
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This paper is third in a series in which I am attempting to compile and evaluate published information on North American Salmonidae. Definition of the relationship among species is extremely complex and although I would preferably avoid the subject, it must necessarily be considered in order to decide on the grouping of taxa for evaluating the significance of various life-history phases. In such a plastic group as the Salmonidae there are all shades of differentiation from the species down almost to the individual. With our present knowledge, probably the best we can hope to do is to gain some appreciation of the relative closeness of the relationships between taxa.

Basically, we are not so much concerned with whether two populations of any one species of Salmonidae differ phenotypically as we are with their response to similar habitats. Differences in physiological reactions may be just as real as those morphological differences which can be demonstrated statistically.

In our zeal to be objective and quantitative, we must not overlook many of the nonmorphological characteristics that, although perhaps more difficult to assess, nonetheless may show very real differences. I am speaking of such things as color, spawning habits, migratory tendency, growth rate, age at maturity, attainable size, temperature tolerance, and doubtless other yet undefined characteristics inherent in different strains.

The use of such new approaches as serological techniques and paper chromotography may furnish a clue to differences not readily discovered by the classical morphological approach. Counts of the chromosomes, while rendered difficult by the large numbers involved, may be of great taxonomic value, at least at the species levels.

In discussing classification of the Salmonidae it is instructive to commence by observing the relationships among the North American genera. Following the basic work done by Vladykov (1954) we chose tentatively to consider *Cristivomer* as a separate genus, resulting in four North American genera, *Cristivomer*, *Salvelinus*, *Salmo*, and *Oncorhynchus*.

Since all salmonids spawn in fresh water (presumably their ancestral home), the anadromous habit may have evolved gradually from population pressure and a higher survival of fish feeding in the sea.

In the genus *Cristivomer* this seagoing habit (if ever present) is almost if not entirely lost. The genus extends in lakes with sufficient cool oxygenated water in summer (only deep, stratified eutrophic lakes toward the southern part of its range) across North America from arctic Alaska to eastern Quebec. Since it is lacustrine and seldom enters streams, the fact that only one species, *C. namaycush*, covers this entire area might seem a little surprising; usually long-isolated populations tend to develop distinguishable morphologic differences. This lack of differences over such an extended range might be cited to postulate a theory of fairly recent origin for the genus, which however is geologically untenable; but there may be other reasons why differences failed to develop. Differences between isolated populations usually develop through environmental selection. In stream-dwelling fish where environmental differences between localities are often large the selection may be rather severe, but *Cristivomer* inhabits a relatively stable lacustrine habitat that differs little from lake to lake. Furthermore, most geneticists support the postulate (National Research Council, 1956, p. 16) that mutations are induced by naturally occurring radiation: "To the best of our present knowledge, if we increase the radiation by X%, the gene mutations caused by radiation will also be increased by X%."

Folsom and Harley (1957), from data of Libby (1955) and George (1952), have estimated that radiation from cosmic rays at latitudes midway between the geomagnetic equator and 55° N. (geomagnetic) decreases, because of the shielding effect of the water, from 35 millirads per year at the water surface to 10.1 millirads at 10 meters, 4.86 at 20 meters, 1.40 at 50 meters, and only 0.47 millirads per year at 100 meters. Folsom and Harley

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also estimate the internal radiation for a large fish at 28 mrad./year. Thus, whereas a fish living near the surface (in fresh water the radiation activity from the water itself is estimated at less than 0.5 mrad./year) would receive a total of 63 mrad./year, the total dose received would fall rapidly with increasing water depth to 38 mrad. at 10 meters and from 33 to 28.5 mrad./year from 20 to 100 meters. A surface-living lake fish would therefore receive about twice the radiation dose of a fish living below 20 meters.

Most of the salmonids would receive an even heavier radiation dosage than the 63 mrad./year for lake fish at the surface since most of them spend some time in streams, often streams too shallow to afford any shielding effect, in which they would receive additional radiation from the naturally occurring radioactive emitters in the rocks, which varies from about 23 mrad./year for sedimentary rock to about 90 for granite, according to Folsom and Harley.

It has been suggested that in part of their range (i.e., in the deep lakes of the Precambrian shield) lake trout might be subjected to considerable radiation, particularly in the egg stage or during extended periods spent on the bottom. In the absence of data to refute this suggestion it must be considered as a valid criticism of the above hypothesis.

To what extent a lowered mutation rate in *Cristivomer* (which we may perhaps assume from the foregoing discussion of radiation received) could have slowed down the evolutionary processes would be difficult to appraise. An alternate possibility is that *Cristivomer*, during its adaptation to severe conditions in the periods of glaciation that preceded its separation into many isolated colonies, may have lost many of the alleles needed for readaptation to less severe climatic conditions. That this could perhaps be the case is indicated by the ultimate upper lethal temperatures tolerated by various salmonids (Rounsefell, 1958). The young of the other genera all tolerate higher temperatures than the young of *Cristivomer*.

Whether *Cristivomer* or *Salvelinus* is more ancient in origin is a moot question that can be argued from different angles. It could be argued that *Cristivomer* developed from *Cristivomer-Salvelinus* ancestry in North America while *Salvelinus* was simultaneously developing in Asia. Later, perhaps, as conditions ameliorated, *Salvelinus* invaded North America, either over an Asian-North American land bridge, or from the sea. *Cristivomer*, now isolated in deep lakes, unable without the nest building habit to spawn effectively in streams and unable to tolerate the higher temperatures found in most streams, would be unable to make a reciprocal invasion of Asia.

The theory that *Cristivomer* became recognizable in its present form at least as early as the last glacial period is supported by Henshall (1907) writing about the Montana grayling—

> It is very probable that the Arctic grayling was the parent stock from which the Michigan and Montana graylings descended; and from the fact that the habitats of the three species are so widely separated, it is not unreasonable to suppose that the Michigan and Montana forms were conveyed thence from the Arctic regions during the Glacial period. This theory is strengthened by the fact that Elk Lake, a half mile from the Montana grayling station, is abundantly inhabited by both grayling and the lake trout (*Cristivomer namaycush*), which latter fish is found nowhere else west of Lake Michigan.

Salmo might seem to be more ancient in origin than *Oncorhynchus*, which is confined to the North Pacific and Arctic Oceans and is much further adapted toward an anadromous existence. *Salmo* ranges in the western Atlantic from New England to Ungava Bay, thence to southern Greenland and Iceland; in the eastern Atlantic from Portugal to the White Sea. Since *Salmo* (Dymond and Vladykov, 1934) is limited on the western side of the Pacific to the Kamchatka Peninsula, it would not seem likely that it had a Pacific origin. Mottley (1934b) suggests that during the next to the last glacial period the joint ancestors of *Salmo* and *Oncorhynchus* were separated into a Pacific and an Atlantic group, the former evolving into *Oncorhynchus* and the latter into *Salmo*. During the interglacial period, *Salmo* was able to migrate from stream to stream across the continent to the Pacific coast—an impossibility for the strongly anadromous *Oncorhynchus*.

Neave (1958) suggests that *Oncorhynchus* evolved from *Salmo* in the western Pacific, citing in support of his theory the fact that *O. masou* is more primitive than other species of *Oncorhynchus* and is more closely related to *Salmo*. He states—

> In due course the newly evolved offshoot spread back through territories occupied by more conservative lines of the ancestral stock. This process of reinvasion was facilitated by increased adaptation to ocean life and was accompanied or followed by a further splitting up into several species.

None of these explanations suffices to explain fully all of the interrelationships.

There are very few morphological characters by which the various species can be unmistakably identified because—

1. The latitudinal range of many of the species is so wide that the meristic characters, which usually show a latitudinal cline, are quite variable for the same species in different localities (see Mottley, 1934a).
2. For those species with fresh-water forms there is a tendency for the geographically isolated populations to develop slight differences.
3. Anadromous and fresh-water dwelling fish of the same population may show environmental differences in form or coloration. Some of these differences, especially color, have been shown by Wilder (1952) to be reversible in *Salvelinus fontinalis.*
4. In fresh-water forms there may also be altitudinal clines. In some instances, these seem to involve retention of juvenile characteristics. For example, the parr marks in the golden trout, *Salmo gairdneri agua-bonita*, and the piute trout, *Salmo clarki seleniris* (see Snyder, 1940).

The foregoing does not mean that there are not valid species. Any experienced fisherman has no difficulty in separating the five species of Pacific salmon at a glance, even though most individual characters overlap in their range. Species are recognized by a combination of characters and most taxonomic descriptions encompass only a few of those most readily taken and easiest to reduce to numbers.

ATTRIBUTES ANALYZED TO INDICATE RELATIONSHIPS

HYBRIDIZATION

One line of inquiry that yields a clue to interrelationships comes from hybridization experiments. Within recent years several investigators have obtained chromosome counts of salmonids (table 1). In the few species studied, the diploid number ranges from 60 to 84. Of course number alone is not always the controlling factor. Thus, in describing experiments with the crossing of *Salmo salar*, *S. trutta*, *Salvelinus alpinus*, and *S. fontinalis*, Alm (1955) writes—

> The chromosomes of the Brown trout and the Char are, in spite of being the same number, greatly differentiated from one another and the former are more homologous with those of the Salmon. The Brook trout and the Char chromosomes are more in agreement with each other than with the other species.

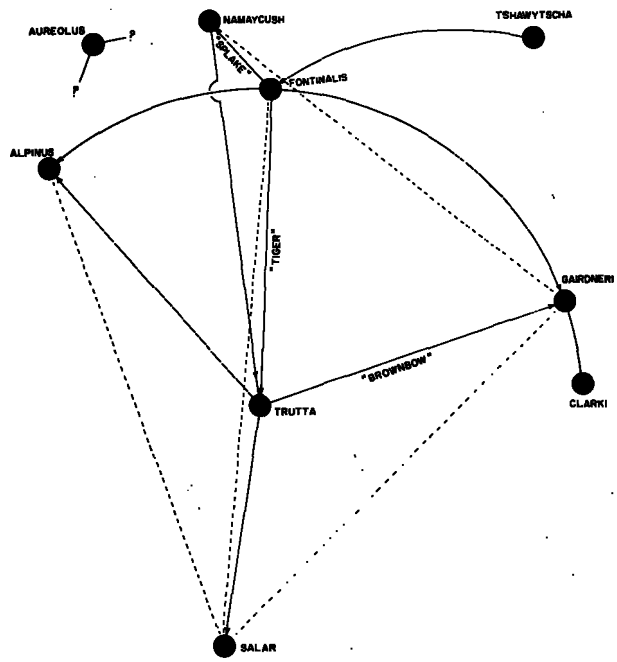

Figure 1.—Relative success of crossbreeding of Salmonidae (except *Oncorhynchus*). (Length of solid lines shows relative success; see table 2; dotted lines indicate failure; arrows, direction of male-female cross.)

In comparing *Salmo gairdneri* and *S. salar sebago*, Buss and Wright (1956) noted that "Bungenberg deJong has indicated (1955) a marked difference in the chromosome structure of these species. . . ."

Table 1.—*Diploid chromosome number in certain Salmonidae*

Species	Chromosomes	Authority
Salmo salar	60	Svärdson (1945).
Salmo salar sebago	60	Buss and Wright (1956).
Salmo gairdneri	60	Svärdson (1945); Wright (1955).
Salmo trutta	80	Svärdson (1945); Wright (1955).
Salvelinus alpinus	80	Svärdson (1945); Alm (1955).
Salvelinus fontinalis	84	Svärdson (1945); Wright (1955).
Cristivomer namaycush	84	Buss and Wright (1956).
Salmo salar × *Salmo trutta*	70	Svärdson (1945); Alm (1955).
C. namaycush × *S. fontinalis* (= "Splake").	84	Buss and Wright (1956).

From several sources we have compiled table 2 showing the results of certain crosses between species of Salmonidae (*Oncorhynchus* is shown in a separate table). To obtain a clearer view of the results we have rated the success of each cross from 1 to 6 (excellent to failure, see table 2). Although this is subjective, it aids in studying the results which are portrayed in figure 1.

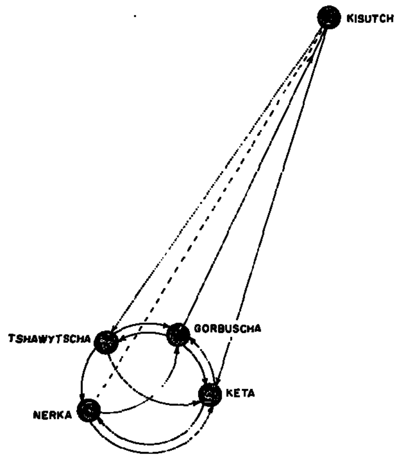

FIGURE 2.—Relative success of crossbreeding of the five eastern Pacific species of *Onchorhynchus*. (Lines indicate relative sucess; see table 3. Arrows indicate direction of male-female cross.)

This figure shows *S. trutta* occupying a position between the Salvelinae and the other species of *Salmo*, approaching closest to *S. salar*. The Salvelinæ appear to be a closely knit group, but not *Salmo*. It is surprising that *trutta* will hybridize, despite the difference in chromosome number with both *salar* and *gairdneri*, yet the latter two so far appear incompatible. No one has been successful in crossing a male *S. gairdneri* with the female of another species, which suggests incompatibility of the male sex chromosome.

The only experiments in crossing *Oncorhynchus* with other Salmonidæ were those of Roosevelt (1880) and Green (1881). In both cases male *O. tshawytscha* from eggs taken in the Sacramento River system were crossed with female *S. fontinalis*, and in both cases hybrids were raised to maturity, but the hybrids were all females, and the eggs would not hatch when fertilized with milt from male *S. fontinalis*.

Within the genus *Oncorhynchus* all five species were crossed in both directions by Foerster (1935); his results are summarized in table 3 and figure 2.

From figure 2, in which the length of each line coincides with the subjective rating of table 3, it is clear that *kisutch* is rather apart from the remainder of the species. This seems to coincide with the conclusions of Milne (1948) from a study of certain morphological characters which will be discussed later. Natural hybrids of *keta* and *gorbuscha* are not uncommon, and Hunter (1949) describes the examination of about 50 such hybrids at Port John, British Columbia; other natural crosses are more rare. The contribution of hybridization toward understanding relationships will have to be evaluated together with other characteristics.

TABLE 2.—*Some interspecific crosses in Salmonidae*

[Excepting *Oncorhynchus*]

Female	Male	Fry survival	Hybrid maturity	Hybrid breeding	Authority	Subjective rating[1]
Salmo salar	*Salmo trutta trutta*	Good	Low	0	Alm (1955)	3
Do	*S. t. fario*	Low	Low	0	do	5
Do	*Salvelinus alpinus*	0			do	6
Do	*S. fontinalis*	0			do	6
Salmo salar sebago	*Salmo gairdneri*	0			Buss and Wright (1956)	6
Salmo trutta trutta	*Salmo salar*	Fair	Low	0	Alm (1955)	4
S. t. fario	do	Very low	Low	0	do	5
Salmo trutta	*S. salar sebago*	0.3%			Buss and Wright (1956)	5
Do	*C. namaycush*	0.08%			do	5
Do	*Salmo gairdneri*	0			do	6
Do	*Salvelinus fontinalis*	4–5%			do	4
Salmo fario	*S. alpinus*	Very low			Alm (1955)	5
Do	*S. fontinalis*	Low			do	4
Salmo gairdneri	do	0–0.6%			Buss and Wright (1956)	5
Do	*Salmo trutta*	0–1.2%			do	5
Do	do	Very low	Yes	Yes	Stokell (1949)	4
Do	*C. namaycush*	0			Buss and Wright (1956)	6
Do	*Salmo salar sebago*	0			do	6
Do	*S. clarki lewisi*	3%			Simon (1946)	4
Salmo clarki	*Salmo gairdneri*			Natural	Miller (1950)	1
Salmo gairdneri	*S. clarki*			Hybrids	do	1
Salvelinus fontinalis	*Salmo trutta*	0.5%			Buss and Wright (1956)	5
Do	*Salmo fario*	0			Alm (1955)	6
Do	*S. gairdneri*	0			Buss and Wright (1956)	6
Do	*Salvelinus alpinus*	Low			Alm (1955)	4
Do	*Cristivomer namaycush*	0.7%			Buss and Wright (1956)	5
Do	do	0			Stenton (1950, 1952)	6
Do	*Oncorhynchus tshawytscha*	Fair	Yes	0	Roosevelt (1880); Green (1881)	4
Salvelinus alpinus	*Salmo fario*	Low			Alm (1955)	4
Do	*Salvelinus fontinalis*	Fair		Fair	do	2
Salvelinus aureolus	"Several other chars"			Yes	Vladykov (1954)	
Cristivomer namaycush	*S. fontinalis*	75%	Yes	Good	Stenton (1952)	1
Do	do	28%		10%	Buss and Wright (1956)	1

[1] Subjective ratings of relative success: 1, excellent; 2, good; 3, moderate; 4, poor; 5, very poor; 6, failure.

TABLE 3.—*Results of crossbreeding species of* Oncorhynchus

[First three columns from Foerster, 1935]

Female	Male	Remarks	Subjective rating [1]
tshawytscha	*nerka*	Very poor. 1 fry from 762 eggs	5
Do	*kisutch*	Very poor. Only 15 abnormal fry from 673 eggs.	5**
Do	*keta*	No hatch. Eggs died in early development.	6
Do	*gorbuscha*	Excellent hatch of healthy fry	1*
kisutch	*tshawytscha*	No hatch. Eggs died at the "eyed" stage.	6
Do	*nerka*	Very poor. Only 3 fry from 1,183 eggs	6
Do	*keta*	No fertile eggs recovered	6
Do	*gorbuscha*	Moderate hatch. Fry abnormal	4**
nerka	*tshawytscha*	Excellent hatch of healthy fry	1*
Do	*kisutch*	Only 50 weak alevins from 900 eggs (all died).	6
Do	*keta*	Good hatch of healthy fry	2*
Do	*gorbuscha*	Only 10 fry from 810 eggs (lived only one month).	5
keta	*tshawytscha*	Moderate hatch of healthy fry ("completely successful").	2***
Do	*nerka*	Good hatch of healthy fry	2*
Do	*kisutch*	Very poor. Only 5 fry from 965 eggs	5
Do	*gorbuscha*	166 healthy fry from 1,196 eggs	3*
gorbuscha	*tshawytscha*	Moderate hatch of healthy fry	3*
Do	*nerka*	Moderate hatch (excellent growth of normal individuals).	2*
Do	*kisutch*	No hatch. Eggs died during development.	6
Do	*keta*	Excellent hatch of healthy fry	1*

*Male hybrids matured and bred successfully with *nerka* females.
**Hybrids held to maturity.
***Hybrids presumably held to maturity.
[1] Subjective ratings of relative success: 1 excellent, 2 good, 3 moderate, 4 poor, 5 very poor, 6 failure.

COLORATION

The fact that a great many taxonomic studies have necessarily been made on faded museum specimens has tended to deemphasize the importance of color in classification. Furthermore, the heightening and changing of color in the breeding season contrasted with the hiding of color by the silvery guanin in marine species and even during the lacustrine existence of adfluvial species, has made color a sometimes unreliable tool for field identification in the salmonids. However, there are several color patterns in Salmonidae that may be diagnostic; the genetic inheritance of color in some taxa has been so well documented (for instance in *Lebistes*) that color should be treated with equal or perhaps greater respect than many anatomical characters. In this discussion we are not looking upon color merely as a handy character for identification; therefore, we are comparing coloration under normal conditions. Some of the more evident color characters of adults, not in breeding color, are given in table 4.

The presence on the body of black spots and black speckling characterizes *Oncorhynchus* and *Salmo* with the exception of *S. trutta*, which has both the black spotting and the bright spots otherwise reserved for the charrs. Since none of the charrs (including *Cristivomer*) shows black spotting, *trutta* is intermediate in this character.

Rainbows and cutthroats agree in both the black spotted tail and the bright lateral band. Both characters are absent in *S. salar* and *trutta*.

The dorsal vermiculations are conspicuous in *fontinalis* and faint in *aureolus* and *namaycush*. This close association is corroborated by the hybridization experiments (fig. 1), which showed *fontinalis* closest to *namaycush*.

The parr markings of young Salmonidae are often useful in field identification, despite the considerable variation both in number and shape of the marks (table 5).

Parr marks are absent in *gorbuscha*. This would seem to be associated with the life history since the young pink salmon normally proceed immediately to the sea so that they are in effect not parr, but very small smolts, when they emerge from the gravel. This theory is somewhat strengthened by the fact that *keta*, which is only slightly less anadromous than *gorbuscha* (Rounsefell, 1958), has parr marks which are not as dark as those of *tshawytscha*, *kisutch*, or *nerka*, and which commence fading at an early age.

TABLE 4.—*Normal coloration in adult North American Salmonidae*

Body spots			Caudal fin spots			Bright lateral band	Red streak under maxillary	Vermiculations on back	Black stripe after white edge on lower fins
Black spots	Black and light spots	Light spots	Large black spots	Black speckling	Without black spots				
gorbuscha			*gorbuscha*						
kisutch				*kisutch*					
tshawytscha				*tshawytscha*					
nerka					*nerka*				
keta					*keta*				
gairdneri			*gairdneri*			*gairdneri*			
clarki			*clarki*			*clarki*	*clarki*		
salar					*salar*				
trutta	*trutta*	*trutta*			*trutta*				
		fontinalis			*fontinalis*			*fontinalis*	*fontinalis*
		namaycush			*namaycush*			*namaycush*	
		aureolus			*aureolus*			*aureolus*	
		alpinus			*alpinus*				
		oquassa			*oquassa*				
		malma			*malma*				

TABLE 5.—*Parr marks in young North American Salmonidae*

Species	Number of marks		Shade	Shape	Relation to lateral line	Remarks
	Range	Average				
gorbuscha	0	0				
keta	[1] 6-12 [2] 6-10		Dusky	Elliptical to oval; slender	Chiefly above line	Marks fade at an early age.
tshawytscha	[1] 6-12		Dark	Long vertical bars equal to or wider than interspaces.	Bisected by line.	
kisutch	[1] 8-9		Dark	Narrow vertical bars, about one-half width of interspaces usually narrower than in *tshawytscha.*	Bisected by line	Marks about one-half depth of body, rounder toward caudal.
nerka	[1] 8-12		Dark	Elliptical to oval	Immediately above line	Row of smaller blotches between parr marks and median dorsal line.
gairdneri [3]	[1] 9-12		Dark	Deep bars, narrower than interspaces.[4]		
trutta				Elliptical, of medium width.[4]	Low on body	Small red blotches between marks.
salar	10-11		Dark	Vertical bars wider than interspaces.		Do.
malma [1]	7-10			Roundish blotches.	On line.	
fontinalis	[5] 7-11	9.0		Large and pear-shaped.[4]		
namaycush [5]	9-11	9.9				
aureolus [5]	11-12	11.7				
marstoni [5]	10-15	12.3				
alpinus [5]	11-15	12.2				

[1] Chamberlain, (1907).
[2] Foerster and Pritchard, (1935b).
[3] Chamberlain (1907) says fry indistinguishable from *S. clarki.*
[4] Bacon (1954, text and plate).
[5] Counts include the incomplete bars; Vladykov (1954).

The young of *S. salar* and *trutta* are difficult to distinguish, as are those of *S. gairdneri* and *clarki.* The former agree in the small red blotches between the parr marks, while the latter two have no colored spots but agree in the light lateral band, which is less conspicuous in *clarki.* The hybridization experiments also show *trutta* closer to *salar* than to *gairdneri.*

The aforementioned relation of parr marks to anadromy is indicated by the retention of parr marks throughout life in some landlocked strains of anadromous species. Thus *Salmo gairdneri agua-bonita*, the golden trout, and *Salmo clarki seleniris*, the piute trout, retain their parr marks.

There are a few other color patterns which have from time to time been used to distinguish between certain species or groups. Because information on these color characteristics is lacking for all of the Salmonidae we shall merely mention the characteristic for the groups with such information.

Color of the mouth is used to distinguish *Oncorhynchus* (mouth black) from *Salmo gairdneri* and *clarki*, whose mouths are white (Snyder, 1940; Shapovalov, 1947).

Color of the roof of the mouth is given by Vladykov (1954) as black for *Salvelinus fontinalis*, blackish for *S. aureolus*, and white for *S. oquassa*, *S. marstoni*, *S. alpinus*, and *Cristivomer namaycush.*

ANADROMY

The degree of anadromy exhibited by various taxonomic groups (see Rounsefell, 1958) may well be of phylogenetic significance. Thus, when the degree of anadromy was scored for each species of Salmonidae according to a subjective rating of several criteria it was found that the most anadromous species belonged to *Oncorhynchus.* The next highest rating for anadromy belonged to *Salmo.* Only slight anadromy characterized *Salvelinus*, while *Cristivomer* was lacustrine. The ratings for anadromy are listed in the following table:

Taxon	Rating [1]	Lacustrine	Adfluvial	Fluvial	Anadromous		
					Optionally	Adaptively	Obligatory
Cristivomer	0	*namaycush*					
Salvelinus	7		*oquassa* *o. marstoni*				
	14		*alpinus* *a. aureolus*		*alpinus*		
	12-16		*fontinalis*	*fontinalis*	*fontinalis*		
	18			*malma*	*malma*		
Salmo	21		*trutta*	*trutta*	*trutta*		
	19-20		*clarki* *c. henshawi*	*clarki* *c. seleniris*	*clarki*		
	29		*gairdneri* *g. kamloops*	*gairdneri* *g. agua-bonita*	*gairdneri*		
	34		*salar* *s. sebago*		*salar*		
Oncorhynchus	40-44		*n. kennerlyi*			*nerka*	
	46					*kisutch*	
	47-50						*tshawytscha.*
	54-60						*keta.*
	56-60						*gorbuscha.*

[1] Degree of anadromy (Rounsefell, 1958: p. 180); the rating of a species is partly dependent on the existence of subspecies, which in some cases occupy a different habitat.

MERISTIC CHARACTERS

In using meristic characters to distinguish between any two populations there are certain things to bear in mind. Several investigators have established that in some species some of the meristic characters exhibit phenotypic variation induced by variations in environmental factors during early developmental stages. For a review of these studies see Tåning (1952) and Seymour (1959).

By incubating and rearing chinook salmon, *O. tshawytscha*, at constant temperatures, Seymour (1959) showed that the fish formed the lowest number of vertebrae at intermediate temperatures (45°–55° F.), and higher vertebral numbers at 40° and at 60°. He found, however, that this phenotypic variation was much less than the genotypic variation when lots of eggs from four rivers, the Sacramento, Green, Skagit, and Entiat, were incubated and the fish reared at several constant temperatures. The mean number of vertebraé for all temperatures was about 66 for the Sacramento, 68 for the Skagit, 69 for the Green, and 72 for the Entiat River. As the spawning season in different localities tends to conform to the optimum local conditions, the temperature-induced variation is probably of even less importance than these controlled experiments might suggest. The number of individuals with abnormal vertebrae increased in temperatures above 60° and below 40° F. Seymour also found that low oxygen content of the water during incubation increased the number of vertebrae.

Branchiostegal Rays

Most meristic data on Salmonidae have not been collected in such a manner, or are not sufficiently extensive, as to yield a reliable measure of the range of variation to be expected between samples taken in different years or in different localities. One of the best series of data is from Chamberlain (1907) for sockeye salmon from six streams in the southern portion of southeastern Alaska for the years 1903 and 1904. Since none of his samples had less than 100 individuals we have made an analysis of his data, shown in table 6, for the mean branchiostegal ray counts on 4,686 specimens.

The number of rays is usually higher on the left side as the left membrane normally overlaps the

TABLE 6.—*Mean count of branchiostegal rays in sockeye salmon, southeastern Alaska, 1903 and 1904*

Locality	Left side		Right side		Total		
	1904	1903	1904	1903	Left side	Right side	Both sides
Quadra	13.579	13.624	13.049	13.092	27.203	26.141	53.344
Yes Bay	13.986	13.930	13.329	13.343	27.916	26.672	54.588
Karta Bay	13.855	13.721	13.339	13.143	27.576	26.482	54.058
Dolomi	13.816	13.800	13.292	13.390	27.616	26.682	54.298
Nowiskay	13.963	13.840	13.384	13.280	27.803	26.664	54.467
Kegan	13.536	13.480	12.931	12.980	27.016	25.911	52.927
Total	82.735	82.395	79.324	79.228	165.130	158.552	323.682
Average:							
1904	162.059 $\bar{y}$=13.505				13.761	13.213	13.487
1903	161.623 $\bar{y}$=13.469						

NOTE.—Data from Chamberlain (1907); total of 4,686 specimens, samples of 100 to 513 individuals each.

right. Chamberlain states that "In no instance was a clearly defined case of right overlapping seen, though occasionally the right membrane carries the higher number of rays." Similarly, Vladykov (1954, p. 909) found the number of branchiostegals on the right side in all charrs somewhat smaller than on the left.

The analysis of table 6 follows.

Source of variation	D.F.	Sum of squares	Mean square	*F*
Total	23	2.423393	0.105365	
Between sides	1	1.802920	1.802920	503.047**
Between years	1	0.007921	0.007921	2.210 N.S.
Between localities	5	0.555203	0.111041	30.982**
Interaction (error)	16	0.057349	0.003584	

The significant difference in the mean number of rays between the left and right sides was confirmed, as well as a significant difference between localities, but the difference between years was very small.

Repeating this analysis, but employing only the number of rays on the left side, a significant difference is again shown between localities, but not between years. If we ignore the possibility of greater differences occurring between years, we still find a maximum mean difference for the left side of 0.506 rays between samples (13.986–13.480). This suggests use of great caution in forming conclusions about interspecific differences in a meristic character on the basis of small samples, especially if the samples are not geographically representative.

If one compares this mean branchiostegal count for *O. nerka* from southeastern Alaska with the average given by Foerster and Pritchard (1935a)

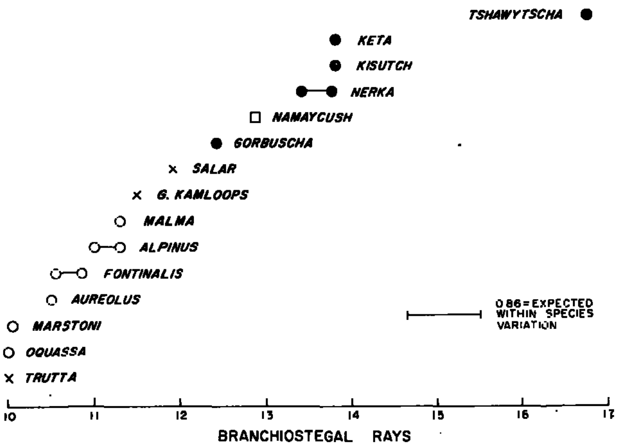

FIGURE 3.—Mean numbers of branchiostegal rays.

for British Columbia and Puget Sound the difference is 0.354. Considering that a difference of 0.506 was noted between adjacent localities in southeastern Alaska, it would seem logical to add this geographical difference of 0.354 to the previous difference of 0.506, which gives a difference of 0.860 rays that can be expected between means of samples of the same species.

The branchiostegal ray counts for various Salmonidae are summarized in table 7 and figure 3. If we apply to the other species the criterion found above for *nerka* of an expected "within species" difference of 0.86 rays between samples we find that the table clearly sets apart *O. tshawytscha*. The next three species of *Oncorhynchus*, *keta*, *kisutch*, and *nerka* are close together but separated from *gorbuscha*.

C. namaycush is clearly distinct from the remaining charrs.

Another interesting point is that *S. trutta* is quite separate from *salar* or *g. kamloops*. This is reminiscent of the position of *S. trutta* (in fig. 1) between the charrs and the other *Salmo*.

TABLE 7.—*Count of branchiostegal rays on left side in North American Salmonidae*

[x in frequency column indicates rays present, but no numbers given]

Species	Number of rays												Number of specimens	Mean number of rays	Standard error
	8	9	10	11	12	13	14	15	16	17	18	19			
Oncorhynchus:															
gorbuscha [1]			8	30	136	121	22	2					319	12.392	0.053
nerka [1]				2	22	128	106	17					275	13.415	.052
Do [2]				2	131	1,420	2,545	569	19				4,686	13.769	.010
kisutch [1]					1	51	50	25					127	13.780	.071
keta [1]					4	52	49	27	3				135	13.800	.077
tshawytscha						1	0	13	43	69	18	9	153	16.758	.083
Salmo salar [3]			x	x	x								65		
salar [4]													41	11.9	
gairdneri [5]			x	x	x										
g. kamloops [6]													213	11.51	.040
clarki [5]			x	x	x										
trutta [4]													41	10.0	
Salvelinus:															
fontinalis [7]		1	19	27	12								59	10.847	.098
Do [8]	1	21	190	193	45								450	10.578	.035
alpinus [7]			3	6	3								12	11.0	
Do [9]													37	11.3	.380
oquassa [7]			4										4	10.0	
aureolus [7]		2	13	17	2								34	10.559	.080
marstoni [7]		4	34	5									43	10.023	.103
malma [9]													57	11.3	.30
Cristivomer:															
namaycush [7]					6	28	2						36	12.889	.244

[1] Foerster and Pritchard (1935a); Puget Sound and British Columbia.
[2] Chamberlain (1907); southeastern Alaska.
[3] Kendall (1935, p. 137).
[4] McCrimmon (1949); eastern Canada.
[5] Shapovalov (1947).
[6] Mottley (1936); Kootenay Lake.
[7] Vladykov (1954).
[8] Wilder (1952); Nova Scotia and New Brunswick.
[9] DeLacy and Morton (1943); Karluk, Alaska.

Pyloric Caeca

Since more material is available for *Oncorhynchus* it has been considered first (table 8). The published material on caeca is usually listed by categories and since different authors have used different breaking points for their categories, some of their material may be listed slightly in error; thus, the number of caeca if listed from 96–105 would be given in table 8 under the category 95–104.

The material for *tshawytscha* is extremely variable but this is caused chiefly by the great difference between the counts for the Sacramento River

(Suisun Bay) and those for the Klamath River. These two samples by McGregor (1923) are the highest and lowest in caecal count. I suspect that this variability is caused by some extraneous factor. When the Klamath River counts are separated into those caught at Requa at the mouth of the river and those taken at the salmon counting weir, 170 miles upstream at Klamathon, the weir-caught salmon show a much lower count. Possibly, the upstream count was lowered on account of the atrophy of the digestive tract prior to spawning.

TABLE 8.—*Number of pyloric caeca in species of* Oncorhynchus

Number of caeca	Number of specimens of—											
	kisutch	*nerka*	*gorbuscha*					*tshawytscha*				
	Milne (1948) [1]	Milne (1948) [1]	Milne (1948) [1]	Pritchard (1945) [2]	Pritchard (1945) [3]	Pritchard (1945) [4]	Sum	Milne (1948) [1]	Townsend (1944) [5]	Townsend (1944) [6]	Townsend (1944) [7]	Townsend (1944) [8]
45–54		1										
55–64	1	6										
65–74	8	15										
75–84	3	30										
85–94	3	40						1				
95–104	1	27	1			5	6					
105–114	1	3	4	49	3	16	72			1		
115–124			7	116	23	65	211				1	4
125–134			8	148	22	95	273		5	7	5	17
135–144			12	119	21	76	228	1	8	14	4	26
145–154			4	77	16	54	151		12	12	21	32
155–164			4	21	8	26	59	1	10	26	9	17
165–174			1	7	2	6	16	2	7	26	11	14
175–184						3	3	1	6	22	11	4
185–194				2		1	3	1	2	6	4	3
195–204								1		4	3	1
205–214										2		
215–224			1				1			1	1	
225–234										1		
235–244									1	1		
245–254												
Number of specimens	17	122	42	539	95	347	1,023	8	51	123	70	118
Mean number of caeca	75.5	85.5	136.3	133.5	137	135.9	134.75	155.0	157.5	165.8	162.5	150.5

Number of caeca	Number of specimens of—							Percentage distribution				
	tshawytscha (con.)						*keta*	*kisutch*	*nerka*	*gorbuscha*	*tshawytscha*	*keta*
	McGregor (1923) [9]		McGregor (1923) [10]	Parker (1943) [11]	Parker (1943) [12]	Sum	Milne (1948) [1]					
	a	b										
45–54									0.8			
55–64								5.9	4.9			
65–74								47.1	12.3			
75–84								17.6	24.6			
85–94		1				2		17.6	32.8		0.2	
95–104		1				1		5.9	22.1	0.6	0.1	
105–114	2	3				6		5.9	2.5	7.0	0.7	
115–124	7	6			3	23				20.6	2.8	
125–134	12	6	2	7	7	69				26.7	8.3	
135–144	9	4	3	22	12	101				22.3	12.1	
145–154	9	3	8	40	14	150				14.8	18.0	
155–164	1		13	43	13	133				5.8	15.9	
165–174			10	48	25	143				1.6	17.1	
175–184			14	31	11	100	4			0.3	12.0	20
185–194	2		18	20	7	63	2			0.3	7.5	10
195–204			10	8	2	29	3				3.5	15
205–214			3	2	3	10	4				1.2	20
215–224						2	5			0.1	0.2	25
225–234						1	1				0.1	5
235–244						2					0.2	
245–254							1					5
Number of specimens	42	24	81	221	97	835	20					
Mean number of caeca	137.5	126.2	176	165.7	162.7	160.68	205.0					

[1] Skeena River, British Columbia.
[2] Queen Charlotte Islands (7 streams).
[3] Vancouver Island, Morrison Creek.
[4] Lower Fraser River (5 streams).
[5] Cowlitz River, Wash.
[6] Middle Fork, Willamette River, Oreg.
[7] McKenzie River, Oreg.
[8] South Santiam River, Oreg.
[9] Klamath River (a, at Requa, mouth of river; b, at Klamathon racks, 170 miles upstream).
[10] Sacramento River.
[11] Sacramento River.
[12] Sacramento and San Joaquin Rivers.

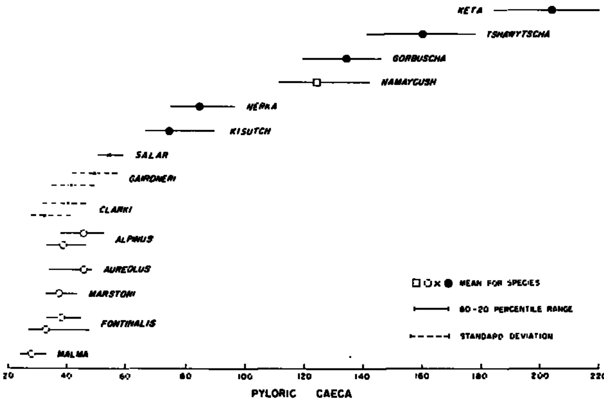

FIGURE 4.—Mean numbers of pyloric caeca. (Lines indicate the 20th and 80th interpercentile range.)

If we disregard McGregor's samples the intraspecific variation in the mean caecal count is small, ranging from 150.5 to 165.8 for *tshawytscha* and from 133.5 to 137 for *gorbuscha*. This is a small range in relation to that for the five species—from 75.5 for *kisutch* up to 205.0 for *keta*.

The data for the remaining genera are far less extensive so they are combined with the summary for *Oncorhynchus* in table 9. In figure 4 the means are given as well as the approximate 20th and 80th percentiles. Obviously, *Oncorhynchus* and *Cristivomer* differ markedly from *Salmo* and *Salvelinus* in number of caeca.

In number of pyloric caeca, as in number of branchiostegal rays, *C. namaycush* differs markedly from *Salvelinus* and is close to *Oncorhynchus*.

TABLE 9.—*Count of pyloric caeca in North American Salmonidae*

Species	Range in number [1]		Approximate percentiles		Mean number of caeca	Number of specimens
	Minimum	Maximum	Q20	Q80		
Oncorhynchus: [2]						
kisutch	55	114	67	90	75.5	17
nerka	45	114	75	97	85.5	122
gorbuscha	95	224	120	147	134.8	1,023
tshawytscha	85	244	142	179	160.7	835
keta	175	249	185	221	205.0	20
Salmo:						
salar [3]	40	74	(4)	(4)	55.4	561
gairdneri [5]	25	54	35	50	42	11
Do. [6]	39	61	------	------	50	16
clarki [6]	27	40	------	------	33	11
Do. [7]	23	60	------	------	40.3	71
Salvelinus:						
fontinalis [8]	20	49	33	45	38.4	30
Do. [9]	23	46	27	38	32.5	47
malma [9]	20	39	24	32	27.9	114
alpinus [9]	30	64	38	53	46.0	62
Do. [8]	20	59	33	47	39.1	16
aureolus [8]	30	[10] 99	34	49	45.9	35
oquassa [8]	------	------	------	------	39	1
marstoni [8]	20	49	33	44	37.7	34
Cristivomer:						
namaycush [9]	95	170	112	143	126.7	55

[1] Upper and lower limits of groups unless given by authors.
[2] References for *Oncorhynchus* in table 8.
[3] Belding (1940); eastern Canada.
[4] Standard deviation, 4.03.
[5] Milne (1948); Skeena River.
[6] Townsend (1944); Oregon.
[7] DeWitt (1954); northern California.
[8] Vladykov (1954).
[9] Morton and Miller (1954); presumably these data include counts for *malma* and *alpinus* by DeLacy and Morton (1943), Karluk, Alaska.
[10] Only 1 specimen beyond category of 70–79; distribution extremely skewed.

Fin Rays

The comparison of fin-ray counts is rendered difficult by differences in counting methods used by different investigators. For instance, for the anal fin counts of *O. nerka* in table 10, Foerster and Pritchard (1935a, p. 91) write—

> In counting fin rays only developed rays, those which had attained a length of one-half the length of the longest ray, were included. The remainder were considered as undeveloped. Care was taken to ensure that branched rays did not lead to error in the count.

Milne (1948) apparently used the same method since he comments (p. 73) concerning his difference in average count between 1946 and 1947—

> . . . it is possible although not probable, that during the first year (1946) less attention was focussed on omitting rays less than one-half the length of the fin or in counting branched rays as two with the result that a higher count might have been recorded in error for 1946.

Chamberlain (1907, p. 89) writes—

> In the fin-ray counts the totals of rudimentary and branched rays are used, but the terminal half ray, which varies greatly in development, is in all cases omitted.

It will be noted that the counts for *O. nerka* given by Chamberlain are about 3 rays higher than the others, owing doubtless to his inclusion of the rudimentary rays. A good summary of this difficulty is given by Vladykov (1954, p. 911), who writes—

> . . . there are technical difficulties in counting small simple rays in front of the dorsal and anal fins. The best way is to remove the skin and stain the rays with alizarin. In larger specimens the stained fins should be dissected and made transparent by placing in glycerine. To avoid error in counting these small rays in unstained specimens, some authors, as Kendall (1914, p. 24), counted only "fully-developed" rays in the dorsal and anal fins. Unfortunately there is no definition of the term "fully-developed." Some other authors count only branched rays, which are plainly seen even without staining with alizarin. Unfortunately the number of branched rays in younger fish (parr) is smaller than in older individuals of the same species . . . .

TABLE 10.—*Count of anal fin rays in* O. nerka

Locality	Number of specimens with fin ray count of—									Number of specimens	Mean number of rays	Year
	12	13	14	15	16	17	18	19	20			
Southeastern Alaska: [1]												
Quadra					2	56	277	167	8	[2] 510	18.24	1904
Do						65	276	146	10	497	18.20	1903
Yes Bay					3	82	322	97	5	509	18.04	1904
Do					1	42	207	49	1	300	18.02	1903
Karta Bay					1	133	307	71		512	17.88	1904
Do					1	114	268	37		420	17.81	1903
Kegan				1	6	150	315	38		510	17.75	1904
Do					2	32	56	8	2	100	17.76	1903
Dolomi					10	248	238	15		511	17.51	1904
Do					13	85	96	6		200	17.48	1903
Nowiskay				1	33	257	212	9	1	513	17.39	1904
Do					7	44	46	3		100	17.45	1903
Sum:												
1904				2	55	926	1,617	397	14	3,065	17.80	
1903					24	382	949	249	13	1,617	17.90	
Both years				2	79	1,308	2,620	646	27	4,682	17.84	
Unweighted average:												
1904											17.80	
1903											17.79	
Both years											17.80	
Skeena River, British Columbia: [3]												
Prince Rupert		1	4	36	60	1	1			103	15.57	1946
Do		3	27	39	17					86	14.81	1947
Moricetown		5	42	18	2					67	14.25	1946
Do		2	11	17	11		1			42	14.98	1947
Babine		5	14	8	3					30	14.30	1946
Do		1	9	4						14	14.21	1947
Lakelse		1	8	3						12	14.71	1946
Do	2	4	5	4						15	13.73	1947
Sum:												
1946		12	68	65	65	1	1			212	14.90	
1947	2	10	52	64	28		1			157	14.70	
Both years	2	22	120	129	93	1	2			369	14.81	
Unweighted average:												
1946											14.57	
1947											14.43	
Both years											14.50	
Southern British Columbia, and Puget Sound [4]		4	53	38	8					103	14.49	Mixed

[1] From Chamberlain (1907).

[2] Because published data by Chamberlain is in percentages a few of the samples reconverted to actual numbers differ slightly from original sample size, undoubtedly owing to rounding off of percentages.

[3] From Milne (1948).

[4] From Foerster and Pritchard (1935a).

In determining how much variation to expect between anal-ray counts within a species (table 10) we can only compare counts made by the same investigator. In Chamberlain's data, the maximum difference between sample means is 0.85 (18.24−17.39). In Milne's (1948) data we can compare only the 1947 data (see quotation above) which leaves a difference of 1.25 (14.98−13.73). Because of the small size of the Lakelse sample this difference may be too large.

A comparison of the means and ranges of the anal-ray count in table 11 shows that counts in all *Oncorhynchus* are definitely higher than in the other genera. *Salmo gairdneri* occupies an intermediate position between *Oncorhynchus* and the charrs.

For dorsal rays, as for the anal, counting methods differed between investigators. Table 10 indicates that Foerster and Pritchard (1935a) were counting about 3 less anal rays than Chamberlain was. The dorsal-ray count appears to vary somewhat less than the anal-ray count; thus, for Chamberlain's data on southeastern Alaska sockeye the maximum difference between sample means is 0.85 rays for the anal-fin count but only 0.51 for the dorsal count (table 12).

TABLE 11.—*Count of anal fin rays in North American Salmonidae*

[Counts adjusted to a complete count (see text); x indicates rays present in frequency column but no number given]

Species	Number of specimens with anal-ray count of—															Number of specimens	Mean number of rays
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		
Oncorhynchus:																	
nerka [1]								2	79	1,308	2,620	646	27			4,682	17.84
Do.[2]								2	22	120	129	93	1	2		369	17.81
Do.[3]									4	53	38	8				103	17.49
gorbuscha [2]										8	49	54	20			131	18.66
Do.[3]									4	34	190	76	3.			307	18.13
kisutch [2]								5	8	24	21	2				60	17.12
Do.[3]								4	37	55	10	3				109	16.73
keta [2]									1	5	18	12	2			38	18.24
Do.[3]									24	64	36	11	2			137	17.29
tshawytscha [2]									1	9	26	26	13	1		76	18.58
Do.[3]											18	60	20		1	99	19.05
Salmo:																	
gairdneri [4]						12	15	3	1							31	13.77
Do.[5]				x	x	x	x										
g. kamloops [6]																215	12.90
clarki [5]				x	x	x											
salar [7]		x	x	x												65	
trutta [8]		x	x	x													
Cristivomer:																	
namaycush [9]			2	12												14	10.86
Salvelinus:																	
fontinalis [10]		4	111	274	66											455	10.88
Do.[9]	3	8	9	2												22	9.46
oquassa [9]				1												1	11.00
marstoni [9]		5	15	16	2											38	10.39
aureolus [9]		8	13	3												24	9.79
alpinus [9]		8	7	3												18	9.72
Do.[11]																57	9.0(?)
malma [11]																63	9.0(?)

[1] Chamberlain (1907); southeastern Alaska; complete count made.
[2] Milne (1948); Skeena River; data adjusted by adding 3 rays (see table 10).
[3] Foerster and Pritchard (1935a); southern British Columbia and Puget Sound; data adjusted by adding 3 rays (see table 10).
[4] Milne (1948); Skeena River; data adjusted by adding 2 rays (McCrimmon (1949) says 1 rudimentary and 1 unbranched in *S. salar* and *S. trutta*).
[5] Shapovalov (1947); California; 2 rays added.
[6] Mottley (1936); Kootenay Lake, British Columbia; 2 rays added; standard deviation 0.5.
[7] Kendall (1935, p. 137); Penobscot River; 2 rays added; McCrimmon (1949).
[8] McCrimmon (1949); count includes rudimentary rays.
[9] Vladykov (1954); complete count.
[10] Wilder (1952); Nova Scotia; complete count.
[11] DeLacy and Morton (1943); Karluk, Alaska; count may be incomplete.

TABLE 12.—*Count of dorsal fin rays in* O. nerka

Locality	Number of specimens with fin ray count of—										Number of specimens	Mean number of rays	Year
	9	10	11	12	13	14	15	16	17	18			
Southeastern Alaska:[1]													
Quadra					12	225	265	11	1	1	515	14.55	1904
Do					13	212	256	19			500	14.56	1903
Yes Bay					9	211	274	13	2		509	14.58	1904
Do					5	109	183	2	1		300	14.62	1903
Karta Bay					3	162	312	35			512	14.74	1904
Do					2	122	265	30	1		420	14.78	1903
Kegan					13	277	211	10			511	14.43	1904
Do					2	57	40	1			100	14.40	1903
Dolomi				1	13	274	211	10			509	14.42	1904
Do					6	107	82	5			200	14.43	1903
Nowiskay					28	299	175	10			512	14.33	1904
Do					7	61	30	2			100	14.27	1903
Sum:													
1904				1	78	1,448	1,448	89	3	1	3,068	14.51	
1903					35	668.	856	59	2		1,620	14.58	
Both years				1	113	2,116	2,304	148	5	1	4,688	14.53	
Unweighted average:													
1904												14.51	
1903												14.51	
Southern British Columbia and Puget Sound [2]	1	12	66	23	2						104	11.13	

[1] Chamberlain, 1907. Because his published data are in percentages, a few of the reconstructed samples differ slightly in sample number.
[2] Foerster and Pritchard, (1935a); counts do not include all rays.

The meager data on dorsal-ray counts for all species are summarized in table 13, in which I have attempted to adjust all data to a complete count. This shows that the overlap in the frequency distributions of the dorsal-ray count is sufficiently large that many individuals of *Oncorhynchus* can not be distinguished from the charrs on the basis of dorsal-ray count.

It is worthy of note that *O. kisutch* is lower than the remaining *Oncorhynchus* in both anal- and dorsal-ray counts, suggesting a closer approach to the other genera. This coincides with the distant relation of *kisutch* to the other *Oncorhynchus* species as shown in figure 2.

TABLE 13.—*Count of dorsal fin rays in North American Salmonidae*

[Count adjusted to complete count (see text); x indicates rays present in frequency column, but numbers not given]

Species	Number of specimens with dorsal ray count of—										Number of specimen	Mean number of rays
	9	10	11	12	13	14	15	16	17	18		
Oncorhynchus:												
nerka [1]				1	113	2,116	2,304	148	5	1	4,688	14.53
Do.[2]				1	12	66	23	2			104	14.13
gorbuscha [2]					3	69	210	24			306	14.83
kisutch [2]				3	26	61	19				109	13.88
keta [2]					5	47	82	3			137	14.61
tshawytscha [2]					1	32	54	11	1		99	14.79
Salmo:												
salar [3]				x	x	x						
trutta [3]				x	x	x						
gairdneri [4]				x	x	x	x					
g. kamloops [5]											216	13.08
clarki [4]		x	x	x	x							
Cristivomer:												
namaycush [6]		2	8	4							14	11.14
Salvelinus:												
fontinalis [7]		2	90	268	93	2					455	12.01
Do.[6]	3	11	6	2							22	10.32
oquassa [6]				1							1	12.00
marstoni [6]		2	16	20	1						39	11.51
aureolus [6]	1	8	12	3							24	10.71
alpinus [6]	1	4	6	6							17	11.00
Do.[8]											57	10.00
malma [8]											64	10.50

[1] Chamberlain (1907), southeastern Alaska, complete count.
[2] Foerster and Pritchard (1935a), southern British Columbia and Puget sound, data adjusted by adding 3 rays.
[3] McCrimmon (1949).
[4] Shapovalov (1947), 2 rays added.
[5] Mottley (1936), Kootenay Lake, British Columbia (2 rays added, standard deviation, 0.5.
[6] Vladykov (1954), complete count.
[7] Wilder (1952), Nova Scotia, complete count.
[8] DeLacy and Morton (1943), Karluk, Alaska, count may be incomplete

Vertebrae

Because the methods used in counting vertebrae vary, it is difficult to place all counts on a common basis. Vladykov (1954) says that "all vertebrae were counted, including three of the hypural." DeLacy and Morton (1943) state "In the up-turned posterior end of the vertebral column the fused vertebrae were counted as one." Wilder (1952) says "In counting the vertebrae the urostyle was excluded."

Obviously, vertebral counts of different investigators may differ by as much as three vertebrae, according to their method of recording. To place all counts on a comparable basis (using the total count) some of the published counts must be increased by either two or three vertebrae. Data on vertebral counts are meager. Mottley (1937) gives data, shown in table 14, which include counts for all of the North American *Salmo*.

TABLE 14.—*Count of vertebrae in genus* Salmo

[Counts from Mottley, 1937]

Species	Number of specimens with vertebral count of—											Number of Specimens	Mean Number of vertebrae	Variance	Standard deviation	Standard error
	57	58	59	60	61	62	63	64	65	66	67					
gairdneri [1]							14	10	1			25	63.48	0.35	0.59	0.117
g. kamloops [2]						4	22	21	3			50	63.46	.53	.73	.104
Do.[3]								12				12	64.00	.0	.0	
Do.[4]						4	10	8	3			25	63.40	.83	.91	.183
Do.[5]						1	7	11	5	1		25	63.92	.83	.91	.182
Do.[6]						1	5	6	5			17	63.88	.86	.93	.225
Do.[7]							13	12				25	63.48	.26	.51	.102
Do.[8]							2	11	9	2	1	25	64.56	.85	.92	.184
g. whitehousei [9]						7	17	17	6	2		49	63.57	1.04	1.02	.146
Do.[10]						6	25	15	4			50	63.34	.44	.66	.093
Do.[11]							4	11	6	4		25	64.40	.92	.96	.191
clarki [11]					1	12	10	2				25	62.52	.50	.71	.143
trutta [12]	3	12	9	1								25	58.32	.56	.75	.150
salar [13]		5	15	4	1							25	59.04	.53	.73	.147

[1] Cowichan River, Vancouver Island, 1931; reared at Cowichan hatchery.
[2] Redfish Creek, 1930.
[3] Lardeau River, 1930.
[4] Penask Lake, 1930; reared at Nelson hatchery.
[5] Paul Creek, 1931.
[6] Paul Lake, 1931; reared at Lloyd's Creek hatchery.
[7] Paul Lake, 1932.
[8] Paul Lake, 1932; reared at Lloyd's Creek hatchery.
[9] 6-mile Lake, 1930.
[10] 6-mile Lake, 1930; reared at Nelson hatchery.
[11] Cottonwood Lake, 1930; reared at Nelson hatchery.
[12] Wisconsin stock, 1931; reared at Cowichan hatchery.
[13] From Thurso River, Scotland, 1933; reared at Cowichan hatchery.

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Mottley's counts are chiefly on fry or fingerlings 20 to 75 mm. in length. He stained the tissues with alizarin and counted the last stained centrum; since the urostyle did not stain it was not counted. He writes—

In making a comparison with the data of other investigators, however, it should be noted that in the caudal region, if the centra were stained as discrete blocks they were counted separately, if the separation was not complete they were counted as one.

Because the last two or three vertebrae were not always separated in the very small fish, he found a slight tendency toward a lower vertebral count in the smaller fry. Therefore, although his data can be used for interspecific comparisons in *Salmo*, they must be used cautiously in making comparisons with species of other genera.

The maximum mean difference between any 2 of the 11 samples of *Salmo gairdneri* is 1.22 vertebrae (64.56 minus 63.34). Obviously *S. gairdneri* and *clarki* differ significantly from either *salar* or *trutta*. Whether *clarki* and *gairdneri* or *salar* and *trutta* can be distinguished by vertebral count cannot be answered without additional data.

For the genus *Oncorhynchus*, all available counts except those for two small samples of adult *tshawytscha* were made by Foerster and Pritchard (1935b) on unstained young ranging from ⅞ inch to 3 inches in length. According to their statement it would appear that their counts do not include the three upturned vertebrae in the tail. Furthermore, there is some reason to suspect that the number counted is related to size. Table 15 gives the estimate of the statistical parameters for the five species and it may be noted that the variance was highest (7.84) for *nerka*, which has the smallest fry, and smallest (2.20 and 1.44, respectively) for *gorbuscha* and *tshawytscha*, which have the largest fry.

For *nerka*, the distribution of vertebral counts is negatively skewed so that the mean, 63.73, is about 2 counts below the mode (about 65.5). In the bottom part of table 15 are shown the resulting estimates of the parameters for four species of *Oncorhynchus*, when the counts causing this extreme negative skew are disregarded. Although *tshawytscha* shows the highest average count it would seem unwise to use vertebrae as a distinguishing character between species of *Oncorhynchus* until further data are available.

TABLE 15.—*Count of vertebrae in genus Oncorhynchus*

Number of vertebrae	Number of young (7/8 to 3 in.)[1]					Number of adult[2] *tshawytscha*		Sum of *tshawytscha*
	nerka	*kisutch*	*keta*	*gorbuscha*	*tshawytscha*	McKenzie River	Willamette River	
56	2							
57								
58	2	1						
59	3	1	1					
60	3	5		1				
61		5	3					
62	6	2	2					
63	9	18	2	1				
64	5	*21*	7	2				
65	12	10	8	14	1	1		2
66	*13*	5	*21*	11	1	6		7
67	7		17	*16*	2	2	7	11
68			6	4	15		9	24
69				1	*25*		6	31
70					18			18
71					6			6
72					1			1
Number of specimens	62	68	67	50	69	9	22	100
Mean number of vertebrae	63.73	63.29	65.57	66.00	69.10	66.11	67.95	68.58
Variance	7.84	3.11	3.61	2.20	1.44	.37	.62	1.98
Standard deviation	2.80	1.76	1.90	1.48	1.20	.61	.79	1.41
Standard error	.359	.214	.232	.210	.145	.204	.130	.141
Range[3]	62–67	62–66	62–68	63–69				
Number	52	56	63	49				
Mean	64.73	63.96	65.89	66.12				
Variance	2.54	1.02	2.04	1.48				
Standard deviation	1.59	1.01	1.43	1.22				
Standard error	.220	.142	.180	.174				

NOTE. Believe these are 3 vertebrae short of total number, as Foerster and Pritchard say, ". . . the segments beginning with the one immediately behind the skull and ending with the one immediately in front of the long vertebrae projecting up into the tail can be counted".

[1] Foerster and Pritchard (1935b); Cultus Lake, British Columbia, except *gorbuscha* which were from Masset Inlet, British Columbia.

[2] Townsend (1944); Oregon.

[3] Recapitulation of estimated sample parameters rejecting counts below 62 vertebrae (see text).

Vladykov (1954) does not give the source of his samples of *Salvelinus* (table 16) but comparison of the variances and ranges of his sample counts with those of Mottley suggests (table 17) that each of his individual samples may not be from one locality. The great variation in both ranges and variances casts doubt on the utility of making any but very broad generalizations from these available data, and also casts serious doubt on the utility of using normal probability estimates for describing distributions of discrete variables that have such a small range.

Salvelinus fontinalis, apparently, is significantly lower in vertebral count than either *C. namaycush* or other species of *Salvelinus*.

The extremely large variances (table 17) in some of the samples of *Oncorhynchus* are apparently caused by undercounting in the smaller fry. Therefore, in table 18 the adjusted values are used for four of the species of *Oncorhynchus*.

The values for the vertebral counts are summarized in figure 5, which shows that the count is highest in *Oncorhynchus* and lowest in *Salmo salar*, *S. trutta*, and *Salvelinus fontinalis*. All of the other species occupy an intermediate position with respect to this character.

TABLE 16.—*Count of vertebrae in* Salvelinus *and* Cristivomer

[x indicates vertebrae present in frequency column, but no numbers given]

Species	Number of specimens with vertebral count of —												Number of specimens	Mean number of vertebrae	Variance	Standard deviation	Standard error
	58	59	60	61	62	63	64	65	66	67	68	69					
S. alpinus [1]				1	1	4	0	3	2	5			16	64.81	4.16	2.04	0.510
Do.[2]								x	x	x	x	x	53	66.7	1.54	1.24	.17
S. marstoni [1]			1	1	1	5	13	7	2				30	63.90	1.69	1.30	.237
S. aureolus [1]				1	3	2	5	7					18	63.78	1.72	1.31	.308
S. oquassa [1]									1				1	66			
S. malma [2]					x	x	x	x	x				37	64.3	1.06	1.03	.17
S. fontinalis [1]	2	5	4	1	1								13	59.54	1.28	1.13	.312
Do.[3]													25	59.68			
Do.[4]													24	60.04			
C. namaycush [1]				1	8	7	4	2	1				23	63.04	1.49	1.22	.255

[1] Vladykov (1954).
[2] DeLacy and Morton (1943); Karluk River, Alaska; count increased by 2 to include all vertegrae.
[3] Wilder (1952); anadromous stock, Moser River, Nova Scotia; count increased by 3 to include all vertegrae.
[4] Wilder (1952); resident stock, Moser River, Nova Scotia; count increased by 3 to include all vertegrae.

TABLE 17.—*Ranges and variances of vertebral-count distributions*

[Presumably individual samples]

Count	Mottley (1937)	Townsend (1944)	DeLacy and Morton (1943)	Vladykov (1954)	Foerster and Pritchard (1935b)	All authors	Foerster and Pritchard adjusted [1]	Total using adjusted values
Range:								
0	1					1		1
1	1					1		1
2	1	2				3		3
3	8					8		8
4	3		2	2		7		8
5				1		1	1	2
6				2		2	2	4
7					1	1	1	1
8					1	1		
9					2	2		
10						0		
11					1	1		
Average range	2.8	2.0	4.0	5.0	8.0	4.3	5.6	3.7
Variance:								
0–0.40	3	1				4		4
0.41–0.80	5	1				6		6
0.81–1.20	6		1			7	2	9
1.21–1.60			1	2	1	4	1	4
1.61–2.00				2		2		2
2.01–2.40					1	1	1	1
2.41–2.80						0	1	1
2.81–3.20					1	1		
3.21–3.60						0		
3.61–4.00					1	1		
7.81–8.00					1	1		

[1] See bottom of table 15.

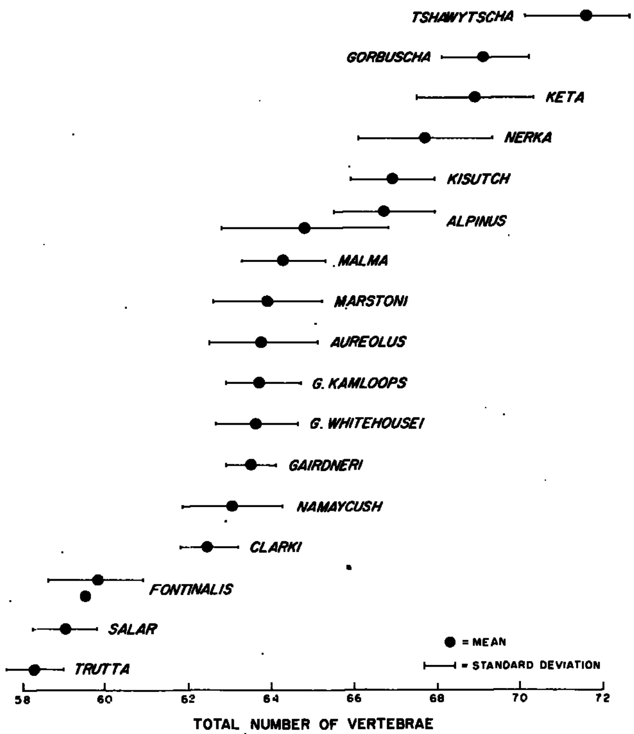

FIGURE 5.—Mean number of vertebrae.

Gill rakers

Counts of gill rakers made by different investigators are somewhat more comparable than are those of the vertebral counts. Even here, however, there seems to be some question concerning the comparability of counts between fish of different sizes. Thus Wilder (1952, p. 187) says that all the gill rakers on both limbs of the first gill arch were counted including rudimentary rakers sometimes present on large trout. He also writes that—

> The exceptionally low raker count for Bocabec trout is possibly a result of the low average size (115 mm. SL) of the fish in this sample as there is some evidence to indicate that raker count increases with size in salmonoids. . . .

Foerster and Pritchard (1935b) write concerning young *Oncorhynchus*—

> From Table 1, in which is presented a summary of the average numbers of gill-rakers for each ⅛-inch length group for all species, it appears that in the very early stages up to a length of 1¾ inches, there is an increase in the number of gill-rakers with increase in size. Such a change might be attributed to the overlooking of some of the rudimentary rakers on the very small arches, but in view of the fact that all counts were carefully made under comparatively high magnification, it is unlikely that such an error would have occurred.

The available gill-raker counts for *Oncorhynchus* are given in table 19. Obviously, the count of *O. nerka* is significantly higher than that of *gorbuscha*, which in turn is significantly higher than the counts of the remaining three species. Because the counts for *Oncorhynchus* are all for mature adults returning from the sea on a spawning migration, the factor of size of fish on gill-raker count may be entirely disregarded.

If we disregard the two smaller samples of *tshawytscha* (14 and 17 specimens), the largest differences between means of samples of the same

TABLE 18.—*Number of vertebrae in North American Salmonidae*

Species	Number of specimens	Mean number of vertebrae	Adjusted values [1]		Unadjusted range			Standard deviation [2]	Standard error [2]
			Number	Mean	Minimum	Maximum	Total		
Oncorhynchus:									
tshawytscha	100	71.58			68	75	7	1.41	0.141
gorbuscha	50	69.00	49	69.12	63	72	9	1.22	.174
keta	57	68.57	63	68.89	62	71	9	1.43	.180
nerka	62	66.73	52	67.73	59	70	11	1.59	.220
kisutch	68	66.29	56	66.96	61	69	8	1.01	.142
Salmo:									
gairdneri kamloops	179	63.75			62	67	5	.87	.065
g. whitehousei	124	63.65			62	66	4	.99	.090
gairdneri	25	63.48			63	65	2	.59	.117
clarki	25	62.52			61	64	3	.71	.143
salar	25	59.04			58	61	3	.73	.147
trutta	25	58.32			57	60	3	.75	.150
Salvelinus:									
alpinus	53	66.7			65	69	4	1.24	.17
Do	16	64.81			61	67	6	2.04	.510
malma	37	64.3			62	66	4	1.03	.17
marstoni	30	63.90			60	66	6	1.30	.237
aureolus	18	63.78			61	65	4	1.31	.308
fontinalis	13	59.54			58	62	4	1.13	.312
Do	49	59.86							
Cristivomer:									
namaycush	23	63.04			61	66	5	1.22	.255

[1] See bottom part of table 15 for treatment of these data.
[2] Based on adjusted values for *Oncorhynchus*.

NOTE.—Insofar as possible was put on basis of total number of vertebrae; for details see tables 15-17.

species are 1.78 for *gorbuscha* and 1.19 for *nerka*, which gives us some basis for judging the differences between the means of the much smaller samples of the other genera. The distributions of gill-raker count are given for *Salmo*, *Salvelinus*, and *Cristivomer* in table 20.

TABLE 19.—*Number of gill rakers on first gill arch (left side) in* Oncorhynchus

Number of gill rakers	Number of specimens of— *nerka*: Foerster and Pritchard (1935a) [1,2]	*nerka*: Milne (1948) [3,4]	*nerka*: Milne (1948) [3,5]	*nerka*: Milne (1948) [4,6]	*nerka*: Milne (1948) [5,6]	*nerka*: Sum	*gorbuscha*: Foerster and Pritchard (1935a) [7,8]	*gorbuscha*: Milne (1948) [4,6]	*gorbuscha*: Milne (1948) [5,6]	*gorbuscha*: Pritchard (1945) [9,10]	*gorbuscha*: Pritchard (1945) [10,11]	*gorbuscha*: Pritchard (1945) [12,13]	*gorbuscha*: Pritchard (1945) [12,14]	*gorbuscha*: Sum
24								2			1			3
25								2						2
26								3			1			4
27							3	8	1		6	2	2	22
28		1				1	20	14	1	1	18	10	18	82
29							70	22	4	13	65	22	91	287
30	1	1		1	1	4	111	24	11	23	118	38	146	471
31	2	3		1		6	79	9	15	37	110	23	125	398
32	6	2	3	2	1	14	30	2	8	21	55	8	62	186
33	18	8	6	5	4	41	5	1	5	3	10		10	34
34	51	19	16	9	6	101		1	1	1	1		3	7
35	74	15	20	23	9	141					1			1
36	72	15	14	24	22	147								
37	48	14	10	20	11	103								
38	32		8	10	10	60								
39	13			3	2	18								
Number of specimens	317	78	77	98	66	636	318	88	46	99	386	103	457	1497
Mean number of rakers	35.62	34.72	35.27	35.73	35.91	35.52	30.11	29.11	30.89	30.78	30.34	29.91	30.35	30.23

Number of gill rakers	Number of specimens of— *tshawytscha*: Foerster and Pritchard (1935a) [1,2]	*tshawytscha*: Milne (1948) [6,15]	*tshawytscha*: Townsend (1944) [16]	*tshawytscha*: Sum	*keta*: Foerster and Pritchard (1935a) [1,2]	*keta*: Milne (1948) [6,15]	*keta*: Sum	*kisutch*: Foerster and Pritchard (1935a) [1,17]	*kisutch*: Milne (1948) [6,15]	*kisutch*: Sum	Percentage distribution: *nerka*	*gorbuscha*	*tshawytscha*	*keta*	*kisutch*
19						1	1	4	1	5				0.5	3.3
20	3	4		7	2	2	4	3	5	8			3.8	2.1	5.3
21	10	1		11	15	5	20	14	8	22			6.0	10.6	14.6
22	32	3		35	36	14	50	37	7	44			19.0	26.6	29.1
23	45	6	2	53	60	13	73	50	5	55			28.8	38.8	36.4
24	43		4	47	34	2	36	13		13		0.2	25.5	19.1	8.6
25	12		6	18	3		3	14		4		0.1	9.8	1.6	2.6
26	6		1	7	1		1					0.3	3.8	0.5	
27	1	2	1	4								1.5	2.2		
28	1	1		2							0.2	5.5	1.1		
29												19.2			
30											0.6	31.5			
31											0.9	26.6			
32											2.2	12.4			
33											6.4	2.3			
34											15.9	0.5			
35											22.2	0.1			
36											23.1				
37											16.2				
38											9.4				
39											2.8				
Number of specimens	153	17	14	184	151	37	188	125	26	151					
Mean number of rakers	23.22	22.76	24.64	23.28	22.81	22.14	22.68	22.45	21.38	22.26					

[1] Puget Sound to Butedale, British Columbia.
[2] 1925, 1926, 1934.
[3] Prince Rupert, British Columbia.
[4] 1946.
[5] 1947.
[6] Skeena River and tributaries, British Columbia.
[7] Fraser River to northern British Columbia.
[8] 1928, 1930, 1932, 1934.
[9] Morrison Creek, Vancouver Island, British Columbia.
[10] 1941.
[11] Four tributaries of lower Fraser River, British Columbia.
[12] 1940.
[13] Two Moresby Island streams, Queen Charlotte Islands, British Columbia.
[14] Five streams in Masset Inlet, Graham Island, Queen Charlotte Islands, British Columbia.
[15] 1946, 1947.
[16] McKenzie River, Oregon.
[17] 1934.

TABLE 20.—*Count of gill rakers on first gill arch, left side, in* Salmo, Salvelinus, *and* Cristivomer

[x indicates gill rakers present in frequency column, but numbers not given]

Species	Number of specimens	Number of specimens with raker count of—														Mean number of rakers
		14	15	16	17	18	19	20	21	22	23	24	25	26	27	
Salmo:																
salar [1]	65				x	x	x	x	x							
Do.[2]	41															19.8
trutta [2]	41															17.0
gairdneri [3]	28			1		1	10	9	5	2						19.75
g. kamloops [4]	214															19.84
clarki [5]		x	x	x	x	x	x	x	x							
Salvelinus:																
alpinus [6]	9				1	1	1	1	2		1			1	1	21.3
Do.[7]	71								x	x	x	x	x	x		23.4
malma [7]	62		x	x	x	x	x	x	x	x						18.1
oquassa [6]	1									1						
marstoni [6]	38					2	5	13	12	5	1					20.4
aureolus [6]	16		1	4	1	2	3	1	2		1	1				18.6
fontinalis [6]	50			15	13	9	5	4	2	2						17.7
Do.[8]	171	1	10	31	53	42	28	6								17.36
Do.[9]	150	2	14	35	35	33	20	10	1							17.25
Do.[10]	29	2	2	10	6	5	3	1								16.79
Total *fontinalis*	400	5	26	91	107	89	56	21	3	2						17.32
Cristivomer namaycush [6]	25						7	10	9		1					20.2

[1] Kendall (1935); Penobscot River.
[2] McCrimmon (1949).
[3] Milne (1948); Skeena River, British Columbia.
[4] Mottley (1936); Kootenay Lake, British Columbia.
[5] Shapovalov (1947).
[6] Vladykov (1954).
[7] DeLacy and Morton (1943); Karluk River, Alaska.
[8] Wilder (1952); anadromous stock, Moser River, Nova Scotia.
[9] Wilder (1952); resident stock, Moser River, Nova Scotia.
[10] Wilder (1952); from 3 brooks in Nova Scotia. Sample from Bocabec Brook in New Brunswick omitted because of small size of the fish.

The gill-raker counts of tables 19 and 20 are summarized in table 21, in which I have endeavored to give some indication of dispersion. Many of the samples were so small, with the distribution either discontinuous or skewed, that the standard deviation was discarded and instead I have shown the range and the interpercentile range from the 80th to the 20th percentile (see fig. 6).

It is interesting to note that *trutta* shows the lowest average for gill rakers (fig. 6), as it also does for branchiostegal rays and vertebrae (fig. 3 and 5). *Fontinalis*, which is next to the bottom in gill-raker count, occupies the same position for number of pyloric caeca and is quite low in number of branchiostegal rays and vertebrae.

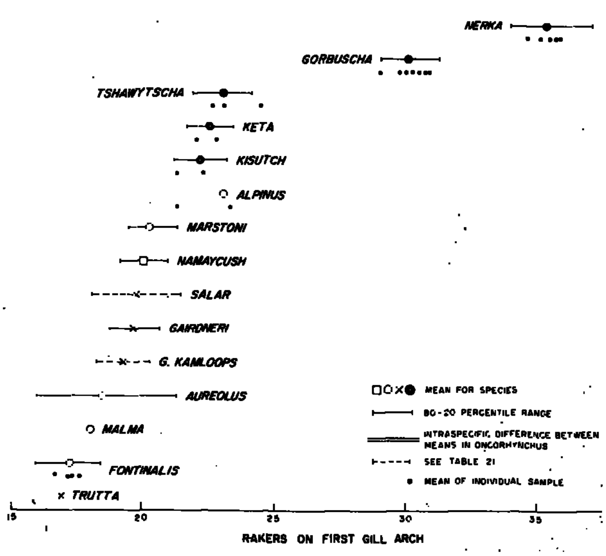

FIGURE 6.—Gill rakers on first gill arch.

The question of gill rakers on other than the first gill arch will be discussed later.

Scales

Although scale counts are widely used in taxonomic work they must be used cautiously because of the variation in counting practice among different investigators. Neave (1943) gives an excellent discussion of the various counting methods in vogue. One difficulty arises from the failure of many authors to recognize that the number of scales in the lateral line does not usually correspond either to the number of diagonal (oblique) rows just above the lateral line or to the number of diagonal rows counted along any horizontal row several rows above the lateral line. As a result many published data on the count of lateral-line scales, or "scales along the lateral line," actually refer to a count of diagonal rows made either just above the lateral line (usually a somewhat higher count) or of diagonal rows counted several longitudinal rows above the lateral line (usually a still higher count).

Some investigators have varied these practices by counting the lateral-line tubes or sensory pores and considering them equal in number to lateral-line scales. A fifth method has been to count the rows of diagonal scales 10 or 15 rows above the

TABLE 21.—*Summary of gill-raker count of North American Salmonidae*

[First gill arch, left side]

Species	Number of specimens	Mean number of gill rakers	Range		Percentile			Total range
			Minimum	Maximum	20	80	80–20	
Oncorhynchus:								
nerka	636	35.52	28	39	34.10	37.32	3.12	11
gorbuscha	1,497	30.23	24	35	29.11	31.35	2.24	11
tshawytscha	184	23.28	20	28	22.04	24.28	2.24	8
keta	188	22.68	19	26	21.75	23.56	1.81	7
kisutch	151	22.26	19	25	21.28	23.26	1.98	6
Salmo:								
salar	41	19.8	17	21	[1] (18.1)	[1] (21.5)	[1] 3.36	4
trutta	41	17.0						
gairdneri	28	19.75	16	22	18.86	20.78	1.92	6
g. kamloops	214	19.34			[2] (18.4)	[2] (20.3)		
clarki			14	21				7
Salvelinus:								
alpinus [3]	9	21.3	17	27	18.5	25.5	7.00	10
Do.[4]	71	23.4	21	26				
malma	62	18.1	15	22				
marstoni	38	20.4	18	23	19.55	21.37	1.82	5
aureolus	16	18.6	15	24	16.05	21.40	5.35	9
ontinalis [3]	50	17.7	16	22	16.17	19.10	2.93	6
Do.[5]	171	17.36	14	20	16.25	18.50	2.25	6
Do.[6]	150	17.25	14	21	15.90	18.55	2.65	7
Do.[7]	29	16.79	14	20	15.68	18.14	2.46	6
Total, *fontinalis*	400	17.32	14	22	16.03	18.54	2.51	8
Cristivomer:								
namaycush	27	20.2	19	23	19.27	20.99	1.72	4

[1] Standard deviation of 1.6 multiplied by 2.1. McCrimmon (1949) gives 1.6 as standard error of mean for *salar* and 0.01 as standard error of mean for *trutta*. The first must be standard deviation, the second is improbably small since standard deviation would be only 0.06.

[2] Assuming same interpercentile range as for *S. gairdneri* above.

[3] Eastern Canada.

[4] Karluk River, Alaska.

[5] Anadromous stock, Moser River, Nova Scotia.

[6] Resident stock, Moser River, Nova Scotia.

[7] Three small brooks in Nova Scotia.

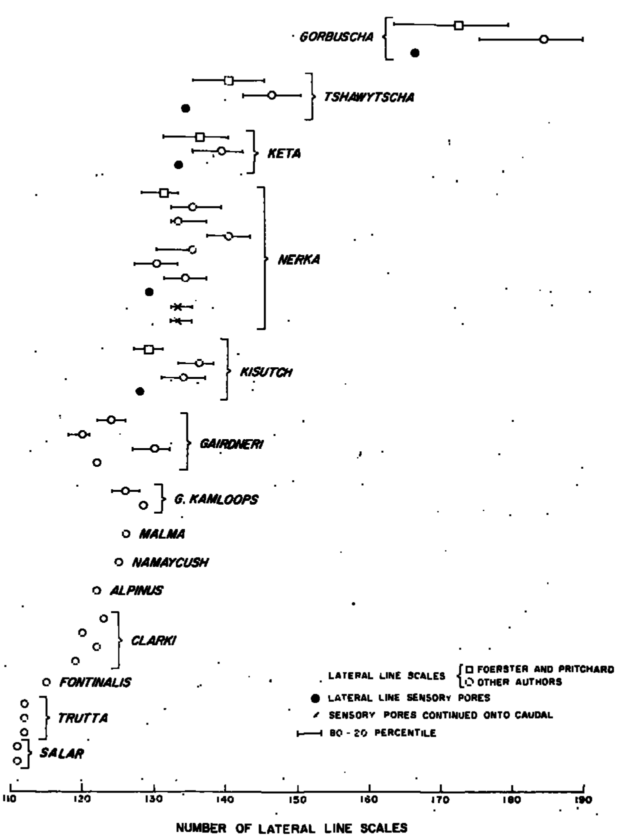

FIGURE 7.—Number of lateral-line scales.

lateral line from the gill aperture to the adipose fin and, then, to continue the count at a lower level from the adipose fin to the caudal. The five methods are briefly summarized as follows, in the order of usually increasing count:

1. Number of sensory pores on lateral line.
2. Number of scales on lateral line.
3. Number of diagonal scale rows in the horizontal row just above the lateral line.
4. Number of diagonal scale rows from top of gill aperture to caudal.
5. Number of diagonal scale rows from top of gill aperture to caudal, counting on a lower horizontal row posterior to adipose fin.

Most investigators terminate the count at the base of the caudal fin (standard length), but some count the scales that extend on to the caudal fin.

Available counts of lateral-line scales (methods 1 and 2) are summarized in table 22 and in figure 7.

It is obvious from figure 7 that the variation between the mean numbers of lateral-line scales from different localities (and perhaps between counts by different investigators) is so great that only a few of the species can be separated by this character. However, there is a general trend with species of *Oncorhynchus* the highest, and *fontinalis*, *salar*, and *trutta* the lowest counts.

TABLE 22.—*Counts of scales in lateral line of North American Salmonidae*

Species	Number of specimens	Mean number of scales	Range			Percentile			Year
			Minimum	Maximum	Total	20	80	80–20	
Oncorhynchus:									
gorbuscha [1]	254	172	148	198	50	163	179	16	
Do [2]	41	184	160	198	38	175	189	14	1946–47
Do [3]	3	166	147	180	33				
tshawytscha [1]	133	140	130	153	23	135	145	10	
Do [2]	41	146	130	165	35	142	150	8	1946–47
Do [3]	9	134	130	138	8				
keta [1]	155	136	124	153	29	131	140	9	
Do [2]	27	139	130	147	17	135	142	7	1946–47
Do [3]	6	133	129	139					
nerka [1]	145	131	124	138	14	128	133	5	
Do [4]	50	135	127	141	14	132	138	6	1946
Do [4]	76	133	130	141	11	132	137	5	1947
Do [5]	46	140	124	150	26	137	143	6	1946
Do [5]	42	135	124	141	17	130	135	5	1947
Do [6]	37	130	124	138	14	127	133	6	1946–47
Do [7]	20	134	127	141	14	131	137	6	1946–47
Do [3]	10	129	122	135					
Do [8]	3,068	133.1	126	143	17	132	135	3	1904
Do [8]	1,612	133.3	127	141	14	132	135	3	1903
kisutch [1]	127	129	121	138	17	127	131	4	
Do [2]	27	136	130	144	14	133	138	5	1946
Do [2]	24	134	130	141	11	131	137	6	1947
Do [3]	10	128	123	132	9				
Salmo:									
salar [9]	11	111	106	113	7				
Do [10]	41	111							
gairdneri [11]	122	124	119	131	12	122	126	4	
Do [12]	61	120	114	124	10	118	121	3	
Do [2]	23	130	124	138	14	127	132	5	1946–47
Do [13]	11	122	119	125	6				
g. kamloops [14]	25	126	121	130	9	124	128	4	
Do [9]	1	128							
clarki [15]	50	123	116	133	17	120	126	6	
Do [16]	30	120	116	126	10	117	122	5	
Do [17]	6	122	120	129	9				
Do [18]	13	119	116	126	10				
trutta [9]	11	112	107	117	10				
Do [12]	25	112	105	116	11	110	114	4	
Do [10]	41	112							
Cristivomer:									
namaycush [3]	19	125	121	130	9				
Salvelinus:									
alpinus [3]	12	122	111	130	19				
fontinalis [3]	28	115	109	127	18				
malma [3]	18	126	120	131	11				

[1] Foerster and Pritchard (1935a); Fraser River to northern British Columbia.
[2] Milne (1948); Skeena River, British Columbia.
[3] Morton and Miller (1954); count is of sensory pores.
[4] Milne (1948); Prince Rupert, British Columbia.
[5] Milne (1948); Moricetown, Skeena River, British Columbia.
[6] Milne (1948); Babine Lake, Skeena River, British Columbia, in 1946 and 1947.
[7] Milne (1948); Lakelse Lake, Skeena River, British Columbia, in 1946 and 1947.
[8] Chamberlain (1907); tubes on lateral line continued onto caudal for 6 localities in southeastern Alaska.
[9] Morton and Miller (1954); count is of lateral line scales.
[10] McCrimmon (1949).
[11] Neave (1943); anadromous stock, Cowichan River, British Columbia.
[12] Neave (1943); resident stock, Cowichan River, British Columbia.
[13] Morton and Miller (1954); resident stock, Rush Creek, Modoc County, Calif.
[14] Neave (1943).
[15] Neave (1943); reared at Cowichan Lake Hatchery, Vancouver Island, British Columbia.
[16] Neave (1943); reared at Veitch Creek Hatchery, Vancouver Island, British Columbia.
[17] Morton and Miller (1954); coastal strains of Oregon and Washington.
[18] Morton and Miller (1954); *S. c. pleuriticus* from Colorado River Basin.

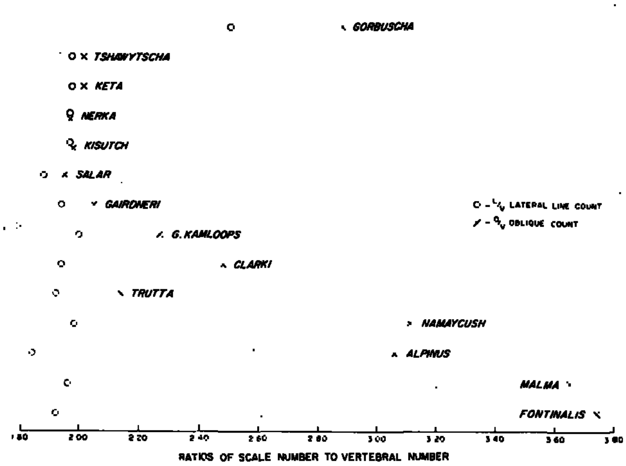

FIGURE 8.—Relation between numbers of vertebrae and scales.

Before commenting further on this character, in table 23 we have compiled the numbers of oblique scale rows counted (with exceptions noted) along the first row of scales above the lateral line. In discussing the lateral scale count, it is instructive to compare the results of counts made on the lateral line and counts made one row (or more) above the lateral line. This comparison is shown in table 24 and figure 8.

It may be noted in comparing the number of vertebrae (fig. 5) with the number of lateral-line scales (fig. 7) that the different species maintain approximately the same ranking in the two characters (see table 24). Even though for several of the species the vertebral counts and scale counts are not all—in some cases none—from the same

TABLE 23.—*Number of diagonal (oblique) scale rows in first row above the lateral line in North American Salmonidae*

Species	Number of specimens	Mean number of rows	Range			Percentile		
			Minimum	Maximum	Total	20	80	80–20
Oncorhynchus:								
gorbuscha [1]	195	199	169	231	62	190	209	19
Do [2]	8	213	194	226				
tshawytscha [1]	110	143	133	153	20	138	148	10
Do [2]	47	149	138	158				
keta [1]	135	139	130	153	23	136	142	6
Do [2]	5	141	137	145	8			
nerka [1]	173	133	124	144	20	129	137	8
Do [2]	16	138	130	146				
kisutch [1]	124	131	118	147	29	127	134	7
Do [2]	9	138	133	145				
Salmo:								
salar [2]	11	115	111	118				
gairdneri [3]	122	132	123	159	36	128	136	8
Do [4]	61	122	115	130	15	119	125	6
Do [5]	8	137	125	149	24			
Do [6]	11	154	146	164	18			
g. kamloops [7]	25	143	130	155	25	134	150	16
Do [2]	1	148						
Do [8]	216	145	130	160	30	140	151	11
clarki [7]	50	160	146	177	31	154	166	12
Do [9]	30	137	122	154	32	128	143	15
Do [10]	6	165	157	170	13			
Do [11]	13	191	180	208	28			
Do [12]	78	152	122	188	66			
trutta [2]	11	125	120	131	11			
Do [4]	25	125	116	136	20	121	131	10
Cristivomer:								
namaycush [2]	30	196	175	228	53			
Salvelinus:								
alpinus [2]	28	195	154	236	82			
Do [13]	15	217	195	236	41			
malma [2]	31	231	186	254	68			
Do [13]	13	243	218	254	36			
fontinalis [2]	25	218	197	236	39			
Do [14]	83	225	200	243	43	217	232	15

[1] Foerster and Pritchard (1935a); Fraser River to northern British Columbia.
[2] Morton and Miller (1954).
[3] Neave (1943); anadromous stock, Cowichan River, British Columbia.
[4] Neave (1943); resident stock, Cowichan River, British Columbia.
[5] Morton and Miller (1954); anadromous stock, Clackamas River, Oreg.
[6] Morton and Miller (1954); resident stock, Rush Creek, Modoc County, Calif.
[7] Neave (1943); reared at Cowichan Hatchery, Vancouver Island, British Columbia.
[8] Mottley (1934a); Kootenay Lake, several rows above lateral line.
[9] Neave (1943); reared at Veitch Creek Hatchery, Vancouver Island, British Columbia.
[10] Morton and Miller (1954); coastal streams of Oregon and Washington.
[11] Morton and Miller (1954); *S. c. pleuriticus*, from Colorado River Basin.
[12] DeWitt (1954); northern California coastal streams, counted along second scale row above lateral line.
[13] DeLacy and Morton (1943); Karluk Lake, Alaska.
[14] Wilder (1952); Moser River, Nova Scotia, count is from posterior margin of head to end of vertebral column (presumably several scale rows above the lateral line).

TABLE 24.—*Comparison of number of vertebrae and number of lateral-line scales, in North American Salmonidae*

Species	Mean number of—			L/V	O/V
	Vertebrae [1] (V)	Lateral-line scales [2] (L)	Scales in first row above lateral line (O)		
Oncorhynchus:					
gorbuscha	69. 12	173. 7	199. 6	2. 51	2. 89
tshawytscha	71. 58	141. 4	144. 8	1. 98	2. 02
keta	68. 89	136. 4	139. 1	1. 98	2. 02
nerka	67. 73	133. 3	133. 4	1. 97	1. 97
kisutch	66. 29	130. 7	131. 5	1. 97	1. 98
Salmo:					
salar	59. 04	111. 0	115. 0	1. 88	1. 95
gairdneri	63. 48	123. 4	130. 4	1. 94	2. 05
g. kamloops	63. 75	126. 1	144. 8	2. 00	2. 27
clarki	62. 52	121. 5	155. 0	1. 94	2. 48
trutta	58. 32	112. 0	125. 0	1. 92	2. 14
Cristivomer: namaycush	63. 04	125. 0	196. 0	1. 98	3. 11
Salvelinus:					
alpinus	66. 26	122. 0	202. 7	1. 84	3. 06
malma	64. 3	126. 0	234. 5	1. 96	3. 65
fontinalis	59. 79	115. 0	223. 4	1. 92	3. 74

[1] From table 18, weighted means.
[2] Weighted mean, excluding counts of sensory pores where lateral-line scale count is available.

samples or localities, the scale count (L) closely approaches twice the vertebral count (V) with one notable exception. The lateral-line scale count for *O. gorbuscha* is 2.5 times the vertebral count.

Neave (1943) noted this anomaly in *O. gorbuscha* and wrote—

> After examining a few small pink salmon fingerlings the present writer believes that the first scale papillae show the same distribution as in other species but that subsequently papillae develop between the primary members of the lateral line series, as well as dorsad and ventrad to the latter. This development can perhaps be correlated with the comparatively large size attained by this species before scale formation begins, resulting in a wider spacing between the sense organs and thus leaving room for the establishment of papillae.

This close relation (except in *gorbuscha*) between vertebral count and lateral-line scale count (approximately twice the verterbral count) is depicted in figure 8. Since these two characters are not independent they should not be used independently in any racial analysis involving a "character" index. The relation between number of vertebrae and number of oblique scale rows (O/V in fig. 8) on the other hand shows that there is a wide variation in the degree of branching of the lateral-line scale papillae: *malma* and *fontinalis* with an O/V ratio of 3.65 and 3.74, respectively, represent the extreme in fine scaling; *alpinus* and *namaycush* with O/V ratios of 3.06 and 3.11 form another distinct group; *gorbuscha*, with an increase in both types of scale counts, occupies a unique position. All of the species of *Salmo* show a slight to moderate increase in the number of oblique scale rows over the number of lateral-line scales.

Surprisingly, in view of the position of *gorbuscha*, the other species of *Oncorhynchus* show no detectable increase in number of oblique scale rows over their lateral-line scale counts.

The number of horizontal scale rows is available for so few species that counts for all genera are combined in table 25. The data for *Salmo salar* and *S. trutta* differ in the method of counting and these species cannot be compared with the others. The published values of 0.82 and 0.16, given presumably as standard errors of the mean for *salar* and *trutta*, differ widely. This suggests strongly that the number of specimens whose scales were counted (at least for *salar*) was much less than the 41 given by McCrimmon (1949). It is therefore doubtful whether the means for the two species should be considered significantly different without additional data.

TABLE 25.—*Number of horizontal scale rows in certain species of Salmonidae*

Species	Number of specimens	Mean number of rows	Range: Minimum	Range: Maximum	Range: Total	Percentile: 20	Percentile: 80	Percentile: 80–20	Year
			FROM ANTERIOR OF DORSAL FIN TO LATERAL LINE						
Oncorhynchus:									
gorbuscha [1]	320	34.3	26	40	14	32	37	5	----------
Do.[2]	16	33.4	27	37	10	32	35	3	1946
Do.[2]	25	36.7	33	40	7	35	38	3	1947
tshawytscha [1]	135	30.8	27	37	10	29	33	4	----------
Do.[2]	21	30.9	23	37	14	30	32	2	1946
Do.[2]	16	30.7	26	35	9	30	32	2	1947
kisutch [1]	127	26.5	23	31	8	25	28	3	----------
Do.[2]	25	27.4	24	31	7	25	29	4	1946
Do.[2]	22	27.5	23	30	7	26	30	4	1947
keta [1]	154	22.9	19	31	12	21	25	4	----------
Do.[2]	14	25.5	22	32	10	24	27	3	1946
Do.[2]	12	24.1	22	26	4	23	26	3	1947
nerka [1]	183	21.8	18	26	8	21	23	2	----------
Do.[3]	47	22.5	18	24	6	20	23	3	1946
Do.[3]	76	22.4	19	27	8	21	23	2	1947
Do.[4]	63	22.8	21	26	5	22	24	2	1946
Do.[4]	16	22.2	20	24	4	22	24	2	1947
Do.[5]	22	22.0	19	24	5	21	23	2	1946–47
Do.[6]	16	23.6	22	26	4	23	24	1	1946–47
Salmo:									
gairdneri [2]	23	25.5	22	30	8	23	27	4	1946–47
Salvelinus:									
malma [7]	15	42.0	----------	----------	----------	----------	----------	[8] 2.8	1939–41
alpinus [7]	15	34.0	----------	----------	----------	----------	----------	[8] 3.7	1939–41
			FROM ANTERIOR OF VENTRAL (PELVIC) FIN TO LATERAL LINE						
Oncorhynchus:									
gorbuscha [1]	319	32.4	25	40	15	30	35	5	----------
tshawytscha [1]	109	30.0	23	39	16	27	33	6	----------
kisutch [1]	127	25.7	19	37	18	24	28	4	----------
nerka [1]	113	21.5	17	27	10	20	22	2	----------
keta [1]	155	21.4	17	27	10	19	24	5	----------
Salvelinus:									
malma [7]	15	42.1	----------	----------	----------	----------	----------	[8] 2.8	1939–41
alpinus [7]	15	35.7	----------	----------	----------	----------	----------	[8] 3.7	1939–41
			FROM POSTERIOR BASE OF ADIPOSE FIN TO LATERAL LINE						
Salmo:									
salar [9]	41	10.8	----------	----------	----------	----------	----------	[10] 0.82	----------
trutta [9]	41	15.2	----------	----------	----------	----------	----------	[10] 0.16	----------

[1] Foerster and Pritchard (1935a); Fraser River to northern British Columbia.
[2] Milne (1948); Skeena River, British Columbia.
[3] Milne (1948); Prince Rupert, British Columbia.
[4] Milne (1948); Moricetown, Skeena River, British Columbia.
[5] Milne (1948); Babine Lake, Skeena River, British Columbia.
[6] Milne (1948); Lakelse Lake, Skeena River, British Columbia.
[7] DeLacy and Morton (1943); Karluk Lake, Alaska.
[8] Standard deviation.
[9] McCrimmon (1949).
[10] These values are presumably the standard error of the mean, but for *salar* the error is inexplicably large if the number of specimens is 41 as stated by McCrimmon (1949, p. 11).

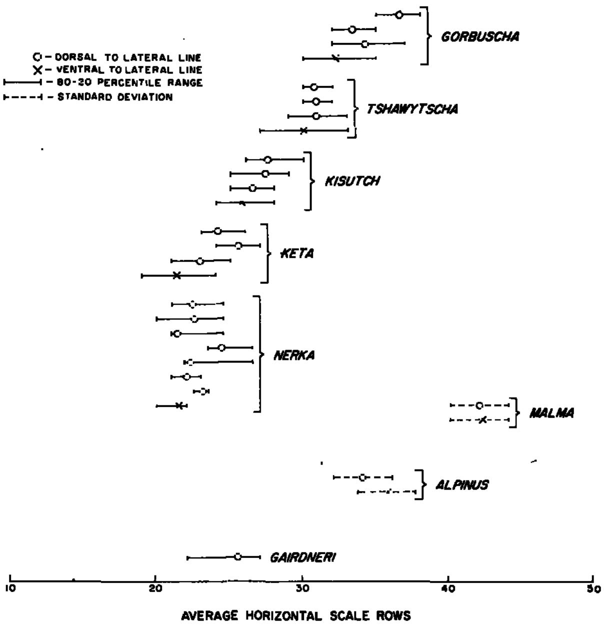

FIGURE 9.—Number of horizontal scale rows.

The average horizontal scale counts for *Oncorhynchus*, two species of *Salvelinus*, and *Salmo gairdneri* are shown in figure 9. *Malma* has the largest number, followed by *alpinus* and *gorbuscha*. The variation in number of scales within species is large, the maximum between means for *gorbuscha* being 3.3 in the number of scale rows above the lateral line.

Despite large differences in the sample means a definite trend exists in *Oncorhynchus* from the fine-scaled *gorbuscha* to the relatively coarse-scaled *keta* and *nerka*.

ANALYSIS OF MERISTIC CHARACTERS

All meristic characters were placed on a common basis to facilitate their comparison. Such a basis was established by determining the lowest and highest species means for any given character and then using the numerical difference between the two means as a yardstick. The lowest mean has been rated as 0, the highest as 10, and the intermediate means have been rated in between according to their position on the scale. The ranking of characters is given by species in table 26.

As explained earlier, not all of these characters are independent variables. Therefore, if we use two closely correlated characters in attempting to weigh differences between species from several characters, we are in effect giving double weight to the same measure. Figures 10 to 12 show the close correlation between three pairs of characters.

To obtain a joint ranking of these pairs of correlated characters, the rankings were adjusted (table 27) according to a correction factor (table 26) to equalize the average ranking for the species with available data. After obtaining the joint rankings for three pairs of correlated meristic characters, we are left with six presumably independent meristic rankings, which are listed by species in table 28.

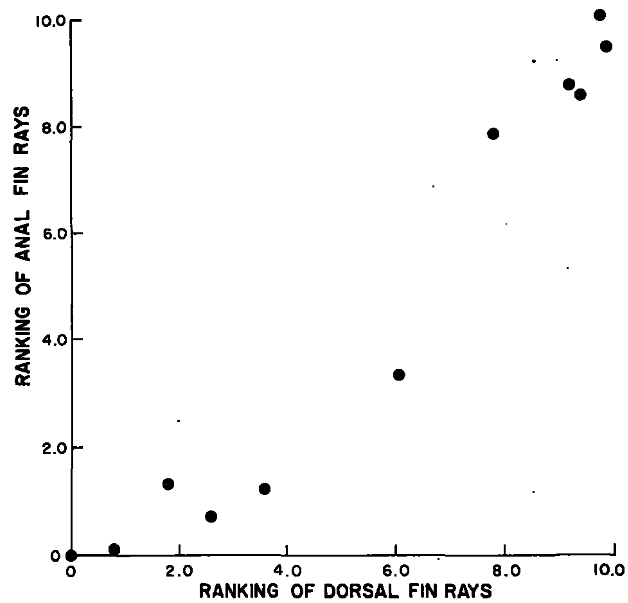

FIGURE 10.—Relation between dorsal and anal fin rays.

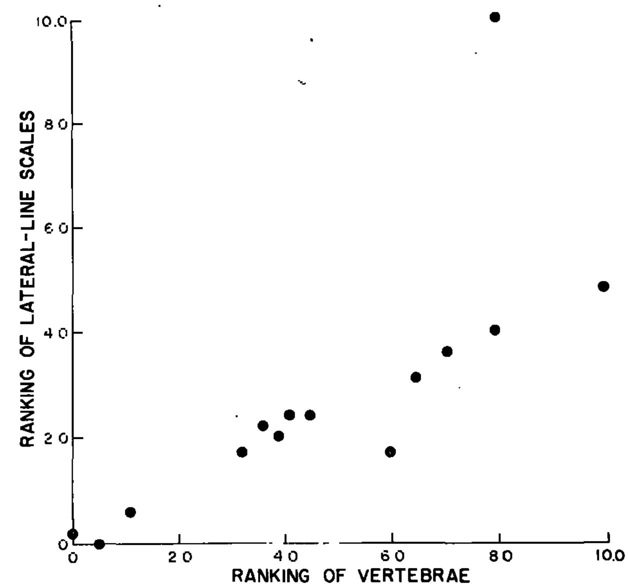

FIGURE 11.—Relation between vertebrae and lateral-line scales.

TABLE 26.—*Summary of ranking of means of meristic characters, by species*

Species	Branchiostegal rays	Pyloric caeca	Rays in— Anal fin	Rays in— Dorsal fin	Rakers on first gill arch	Vertebrae	Scales: On lateral line	Scales: Oblique rows	Scales: Dorsal fin to lateral line
Oncorhynchus:									
tshawytscha	10.0	7.5	10.0	9.9	3.4	10.0	4.8	2.5	4.4
gorbuscha	3.4	6.0	9.4	10.0	7.1	8.1	10.0	7.1	6.2
kisutch	5.7	2.7	7.8	7.9	2.8	6.5	3.1	1.4	2.3
keta	5.7	10.0	8.5	9.5	3.1	8.0	4.0	2.0	0.8
nerka	5.3	3.2	8.9	9.3	10.0	7.1	3.6	1.5	0.0
Cristivomer:									
namaycush	4.2	5.6	1.3	1.8	1.8	3.6	2.2	6.8	
Salmo:									
salar	2.8	1.6			1.5	0.5	0.0	0.0	
gairdneri		0.8	4.4		1.5	3.9	2.0	1.3	1.7
g. kamloops	2.2	1.2	3.5	6.1	1.3	[1] 4.1	2.4	2.5	
clarki		0.3				3.2	1.7	3.4	
trutta	0.0	0.7			0.0	0.0	0.2	0.8	
Salvelinus:									
alpinus	2.0	0.9	0.0	0.0	3.3	6.0	1.7	7.3	6.0
aureolus	1.1	1.0	0.1	0.8	0.9	4.1			
marstoni	0.0	0.6	0.7	2.6	1.8	4.2			
oquassa	0.0								
malma	2.1	0.0		0.4	0.6	4.5	2.4	10.0	10.0
fontinalis	1.1	0.4	1.2	3.6	0.2	1.1	0.6	9.1	
Correlated characters:									
Number of paired entries			11			13		8	
Sum of ranks			51.4	61.5		[2] 58.5	[2] 28.7	33.1	31.4
Average rank			4.67	5.59		4.50	2.21	4.14	3.93
Average rank, both characters			5.13			3.35		4.03	
Correction factor [3]			1.10	.92		.74	1.52	0.97	1.03

[1] *g. whitehousei*=4.0.
[2] Exclusive of *gorbuscha*.
[3] To put on a common basis.

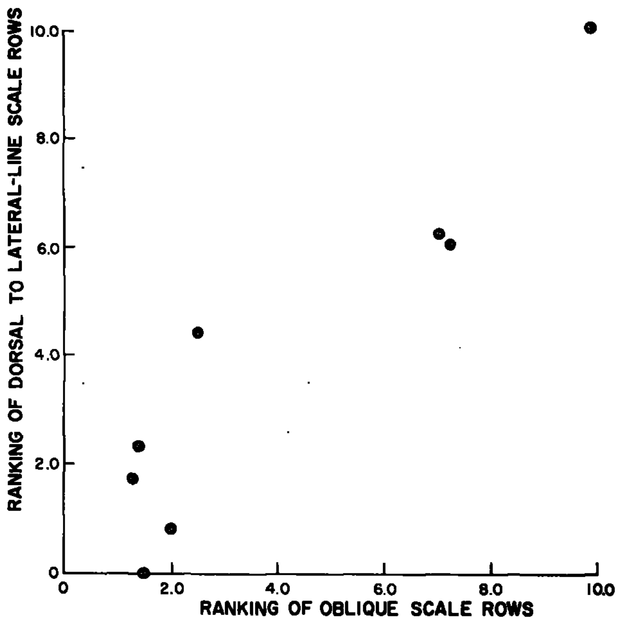

FIGURE 12.—Relation between oblique scale rows and scale rows from the dorsal to the lateral line.

Throughout the enumeration data there is a clear tendency for the variances to be correlated with their means. This tendency is easily seen in figures 4, 5, and 7, in which the 80 to 20 interpercentile range increases with an increase in the mean. This of course implies that the differences between mean rankings must be larger for higher rankings to be equally as significant as the smaller differences between mean rankings for lower rankings.

TABLE 27.—*Adjusted rankings of certain correlated meristic characters, by species*

I. Anal and dorsal fin rays

Species	Anal fin rays	Dorsal fin rays	Sum	Average rank
Oncorhynchus:				
tshawytscha	11.00	9.11	20.11	10.1
gorbuscha	10.34	9.20	19.54	9.8
kisutch	8.58	7.27	15.85	7.9
keta	9.35	8.74	18.09	9.0
nerka	9.79	8.56	18.35	9.2
Cristivomer:				
namaycush	1.43	1.66	3.09	1.5
Salmo:				
salar				
gairdneri	4.85		4.84	4.8
g. kamloops	3.85	5.61	9.46	4.7
clarki				
trutta				
Salvelinus:				
alpinus	0.00	0.00	0.00	0.0
aureolus	0.11	0.74	0.85	0.4
marstoni	0.77	2.39	3.16	1.6
malma		0.37	0.37	0.4
fontinalis	1.32	3.31	4.63	2.3

II. Vertebrae and lateral-line scales

Species	Vertebrae	Lateral line scales	Sum	Average rank
Oncorhynchus:				
tshawytscha	7.40	7.30	14.70	7.4
gorbuscha	5.99	15.20	21.19	10.6
kisutch	4.81	4.71	9.52	4.8
keta	5.92	6.08	12.00	6.0
nerka	5.25	5.47	10.72	5.4
Cristivomer:				
namaycush	2.66	3.34	6.00	3.0
Salmo:				
salar	0.37	0.00	0.37	0.2
gairdneri	2.89	3.04	5.93	3.0
g. kamloops	3.03	3.65	6.68	3.3
clarki	2.37	2.58	4.95	2.5
trutta	0.00	0.30	0.30	0.2
Salvelinus:				
alpinus	4.44	2.58	7.02	3.5
aureolus	3.03		3.03	3.0
marstoni	3.11		3.11	3.1
malma	3.33	3.65	6.98	3.5
fontinalis	0.81	0.91	1.72	0.9

TABLE 27.—*Adjusted rankings of certain correlated meristic characters, by species*—Continued

III. Oblique and dorsal-to-lateral-line scale rows

Species	Oblique rows	Dorsal to lateral rows	Sum	Average rank
Oncorhynchus:				
tshawytscha	2.42	4.53	6.95	3.5
gorbuscha	6.89	6.39	13.28	6.6
kisutch	1.36	2.37	3.73	1.9
keta	1.94	0.82	2.76	1.4
nerka	1.46	0.00	1.46	0.7
Cristivomer:				
namaycush	6.60		6.60	6.6
Salmo:				
salar	0.00		0.00	0.0
gairdneri	1.26	1.75	3.01	1.5
g. kamloops	2.42		2.42	2.4
clarki	3.30		3.30	3.3
trutta	0.78		0.78	0.8
Salvelinus:				
alpinus	7.08	6.18	13.26	6.6
malma	9.70	10.30	20.00	10.0
fontinalis	8.83		8.83	8.8

To correct for this correlation between the means and their variances, the adjusted rankings (table 28) were converted to logarithms. In order to avoid dealing with minus logarithms, and with the absence of any logarithm for a zero ranking, all rankings were first increased by 1 and then multiplied by 10. The logarithms of the rankings so derived are given in table 29.

One method of assessing the value of these meristic characters (table 29) is to determine whether the variation within each genus differs significantly from the variation between genera. Because the number of species varies from genus to genus, calculation of the variance must recognize unequal sample size (Snedecor, 1956: p. 268), considering each species as one sample mean.

TABLE 28.—*Adjusted rankings of meristic indices*

	Branchiostegals	Pyloric caeca	Anal and dorsal fin rays	Rakers on first gill arch	Vertebrae and lateral line scales	Oblique and dorsal-to-lateral-line scale rows
Species:						
Oncorhynchus:						
tshawytscha	10.0	7.5	10.1	3.4	7.4	3.5
gorbuscha	3.4	6.0	9.8	7.1	10.6	6.6
kisutch	5.7	2.7	7.9	2.8	4.8	1.9
keta	5.7	10.0	9.0	3.1	6.0	1.4
nerka	5.3	3.2	9.2	10.0	5.4	0.7
Cristivomer:						
namaycush	4.2	5.6	1.5	1.8	3.0	6.6
Salmo:						
salar	2.8	1.6		1.5	0.2	0.0
gairdneri		0.8	4.8	1.5	3.0	1.5
g. kamloops	2.2	1.2	4.7	1.3	3.3	2.4
clarki		0.3			2.5	3.3
trutta	0.0	0.7		0.0	0.2	0.8
Salvelinus:						
alpinus	2.0	0.9	0.0	3.3	3.5	6.6
aureolus	1.1	1.0	0.4	0.9	3.0	
marstoni	0.0	0.6	1.6	1.8	3.1	
malma	2.1	0.0	0.4	0.6	3.5	10.0
fontinalis	1.1	0.4	2.3	0.2	0.9	8.8
Genus:						
Oncorhynchus	6.02	5.88	9.20	5.28	6.84	2.82
Cristivomer	4.20	5.60	1.50	1.80	3.00	6.60
Salmo	1.67	0.92	4.75	1.08	1.84	1.60
Salvelinus	1.26	0.58	0.94	1.36	2.80	8.47

TABLE 29.—*Logarithm of adjusted rankings of meristic indices*

[Rankings: + 1 × 10]

	Branchiostegals	Pyloric caeca	Anal and dorsal fin rays	Rakers on first gill arch	Vertebrae and lateral line scales	Oblique and dorsal to lateral-line scale rows
Species:						
tshawytscha	2.04	1.93	2.05	1.64	1.92	1.65
gorbuscha	1.64	1.85	2.03	1.91	2.06	1.88
kisutch	1.83	1.57	2.00	1.60	1.76	1.46
keta	1.83	2.04	2.00	1.61	1.85	1.38
nerka	1.80	1.62	2.01	2.04	1.81	1.23
namaycush	1.72	1.82	1.40	1.45	1.60	1.88
salar	1.58	1.42		1.40	1.08	1.00
gairdneri		1.26	1.76	1.40	1.60	1.40
g. kamloops	1.51	1.34	1.76	1.36	1.63	1.53
clarki		1.11			1.54	1.63
trutta	1.00	1.23		1.00	1.08	1.26
alpinus	1.48	1.28	1.00	1.63	1.65	1.88
aureolus	1.32	1.30	1.15	1.28	1.60	
marstoni	1.00	1.20	1.41	1.45	1.61	
malma	1.49	1.00	1.15	1.20	1.65	2.04
fontinalis	1.32	1.15	1.52	1.08	1.28	1.99
Genus:						
Oncorhynchus	9.14	9.01	10.09	8.80	9.40	7.60
Cristivomer	1.72	1.82	1.40	1.45	1.60	1.88
Salmo	4.09(3)	6.36	3.52(2)	5.16(4)	6.93	6.82
Salvelinus	6.61	5.93	6.23	6.64	7.79	5.91(3)

The analysis of variance of the logarithms of the adjusted rankings of meristic characters follows:

Character index	Mean square		*F* value
	Between genera	Within genera	
Branchiostegals	0.2594	0.0438	5.92*
Pyloric caeca	.4210	.0229	18.38**
Anal and dorsal fin rays	.5255	.0203	25.89**
Rakers on first gill arch	.2171	.0421	5.16*
Vertebrae and lateral-line scales	.0430	.0808	.53
Oblique and dorsal to lateral-line scale counts	.2657	.0510	5.21*

For five of the six meristic indices, the variance within is significantly less than the variance between genera. This tends to confirm the validity of the generic groupings as established even though it does not yield much information concerning affiliations of particular species.

To show the relationships between species, both the maximum and the average differences in the logarithms of the six meristic indices are given for 16 species in table 30.

The interrelationships of the various species as shown by these meristic indices are depicted in figure 13. The genus *Oncorhynchus* is quite well separated from the other genera except for a close link between *O. kisutch* and *Salmo gairdneri*.

Cristivomer shows a loose affinity with *Salvelinus alpinus* and remote connections with several other species.

Salvelinus is a rather closely knit group, with *S. marstoni* the closest link between *Salmo gairdneri* and the other *Salvelinus*.

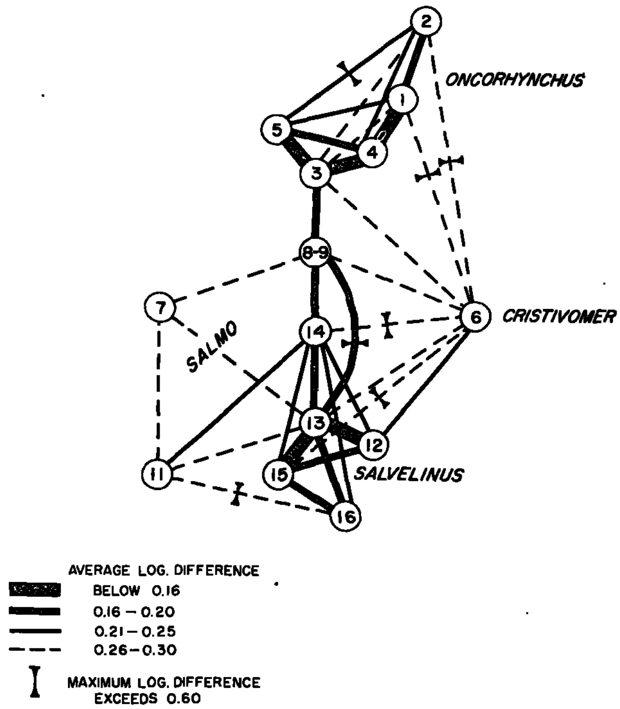

FIGURE 13.—Relationships of species of Salmonidae, as shown by meristic indices. (See table 30 for key to species' numbers in circles.

TABLE 30.—*Differences between logarithms of six meristic indexes, average differences between species (lower left), maximum differences (upper right)*

Species [1]	No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
tshawytscha	1		.40	.36	.27	.42	.65	.84	.67	.59	.82	1.04	1.05	.90	1.04	.93	.78
gorbuscha	2	.19		.42	.50	.65	.63	.98	.59	.55	.74	.98	1.03	.88	.65	.88	.83
kisutch	3	.26	.26		.47	.44	.60	.68	.31	.32	.46	.83	1.00	.85	.83	.85	.53
keta	4	.12	.24	.11		.43	.60	.77	.78	.70	.93	.83	1.00	.85	.84	1.04	.89
nerka	5	.25	.25	.14	.18		.65	.73	.64	.68	.51	1.04	1.01	.86	.80	.86	.96
namaycush	6	.30	.28	.28	.31	.39		.88	.56	.48	.71	.72	.54	.52	.72	.82	.67
salar (5)	7	.54	.57	.35	.45	.40	.40		.52	.55	.63	.58	.88	.52	.58	1.04	.99
gairdneri (5)	8	.35	.46	.19	.30	.33	.29	.27		.13	.23	.52	.76	.61	.35	.64	.59
g. kamloops	9	.35	.37	.20	.31	.33	.25	.25	.00		.23	.55	.76	.61	.51	.61	.46
clarki (3)	10	.41	.50	.28	.50	.39	.34	.45	.15	.14		.46	.25	.19	.09	.41	.36
trutta (5)	11	.72	.75	.53	.63	.60	.58	.29	.27	.36	.31		.63	.52	.53	.78	.73
alpinus	12	.46	.41	.37	.47	.48	.24	.38	.31	.25	.18	.47		.35	.48	.43	.55
aureolus (5)	13	.59	.57	.42	.54	.53	.27	.26	.19	.19	.22	.30	.15		.32	.30	.37
marstoni (5)	14	.58	.56	.40	.53	.53	.27	.34	.12	.22	.08	.25	.24	.17		.49	.37
malma	15	.58	.53	.48	.54	.60	.29	.46	.35	.28	.21	.45	.17	.12	.25		.37
fontinalis	16	.60	.54	.49	.60	.62	.33	.41	.32	.28	.22	.28	.31	.21	.24	.20	

[1] Figures in parentheses show number of comparisons when less than 6.

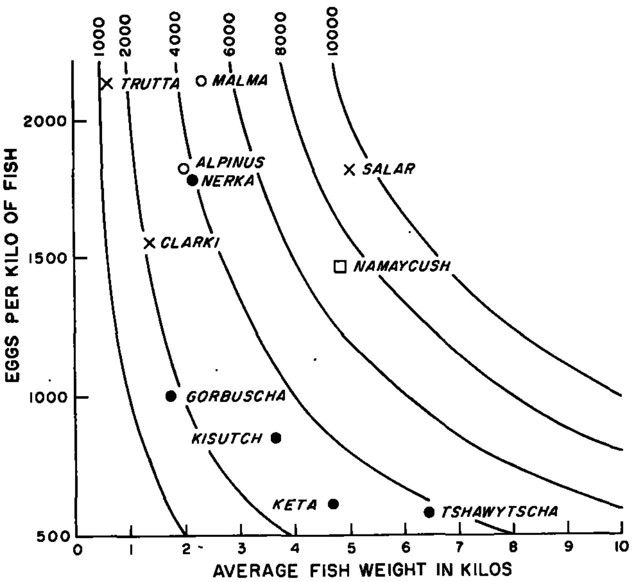

FIGURE 14.—Fecundity isopleths based on number of eggs per kilo of total weight versus the average weight of the adult fish.

The genus *Salmo* presents a very different picture. Of the three species, *salar*, *trutta*, and *gairdneri*, *S. trutta* shows connections with *Salvelinus marstoni*, only a remote affinity with *Salmo salar*, and none with *Salmo gairdneri*. *Salmo salar* shows equally remote associations with *Salmo trutta*, *Salvelinus aureolus*, and *Salmo gairdneri*. *Salmo gairdneri* is closely linked with *Oncorhynchus* (*kisutch*) on one hand and with *Salvelinus* (*marstoni*) on the other, and shows only a remote affinity with *Salmo salar* and none with *Salmo trutta*.

FECUNDITY

Although the term "fecundity" is normally used to denote the numbers of ova produced, we must also deal with the size of the ova. For each species of Salmonidae there is a normal range for both number and size of egg. For *Oncorhynchus*, which mature and spawn only once, this range is not too difficult to define. For species that live to spawn two or more times, the number of eggs varies widely, since the number is correlated with the weight of the fish (Rounsefell, 1957). Size of the egg is more constant for each species than the number, but tends to be larger in larger individuals.

Most of the available data on fecundity in the Salmonidae are given in some detail by Rounsefell (1957). From these data the average fecundity of the species for which data are available was plotted in figure 14. It will be noted at once that the lowest number of eggs per kilo of fish weight occurs in the fluvial anadromous *Oncorhynchus*. That this lower number of eggs per kilo of fish weight is not caused by a lower total weight of ova but rather to larger individual eggs is shown by figures 15 and 16, which show for available data the number of eggs per kilo of fish weight plotted against egg diameter and weight of fry, respectively.

Figures 15 and 16 show that the fluvial anadromous *Oncorhynchus* differ markedly in egg size from the other Salmonidae. The lacustrine anadromous *O. nerka* appears to be only slightly ahead of *S. salar* in egg size.

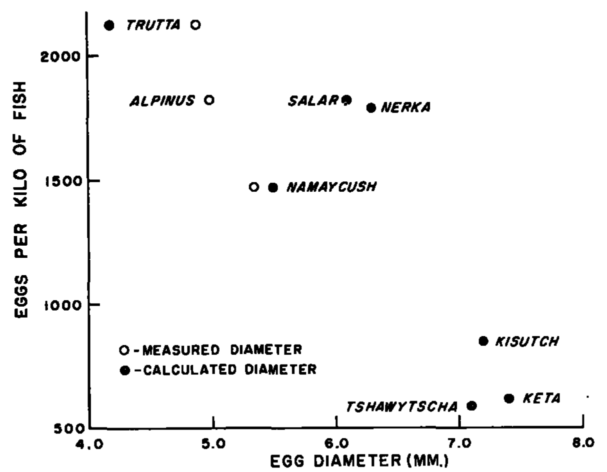

FIGURE 15.—Number of eggs per kilo of total weight versus the egg diameter.

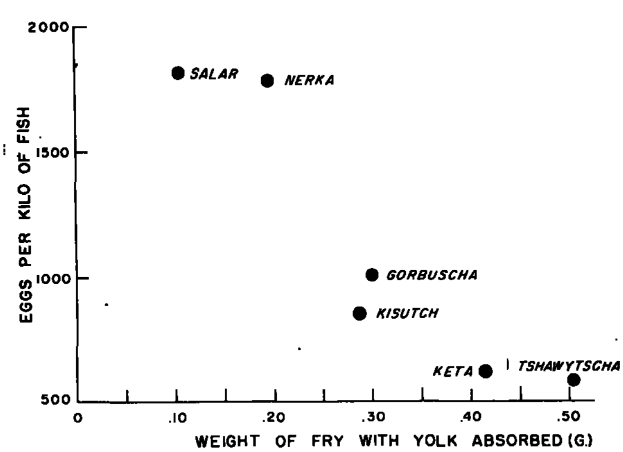

FIGURE 16.—Number of eggs per kilo of total weight versus the average weight of fry after absorption of the yolk.

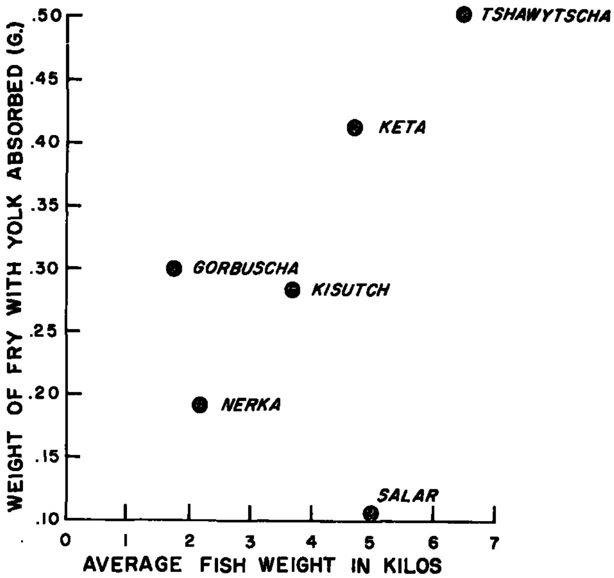

FIGURE 17.—Average weight of fry after absorption of the yolk compared with the average total weight of the species.

In considering egg size in relation to fish weight, however, it is obvious that *Oncorhynchus* can be distinguished even more clearly by this character. Thus, in figure 17, in which the weight of fry with the yolk absorbed is plotted against the average weight of the fish, *S. salar* has small fry for the size of the parent fish. In fact all five species of *Oncorhynchus* except *gorbuscha* fall in a straight line. The larger size of the fry (and of course the egg) of *gorbuscha* may be related to the extreme degree of anadromy in this species, whereby the fry emerge from the gravel as soon as the yolk is absorbed and migrate seaward at once.

DISTRIBUTION IN RELATION TO TEMPERATURE

Species may range over a wide area and yet avoid extreme conditions by changing spawning seasons and by occupying different ecological niches. A further complication is the tendency of isolated populations to change genetically. Despite these difficulties the overall picture shows that some of the species are definitely arctic or subarctic, whilst others range far to the south. The approximate latitudes given in table 31 are not too descriptive of the actual temperatures encountered because of the great differences in both sea-water and fresh-water temperatures at comparable latitudes on different coasts and the complicating factor of the lowering effect of altitude on fresh-water temperature.

TABLE 31.—*Limits of ranges of North American Salmonidae, ranked according to temperature of water frequented*

Species	Coldest water			Warmest water			Average cold rank	Final rank
	Locality	Latitude north	Cold rank	Locality	Latitude north	Cold rank		
alpinus	Ellesmere Island [1]	82°	1	Kodiak Island lakes	57°	4	2.5	1
namaycush	Banks Island [2]	73°	2	Lake Erie	41°	3	2.5	1
oquassa	Quebec lakes	50°	2	Lakes, northern Maine	45°	3	2.5	1
malma	Herschel Island [3] Cape Lisburne [4]	71°	2	High streams, California	39°	4	3.0	2
keta	MacKenzie River [5]	70°	2	Klamath River [6]	41°	5	3.5	3
gorbuscha	MacKenzie River [5]	70°	2	Russian R., California [7]	38°	5	3.5	3
nerka	Yukon River [8]	66°	3	Wallowa lakes, Oregon	45°	4	3.5	3
salar	Koksoak R., Ungava [9]	60°	2	Housatonic R., Connecticut	41°	6	4.0	4
fontinalis	Hudson Bay	59°	2	High streams, Georgia	35°	6	4.0	4
clarki	Southeast Alaska	60°	4	Eel River, California	39°	5	4.5	5
tshawytscha	Yukon River	66°	3	San Joaquin River	36°	7	5.0	6
kisutch	Norton Sound [10]	64°	3	Salinas R., California	36°	7	5.0	6
gairdneri	Kuskokwim R.	61°	3	Rio Presidio, Durango [11]	24°	8	5.5	7

[1] Fisheries Research Board (1959, p. 112).
[2] Fisheries Research Board (1959, p. 12).
[3] Scofield (1899).
[4] Bean (1882).
[5] Dymond (1940).
[6] Snyder (1931).
[7] Taft (1938).
[8] Evermann and Goldsborough (1907).
[9] Dunbar and Hildebrand (1952).
[10] Nelson (1887).
[11] Needham and Gard (1959).

In order to obtain a picture of the effect of temperature on distribution, I have disregarded latitude in favor of generalized temperature isotherms. The mean surface ocean temperatures (see Davidson and Hutchinson, 1938) differ considerably at comparable latitudes on the eastern and western shores of the continent. In table 31, the water temperatures at the extreme ranges of the distribution have been ranked subjectively by species. This empirical method shows definite trends when the species are grouped according to their temperature distribution (averaging both extremes of the range).

The final rankings, by species and genus, according to distribution in cold waters, are as follows:

Rank and species	*Cristivomer*	*Salvelinus*	*Oncorhynchus*	*Salmo*
Rank 1:				
namaycush	X			
alpinus		X		
oquassa		X		
Rank 2:				
malma		X		
Rank 3:				
keta			X	
gorbuscha			X	
nerka			X	
Rank 4:				
fontinalis		X		
salar				X
Rank 5:				
clarki				X
Rank 6:				
tshawytscha			X	
kisutch			X	
Rank 7:				
gairdneri				X
Rank by genus	1	2	4.2	5.3

Cristivomer and *Salvelinus* are arctic and subarctic genera, except that *S. fontinalis*, which differs most widely from the other species of *Salvelinus* in respect to other characteristics is more southerly. All *Oncorhynchus* species range far to the north, but *tshawytscha* and *kisutch* are more tolerant than the others of warmer water. *Salmo salar* lives in colder water than either of the Pacific species of *Salmo*. The range of *clarki* is peculiar in that it extends neither far to the north nor far to the south, but inhabits the temperate waters between. While it extends to Bristol Bay, *gairdneri* avoids the colder streams and extends into much warmer waters than any of the other species.

COMPARISON OF NORTH AMERICAN AND ASIATIC GENERA

Some authors classify the salmons and trouts, together with the graylings and whitefishes, in a single family, which they call Salmonidae. We prefer to consider them as three families, the Thymallidae, Coregonidae, and Salmonidae. The last is the group discussed below.

In addition to the genera of Salmonidae that occur in North America two fresh-water genera occur only in Asia (Dymond and Vladykov, 1934). *Brachymystax* occurs across Siberia and south to the rivers of Japan and the Okhotsk Sea. *Hucho* consists of three species, one on the Danube, one in the rivers of Siberia, and a third in Sakhalin and the rivers entering the Okhotsk Sea (Dymond and Vladykov, 1934).

Some notion of the relationship between these two purely Asiatic genera and the other four genera is obtained by comparing their osteology since other characteristics are not sufficiently well-documented for the Asiatic genera. Furthermore, morphological material is chiefly available for only one or two species of each genus. The available osteological data are well summarized by Norden (1958). As Norden classed *Cristivomer* under *Salvelinus* and used *Cristivomer namaycush* as his chief representative of *Salvelinus*, we are forced to combine these two genera for the purpose of this comparison (table 32).

TABLE 32.—*Comparison of certain generic characteristics in Salmonidae*

[Osteological characters adapted from Norden, 1958]

Character	*Brachymystax*	*Hucho*	*Salvelinus-Cristivomer*	*Salmo*	*Oncorhynchus*
Mouth:					
Small	A				
Large		B	B	B	B
Jaw hinge:					
Below orbit	C				
Behind orbit		D	D	D	D
Palatine and vomerine teeth:					
In continuous U-shaped band	E	E			
Narrowly separated			F	F	
Widely separated					G
Ova:					
Small	H				
Medium		I	I		
Large				J	
Very large					K
Jaw teeth:					
Small, fine	L				
Strong		M	M	M	M
Shaft of vomer:					
Short, toothless	N	N			
Long, toothless			O		
Long, toothed				P	P
Postorbitals contact preopercle:					
No	Q	Q	Q	Q	
Yes					R
Dorsal fontanelles:					
Persistent	S	S	S	S	
Covered in adult					T
Supraethmoid:					
Long and narrow with posterior projections	U	U	U		
Short, notched posteriorly				V	V
Ascending process of premaxilla:					
Intermediate in size	W	W		W	
Well-developed			X		
Absent in adults					Y

The number of differences between genera in ten characters (from table 32) are summarized in table 33.

The relationships between genera based only on the 10 characters of table 32 are depicted in figure 18, in which the distances between genera are roughly proportional to the number of differences in characters (from table 33).

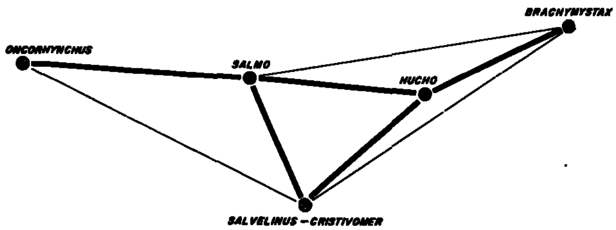

FIGURE 18.—Diagrammatic comparison of genera based on certain characters.

It appears that *Brachymystax* is the most primitive and generalized of the genera, *Hucho* represents an intermediate stage, whilst *Oncorhynchus* is the most specialized.

TABLE 33.—*Number of certain characters differing between genera of Salmonidae*

[Characters from table 32]

	Brachymystax	*Hucho*	*Salvelinus-Cristivomer*	*Salmo*	*Oncorhynchus*
Brachymystax	....	4	7	7	10
Hucho	4	....	3	4	7
Salvelinus-Cristivomer	7	3	....	4	7
Salmo	7	4	4	....	5
Oncorhynchus	10	7	7	5	....

SUMMARY OF RELATIONSHIPS

The foregoing material on hybridization, coloration, anadromy, fecundity, morphological characters, et cetera, show the relationships between the North American species of Salmonidae. In figure 19 the degrees of relationship have been indicated by the relative distances between species. Since many of the differences and similarities are difficult to weigh with the information presently available concerning the relative value of different criteria, I have not attempted to be more precise.

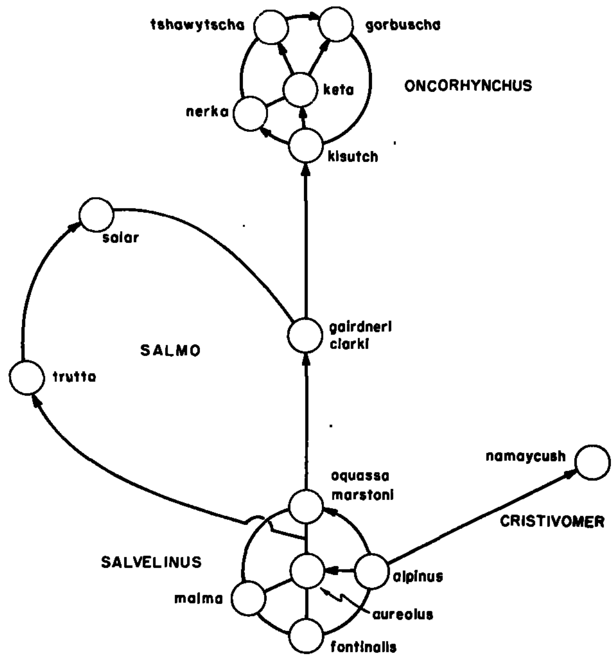

FIGURE 19.—Suggested relationships among North American Salmonidae.

ANNOTATED KEY TO NORTH AMERICAN SALMONIDAE

This annotated key is given in place of the more conventional strictly dichotomous key. Keys are used chiefly to determine the identity of a specimen, and each subdivision should not be interpreted as denoting relationships.

The amount of information available varies widely from species to species, but where available, certain items (such as chromosome number) have been included. Thus, although this section has been arranged as a key, it is also a summarized description of the North American Salmonidae. It should be kept in mind that this paper is based wholly on published data and that no attempt was made to verify points that await further study.

KEY TO GENERA

A. Skeleton cartilaginous, very slight calcification; dorsal fontanelles closed in adults; postorbitals contact preopercle; ascending process of premaxilla absent in adults; branchiostegal rays (left side) 10–19; gill rakers (first arch, left side) 19–39; lateral-line scales 121–198; anal fin rays 15–22; pyloric caeca 55–249; dorsal fin rays 12–18; vertebrae 62–75; only black spots or speckling at all ages (except breeding colors); ova and fry very large in relation to adult size; anadromy obligatory or adaptive; mouth lining dark to black; all adults die after spawning. Genus *ONCORHYNCHUS*, Pacific salmons.

AA. Skeleton fairly well calcified; dorsal fontanelles persistent; postorbitals do not contact preopercle; ascending process of premaxilla persistent; branchiostegal rays (left side) 8–14; gill rakers (first arch, left side) 14–27; lateral-line scales 105–138; anal fin rays 8–16; pyloric caeca 20–170; dorsal fin rays 9–15; vertebrae 57–69; light spots, speckling, or colored areas present at some stage; ova and fry medium to small in relation to adult size; anadromy not adaptive or obligatory; mouth lining white to black; some adults may die after spawning.

B. Teeth on both head and shaft of vomer; supraethmoid short, width medium to broad, notched posteriorly; lateral-line scales 105–138; anal fin rays 9–16; all have black body spots or speckling but may also have light spots or areas at some stages; fins without conspicuous white leading edge.
Genus *SALMO*, Atlantic salmons and trouts.

BB. Teeth on head (anterior end) of vomer only; supraethmoid long, narrow, with posterior projections; lateral-line scales 109–131; anal fin rays 8–12; body spots yellow to red or gray, never black; no lateral body stripe; white leading edge on paired fins.

C. Basibranchial (hyoid) teeth numerous and strong; supralingual (tongue) teeth in parallel rows; pyloric caeca 95–179 (average about 127–138); caudal fin deeply forked; pearl organs in adults; no bright colors, but spotted with gray; egg diameter less than 5.0 mm.; lacustrine; diploid chromosome number 84.
Genus *CRISTIVOMER*, lake trouts.

CC. Basibranchial (hyoid) teeth few or missing, weak; supralingual (tongue) teeth form equal sides of an isoceles triangle; pyloric caeca 20–64 (average about 28–46, 30–99 in *S. aureolus*); caudal fin very little to deeply forked; no pearl organs; brightly colored in fresh water, spotted with yellow, pink, or red, lower fins usually brightly colored; egg diameter usually more than 5.0 mm.; adfluvial, fluvial, or optionally anadromous.
Genus *SALVELINUS*, charrs.

KEY TO SPECIES

Salvelinus. Charrs

A. Basibranchial (hyoid) teeth absent or rare; back with dark wavy "wormlike" vermiculations extending onto dorsal fin; lower fins with white front edge followed by a black stripe; tip of lower jaw black; some of lateral spots may be pink or red with a blue halo; roof of mouth black; end of caudal fin almost square in adults; anal fin falcate; diploid chromosome number 84; optionally anadromous, fluvial, or adfluvial; very short migrations in the sea .... *Salvelinus fontinalis*, Speckled charr or eastern charr (eastern brook trout).

AA. Basibranchial (hyoid) teeth usually present, weak to moderate; vermiculations on back absent or faint; no black stripe on lower fins; tip of lower jaw white to reddish; lateral spots without blue borders; caudal fin slightly to well-forked in adults; optionally anadromous, adfluvial, or lacustrine.

B. Pyloric caeca 20–39 (average about 28–29); numerous red dots on sides (+50) smaller than diameter of pupil; pectoral fins very seldom if ever with white anterior margin; caudal fin almost square in adults; optionally anadromous or fluvial; short migrations in the sea .... *Salvelinus malma*, dolly varden charr.

BB. Pyloric caeca 20–99 (average about 38–46); spots on sides orange; all lower fins with white anterior margin; caudal fin well-forked; optionally anadromous, adfluvial, or lacustrine.

C. Maxillary extending about to posterior margin of eye; lateral spots (orange or yellowish) very small and numerous; roof of mouth white; white margin of lower fins narrow; adfluvial.
Salvelinus oquassa, blueback charr.
Salvelinus o. marstoni, red Quebec charr.

CC. Maxillary extending well beyond posterior margin of eye; orange or yellowish lateral spots small to large; broad white anterior edge on lower fins, roof of mouth white to blackish; optionally anadromous or adfluvial; short migrations in the sea (*alpinus*) .... *Salvelinus alpinus*, Arctic charr.
Salvelinus a. aureolus, golden charr or Sunapee charr.

Salmo. Salmons and trouts

A. Parr with small orange blotches or spots on sides adjacent to lateral line; black spots on caudal fin absent or few; adults may have pink or blue halo surrounding black spots on body; adult *S. salar sebago* may have some colored spots; caudal peduncle stout or slender, anal fin rays 9–11 (complete count).

B. Teeth on head and shaft of vomer strong and well-developed; branchiostegal rays average 10.0; oblique scale rows 116–136; end of maxillary usually not far behind posterior margin of eye; large black spots on body with some often surrounded by pink or red halo; few smaller reddish spots adjacent to lateral line; orange blotch on adipose usually present even in sea-run individuals, no colored lateral band; tail never deeply forked, square to fan-shaped in older fish; tail unspotted; caudal peduncle stout; diploid chromosome number 80; optionally anadromous, fluvial, or adfluvial; short migrations in the sea .... *Salmo trutta*, brown trout.

BB. Teeth on vomer all short, weak; branchiostegal rays average 11.9; oblique scale rows 111–118; maxillary extending to or slightly behind posterior margin of eye; small black spots, often x-shaped, numerous on upper body, sometimes extending slightly onto dorsal, adipose, and anal fins; landlocked varieties may have some lighter spots on body; caudal peduncle slender; no colored lateral band; caudal usually without spots, caudal slightly to well-forked in adults; some adults die after spawning; diploid chromosome number 60; optionally anadromous or adfluvial; long migrations in the sea; not abundant far offshore.... *Salmo salar*, Atlantic salmon.
Salmo s. sebago, landlocked salmon.

AA. Parr with bright lateral band, usually reddish or iridescent; black spots on back, and on dorsal, adipose, and caudal fins; adults without colored spots; caudal peduncle stout, and anal fin rays 11–16 (complete count).

C. Usually with red streak on underside of lower jaw which may be concealed by mandible; maxillary extends well beyond posterior margin of eye; oblique scale rows 122–208; pyloric caeca 27–40; in breeding color, belly suffused with red, lower fins reddish; adults seldom with a red lateral band; mouth lining white; optionally anadromous, fluvial, or adfluvial; very short migrations in the sea.
Salmo clarki, steelhead cutthroat trout or cutthroat trout.

CC. No red streak under jaw, maxillary extends to or slightly beyond posterior margin of eye; oblique scale rows 115–164; pyloric caeca 25–61 (average about 47); wide pink or red lateral band, especially bright in spawning males; mouth lining white; some sea-run adults die after spawning; optionally anadromous, fluvial, or adfluvial; chiefly coastwise migrations at sea---- *Salmo gairdneri*, steelhead rainbow trout or rainbow trout.
Salmo g. kamloops, Kamloops trout.

Oncorhynchus. Pacific salmons

A. Lateral-line scales 160–198 (average about 184); branchiostegals 9–15; pyloric caeca 95–224 (average about 136); anal rays 16–20 (complete count); gill rakers 24–34 (average about 29.7) with minute teeth; large black spots tending to oval on back and on entire caudal fin; young without parr marks; mouth lining dark; very pronounced hump on breeding males; mature at 2 years of age; obligatory anadromous; long sea migrations; abundant far offshore; usually less than 2,000 ova---- *Oncorhynchus gorbuscha*, pink salmon.

AA. Lateral-line scales 124–165; branchiostegals 10–19; pyloric caeca 45–254; anal rays 15–22 (complete count); gill rakers 19–39; no black spots on lower lobe of caudal fin, may be black speckling on dorsal edge of upper lobe; young with distinct parr marks; mature normally at ages 3–8, usually more than 2,500 ova.

B. Pyloric caeca 85–254; lateral-line scales 130–165; branchiostegals 10–19; anal rays 16–22 (complete count); gill rakers 19–28.

C. Lateral-line scales 130–147 (average about 139); branchiostegals 10–16; pyloric caeca 140–254 (average about 205); anal rays 16–20 (complete count); gill rakers 19–26 (average about 22), rakers wide apart and without teeth; caudal peduncle slender; parr marks short, elliptical or oval, extending little, if any, below lateral line; no black speckling on back or fins; breeding color anterior two-thirds of sides with bold jagged reddish line, posterior third of sides with jagged black line; mouth lining dark; obligatory anadromous, long sea migrations, abundant far offshore---- *Oncorhynchus keta*, chum salmon.

CC. Lateral-line scales 130–165 (average about 146); branchiostegals 13–19; pyloric caeca 85–244 (average about 158); anal rays 16–22 (complete count); gill rakers 20–28 (average about 24), rakers wide apart with large teeth; caudal peduncle stout; parr marks large vertical bars almost bisected by lateral line; small black speckling on back, dorsal fin, and upper lobe of caudal fin, sometimes extending onto adipose fin and lower lobe of caudal and faintly onto anal fin; breeding adults without red on sides; mouth lining black; obligatory anadromous; long sea migrations; not abundant far offshore---- *Oncorhynchus tshawytscha*, king salmon.

BB. Pyloric caeca 45–114; lateral-line scales 124–150; branchiostegals 11–16; anal rays 15–21 (complete count); gill rakers 19–39.

D. Pyloric caeca 45–114 (average about 75); lateral-line scales 130–144 (average about 135); branchiostegals 11–15; anal rays 15–19 (complete count); gill rakers 19–25 (average about 21), rakers wide apart with large teeth, none on back of second and fourth gill arches; caudal peduncle stout; parr marks large vertical bars almost bisected by lateral line; anal fin of parr falcate with first ray whitish; other lower fins of parr orange-tinged and white-tipped; in adults black speckling on back, often extending along upper edge of caudal fin and base of dorsal fin; sides of breeding adults may be suffused with light pink, but no definite markings; mouth lining dark; adaptively anadromous; long sea migrations; not abundant far offshore.
Oncorhynchus kisutch, silver salmon.

DD. Pyloric caeca 45–114 (average about 86); lateral-line scales 124–150 (average about 135); branchiostegals 11–16; anal rays 15–21 (complete count); gill rakers 28–39 (average about 35), rakers close together with minute teeth and present on back of second and fourth gill arches; caudal peduncle slender; parr marks short, elliptical or oval, extending little, if any, below lateral line; black speckling, when present, is faint, fins without speckling, except faint speckling on margin of caudal in breeding fish; in breeding adults, body (except lower belly) and all fins except pectorals and caudal lobes a deep crimson to brick red, head a dull green on dorsal half, creamy white below; mouth lining dark; adaptively anadromous; long sea migrations; abundant far offshore---- *Oncorhynchus nerka*, sockeye salmon.
Oncorhynchus n. kennerlyi, kokanee.

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APPENDIX

The scientific names mentioned in text, tables, or footnotes with their English equivalents are listed below. The preferred common name is marked with an asterisk.

SALMONIDAE. SALMONS, TROUTS, and CHARRS

Salvelinus, CHARRS	
alpinus	Arctic charr*, alpine charr, red lake charr
aureolus (or *alpinus aureolus*)	Golden charr*, Sunapee charr
fontinalis	Eastern charr*, speckled charr, eastern brook trout
malma	Dolly varden*, dolly varden charr
marstoni (or *oquassa marstoni*)	Red Quebec charr
oquassa	Blueback charr
Cristivomer, LAKE TROUTS or LAKE CHARRS	
namaycush	Lake trout*, lake charr, togue, namaycush
Salmo, SALMONS and TROUTS	
clarki	Cutthroat trout*, cutthroat steelhead*
clarki lewisi	Black-spotted trout*, Yellowstone trout
clarki pleuriticus	Cutthroat trout*, Colorado River trout
clarki seleniris	Piute trout
gairdneri	Rainbow trout*, rainbow steelhead*
gairdneri agua-bonita	Golden trout
gairdneri kamloops	Kamloops trout
gairdneri whitehousei	Mountain rainbow
salar	Atlantic salmon
salar sebago	Landlocked salmon*, ouaniche, Sebago salmon
trutta	Brown trout, sea trout
trutta trutta	Sea trout*, Loch Leven trout
trutta fario	Brown trout
Oncorhynchus, PACIFIC SALMONS	
gorbuscha	Pink salmon*, humpback salmon
keta	Chum salmon*, dog salmon
kisutch	Silver salmon, coho (Alaska), silverside (Columbia River)
nerka	Sockeye salmon, red salmon (Alaska), blueback (Columbia River)
nerka kennerlyi	Kokanee*, silver trout (Washington), little redfish
tshawytscha	King salmon, spring salmon (British Columbia), chinook (Northwest), tyee
masou	Masu salmon

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