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Volume 9, Number 1.

Monographs on the Natural History of New England.

THE FISHES OF NEW ENGLAND.

THE SALMON FAMILY. PART 2.—THE SALMONS.

By WILLIAM CONVERSE KENDALL.

WITH ELEVEN PLATES.

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PREFACE.

In pursuance of the policy to which reference was made in Part 1 (Kendall 1914) the second part of the monograph of the fishes of New England comprises the genus *Salmo*.

Acknowledgments are again due and are hereby made to the Trustees of the Bache Fund for a grant providing for the colored illustrations, which were painted by Mr. Walter H. Rich, of Portland, Maine.

INTRODUCTION.

Taxonomic Considerations.

While this memoir pertains only to the fishes of New England, and the present part particularly to a very limited number of species of one genus comprised within a restricted area, a proper understanding of them involves more comprehensive consideration than the subject at first would seem to imply. In the previous part (Kendall 1914, p. 5) it was stated that no one of the external or internal structures, usually enumerated as the chief characteristics of the salmon, will alone distinguish it, but that combinations of characters have to be considered. Opinions vary regarding the value of the distinguishing combinations of characters, and a satisfactory classification depends upon a thorough knowledge of comparative anatomy of salmonoid, and related fishes. According to Regan (1913, p. 288–289) the Salmonidæ, in which he includes Thymallidæ of Gill, differ from the salmonoid families Argentinidæ, Microstomidæ, Osmeridæ,[1] Retropinnatidæ, Salangidæ, Galaxiidæ, and Haplochitonidæ, in having an opisthotic, and in having upturned vertebræ at the base of the caudal fin. Again Regan (1914, p. 405–406) follows Gill and recognizes the family Salmonidæ to comprise two subfamilies: *viz.*, Salmoninæ and Coregoninæ. In the former he includes *Salmo*, *Salvelinus*, *Hucho*, and *Brachymystax*, and in the latter *Stenodus*, *Coregonus*, *Phylogephyra*, and *Thymallus*, in which he differs from Gill who established separate families for *Thymallus* and *Stenodus*. The meeting of the parietals on the middle line of the cranium in front of the supraoccipital is the stated differential character of the Coregoninæ, the parietals not meeting in the Salmoninæ.

It was this distinction upon which Cope (1871, p. 333) based the family Coregonidæ. Gill (1895, p. 117) later reduced this family to subfamily rank through some error of interpretation, thinking Cope was mistaken concerning the relation of the parietals and supraoccipital. But chiefly upon the same character he erected the family Thymallidæ.

Later Boulenger (1895, p. 299–302) indicated Gill's error and showed that the whitefishes and grayling were alike in respect to this cranial character. Therefore owing to certain supposed intergradations of cranial and other characters, he recognized only one family, Salmonidæ, and that apparently without subfamily groups. This family comprised all of the previously mentioned genera included in the two subfamilies Salmoninæ and Coregoninæ.

There are undoubtedly two distinct groups distinguished by this one character of the parietals. These are the salmons and trouts on the one side and the whitefishes and graylings on the other. Boulenger's supposed intergradations are exhibited by two other genera, *Brachymystax* and *Stenodus*. In one species of *Stenodus* the parietals are separate,

[1]Regan establishes this family for the smelts, etc., which had been previously successively placed in Salmonidæ, Microstomidæ, and Argentinidæ.

in another narrowly meet. *Brachymystax* resembles *Coregonus* only slightly in the size and shape of the mouth. When the parietal character in each of these genera is considered along with other characters, it is seen, even if they are as stated by Boulenger, that they do not intergrade. If the parietal character alone is considered there is an apparent intergradation, but this disappears when taken in combination. Boulenger (1895, p. 300) calls attention to the small mouth (coregonoid) and small scales (salmonoid) of *Brachymystax*, as evidence of its intermediate position between *Coregonus* and *Salmo*. Derivatively it cannot be so regarded. Published descriptions of *Brachymystax* indicate that the only coregonoid character is that of a small mouth. The other characters are obviously charlike. Its parietals do not meet on the cranial, median line in front of the supraoccipital. In the parietal character and small mouth *Thymallus* is more closely coregonoid, and in its scales and some other characters more salmonoid. But it does not form a link in any connected chain comprising also *Coregonus*, *Brachymystax*, and *Salmo*, or *Salvelinus*. The ensemble of characters is more than generically distinct from the coregonids or salmonids, as probably also is that of *Stenodus*, and doubtless they represent distinct lines of development from ancestral branches of the common salmonoid stock. The respective family characters are those of addition or reduction, as the case may be.

The present memoir recognizes and defines the following New England salmonoid families: all four (Salmonidæ, Coregonidæ, Argentinidæ, and Osmeridæ) have a mesopterogoid.

TABLE 1.

The Differential Characteristics of the Salmonoid Families.

	Salmonidæ	Coregonidæ	Argentinidæ	Osmeridæ
Alisphenoid present	+	+	+	−
Stomach 'siphonal'	+	+	+[1]	−
Stomach with cæcum[2]	−	−	−	+
Opisthotic present	+	+	+[3]	−
Parietals meeting in front of supraoccipital	−	+	+	−
Upturned vertebræ at the caudal end of the vertebral column	+	+	−[4]	−
Ventral mesentery present	+	−[5]	−	−
More than 100 scales in longitudinal series above lateral line	+	−	−	−

[1]The stomach of *Argentina silus* is slightly cæcal, that is, somewhat conic posteriorly, not evenly curved as in Salmonidæ.

[2]This character is negative in all but Osmeridæ, except possibly Argentinidæ.

[3]Regan failed to recognize the opisthotic in *Argentina*. It is present, however, but somewhat concealed by the superimposed and overlapping parietals and frontals.

[4]*Argentina silus* has three upturned vestigial or rudimentary vertebræ following the last fully developed one.

[5]Since this statement was written it has been found that Weber (1886) says that the intestine of *Coregonus oxyrinchus* is attached posteriorly to a ventral mesentery. From what he says of *C. lavaretus* it is inferred that it also was found to have a ventral mesentery. Kendall (1921, p. 197) found none in *Coregonus clupeaformis*.

No one external or internal characteristic will alone distinguish the Salmonidæ. The other salmonoid families are: the Coregonidæ, which comprise the whitefishes and ciscoes; the *Argentinidæ*, which include only a single species, the silver smelt (*Argentina silus*), known as the sea smelt and king herring, and the Osmeridæ, which include the anadromous marine and fresh water smelt (*Osmerus*) and the marine capelin (*Mallotus*).

These are the most salient, family differences, and it is seen that there is one character that distinguishes Salmonidæ from all other families mentioned. In fact no other family of teleosts has yet been observed to possess it. That is the ventral mesentery. However, this exception does not detract from the previous general statement that no one character usually enumerated as the chief characteristic of the salmon will alone distinguish it from all other families.[1] As now restricted, the family Salmonidæ of New England comprises only the salmons, trouts, and chars, which previously constituted the subfamily Salmoninæ. The Coregonidæ comprises the whitefishes and ciscoes; the Argentinidæ but one species, the silver smelt (*Argentina silus*), known to New England fishermen as 'sea smelt' and king herring; and the Osmeridæ includes the anadromous, marine and fresh-water smelt (*Osmerus*) and the marine capelin (*Mallotus*). The Coregonidæ, Argentinidæ, and Osmeridæ in many ways are more closely related to each other than to the Salmonidæ. *Argentina* is the most highly specialized form and doubtless represents the end product of an early diverging line from common isospondylous stock and is not closely related to the Salmonidæ. It possesses a well-developed, spiral valve in the intestine (Kendall and Crawford 1922, p. 10).

Genera of Salmonidæ.

According to Linnæus (1758, p. 308–312) the salmon family comprised only one genus (*Salmo*), although by subdesignations the list of species is subdivided as Truttæ, Osmeri, Coregoni, and Characini. By later writers these divisions were transcribed into the singular, *Trutta*, *Osmerus*, *Coregonus*, and *Characinus* as used by Artedi and previously by Linnæus and accepted as generic names, credited to Linnæus. The division Truttæ comprised 24 species of which only 17 are now recognized by any ichthyologist as belonging to the Salmonidæ, and Americans admit only 15 to the family and 6 to the genus *Salmo*.

Regan (1914, p. 407) has shown that the genus *Oncorhynchus* must be relegated to the synonymy of *Salmo*, or else the Pacific trouts now regarded as *Salmo* must be included in the genus *Oncorhynchus*. Regan appears to be correct as concerns the cranial characters upon which he bases his conclusions. But he seems to be in error as concerns the anal fin-ray character, since the supposed *Oncorhynchus masou*, which he found to have the few rays of *Salmo*, has been shown to be a *Salmo* (Kitahara 1904, p. 118–120, and Jordan 1905*b*). Furthermore the number of anal rays is not the only distinctive character of *Oncorhynchus*.

[1]Since this statement was written it has been found that Weber (1886) says that the intestine of *Coregonus oxyrinchus* is attached posteriorly to a ventral mesentery. From what he says of *C. lavaretus* it is inferred that it also was found to have a ventral mesentery. Kendall (1921, p. 197) found none in *Coregonus clupeaformis*.

If the cranial character described by Regan (1914, p. 407) characterizes the Pacific salmonids as a distinct group from the Atlantic, and *Oncorhynchus* is recognized as a valid genus, then the western trouts now regarded as belonging to the genus *Salmo* unfortunately should have a new name. This the present writer has not the temerity to bestow, as it would serve no purpose of convenience of classification.

As pertains to New England, the only indigenous genera are *Salmo* and *Salvelinus*. The latter constitutes the subject of Part 1 of this memoir. The genus *Salmo* as at present recognized includes only two native species, and the question of their distinctness or identity has been one of long dispute and varied and varying opinion. However, several other species of *Salmo* and three of *Oncorhynchus* have been introduced with more or less success so far as their establishment is concerned.[1]

Geographical Distribution of Genera.

The salmon family occupies the waters of the northern portion of the northern hemisphere, practically restricted to coastwise, and inland fresh waters of the great continents and neighboring islands. Thus geographically there are three oceanic and two continental realms. As relates to oceans, each continental area has a common arctic and an eastern and western division. The common, arctic division is occupied by marine, anadromous chars, almost exclusively, but to some extent the influence of warm, oceanic currents has permitted local invasions by other forms, so that salmon and sea trout occur on the Murman coast and in the White Sea. In the western Atlantic there are no 'sea trout.' The northern limit of the salmon is not positively known.

As regards the fresh-water species of Salmonidæ, the continental areas are subject to more or less subdivision by barriers, of one kind or another, preventing intercommunication. In the circumboreal or common arctic realm *Salvelinus* is predominant. In the eastern Pacific are *Salvelinus*, *Oncorhynchus*, and '*Salmo*.' In the western Pacific, in addition to the foregoing, is *Hucho*. In the eastern Atlantic are *Salvelinus*, *Salmo*, and *Hucho* (ultra-Mediterranean). In the western Atlantic are *Salvelinus* and *Salmo* only. In local, fresh waters of Siberia, where *Salvelinus*, *Hucho*, and the little-known and doubtful genus *Brachymystax* occur, no species of *Salmo* are recorded excepting in the Bering Sea and Pacific drainages.

The northern and southern limits of geographical distribution of all of the nominal species or forms of each genus are not definitely determined. The most northern records for any salmonoid are 'Floeberg Beach' in north latitude 82° 34′ and Cape Sheridan in about the same latitude for one or more species or forms of *Salvelinus*. The most northern record for *Salmo* is the White Sea. The most southern *Salvelinus* is in the mountains of southern Georgia. The most southern species of *Salmo* are in the mountain streams of Algeria, Mexico, and Formosa. In both the Atlantic and Pacific regions the chars are

[1]The introduced species are: Scotch sea trout (*Salmo trutta* or *eroix*); brown trout (*Salmo fario* or *S. ausonii* or both); Loch Leven trout (*Salmo levenesis*); Swiss lake trout (*Salmo lemanus*); steelhead trout (*Salmo gairdnerii* or (and) *S. irideus*) rainbow trout (*Salmo shasta*); king or chinook salmon (*Oncorhynchus tschawytscha*); silver salmon (*Oncorhynchus kisutch*); humpback salmon (*Oncorhynchus gorbuscha*).

the typical salmonoid forms, having their center of abundance and perfection in size in the arctic and sub-arctic regions. Southward in all regions *Salvelinus* gradually gives way to *Salmo*.

The Pacific is peculiar in its genus *Oncorhynchus* which comprises several species. In the far north, comprised in a narrow irregular zone, *Salvelinus* is associated with no other member of the salmon family, although its geographical range encircles the northern hemisphere. There it is essentially a marine fish, occasionally for food, or periodically for procreation, entering fresh water. On each coast of both the Atlantic and Pacific oceans, there are certain extents of southward projections of the anadromous-Salvelinus zones. But these marine forms gradually disappear, becoming almost or quite exclusively fresh-water inhabitants at the southern terminus of each range. Interdigitating with the southward extensions of the *Salvelinus* zone are northward extensions of the species of marine anadromous and fresh-water *Salmo* which has its center of abundance in a more southern zone, the northern geographical limits of which are fully as irregular in extent as is the southern extent of the *Salvelinus* zone.

Species of Salmonidæ.

The genus *Salmo* comprises numerous, more or less valid, taxonomic species which appear to be most abundant in Europe and western North America. The *Manual of the Vertebrate Animals of the Northeastern United States* by David Starr Jordan (1929, p. 50–51) transferred all the species formerly included in the genus, excepting *Salmo salar*, to the genus *Trutta*. In fact, in North America, no species of *Salmo* naturally occurs east of the western mountains, except on the Atlantic coast and in its coastwise waters. Disregarding the chars, the eastern Atlantic has an anadromous salmon, which is also present in the western Atlantic, one or more anadromous trouts, and predominantly fresh-water forms. Besides the salmon, the western Atlantic has only the so-called 'landlocked' salmon.

Pacific North America has its sea trouts and many nominal species of predominantly fresh-water trout. The Asiatic-Pacific region has a limited number of known trouts, anadromous in the north and permanently fresh-water residents in the south. Mention of the Pacific salmons has already been made. Of these there are five well-differentiated species belonging to a very definitely determined genus (*Oncorhynchus*) which occurs on both the North American, and Asiatic coasts.

Jordan (1905*a*, p. 293–294) says, 'The word "species" then, is simply a term of convenience, including such members of a group similar to each other as are tangibly different from others, and are not known to be connected with these by intermediate forms. Such connecting links we may suppose to have existed in all cases. We are only sure that they do not now exist in our collections, so far as these have been carefully studied.

'When two or more species of any genus now inhabit the same waters, they are usually species whose differentiation is of long standing,— species, therefore, which can be

readily distinguished from one another. When, on the other hand, we have "representative species",— closely related forms, neither of which is found within the geographical range of the other,— we can with some confidence look for intermediate forms where the territory occupied by the one bounds that inhabited by the other. In very many such cases the intermediate forms have been found; and such forms are considered as sub-species of one species, the one being regarded as the parent stock, the other as an offshoot due to the influences of different environment. Then, besides these "species" and "sub-species", groups more or less readily recognizable, there are varieties and variations of every grade, often too ill-defined to receive any sort of a name, but still not without significance to the student of the origin of species.'

These quotations are explanatory of the statement that the word 'species' is one of convenience. In other words, it affords the means of labelling specimens in collections, which indicates existing conditions in proportion to the degree of completeness of collections. That part of taxonomy which relates to the classification of existing forms considers the relations of these forms to each other as shown by structural characters alone. In the study of the relationship of existing forms there is tendency to endeavor to account for the origin of some existing species in other existing species.

Jordan (1905*a*, p. 293) wrote: 'Where species can readily migrate, their uniformity is preserved; but whenever a form becomes localized its representatives assume some characters not shared by the species as a whole. When we can trace, as we often can, the disappearance by degrees of these characters, such forms no longer represent to us distinct species. In cases where the connecting forms are extinct, or at least not represented in collections, each form which is apparently different must be regarded as a distinct species.'

From the foregoing it would seem that the statements regarding the 'disappearance by degrees' of characters and the extinction of connecting forms refer to present space and not past time. At any rate, the statement is based upon existing situations. There are geographically intergrading forms with terminals more or less different from each other. There are widely different forms with no geographical intergrading forms. There are closely related forms more or less geographically separated and having no intergrading forms, and there are geographically and structurally distinct forms with indirect irregularly geographical intermediates that do not constitute intergradation. Satisfactorily to apply the usual taxonomic methods to all of these conditions involves certain difficulties, which have caused considerable confusion and lack of uniformity and consistency in nomenclature, particularly of the Salmonidæ. Efforts to regulate these conditions have resulted in the adoption, by some ichthyological authorities[1], of arbitrary rules, to the effect that if one form differs from others by constant characters, however great or small, the form must be considered as a distinct species; the known existence of geographical intergradation of structural characters, would according to priority of description, make one or the other terminal a subspecies. This rule permits the intermediate forms of the last category mentioned to be regarded as distinct species,

[1]Jordan and Evermann in MS.

but in this direction the rules have not been strictly adhered to and lack of uniformity and consistency with attendant difficulties still obtain.

Writing of the genus *Salmo*, which comprised the Salmones and Salvelini, Günther (1880, p. 631) said: 'We know of no other group of fishes which offers so many difficulties to the ichthyologist with regard to the distinction of the species as well as to certain points in their life-history, as this genus.' After enumerating the many characters which vary greatly, some of which he considered more or less constant, and referring to a number of problems relating to their life histories, Günther went on to say (p. 642–643) that 'In accordance with acknowledged principles in zoölogy, forms which differ from their congeners by a combination of two or more constant characters, are to be distinguished under distinct specific names. Most likely they have been derived, at a not very remote period, from common ancestors, but the question of their specific distinctness is no more affected by this consideration than the question whether *Salmo* and *Coregonus* are distinct genera.' Then, in the way of explanation, he added: 'Whenever the zoölogist observes two forms distinguished by peculiarities of organization, such as cannot be conceived to be the effects of an external or internal cause, disappearing with the disappearance of that cause, and which forms have been propagated and are being propagated uniformly through all the generations within the limits of our observations, and are yet most probably to be propagated during the existence of mankind, he is obliged to describe these forms as distinct, and they will commonly be called species.'

To me it seems necessary to present the foregoing as exemplifying the commonly accepted ideas regarding the basis of specific distinction, although to a certain extent modified by some later systematists. It is of common experience to find that some species are harder to distinguish than others, and it is not always easy to determine whether certain characters are produced by causes which, being removed, were removed coincidently with the characters. A species of one locality easily distinguished from another in the same or another locality, in some other place may appear indistinguishable. Referring to the steelhead (*Salmo gairdnerii*) and the cut-throat trout (*Salmo clarkii*), Jordan and Evermann (1896, p. 488) write: 'Among the various more or less tangible varieties and forms of American trout, three distinct series appear which we here provisionally retain as distinct species; these may be termed the Cut-throat Trout series, the Steelhead series, and the Rainbow Trout series . . . '

'Along the western slope of the Sierra Nevada there are also forms of trout with the general appearance of *gairdneri*, but with scales intermediate in number (McCloud River), or with scales as small as in the typical *mykiss*[1] (Kern River). In these smaller-scaled forms more or less red appears below the lower jaw, and they are doubtless in fact what they appear to be, really intermediate between *mykiss* and *gairdneri*.'

In the light of more recent knowledge, the three series of Pacific trouts may be retained, but with different terminology, and distinguished by a different, scale series. The cut-throat or red-throat trout (*Salmo clarkii* [?] or *mykiss* Jordan and Evermann)

[1]In more recent classification the specific term *clarkii* replaces *mykiss*.

series with very small scales; the rainbow (*Salmo shasta*) series with somewhat larger scales; and the steelhead (*Salmo gairdnerii*) series with still larger scales. The latter comprises the form previously known as *Salmo irideus*, which is typified by the marine and coastwise form. The rainbow-trout series comprises the mountain trouts of California of the Sacramento and San Joaquin basins, excepting perhaps the Mount Whitney region. It is possible that the red-throat-trout series permits of a subdivision, the finer-scaled form comprising *Salmo lewisii, virginalis, stomias, pleuriticus*, etc., and a coarser-scaled form, *Salmo clarkii*, etc.

In endeavoring strictly to adhere to the aforementioned rules and practices, one difficulty encountered is in ascertaining wherein certain forms constantly differ and wherein they intergrade. It has long been the custom, and owing to insufficient material necessarily so, to stereotype certain external characters. Naturally the most conspicuous of these were made prominent in description. Some of these characters may show constant differences or they may be comprised in those mentioned by Günther, which disappear with the removal of the cause, whatever that may be. Herein lies another difficulty: the difficulty of ascertaining whether or not certain characters will disappear under changed conditions leads to different conclusions according to the decision regarding them. Besides being one of convenience, the term 'species' has been said to be an expression of ignorance; and it may be added that inability to distinguish species is also due to ignorance. It is believed that the evolution of a species would progress in an unchanged environment by interbreeding, thus transmitting with certain superspecific characters, progressively developing new combinations of characters derived from a large number of individual variations. Isolation according to its degree restricts the transmission of individual characters to a smaller number of individuals, but by selection emphasizes some one or more of these characters, either singly or in combination.

Among the salmonoid species are numerous geographical groups which exhibit various combinations of characters, but apparently all infringe upon each other to such an extent that it seems impossible, in some instances, to distinguish species. They seem to be so interrelated, though in some respects different, that certain authorities do not admit that these geographically distinct groups are distinct species. It would seem that the significance of these groups cannot be understood until the reason of their existence is at least better understood. The reason can hardly be found by studying the structures of the fish alone. It must be sought by considering geological history, not only in respect to phylogeny but in its relation to its probable, or at least possible, past environment and distribution.

Origin of Species of Salmonidæ.

The ancestral salmonids were marine forms which gradually acquired an anadromous habit, and some of them, later, a permanent fresh-water abode. They had invaded every accessible region suitable to their existence, which their present distribution and the

structure of the various species indicate must have been during a time of comparatively free intercommunication of oceans, and of comparatively uniform conditions in those portions of all seas in which they lived.

The ancestral salmonid may have occupied the Pacific, Arctic, and Atlantic Oceans, or it may have been restricted to the Arctic. Changes which were evidently initiated as early as the Miocene may have pushed some arctic ancestors southward into the Pacific, if they did not already occur there. It is well established that in the Pliocene the Pacific was occluded from the Arctic by land connections between Alaska and Siberia. The salmonids were then actually segregated into two groups, Pacific and Atlantic, with no possible means of intercommunication. With the closing of the Arctic-Pacific gateway, two independent lines of development began.

The original ancestral forms doubtless occupied a sort of northern zone, the southern limit of which was a temperature barrier. The advancing glacial conditions pushed the zone southward and formed a northern border-barrier beyond which no aquatic animal could pass. The evolution and oscillation of the environment was accompanied by evolution of the occupants, with the very evident result that there now exist groups of fishes adapted to different environmental conditions.

The Pacific Salmonidæ, with the exception of the chars which were probably of arctic-Atlantic origin, are sharply defined from the Atlantic Salmonidæ by cranial characters (Regan 1914, p. 406–407). The changing environmental conditions and the indirect barrier of distance, which preceded the Pacific-arctic separation, had effected a partial segregation and modification of the ancestral form, which the previously mentioned land-barrier and the glacial period carried on to the results manifested by present distribution of more or less differentiated forms. It is a well-known fact, that, as a rule, northern fishes are characterized by smaller scales and more numerous vertebræ than those of the south.

The present conditions necessary to the existence of the salmonids indicate that they were evolved in and synchronously, with changes of environmental conditions culminating in those of the present time. As the environmental zone and its subordinate marine zones moved northward with the recession of the glacial conditions, the occupants of the respective subordinate zones entered accessible fresh waters. It could not have been until the final recession of the glacial conditions that the marine salmonids were able permanently to occupy inland waters of the glaciated regions, so, as northern waters became accessible, they were occupied by them. Inasmuch, however, as all regions were not provided with accessible fresh waters, the present faunas represent only those which were derived from the respective subordinate zones reaching the outlet of the inland region at the time of accessibility. Such outlets may have been accessible to one or two zones and not to the remaining zones. The salmonids of present inland isolated waters indicate by their structure from which zones they were populated and by what routes they probably reached those waters. Thus through physiological adaptation a complex of environmental factors, seemingly paramount of which was that of temperature, determined the distribution, differentiation, and certain so-called habits and behavior of salmonid fishes.

As concerns the three recognized series of western trouts, *i.e.*, the cut-throat, steelhead, and rainbow series, it is observed that with a few exceptions, which may prove the rule, they are distinguished in at least three ways: (1) geographically; (2) habits; (3) by number or size of scales, and to some extent by (4) number of vertebræ.

In Europe a similar situation exists in the series commonly designated the salmon, the sea trout, and fresh-water trout series. With these series similar difficulties have confused ichthyologists. Many species of sea and fresh-water trouts have been described and as many times relegated to synonymy. Some have regarded all trout, whether marine and anadromous or perfectly fresh-water forms, as constituting a single species. Others, while so regarding them, are compelled to admit that the sea trout differ more or less according to locality, and that there are northern and southern forms of fresh-water trout, which they designate in their terminology as *Salmo fario* and *Salmo ausonii*. Even Smitt (1893–1895), who regards the salmon, sea trout, and fresh-water trout as one species, indicates specific distinctions between the salmon and sea trout, as he does between two forms of *Salvelinus*, in '*Salmo alpinus*' and '*Salmo salvelinus*.'

The structural characters of the sea trout are evidences of its differential advancement, and its restriction to certain coastwise, western European range is evidence in favor of previous isolation of some nature with which its differential characters were associated. If the isolation was geographical the present coincidental geographical range of the salmon can be accounted for only by assuming a later encroachment of either the salmon or trout within the range of the other, and the most natural assumption is that the adventitious form is the salmon. In whatever manner it may or may not be accounted for, it is obvious that, in accordance with accepted views of descent they were not developed in exactly the same environment and probably not in the same geographical range.

On the Atlantic coast of North America the situation is somewhat different from that of the other regions discussed. Of the genus *Salmo*, so far as known, there are only two series, comprising the anadromous, marine salmon and the fresh-water forms commonly called landlocked salmon and ouananiche. Anticipating a discussion which appears in a subsequent chapter, it may be stated here that in my opinion the so-called, 'fresh-water' salmon is just as distinct and almost as easily distinguished from the sea salmon as are the trouts of Europe from the sea salmon; furthermore among the fresh-water salmon there are forms, or species, if you please, just as distinct from each other as are some of the trouts of Europe from each other. In fact, it is more difficult to distinguish certain forms of fresh-water salmon from 'Loch Leven' trout in this country, than it is to distinguish the former from the marine form of the salmon.

Those who hold that all the different forms of a trout of a region, as for example Europe, constitute but one comprehensive species, attribute the differences shown by them to an unstable quality, supposed to be characteristic of salmonoid fishes, which they term 'plasticity.'

'Plasticity' of Salmonidæ.

The marine Salmonidæ ascend rivers to breed. The fresh-water salmonids breed in the lakes and streams. In certain instances fresh-water Salmonidæ descend to the sea presumably to feed, but the strictly marine forms do not interbreed to any appreciable extent with fresh-water forms. In the extreme north the salmonids are almost exclusively marine. In the extreme southern distribution they are exclusively fresh-water, or inland forms. Each of various inland water basins possesses forms which differ more or less from those of other inland water basins, and from those which ascend fresh-water streams from the sea principally to breed.

As previously mentioned, some ichthyologists have regarded each of these differing forms as distinct species, while others have pronounced all forms comprised in one genus a single species and ascribe the differences to 'plasticity.' This use of the term seems to signify that the fish is 'as clay in the hands of the potter,' the potter being environment, and if the clay is transferred to the hands of a different potter, it is moulded accordingly.

It is manifestly impossible to transfer all individuals of one basin to another. A few so transplanted would be another restrictive isolation, and such a group, if it survived, and maintained its integrity, would in time differ from that of the stock from which it was separated, regardless of any difference of environment. So 'plasticity' of segregated forms is only another name for limited interbreeding or 'close breeding.'

THE ATLANTIC SALMON (*SALMO SALAR* LINNÉ).

Plates 1–4.

General Considerations.

Based upon *Systema Naturæ* of Linnæus, 1758, as determined by rules of zoölogical nomenclature and general usage, *Salmo salar* has been designated as the type of the family Salmonidæ.

There are very few other fishes having any vernacular name at all that have the distinction of being everywhere known to the English-speaking peoples by one name only. Everywhere it is 'the Salmon.' Sometimes there are local names for the two sexes, the different stages of growth, or physical condition; or the names of the rivers in which it is caught are added as prefixes, but at the same time it is recognized as salmon. In each foreign language, too, there is one name for the fish, which forms the basis for the names of other salmonids. As in English there is the 'salmon trout,' so other tongues have like names to distinguish the trouts and at the same time indicating a relationship. There are many of such recognized forms and combination names for them, but only one salmon. In most regions the other closely related forms are trout or the equivalent for trout in whatever language, though occasionally a trout with some qualifying word is called salmon, as the Swedish name for the sea trout which translated is 'gray salmon.'

As previously shown, all of these fish are generically salmon, taxonomically speaking, '*Salmo*.' But in common usage all but *Salmo salar* are 'trout.'

The North American Atlantic salmon has always been regarded as specifically identical with the European salmon, although as Prince (1899, p. lxii) says, minor local peculiarities are noticeable, indicating that in the British form the head is smaller and more acuminate, and the body more gracefully attenuated both in the shoulder and the tail region, than in the American fish. Whether these differences and any others that may be present can be regarded as taxonomically specific depends much upon the viewpoint of the taxonomist. The question of species and subspecies has been discussed in foregoing pages, where my own view was indicated, to the effect that there were two kinds of species, *i.e.*, taxonomic species and natural species. A single species of the systematist may be broad enough to comprise several, many, or all of the natural species. Smitt (1893–1895) recognizes but one species of *Salmo*, each of the others, usually regarded as species, by him being designated as *forma*. Some systematists have regarded some of the *formæ* of Smitt as distinct species, others as subspecies or varieties.

Except for convenience and uniformity it makes little difference what the recognized, more or less distinct forms, are called. It does not affect the natural system, which was established by natural laws, not by nomenclatural rules. However, when this natural system is interfered with by fishermen, legislatures, and fish culturists, due cognizance and proper appreciation of the significance of these 'minor local peculiarities' are essential. The classificationist often changes his mind and what is a species at one time may not be at another, or *vice versa*. But these changes of opinion and names of the fish do not change the fish.

So, while taxonomically the European and American salmon are specifically identical, there may exist sufficient natural 'minor local peculiarities' to constitute peculiar American salmon problems, requiring for their solution somewhat different methods of research than do the European problems. Even on the American coast there are minor peculiarities of the habits and phenomena exhibited by the salmon, so that the problem of one section of the coast may differ from that of another, as, for instance, in the Gulf of St. Lawrence and on the coast of New England.

For these reasons, to me it seems not only extremely unfortunate but fatal that so much reliance has been placed upon the applicability of the results of investigations on the other side of the ocean, to the conditions of the western Atlantic and so little done in the way of independent investigation. Canada has made and is still making some effort in that direction but in the United States almost nothing has been done in the past and absolutely nothing is being done now, with the consequence that her Atlantic salmon fishery is almost past history, and the salmon is verging on extinction.

More than sixty years ago Atkins (1874, p. 327) wrote that data for a history of the life of Maine salmon were so exceedingly scanty that, except for assistance afforded by observations made in other countries, it would be largely an unguessed riddle. Atkins was the pioneer and only competent observer then in New England who gave any consideration to practical salmon investigation, and the results of his experiments,

experience, and observations constitute virtually all that is known of the New England salmon to this day. This fact is not directly attributable alone to the scarcity of salmon, but to the lack of adequate effort on the part of anybody else. Consequently, at the present time, for information concerning the salmon, resort must be had to other countries with the assumption that the species is the same and that conditions are similar.

For the foregoing reasons, in this memoir the discussion of the life history and habits of the Atlantic salmon are largely derived from Atkins and European sources, to which is added a small amount from Canadian authorities, and a few of my own observations.

Names Applied to Life Stages.

The names applied to certain stages of growth and conditions of salmon are of British origin, and their use for American salmon presupposes an identity of habits in general, and, as Atkins says, so far as these have been investigated there is nothing to forbid that supposition. The only names adopted in this country are parr, smolt, grilse, kelt, and salmon.

A parr is a young salmon before it leaves the river; a smolt is a young salmon ready to migrate; a grilse is an adolescent salmon, which after it has left the river as a smolt, has spent one winter in the sea. The term grilse, is usually applied to small salmon on their first return to the bays and rivers. A kelt is a salmon deteriorated during breeding. A salmon in relation to the last form mentioned is sometimes designated as a 'clean' salmon, indicating a fish in good condition such as is the case with salmon ascending rivers to breed. Day writes (1887, p. 59, footnote), 'John Josselyn, writing in 1675, refers to the salmon of New England as in the first year a *salmon-smolt*, the second as a *mort*, the third as a *spraid*, the fourth as a *soar*, the fifth as a *sorrel*, the sixth as a *forket-tail*, and the seventh as a *salmon*, showing that even in those days [over 250 years ago] differences had been observed in the various stages of growth of this fish.'

Size Attained by Salmon.

Day (1887, p. 141) says, 'The size to which this fish attains depends upon the extent and character of the water it inhabits, the quantity and quality of its food, temperature, and other circumstances. A considerable amount of caution is necessary before we accept some of the dimensions and weights which have been handed down to us.' In a footnote on the same page presumably as a reason for 'caution,' Day says, 'In Hennesey's *Chronicum Scotorum*, p. 317, mention is made as follows: — "A.D. 1109. A salmon was caught at Luimnech (Limerick) this year, which was twelve feet in length, twelve hands in breadth, without being split open, and the length of its neck fin was three hands and two fingers." A correspondent of *The Field*, February 13, 1886, gave a circumstantial account of one "82 lb. that was taken in a snap-net in the Shannon twelve years ago. It was weighed by the station master before being sent off by train . . . it was also measured." The succeeding month we were informed that the fish was a sturgeon!'

Day then gives some records as follows: 'Respecting those taken by angling in Scotland Lascelles, *Letters on Sporting*, gives 54½ pounds as the largest he had heard of; Young mentions one 67 pounds captured in 1812 in the Nith; Yarrel one killed by Earl Home in the Tweed which weighed 69¼ pounds; Pennant, one of 74 pounds; Buckland cast one of 70 pounds; 4 ft. 5 in. long, taken from the Tay. In 1885 the largest salmon netted in the Tweed were 56 lb., 44 lb., 43 lb., and of those taken by anglers 46 lb., 44 lb., and 43 lb.'

Lawson B. Bell (1887, p. 479) gives weights of his captures as follows: 'In 1884 I killed 11 salmon on the St. Mary's River [Sherbrooke, N. S.] that averaged 30¼ lb. In 1886 I killed 42 salmon on the Restigouche that averaged 23½ lb. This season I have killed eight salmon on the St. Mary's River weighing 28, 27, 32, 47½, 39¼, 28, 24¼ and 28 lb.; total 254 lb., and average 31¾ lb. I was late upon the ground and most of the large fish had passed along before I arrived.'

In March, 1896, A. N. Cheney (1896, p. 199) writes that R. G. Dun killed a 54-pound fish in the Cascapedia, Canada, beating by four pounds the salmon killed in the same stream by President Arthur, which was the record salmon at the time of its capture. Mr. Cheney writes that Mr. A. K. Sloane during the previous summer had killed a salmon which weighed 74 pounds, presumably in the Romaine River, Labrador. This River has not been noted for its large fish as Cascapedia has. Mr. Cheney also writes of Dr. W. H. Drummond, of Montreal, president of the St. Maurice Club, who killed a salmon from the Cascapedia weighing 50 pounds, 8 ounces, and 52 inches long, entitling it to rank between the fish of President Arthur and that of Mr. Dun.

Paulze d'Ivoy (1914, p. 200–201) gives some records of large salmon taken by line. The largest salmon taken by line are those taken in 1750 by Count de Home, which weighed 69 pounds, 10 ounces; one of 61 pounds, 8 ounces, by M. J. Wallace, in 1872; another of the same weight (?) in 1907 by M. T. Stewart, and finally one of 61 pounds, in 1870, by Mr. J. Haggart.

In early July, 1929, there was an unprecedented catch of salmon by the floating traps or pounds at Battle Harbor, Labrador. The largest fish taken, I was told, weighed about 62 pounds. There were many other large fish some of which would have weighed perhaps 30 pounds or more, but I saw none of them weighed. Concerning the weight of salmon in the Gulf of Maine, Bigelow and Welsh (1925, p. 130) say, 'The largest salmon we find mentioned was an English fish of 83 pounds. None even approaching this size is recorded from our side of the Atlantic, where a 50-pounder is unusual, though fish of 40 pounds weight are not uncommon in some of the larger rivers emptying into the Gulf of St. Lawrence. In the Penobscot and St. John Rivers very few fish reach 40 pounds and 30-pounders are rare, the usual run being 10 to 12 pounds. Taking one river with another, large and small, 10 pounds may set as a fair average of the mature Gulf of Maine fish. With due allowance for individual and seasonal variation a two-foot fish will weigh about six pounds, one of three feet, 16 to 20 pounds.'

Geographical Distribution.

The salmon inhabits the North Atlantic and its tributary waters. In Europe its stated occurrence is from the White Sea on the north to Galicia, the most northern province of Spain, in latitude 43° north. Day (1887, p. 141) wrote that 'This fish ranges in the northern hemisphere between latitudes 45° and 75°, and examples have been captured as high as 80° N. Lat. In the United States' report, it is stated to range from the Polar regions to Cape Cod; but their presence in Hudson's Bay and the Arctic coast of America, though probable, is still doubtful. It extends throughout the seas and countries of Northern Europe, around the British Isles, and also the Atlantic coast of France, but does not occur in the rivers which flow into the Mediterranean.

'It is rare in the Orkneys and Zetland (Baikie), but is found in all suitable rivers of England, Scotland, Wales, and Ireland, where it has not been destroyed by pollutions, or obstructions render its ascent impracticable.'

Dahl (1918, p. 1–2) says, 'On the Continent of Europe we find the salmon occurring very scantily in Portugal, somewhat more abundant on the Atlantic coast of France, and numerous along the coasts of the North Sea, the Skagerrack, the Kattegat and the Baltic. It is further distributed along the coast of Norway, the Murman coast, and the White Sea as far as the river Petchora, which flows into the sea a little west of the entrance to the Kara Sea. Further east, in Siberia and in the Arctic islands, salmon do not occur. The salmon of Spitsbergen is really a sea char.'

On the North American coast its northern limit has not been positively determined. Its occurrence in Greenland rested for a long time on the authority of Fabricius (1780, p. 170), who said that it was very rare in Greenland and never seen by him, but it was said to occur in the southern bay Tunnudliorbik, and he had heard that it had been seen in a bay in the neighborhood of the colony of Gothaab.

Dr. Morten Porsild, whom the present writer met in Syracuse, N. Y., stated that there was a regular fishery for 'salmon' at Amerdlog-Fjord Trading District of Holstenborg, near the settlement of Sarfánguag, west Greenland, but that this salmon had not been authoritatively identified. However, owing to its large size, large scales and other characters it was regarded as *Salmo salar*. The Eskimos recognized it as different from the common char. It was stated that it also occurred south of this locality but that only one individual had ever been found as far north as Christianhaab.

Later Dr. Porsild sent a dried skin of a specimen which in his letter dated June 14, 1924, he said was taken in the preceding fall at Sarfanguag, 66° 56′ north latitude, 'the only place where a small number of this species are regularly caught.' The label stated that the fish weighed 4 kilos (8.8+ lbs.) evidently on the authority of David Olsen, presumably the collector. The skin was about 29 inches in total length and about 28⅓ inches to the extremity of the shortest caudal-ray.

Jensen (1925, p. 20) writes, 'Two species of salmon are found in the Greenland rivers and fjords, the large salmon proper (*Salmo salar* Linné), called by the natives Kapisilik ('scale salmon'), and the smaller, fine-scaled char (*Salmo alpinus* Linné), which they call Ekaluk. The former appears only in small numbers and at a few places (only known

from Amerdlok Fjord at Holstenborg and Kapisilik in the Gothaab Fjord). The char on the other hand, occurs all along the coast.' In another connection on page 35 Jensen said, 'The true salmon (*Salmo salar*), as already mentioned, occurs in too small numbers to be of any importance.'

On the authority of Ludwig Kumlien, Bean (1879, p. 134) records *Salmo salar* as obtained in quantities in Cumberland Gulf waters, but says no specimens were obtained that were not split or otherwise mutilated. Low (1897, p. 329–330) states that it is abundant in the rivers flowing into Ungava Bay, but says that it is absent from Hudson Bay.

The late Dr. Wakeham (1898, p. 77) stated that salmon are found in all the bays and larger streams of Labrador and that an extensive salmon fishery is made in August by the Hudson's Bay Company at Georges, Whale, and Ungava or Koksoak rivers. He stated that salmon are found as far north as Lancaster Sound, and that these and the salmon on the eastern shore of Baffin Land are exactly like those taken in the Gulf of St. Lawrence.

While the foregoing accounts appear authentic, there is considerable direct and indirect evidence that some other salmonid was mistaken for salmon and Dr. Wakeham's report does not indicate that he actually saw the fish. Kumlien's statement is plainly open to doubt, but Wakeham's statement that the fish were exactly like those entering the rivers of the Gulf of St. Lawrence appears positive enough. Yet there is the possibility that even he was mistaken, as will appear later. Low's record is likewise open to doubt, for there is no evidence that the fish were positively identified.[1]

In various other reports and publications pertaining to these northern regions there are frequent references to 'salmon' but all are reducible to northern chars. Thus Wakeham mentioned a small salmon in Hudson's Bay which he thought might be 'Hearn's Salmon.' '*Salmo hearnii*' is known to be a char.

Packard (1891, p. 399) stated that at Hopedale the salmon were quite rare and that he was informed that it was not common north of that point. Hopedale is in about north latitude 55°, or approximately halfway between the Strait of Belle Isle and the entrance to Hudson Strait, a little beyond lat. 60° N. Low (1897, p. 330) stated that there was no evidence that the salmon migrated along the coast.

However salmon are fairly common at least as far north as Jack Lane Bay in about lat. 56° N., beyond which there are no fisheries especially for salmon. But straggling salmon are occasionally caught in cod traps at Nachvak Bay, which lies a little north of lat. 59°. At Saglek Bay, about 58° 20′ north latitude, on July 30, 1929, the captain

[1]Since the above was written I find that Prof. J. R. Dymond has published a note (Dymond 1932, p. 185) stating that Captain John Hearn, C.G.S. Mikula, Quebec, reports that Atlantic salmon (*Salmo salar*) occurs in the following rivers of Ungava Bay: — Koksoak, Chimo, St. George's, and Leaf; that considerable numbers are caught and salted in some years at the Hudson's Bay posts on these rivers; that they are not found west of Cape Hope's Advance; that discussions with Captain Hearn convinced Prof. Dymond that the fish were 'properly distinguished'.

Prof. Dymond does not say how Captain Hearn convinced him that the salmon of Ungava Bay were 'properly distinguished' as Atlantic salmon. From Prof. Dymond's note alone I can but suspect that the supposed salmon is a large char which has been stated to attain a very large size in that region. My suspicion is supported somewhat by the fact that Captain Hearn does not mention Ungava Bay among those localities where he said he had seen 'Sea trout.' He says he had seen the species taken as far north as Resolution Island, also in McClure Strait, and at Port Burwell.

of a Newfoundland fishing schooner told me that he had caught some salmon, but not many, in Ryan's Bay, which is as far north as he had fished. Ryan's Bay is not named on any map available to me but from Jordan's notes (Islin-Jordan Expedition, 1926) I judge it to be between Nachvak Bay and Ekortiorsoak in about north latitude 59° 30′.

In a collection of fishes from Labrador obtained by the Islin-Jordan Expedition and turned over to me for study is a salmon of nearly 30 inches total length, which is said to be one of the only three that had been taken in a cod trap at Saglek Bay that season up to August 11. Mr. Jordan was of the opinion that these northern salmon were strays which had fallen in with schools of sea trout (chars), while the bulk of the salmon remained in the warmer southern region of Labrador. Mr. Jordan said that no salmon had been reported in Nachvak Bay that year although several are usually caught every season. There were no signs of parrs in the streams. On July 30, 1929, two salmon were taken in a cod trap at Saglek Bay.

While such roving salmon apparently occur in very small numbers almost up to Cape Chidley, as Low (1897, p. 330) said, there is no evidence of a migration along the coast.

If the salmon do not migrate in numbers along the coast it would hardly be expected that they would reappear in quantities in Ungava Bay unless they come from some other direction. Low's (1897, p. 330) reference to the temperature barrier to Hudson's Bay may possibly apply to northern Labrador. Packard says that the Labrador midsummer corresponds in temperature to that of the middle of May in New England. Farther north the same seasonal conditions cannot obtain. The geographical distribution of the salmon, then, may be determined by the range of temperature conditions represented by those New England spring months, varying more or less either way from the month of May.

Professor E. E. Prince (1899, p. lxii), Dominion Commissioner of Fisheries, says that long conversations with residents from Fort Churchill [Hudson Bay], Chesterfield Inlet, etc., who have lived upon the various rivers in question, have shown rather that the large salmonlike fish captured for food have been enormous sea trout or species of *Salvelinus;* also, he stated that he had examined specimens of large salmonids supposed to be salmon from northern Labrador and every example proved to be a recognized species of northern trout [*Salvelinus*]. Professor Prince indicated that the range of the true salmon ceased north of Hamilton Inlet and that it is not found in the rivers of the District of Ungava.

The range as pertains to reproduction may cease somewhere not far north of Hopedale and the wanderers farther north may signify no more than do the summer stragglers of more southern species of fishes in the waters of New England. However, the opinion has been advanced that the reason the salmon do not occur more abundantly northward is the lack of suitable rivers in which to spawn. If these northern so-called 'salmon' are chars, the northern reproductive range of the salmon but slightly overlaps the southern range of arctic chars, the southernmost recorded locality for which is Newfoundland. The more northern extensions of the range of the salmon in Europe and its

occurrence in Iceland and southwestern Greenland may perhaps be attributed to the influence of the Gulf Stream or other climatic or physical conditions.

Almost every accessible stream from the north shore of the Gulf of St. Lawrence to southern New England was once frequented by salmon, but throughout this extent they have greatly decreased in numbers, which decrease is most marked in New England. There is no historical indication of salmon having ascended any rivers south of the Hudson River except as the result of fish-cultural distribution. Some years following the introduction of young salmon, adult fish have appeared in the Delaware. A record for the Potomac seems to have been exaggerated and of a young fish, and the identity of one in the James River is uncertain. That adult salmon appeared in the Delaware indicates that the river was at least in some way favorable and may have been a salmon river at some early period.

While there may have been some doubt regarding Henrich Hudson's observation in 1609, the fact that in Mitchill's (1815, p. 355–492) time it occasionally appeared in the river and in recent years it gave temporary promise of becoming a salmon river through fish-cultural effort, indicated that it is quite possible that Hudson actually saw 'great stores of salmon in the river' as he passed the Highlands. Dekay (1842, p. 242) stated that 'The Sea Salmon rarely appears on the coast, except as a straggling visitor. Such an occurrence took place in August, 1840, when a Salmon, weighing eight pounds, entered the Hudson river and ascended it more than one hundred and fifty miles, when it was taken near Troy.'

Goode (1888, p. 442) says that many stragglers have been taken in the Housatonic and Hudson, but Linsley (1844) does not mention the Housatonic as a salmon river. Authentic history, however, permits the Connecticut River to be regarded as the only real salmon river of southern New England, although it is not beyond the bounds of reason to assume that in the days of abundance of salmon and before the advent of the white man, some of the other, smaller streams may have been more or less frequented by salmon.

Marine Habitat.

G. Brown Goode (1884, p. 469) stated that at least half of the salmon's life is spent in the ocean. This period, however, is more or less intermittent, depending upon the number of times a salmon breeds and the time of the year when it enters fresh water for breeding purposes. It has been stated that young salmon remain in the rivers from two to three or four years and rarely five years before descending to the sea, and after their descent as smolts, individuals may remain in the sea similar lengths of time, although the majority are short-period fish.

Where the salmon lives while in the sea is a subject of much discussion, and a question which has not been fully answered. Some views regarding the question have been purely speculative with absolutely no evidence to support them. As late as 1905 Charles Hallock (1905, p. 236), like some of more scientific reputation who preceded him, suggested

that all migratory fishes, in winter, resort to the warm waters and abundant food of the Gulf Stream. Such opinions hardly rise to the dignity of theories, for they lack knowledge of the conditions of the Gulf Stream even, to say nothing of any supporting evidence in those conditions.

Movements of Salmon in the Sea.

The movements of salmon may be considered in two classes: (1) for feeding; (2) for breeding. Feeding is largely in the sea where the fish are beyond observation. Now and then a salmon is taken at sea, which indicates a little concerning the movements. Most that is known is derived from fish on the coast and from marking experiments. Some little may be inferred from the time and place of appearance on the coast.

More than 50 years ago Henry Youle Hind (1880, p. 126–127), of Windsor, Nova Scotia, advanced some plausible theories concerning 'The movements of Salmon in the sea,' substantiated by observational and investigational evidence, which later appear to have been disregarded or overlooked. His observations principally pertain to Newfoundland and Labrador, and as concerns the movements of salmon the statements are evidently accurate. His theory as to the winter abode of the fish is largely conjecture based upon analogy, although the movements and habits of the fish while under observation perhaps to some extent support his views.

He says: 'The winter homes of the great body of salmon are on the seaward slopes of the sea-bottom outside of the 100-fathom line of soundings or thereabouts, and generally it would seem just out of the reach of the harp-seals. There are probably two million harp-seals wintering on the coast of Newfoundland, but although these active marauders frequently bring cod and "turbot", the Greenland halibut, and flat-fish generally to the ice-floes and ice-pans, I have not heard of a single salmon being brought up by seals. Nevertheless, since large salmon are caught in deep water off the Island of Fogo up to Christmas, schools of this fish are on the coast, in deep water, at that period and they have been taken there in seal nets. In such deep bays as Trinity, where there are from 120 to 320 fathoms of water, salmon are not unfrequently cast upon the shore during winter storms, but these are probably either spring-spawning fish, or schools swiftly resisting fresh water under the ice.'

Having spoken of the deep waters of the various bays of Newfoundland and Labrador, the author went on to say:

'It is from these profound and populous depths where cod, young herring, caplin, and probably launce range, with an innumerable multitude of sub-arctic fishes, and an infinite host of the lower forms of life, all fed directly or indirectly by the unfailing Labrador current, that the full-grown silver-sided salmon rises in the spring to pursue his food along the islands, headlands, promontories and wall-like escarpments of the south coast of Newfoundland. On the east Atlantic coast of the Island and the Labrador coast, these features are reproduced in various localities on a less grand scale, and in

many parts the steep escarpments are replaced by gentle slopes which lead, within from five to 50 miles from the land, to profound depths.'

'In order to form a proper conception of the general spring movement of salmon in the sea on a grand scale it is necessary to refer to a map of Newfoundland and Labrador. The distance from Burgeo Islands (longitude 57°, 40′, latitude 47°, 30′) on the south coast of the island (Newfoundland) to Ukkasiksalik (latitude 56°) on the northern Labrador is about 1500 miles. The salmon strike the whole of this long extent of coast line between May 16th and July 16th, a period of 60 days. . . . The presence or the the incoming of food at the spring season of the year brings the great body of salmon shoreward at that period.

'A vast army of fish bearing the colors of *Salmo salar* advance from the continental submarine slopes in successive battalions toward the coasts through nine degs. of latitude as far as Fern Bay, some twenty miles beyond Ukkasikaslik, for there the salmon may be said to cease. They do not appear again until Ungava Bay is reached, inside of Hudson Straits.'

'We are now in a position to consider the movements of salmon in the sea as far as regards the large schools of adult fish which are first taken at the headlands during the earliest visible runs in the spring. The schools come inshore from deep water with and against the rising tide, and begin to feed without any special regard to river estuaries or fresh water, for they strike and coast about small islands and bold promontories stretching far into the ocean and destitute of rivers, just as frequently as they visit the headlands which guard the estuaries. They pursue a course in shallow water parallel to the shore line and against the tide; they go out to sea again just as the tide begins to turn, and when in deep water they turn round and swim against the ebb tide. At the turn of the ebb they approach the shore again and pursue their course as before, against the flood, going out to sea at the turn. Their movements, as will presently be shown, are in the form of a series of loops or ellipses along the coast, the straight line connecting these loops being in deep water.

'If these movements of the feeding fish be plotted they will form a continuous line parallel to the coast, with loops in it at irregular intervals. The loops represent the movements of the fish toward and on the coast, the straight parts in deep water the progress up the bay or along the coast line.'

In the same publication I. Henry Phair (1888, p. 291), of Fredericton, New Brunswick, wrote of winter salmon in the St. John River region. He said that in Belle Isle Bay, an inlet or bay on the St. John River in New Brunswick, about 28 miles above the mouth, in one season from the latter end of December to the end of March upward of 200 salmon were taken by one fisherman. It was stated that in the early part of winter the fish were poor and dark colored, but as the season advanced they improved rapidly and were exceedingly fat and well colored. The author was inclined to believe that the Belle Isle Bay fish belonged to a late run of salmon which entered the river, deposited their spawn, and on their way back to the sea, finding an abundance of food in the bay, remained there for the winter and in the spring continued their journey to salt water.

These fish undoubtedly belonged to the 'winter' run of salmon which enter this river in the late fall and do not spawn until the following fall one year later.

A later article signed by 'A. N. C.' (1892, p. 152) in the same publication suggests that the salmon of each river go out to sea sufficiently far to find conditions of temperature and food which suit them and there they remain separate from the salmon of other rivers, until it is time for them to return to fresh water. It was stated that the movements of salmon were governed by their food, and if they find it near the mouths of rivers, there they remain, and if not, they seek it farther away, in some instances at a great distance from the rivers, and apparently no particular kind of food, but quantity rather, was sought.

In support of this theory instances of winter capture of salmon were cited. Mr. Blackford of Fulton Market reported that every winter he got a few fish from the Atlantic coast that were evidently part of schools of fish that run up into the Kennebec, Penobscot, and other eastern rivers, and that during November and December 15 or 20 fish weighing from 12 to 24 pounds each were received. They had been caught in mackerel nets in the vicinity of Provincetown and North Truro, Mass. It was stated that these nets were set out from the Cape in very deep water. Also, about the first part of February, several specimens of very handsome salmon were received from Maine, where they had been caught by smelt fishermen. Such records are strong indications that the salmon do not necessarily go far from the coast, and the multiplicity of records of winter coastwise catches strengthens the evidence. There are probably more winter salmon caught than are ever brought to public attention.

According to Calderwood (1930, p. 18–19), 'In the Baltic, a regular line fishery for salmon is carried on in the neighborhood of the island of Bernholm. This fishery is carried on from November to May, the lines being hung at a moderate depth and the hooks baited with herring.'

On the Atlantic coast of North America there is no special line fishery for salmon, but now and then the capture of one on a trawl in the ground-fish fishery is heard of. A few of such records are referred to on following pages.

Calderwood (1930, p. 19) says: 'In the Skagerrack between the south of Sweden and the north of Denmark, men fishing for mackerel appear to capture a fair number of salmon. In Ireland a regular drift-net fishery for salmon is carried on off the western counties, the nets being set at distances off the coast ranging to about 15 miles. For some reason or other attempts to catch salmon in this way off the coasts of Scotland resulted in complete failure.'

Salmon are more or less common on our coast during the spring and early summer, and in the fall. Occasionally one is caught at sea. Spring and early summer fish have been supposed to be related to the spawning runs, since in these early months some are known to ascend rivers.

In this connection Calderwood's remarks concerning the wanderings of salmon in the sea are of special interest as they indicate how little is known about the subject at this late date even in Europe where salmon study for many years has been intensively carried on, particularly in Great Britain and Norway.

Calderwood (1930, p. 14) says: 'Their wanderings in the sea have been wide, wider than perhaps we know, and when they leave the open water, they give up the search for food in order to follow the other great instinct of all creatures and they make a passage to the coast.'

In another place (1930, p. 19) he says: 'Chance captures of adult fish are, however, made from time to time, and these show us that salmon are to be found at great distances from land.'

He goes on to say: 'Two of the captures are of special interest as indicating that the fish go very far from any fresh waters where salmon are commonly to be found. One was taken by a herring drifter fishing 67 miles E. by N. from Lerwick (Shetland Isles), the other by a trawler about 40 miles W. of the Fair Isle. There is a great herring fishery conducted every summer round the Shetland Isles, and it is clear that some salmon know where the shoals are. In this connection I recall a statement of Prof. Dahl's that Norwegian fishermen have told him how they saw great numbers of salmon in shallow water in the neighborhood of the Fair Isle. It is hearsay evidence, but it has a certain amount of application in view of the captures mentioned.

'It is necessary, I feel sure, that we should realize how completely separated from all fresh waters salmon are during their sea life. They can rove hundreds of miles away off the coast, as they follow the creatures upon which they feed. Instead of regarding those chance captures as telling us little or nothing, I am inclined to regard them as valuable indications of where salmon go in the sea.'

Salmon Taken in Casco Bay, Maine, by Traps, Nets and Pounds.

On the Massachusetts coast salmon are now regularly taken each year at most of the important pound-net and trap fisheries. The largest numbers are caught in Cape Cod Bay.

Beginning with 1917, in connection with his statistical work pertaining to the vessel fisheries landing at Portland, Mr. Walter H. Rich, agent of the United States Bureau of Fisheries, kindly collected for the writer such data concerning salmon as came to his notice. Necessarily the records are not complete in every respect and are not full for every year. Many of the salmon taken at the pounds in and about Casco Bay are sold locally to summer people or to towns nearer the traps. Probably the receipts at Portland would not amount to more than one-third of the catch. It is further noted that a large number of the fish which enter the traps do not remain; they jump the corkline to make their escape. Most of the records pertain to salmon incidentally caught in floating traps or pounds or other nets operated for other fishes.

Table 2 embodies these records in a general way without specifying the exact locality, but all are Casco Bay data. It shows the total number of pounds of salmon caught in the traps or pounds, and nets, from May to September, inclusive. Of the total catch of 10,419¾ pounds, 9,303 pounds were taken in traps or pound nets.

Although incomplete and more or less deficient in some respects, the data are interest-

ing for two reasons: They show a fishery, which though small, adds considerably to the returns to the fishermen, as salmon are only incidental to the principal object of the fishery but bring a good price in the market. They show also that salmon of various sizes are present in the shorewise waters in varying numbers throughout the summer months, although the localities of capture may be a long way from accessible spawning places.

TABLE 2.

Total Amount of Salmon Caught by Traps or Pounds, Drift-gillnets and Purse Seines in Casco Bay and Vicinity, Maine, as Brought to the Port of Portland.

Year	May	June	July	August	September	Total
1917			11½[1]	36	116	163½
1918	12	11	208½	131½	8[1]	371
1919	30½	267½	213	35	18¾	564¾
1920		61½				61½
1921	14½	801½	1573	240	7½	2636½
1922		136¾	459	170	41	806¾
1923			75½	1073½	83½	1232½
1924	46	237	335¾			618¾
1925	4[1]	354	637½	10[1]		1005½
1926	2[1]	57	5½			64½
1927	5½	148¾	90½	24½		269¼
1928		96½	94¾	15		206¼
1929	36	190½	36½			263
1930		258	63	8	11	340
1931	11½[1]	157	402½			571
1932	11[1]	745	469	20		1245
Total	173	3522	4675½	1763½	285¾	10,419¾

[1]Recorded as single fish.

The presence of salmon in the Casco Bay region, not only in the summer, but to some extent in other months gives rise to the question of their origin. Are they naturally bred or the product of the Craig Brook hatchery? If they are naturally bred in what streams were they hatched? It is possible that there are some limited spawning places in the lower Kennebec. There is one tidal stream connecting a small fresh-water pond on Small Point with the Kennebec which a few salmon are said to ascend. If they do spawn here, the known spawning places are very limited in both number and area. The writer has seen an occasional salmon among the alewives in May at the dam in a small stream at Woolwich connecting Nequassett Pond with the Kennebec River. There may be other small streams affording very limited spawning places between this region and the Penobscot River, also between the Penobscot and Passamaquoddy Bay. If there are, there is no definite information concerning them. Perhaps in the aggregate such creeks and small streams may be responsible for the Casco Bay Fish, but this is very doubtful.

It has been demonstrated by marking experiments that at least some salmon wander a long way from their birthplaces. The distance traveled by one of the fish marked by Dahl suggests the possibility that the salmon occurring on the western coast of Maine

could have originated in the St. John River of New Brunswick or in some Nova Scotia stream. But it is difficult to believe that the fish caught on the coast of Delaware, New Jersey and other places south of Cape Cod ranged so far, although it is not beyond the bounds of possibility. It should be remembered, however, that most of these fish were caught 40 years ago, more or less, when fish cultural efforts were made to stock the Delaware, Hudson, Connecticut, Merrimack and other rivers, and there were occasional appearances of salmon in the streams where the young salmon were planted, notably the Hudson.

In the writer's possession is a young salmon, 229 millimeters (slightly over nine inches) long, with red spots on its side, taken at Bayside, New Jersey, in tide water May 1, 1899. There can be little doubt that the fish came from the Delaware River, where it probably had been planted by the Pennsylvania Fish Commission, as the United States Fish Commission had delivered some thousands of Atlantic salmon eggs to the state hatchery at Allentown in both 1898 and 1899.

Young Salmon in the Sea.

The second stage of the salmon's life begins with the departure of the smolt for the sea. From the beginning to the end of its existence in the river it has been comparatively easy of observation, but after leaving the river it has been more or less 'shrouded in mystery.'

Calderwood (1930, p. 16–17) says, 'The descending salmon smolt when it gets into the tide goes straight out with the ebb, and does not return the same year.'

Atkins wrote (1874, p. 335) that little is known of the movements of salmon during the growth from smolt to grilse and from grilse to adult. He remarked that it could be safely said that they were feeding; but of the location of the feeding grounds and the nature of their food scarcely anything was known. He said that at their disappearance and at their reappearance their stomachs were alike empty of food, except in rare instances.

According to Dahl, mackerel fishermen took three young salmon measuring respectively 6⅞, 15⅜ and 17 inches off the coast of Norway, and he himself by means of a small-meshed fish trap set in Trondhjem Fjord, took a few small salmon measuring 17⅝ to 27½ inches. Dahl also reports that after exhaustive search in European museums for young salmon, he found in Bergen University two examples, 9¼ and 11 inches long, which, he was informed, had been found among young mackerel in a Christiania fish market. These occurrences indicated to him the direction which he should pursue in his efforts to locate young salmon at sea. He later, in two successive years during the winter, spring and summer up to and including September, secured a number of salmon and grilse, some of the latter being under 18 inches in length. From the attendant circumstances pertaining to these captures his conclusions were that the young salmon, after leaving the river and fjords, pass to the open sea and frequent the natural habitats of young mackerel and herring.

As pertains to the New England coast, in 1894 (1895, p. 98), Smith wrote that for two or three years large numbers of young salmon about six inches long have been noticed in the pound nets, at North Truro, Mass., according to Capt. Atkins Hughes. Smith (1898, p. 119) further said that at Matinicus, in August and September fish too small to utilize are taken in considerable quantities. In 1895 and 1896 the smallest taken was one-half pound. The present writer observed a young salmon of about one-quarter pound taken in a pound net at Small Point, Maine, July 6, 1896. This fish was 7½ inches long.

According to Mr. Rich an eight and one-half inch salmon was taken in a pound net at Richmonds Island, July 1 and another about $9^1/_3$ inches on July 12, and Will Richardson and Gus Wallace of Small Point say that 1,000 pounds of six-inch salmon were taken in their pounds and liberated this year. One of about $9^3/_8$ inches long was taken in a trap near Harpswell, August 16, 1923. August 2, 1928, Charles Pye of Bald Head, Small Point, stated that many small salmon 'smelt size,' were caught by him: '15 or 20 every day; 500 so far.' A 'pre-grilse' $11^4/_5$ inches long was caught about September 16, and another about $13^1/_5$ inches long on October 3, 1923, in a pound net at Small Point, Casco Bay.

Records of Salmon Caught in the Sea.

In a study of the marine habitat of the salmon, I have collected a record of over 200 instances of these fish taken in the sea. To enumerate each would but accent the obvious. Sufficient then but to note that the extreme range covered by these takings is long and wide, extending from well off the coast of Delaware on the south, northward to the coast of Labrador, in the vicinity of the Strait of Belle Isle latitudinally and from the coast lines of Maine, Massachusetts and New Jersey to the southeastern part of Georges Bank, distant from Cape Cod, the nearest land, 160 miles longitudinally. The recorded takes were made by hook and line, traps, weirs, gill and pound nets, line and otter trawls and mackerel seines and at all seasons of the year. The range of years covered by these individual reports extends from 1879 to 1930 and show weights of salmon taken from 'smelt size' to 35 pounds.

Few if any small fish are among those taken other than by the fish-catching appliances close to or not far from the coast line and none of the salmon included in these over 200 separate cases are contained in the preceding table in this paper. In general these reports of individual takes are well authenticated and are taken from newspapers published at fishing ports, fisheries publications, reports of fishermen and fish dealers and from a collection of these occurrences gathered by Dr. Hugh M. Smith of the United States Bureau of Fisheries and for several years its commissioner, who noted in 1898 that instances were multiplying of the taking of salmon at sea on trawl lines on the New England coast, usually during the time when the fish were running in the rivers, but occasionally in midwinter.

As an indication of the scope of these reports as to the season of catch, size range, dis-

tance from shore, general locale of taking, and catching apparatus, the following are culled from the reported incidents of capture:

A salmon weighing eight pounds was caught on a line trawl on the southeastern part of Georges Bank in 20 fathoms of water by schooner *Hattie I. Phillips* in 1896. The location indicated is 160 miles from the nearest land, Cape Cod.

A ten pound salmon, the first reported caught off Cape Ann in 30 years, was taken in a trap off Magnolia in June, 1879.

In June, 1888, two salmon, 17 and 19 pounds were taken at Cranberry Isles, Maine, almost 35 miles in a straight line from the mouth of the Penobscot River. During the following July six salmon were caught at the same place.

About April 10, 1893, the mackerel schooner *Ethel B. Jacobs* of Gloucester, Mass., was cruising for mackerel off the coast of Delaware. When in latitude 38 degrees, at a point about 50 miles east southeast of Fenwick Island lightship, the vessel fell in at night with a large body of mackerel, and a seine was thrown round a part of the school. Among the mackerel taken was an Atlantic salmon weighing 16 pounds. The fish was fat and in good condition. Another was reported to have escaped over the corkline. This would be about 60 miles offshore from the nearest land.

In 1895 a Penobscot River salmon exhibited in a Bangor market tipped the beam at a trifle less than 35 pounds. It was taken in a weir at Stockton Springs.

While salmon are caught in nets and weirs in the vicinity of Islesboro, Maine, the experiences of a Searsmont man fishing from the steamboat wharf, presumably with a hand line, while waiting for a boat at that place, is unprecedented. To his own astonishment, and that of others, he landed a salmon of 21 pounds.

In December a salmon of 28 pounds was caught on a trawl near Halfway Rock off Salem Harbor. In 1896 I personally recorded the following: At North Truro, Cape Cod, June 15, a salmon of 12 pounds, and on June 17 two salmon of 15 and 18 pounds were taken in a trap.

In the first week of June, 1890, a salmon was taken on a trawl by boat fishermen off Gloucester. On June 11, 1893, a salmon of 15 pounds, and on various other occasions, in the same month salmon from 12 to 15 pounds were taken on trawls by boat fishermen, off Gloucester. Also on a trawl of a hake fisherman one was caught. The weight was not stated.

In April or May, 1917, the schooner *Ida and Frances*, Captain Ralph Bickford, purse-netting pollock, set around a supposed school of those fish. All but five fish jumped out. These five were salmon averaging ten pounds each. It was estimated that there must have been at least 200 salmon in the school.

On March 18, 1929, a 30-pound salmon was caught on a trawl of the schooner *Virginia*, on Browns Bank, 60 miles south of Cape Sable, N. S., and on August 6 the schooner *Oretha F. Spinney* took a 19-pound salmon on a halibut trawl off the Labrador shore in the Strait of Belle Isle. In March, 1924, Captain Reuben Doughty took a five-pound salmon from the stomach of a 'steak' cod of 30 pounds caught on Jeffreys, 36 miles southeast of Portland Lightship, in 70 fathoms.

In 1932, June 2, off Cape Porpoise two and one-half pounds of salmon (number not stated) were caught in mackerel gill nets by a small-boat fisherman; on June 8 the schooner *Reliance* got one of 11 pounds east of Boon Island. On June 2, 1926, steamer *Elizabeth C.* fishing with bottom gill nets on the 'Kettle Bottom,' ten miles south from Seguin, in 70 fathoms, took one salmon of 20 pounds. On February 17, 1931, steamer *Pofisco*, similarly equipped, on 'Tanta,' 12 miles south from Cape Elizabeth, took a salmon of ten pounds in 80 fathoms; on March 1 the same vessel on the same ground took two fish, one of ten, the other of 13 pounds; and April 2, the same vessel on the same ground took one fish of 23 pounds. On June 11, 1932, steamer *Richard J.* caught one salmon of 18 pounds 20 miles south from Portland Lightship and on June 13, the same vessel in the same locality got one of 18½ pounds, both in gill nets.

On February 12, 1925, steamer *Sea Gull*, an otter trawler, took a large salmon on Georges Bank, 172 miles southeast from Boston Lightship. In 1929 steamer *Lewis M. Winslow* of Boston, reported to the United States Bureau of Fisheries that in the year's catch of the vessel, 100 pounds of salmon, valued at $40, were taken in her otter trawl on Georges Bank. On April 2, 1932, a ten-pound salmon was taken by the steam otter trawler *Tremont* in the South Channel, 100 miles southeast from Highland Light, Cape Cod. On April 7, of the same year, the steamer *Brookline* took a salmon of eight pounds on La Have Bank, 100 miles south from Halifax, N. S., in her otter trawl.

Feeding Habits.

Feeding in the Sea.

'The salmon while it remains in the sea or in the brackish estuaries takes particular delight in feeding on crustaceans and their eggs, small shrimps, and young crabs [Goode 1884, p. 470].' This and similar statements concerning the food of the salmon have been handed down in salmon literature from time immemorial. Owing to the fact that salmon near shore or in the rivers were usually the only fish possible of observation concerning their food, for a long time little was known. But in the light of more recent observations it would seem that the foregoing bill of fare is somewhat incomplete. Day (1887, p. 107) says that he had found the remains of sand eels, *Ammodytes*, herrings, and crustacea in their stomachs. Both Jardine and Thompson indicated that the salmon eat sand eels. Morrison recorded salmon taken in tidal water which contained full-sized herring. The British Museum has the remains of a silver gar, *Belone*, taken from a salmon in fresh water, but just from the sea.

The *Fishing Gazette*, December 20, 1879, mentions a 24-pound salmon which contained two trout, each about one-sixth of a pound in weight. In a footnote Day (1887, p. 107) cites the statement of a Mr. Gosden (*Land and Water*, March 8, 1886) to the effect that in 1874 he opened 490 salmon in which he found eels, minnows, loach, gudgeon, sand eels, shrimp, etc.

Day (1887, p. 108) states that a fishmonger in the Promenade, Cheltenham, drew his attention to the condition of the belly of a 12-pound clean male salmon, received by him

the previous day from the tidal portion of the Severn. The stomach was very distended, and on being removed from the fish was found to measure seven inches in length and contained 22 quite fresh entire sprats (*Clupea sprattus*), the smallest being 2.6 inches and the largest 4½ inches long. Hind (1880, p. 126) said that on approaching the coast in the spring, the salmon feed ravenously upon capelin, sand eels, and young herring, which were also at the same time nearing the shore. At this season adult salmon first follow the capelin from the depths, and are caught with capelin in their stomachs.

Calderwood (1907, p. 113–114) refers to investigations concerning salmon fresh run from the sea, giving a table taken from the *Fourteenth Annual Report of the Fishery Board for Scotland*, part II, no. 2. The table shows that the greatest number with food was taken during the months of March, April, May, and June, when the monthly percentage of the number of fish ranged as follows: March, 43.4; April, 36.9; May, 16.7; June, 13.1. He states that the food consisted largely of herring, while other contents observed were sand eels, whiting, and haddock. Some, however, contained crustaceans and marine worms, and as 'curious oddments' he mentions a caterpillar, four feathers, a leaf of a beech tree, moss, blades of grass, and spikelets of sedge, which he regarded as interesting when we recollect the nature of the salmon fly. The crustaceans observed were mostly amphipods which were thought to have been first ingested by herring which the salmon afterwards swallowed.

The Norwegian investigator, Knut Dahl (1918, p. 15) states that in the year 1909, between June 30 and July 2, he opened and examined the stomachs of 46 grilse, caught between Trondhjem and Finmarken. In 26 cases the stomachs were empty or contained indefinable pulp. In 17 fish he found herring up to 20 centimeters in length, and in some cases the stomachs were absolutely crammed with these fish. In three cases the contents consisted of capelin (*Mallotus villosus*). In two cases the stomachs were full of Euphausidæ, partly mixed with pelagic amphipods (*Parathemisto oblivia*).

The foregoing are a few concrete examples of the many scattered references to the food found in the stomachs of salmon fresh from the sea. The present writer has examined the stomachs of many fish, particularly from the weirs of the Penobscot River and from the St. John River in New Brunswick. In most instances the stomachs were empty but in some Penobscot fish smelts were found and in a few of the St. John River fish medium-sized alewives were observed. From these notes it is quite evident, that, as suggested by a previously referred-to observer, the salmon are not very discriminating in the pursuit of food. The fact that a comparatively small percentage of the fish taken in their approach to the rivers contain food, does not necessarily indicate that they have ceased to take food. It would seem, rather, that the empty stomachs may be accounted for in some such way as suggested by Jordan and Evermann (1902, p. 165–166), 'The assumption that salmon do not feed after entering fresh water is founded upon the fact that seldom is anything found in their stomachs when caught in traps or by hooks. In traps and weirs it is the habit of most fishes either to disgorge the food from fright or, if not immediately removed, to digest it.' The present writer has opened scores of the notoriously voracious dogfish (*Squalus acanthias*) and found a large majority

of their stomachs empty. It can hardly be inferred from this fact, that the dogfish was for any reason abstaining from food, if it were available. The probability is that the food is rapidly digested, and only those which have recently ingested food are found to contain it. Having ascended rivers toward their breeding places and near breeding time it is a different proposition.

Feeding in Fresh Water.

The question whether or not salmon feed during their ascent of rivers is an old one which has given occasion for many lay arguments pro and con as well as much scientific investigation.

Much of the evidence that salmon feed in fresh water has been based upon the facts that food has been found in fresh-run salmons' stomachs and that they will take bait or fly.

At Basel, some 500 miles up the Rhine, Dr. F. Miescher-Rüsch (1883, p. 429–430), professor of physiology at Basel, made observations upon the Rhine salmon the account of which became almost a classic. Having for four years examined the intestines of Rhine salmon, he was forced to the conclusion that the salmon, from the time they ascend the river from the sea until they have finished spawning, never take food, and that, as a rule, they do not take any food afterwards. He stated that occasionally he found a small stone, a piece of a blade of grass, or a stalk of some plant, which had been swallowed. Once a tolerably large larva of an insect was found in the small intestine, but entirely undigested and intact. He also decided that, with the exception of the bile, no effective gastric juice is secreted.

On the lower Rhine an examination of 2,000 salmon by Hoek revealed only seven with remains of food in their stomachs. In Scotland after a number of years of exhaustive research Dr. D. Noël Paton (1898) reached the conclusion that salmon did not feed in fresh water.

The fact remains that salmon seldom take food during their ascent of rivers, the best evidence of which is that seldom is anything of the nature of food found in the stomachs of those caught, and that there is not sufficient food in the rivers to support the number of salmon that ascend them. The general absence of parasites in the intestinal tract of salmon after they have been some time in fresh water has been offered as evidence that salmon do not feed. The foregoing are a few of the specific observations upon which the general assumption that all Atlantic salmon practically cease to feed in fresh water is based; also, which convey some positive evidence that occasionally or in some instances food substances are to some extent taken.

On the other side of the question as late as 1921, *The Fishing Gazette* published a communication by R. F. Miles (1921, p. 136) which the editor, Mr. Marston, pronounced 'interesting testimony.' Mr. Miles wrote: 'I was very high up the river, say seven or eight miles, where it was so narrow one could almost jump across. Fishing in clear water just below a little fall, I hooked a grilse of about 7 lb. Both I and my gillie

plainly saw him eject a sea-trout ¼ lb. to ½ lb. in weight, which we picked up, scarred a good deal and, of course, dead, but quite fresh. I was fishing with worm, and killed a good many salmon with worm that month, but a very few with a fly.

'My opinion always has been that salmon in fresh water though they of course get poorer and more out of condition the longer they are away from the sea, feed sufficiently to avoid starvation, but directly they are hooked eject everything in the stomach, though there is usually difficulty in observing this.'

As the exception that proves the rule that salmon do not feed in fresh water, Calderwood (1930, p. 73) cites the following instances, 'I have known four instances of fish in rod-caught salmon in the last thirty years; a trout in a salmon caught in Loch Shiel, a char in a salmon taken, if I remember rightly, in Loch Tay, a trout in a salmon caught in the Thurso, and five parr taken in a salmon caught in a tributary of the Tweed.'

But as Miescher-Rüsch (1883, p. 462) remarked in connection with another subject pertaining to the Rhine salmon, 'I feel compelled to warn people not to apply the experiences gained in other rivers to the Rhine salmon, and *vice versa*.' The fact that conditions in different rivers greatly differ and that the habits of the salmon may differ accordingly, should not be lost sight of, and that generalizations from specific localities may lead to confusion. While the basic physiological impulse to ascend fresh-water rivers is doubtless the same in all salmon, it may be modified more or less by local conditions and the necessities imposed by those conditions. Or, as succinctly expressed by Gurley (1902, p. 422), the habit of abstinence from food 'has many degrees and probably is strict in direct ratio to the length of time required ad minimum and the amount of time available ad maximum, for the species to reach the spawning grounds,' and so 'Natural selection would then gradually weed out those individuals which had the feeding impulse strong, and favor those which tended to concentrate their feeding and motor-sexual functions into different portions of the yearly cycle.'

It has previously been suggested that with the Atlantic salmon there may be some local structural racial differentiation, something like that manifested by some of the Pacific salmon, as shown by Gilbert (1918, p. 37). Or, there may be a correlated physiological differentiation. In fact, this is to be expected. The salmon which ascend the Rhine 500 miles or more have conditions to meet which do not obtain in the comparatively short rivers of Scotland or Norway. Fish which live in the Baltic and ascend the rivers of Finland or Sweden can hardly be comparable in every respect with those which ascend the Rhine or the rivers of Great Britain. While in the case of all, the 'feeding and motor-sexual functions' are largely 'concentrated in different portions of the yearly cycle,' the degree of concentration and the abruptness of transition from the one to the other may and probably do differ according to conditions. Furthermore, it could hardly be expected that in any case would a sudden suppression of the feeding impulse take place. The switch-board of the 'nerve responsive' mechanism could hardly be expected to be under such complete automatic control. So while the breeding impulse more or less gradually becomes paramount, and the feeding impulse correspondingly subordinated to it, it may be expected that the nerve mechanism may be for a

time occasionally excited by objects of the nature of food or having that appearance, and that this excitability grows weaker as the breeding time and place is approached.

This seems to be in accord with the facts as indicated by the observations mentioned and by general experience, and would account for the fact that salmon occasionally eat a fish, or insect, swallow a leaf, or piece of bark, or take a bait or artificial fly. It would also perhaps account for what have been regarded as peculiar idiosyncracies of the salmon. It also may suggest the reason why the best angling season is in the spring or early summer. It appears also from observations cited and from general experience, statements to the contrary notwithstanding, that salmon kelts do not abruptly begin to feed in ravenous manner, and those kelts most commonly found with food within their stomachs are males. This latter fact possibly is connected with what appears to be a fact that at least some males linger longer than females in fresh water after spawning.

Anadromy.

General Considerations.

The habit of ascending fresh-water streams from the sea for the purpose of procreation is common to a considerable number of fishes which pass the adult stages feeding and maturing in the sea. This habit may be regarded merely as an elaboration of the movements of other fishes in the sea for the same purpose. Doubtless all such movements are in conformity to 'natural laws.' The so-called spawning migration, however, is not always sharply defined from movements of other kinds or 'purposes.' In fact, the spawning migration may apparently begin as one distinctly of another kind, as, for instance, pursuit of food. Yet both are doubtless correlated, the latter in many instances being a necessary preliminary and preparatory stage of the other. Various spring 'migratory' fish, as mackerel, menhaden, etc., are poor when they first appear, and their vernal movements are plainly influenced by the food supply. The mackerel, it is known, gorge themselves with food, by which they are nourished, and the reproductive organs rapidly develop.

Some 'migratory' species spawn at sea, either at the surface or at some varying depths. Others require shoals or 'banks;' others approach the shore and spawn in the shoal water of bays; others spawn upon the open shore or beaches; others ascend estuaries into brackish water; others spawn just above the influence of tide water; and still others ascend to fresh-water streams, in some instances even to their headwaters. All are impelled to attain certain requisite conditions. These must be attained, for no other conditions will avail and, the requisite conditions failing, the species 'perishes from the earth' or, rather, from the waters.

The anadromous habit is not restricted to marine fishes. Among fresh-water fishes there appear to be similar movements, of like variability, except that there are no surface or pelagic spawners, or, rather, no species producing floating eggs.

Meek (1916, p. 18) says that all degrees of anadromous migration from mid-ocean to

the upper limits of streams, may take place, and he classifies as anadromous migrations those movements from oceanic to continental waters, whether demersal or pelagic, from deep to shallow water, from offshore to inshore, and estuaries, from river to the stream, etc.

This classification is a logical one, for the movements all lead up to the same end and are in obedience to the same demands of 'the laws of nature.' But to state that the 'laws of nature' are responsible for the movements merely restates the question of why the fish are migratory or anadromous. The question is, what are these 'laws of nature' which impel the king salmon, for instance, to cease to feed and to ascend Pacific coast streams a thousand miles or more, reproduce its kind once only in its lifetime, then perish? Or, what are the laws which impel the sockeye salmon to ascend certain streams only which have lakes at their head fed by waters from melting snows, there, like the king salmon to reproduce but once in its life and die? To state that the impulse is 'instinct' without defining the term, also simply restates the question.

'Instinct,' Jordan (1905*a*, p. 154) says, 'is automatic obedience to the demands of conditions external to the nervous system.' He again says: 'The greater the stress of environment, the more perfect the automatism, for impulses to safe action are necessarily adequate to the duty they have to perform. If the instinct were inadequate, the species would have become extinct. The fact that its individuals persist shows that they are provided with the instincts necessary to that end. Instinct differs from other allied forms of response to external conditions in being hereditary, continuous from generation to generation.'

Referring to the view of various investigators, Jordan mentions that some regard instinct as the natural survival of automatic responses which were most useful to the life of the animal, the individual having less effective methods of reflex action perishing, leaving no posterity.

Anadromy, then, is one 'adequate' means to an end, that of reproduction, which occurs periodically; or in the words of Gurley (1902, p. 409) '. . . cyclical recurrence of instinct is the outcome of cyclical recurrence of environmental stimuli.' In a consideration of movements attributed to the 'constitution of the nervous system,' Gurley indicates (p. 408) that the real question is: 'How did the nervous system come to be such as it is; that is, how has it come about that there has been developed just that series of nerve mechanisms which corresponds to the demands made upon the organism by its environment?' He further indicates that in a progressive change of conditions of environment has originated a definite correlative change of function in the organism.

Some may regard the foregoing questions as properly belonging to biological philosophy and as having no practical significance, and their solution no practical utility. But let it be said that, had the answers to these seemingly purely scientific questions been realized and regarded in time, they would have conveyed the solution of practical fishery and fish-cultural problems which have for years been the subject of debate by scientist, fish-culturist, and fisherman, and the object of inadequate legislation, to say nothing of the research, inquiries, and fish-cultural effort that are still going on, as well as continued and changing legislative action.

While recognizing various known and unknown supercessory, subcessory, and accessory factors as involved in the evolutional development and present manifestation of the anadromous 'habit,' Gurley (p. 414) emphasizes that of temperature as of prime significance, stating that the facts '. . . demonstrate the presence of a temperature responsive nerve mechanism . . .' and indicate the necessity of recognizing that, '. . . besides the convenient, naked eye anatomical characters utilized for classification, a number of physiological characters exist which are perhaps less immediately evident, but which are none the less real and important.'

In fish culture and artificial distribution, if not elsewhere, these physiological characters are the essentials to be regarded. The fact that this or that ichthyologist pronounces the rainbow trout, and steelhead trout, or the Atlantic salmon and 'landlocked salmon' identical or distinct, affects the culture and distribution of the forms favorably or unfavorably only to the extent that the pronouncement conforms to the physiological characters and their significance.

Gurley very forcibly argues that the environmental factor, or the immediate stimulus to which the spawning migration is a physiological response, is a definite temperature trend. This fact 'plays a dominant role in the fish's life.' The tendency of Salmonidæ to seek cooler water for procreation is, he states (p. 415) ' . . . their fundamental dynamic character, the character which is back of their migrations and habitats, which latter have, in turn, developed their generic and specific differences.'

Day (1887, p. 27–28) adduces a few instances of change of spawning time by acclimatized fish in conformity to differences of temperature. In consideration of whether seasons or changes of temperature exercise any marked influence on the time of the year when fishes spawn, he says:

'If they do we ought to be able to observe such among the trout and *Anadromous Salmonoids* despatched in the form of ova to Tasmania from this country [Great Britain]. Turning to Mr. Allport's account (Proc. Zoöl. Soc., 1870, p. 25) we find a most marked instance of such a result. We know the cold season in that portion of the globe corresponds with our summer, and the first brook trout which were spawned in Tasmania occurred on July 3rd, 1866; by the 7th of August fourteen females had been stripped, and shortly afterwards five pair of trout were observed constructing redds in the River Plenty. During June, July and August, 1867, the trout were again stripped of their ova artificially. In this country [Great Britain] trout spawn at different periods in different rivers, from about September to February. The very first Tasmanian bred trout hatched from English trout eggs have not selected for spawning the months adopted by their ancestors in this hemisphere, but have chosen others which are better suited for their purpose, clearly demonstrating the possibility of trout being capable under changed conditions of varying the period of the breeding season.'

From the foregoing it is evident that salmonids do not spawn by the calendar, and are not only 'capable' of varying the breeding season under changed conditions, but are also compelled to do so or fail in reproduction. In the early days of fish culture, data were not available to indicate this essential fact, and for years thousands of dollars

were expended in the vain attempt to acclimatize salmonids in waters in which the requisite conditions did not obtain. Even today, although there are volumes of data, they have never been adequately correlated and fish culture and efforts toward acclimatization are still conducted in much the same blind way.

Granting that all salmonids require cooling water in which to spawn, how has it come about that the fish are impelled to ascend the rivers from the sea when the same temperature may be within as easy or easier attainment in the sea?

It should here be mentioned that temperature is only a saliently observable factor among perhaps many active, reactive, and interactive factors. The difference of method or degree of response to external conditions shown by different species, is doubtless due to different combinations of factors referred to. While among salmonoid fishes the differences of method and degree are evident, as previously indicated, they are all manifested, as Gurley maintained, in the 'to-cooler migration.' The direction of such migrations is either horizontal or vertical.

It has already been indicated that the common salmonoid ancestral form was marine, and that, while some of the present forms are beach or shore spawners and have demersal eggs, others periodically ascend the streams as anadromes for procreation. This anadromy, then, must have originated in the beach-spawning ancestry. The cause must have been the same which determined the present distribution.

By invoking natural selection, Gurley adduces a logical, though somewhat theoretical, explanation of the formation or evolution of the anadromous habit. He proposes but does not demonstrate a special nerve mechanism which responds or reacts to a downward temperature trend. His argument necessarily implies that at sometime during the development of the genitalia, the 'nerve mechanism' generates in the fish a desire or necessity to seek cooler water which it finds, first near the river mouth, then in the river. Then having obtained the cooler water of the river 'the gear is shifted' so that the motile stimulus is the current of the stream. This in turn signifies another special nerve mechanism which responds to the stimulus of the current.

Atlantic salmon ascend the same river at different seasons of the year. They avoid some rivers entirely. Some salmon enter a river in the spring, where they linger until near the spawning time at a distance short of the spawning place. It has been stated that in the Rhine some salmon pass the winter and do not spawn until the succeeding fall when salmon which have ascended later are spawning in the same region. Gurley's theory was supposed to apply to all salmonids whether of the sea or inland fresh waters, and there are instances of so-called 'landlocked salmon' migrating into the outlet at the approach of the spawning season. It is hard to reconcile this fact with the to-cooler-water and head-to-current impulses. Indeed, there is still an unknown quantity, to use a mathematical term.

The more clearly anatomical structures and their physiological functions are understood the more evident it is that organisms of similar structure have similar physiological functions, so it seems that it may be assumed that like salmonids of like distribution, which migrate to dissimilar places for the purpose of breeding are impelled to those

places because the conditions in them and leading to them satisfy the physiological demands and that they arrive at those places by force of similar stimuli. A salmon, then, is led down into an outlet by the same sort of forces that induces another to ascend an inlet for the same purpose, reproduction.

From observation and experiment made upon various rivers of France, Roule (1920) came to the conclusion that dissolved oxygen is the inducing agent leading salmon into and up the streams to the breeding places. He supports his argument by statements of the results of these experiments and studies of the streams, both those which are and which are not ascended by salmon. It is very clear, too, that so far as the conditions of the rivers are concerned his argument is well sustained. Roule's idea is that the migrations of salmon appear to be due to some forces of the nature of tropisms, and his theory, briefly stated, is that the fish during life and growth in the sea assimilates intensively, accumulates in its tissues numerous reserves, and reaches that condition of physiological surfeit, when further acquisition of that kind becomes uncomfortable.

Roule's theory is thoroughly logical and in full accordance with all the known facts concerning the conditions of rivers, both those frequented and avoided by salmon. But like Gurley's theory it fails to explain clearly certain questions which arise in connection with it. He states that fresh-water salmonids are affected in a similar manner but to a lesser degree, but he, like Gurley, fails to explain why fresh-water salmon sometimes resort to outlets to breed. Indeed he does not refer to the fact at all.

There still remains the question, pertaining to the sea life of the salmon, as to what is the actuating factor that brings it in contact with the exact proportions of oxygen, cold water, etc., which starts it up river. Chance contact in search for relief from discomforts of satiety is not in accordance with a 'reign of law.' If it were so, many salmon might never migrate and reproduce. The old plethora theory from intensive feeding in the sea, which has been advanced from time to time, appears formerly to have been regarded as a sort of psychological effect. More recently Taylor (1922, p. 121–126) has enlarged upon the idea by connecting it with the specific gravity of the salmon. His theory is based on several demonstrated facts, one of which is that the specific gravity of fish varies with the amount of fat present in the tissues.

He finally reaches the following conclusions:

'1. Fish on migrating from water of low salinity to that of high salinity may adjust specific gravity by reducing the size of air bladder. In the reverse direction there is no apparent means for voluntary adjustment.

'2. As a fish puts on fat its body specific gravity diminishes, *pari passu*, and in proportion to the amount of fat present (*a*) its navigation in salt water is more difficult; (*b*) fresher water is better suited as a physical medium. Until a certain amount of fat is accumulated migration from salt to fresh water must be difficult or impossible.

'3. Reduction of volume of air bladder may possibly be effected by (*a*) resorption of gas from bladder to blood and expulsion through gills; (*b*) direct expulsion of gas through pneumatic duct (except in Acanthopteri); (*c*) diving, whereby hydrostatic pressure reduces the volume. The effect produced by diving a given depth is proportional to the absolute volume of the air bladder.

'4. Diminishing specific gravity consequent upon increasing fatness probably constitutes a strong directive influence governing the movements of fishes, both marine and anadromous.'

Specific gravity would thus tend to bring the fish to the surface and if thereby it comes in contact with fresh water it would, as Roule says, follow it up. For salmon far from shore, to find the fresh-water factor, some other *vis a tergo* is required to force it toward the fresh water. Furthermore Taylor seems satisfied to have got his fish into the fresh water and does not explain how it is that the salmon is able 'to float' in fresh water after its specific gravity is increased through the reproductive changes.

Yet, it is not impossible that the seasonal food of the salmon such as smelt, capelin, herring, sand eels, etc., may concentrate in those regions where the salmon may come in contact with the requisite stimuli. In fact we have already cited instances of marine food being found in the stomachs of salmon after they had entered the river. There are also known instances of salmon pursuing smelts and young herring well up in the mouths of the rivers. There is also considerable evidence that salmon do not habitually go far enough away from shore to entirely avoid fresh water, at least at the surface and at certain seasons.

After making other comparisons and statements concerning characters of streams referred to, Calderwood (1907, p. 133) concludes from the facts that the theory that salmon enter rivers warmer than the sea is erroneous and that temperature has nothing to do with the seasonable character of the river in Scotland, in so far as the actual entrance of salmon from the sea is concerned. But he goes on to say that after a fish has once entered the mouth of a river fluctuations of temperature exercise a distinct influence, but in making an early or late river temperature does not appear to play a part.

This latter conclusion is probably quite true so far as warmer river water is concerned but it has not been shown that when salmon enter a river its water is not colder than the immediate sea at the time of entrance. It is natural to assume that in summer river water is necessarily warmer than the sea into which it flows. But there appears to be no evidence that the time of entrance is not during one of those 'fluctuations' when the river is relatively colder than the immediate sea water, as it has been shown that various streams differ more or less from each other in character and time of salmon runs, and that the same river sometimes varies in those respects according to the season or condition therein. Neither Gurley's nor Roule's theory predicates definite degrees of difference of temperature affecting salmon runs, but that the runs are related to cooler water in the one theory and to greater oxygen content in the other. But, as has been stated, the one involves the other.

In this connection the conclusions reached by Nordquist (1924, p. 5–6) may be considered. In his studies of the salmon rivers of Finland, Nordquist had previously come to the conclusion that the time of the breaking up of the ice, temperature of the water, and direction of the wind had no direct connection with the time of entering of salmon into the rivers, but that the water level in the river did have an influence in that direction.

After presenting other rivers in evidence that it is the volume of water rather than

other factors that primarily induces salmon to ascend, Nordquist (1924, p. 50) thus refers to Roule's conclusions: 'Roule (1920, p. 41–53) says that the salmon in entering rivers are guided by the amount of oxygen in the water, but not by any instinct or other psychical faculty. The salmon thus enter the rivers with a lower amount of this gas.' Also: 'Roule (p. 45) pretends also that the interruption of the ascent of salmon, which takes place in French rivers in summer is caused by a lower amount of oxygen.'

The unfavorable effects of turbidity of the water and other conditions are then discussed, all of which lead to his final conclusion, *viz.:* 'notwithstanding that we yet want more details about the connection between the ascent of salmon and other factors, the facts brought forth above, seem to show that high water in the rivers, when not connected with an excessive turbidity, promotes the ascent, while skreed and great turbidity of the water prevent it.'

In another connection on page 48 Nordquist says: 'I have here tried to show that the time of ascent of the salmon stands in direct relation to the water level in the respective rivers. *Of course it is not the water level itself but accompanying circumstances that affect the ascent, viz.:* how far out in the sea the river water extends; the swiftness of the water, and the height of the water-falls. *But there may still be other factors that affect the time of ascent.*' (Italics the present writer's.)

The following quotation from page 52 should be compared with Gurley's theory: 'The influence of the height of water upon the ascent of salmon manifests itself in two different ways, *viz.:* the high water-level directly promoting, the low water checking the ascent and further so that the favourable height of the water recurring every year about a certain time, has brought about a concentration of the chief entering of the salmon to this time. *This latter effect has probably been caused indirectly by selection and heredity* [italics the present writer's], so that individuals that ascend during a period with a favourable height of the water are more likely to attain the spawning places than individuals that ascend later, when the water has sunk so much that the surmounting of high waterfalls becomes impossible.'

Shelford and Powers (1915, p. 331–332), concerning the results of their experiments, say that in connection with the entrance of salmon into fresh water, the orientation of the specimens concerned in the experiment was with reference to acidity and alkalinity rather than salinity. Sea water is less acid than fresh and the reactions of the salmon accord with their recent entrance into salt water. They also found that the fish *selected aerated water in preference to water directly from the tap and further that when oxygen was added to the water in opposition to that drawn directly from the tank the preference for the higher oxygen content was decided.*

The authors concluded that the extreme sensitiveness of the fish enabling them to detect slight deviations from neutrality, makes it clear that there is no difficulty in fishes determining the direction to large rivers from hundreds of miles out at sea or of finding their way into a bay or harbor or river or other arm of the sea which their particular physiological condition at a given time demands; and that it is not necessary to appeal to 'instinct' to explain the return of certain salmon to certain rivers.

Wells (1915, p. 276) remarks that: 'There are two general complexes of factors to be considered in an attempted explanation of the reactions of the anadromous fishes, namely, the fish and the environment. Both are made up of physico-chemical factors which are measurable and to a large degree quantitatively. Of the two complexes, that of the living organism is least understood and perhaps, because it is much more variable and changing than the environmental complex, which, especially in the case of the sea-water, varies hardly at all. For the fishes to live normally in the environment there must exist between the two complexes a more or less complete equilibrium.' After further discussion Wells concludes on page 281 that, 'The migrations of anadromous fishes are probably correlated with rhythmic changes in metabolism. These alterations in metabolic activity are largely the result of internal changes such as occur with the ripening of the sexual products.'

Well's argument appears to warrant his conclusions, excepting in his speculation pertaining to the ripening of the sexual products. Paton (1898, p. 169) came to the conclusion that the migration of the fish is not governed by the growth of the genitalia and by the *nisus generativus* as shown by the fact that salmon are ascending the rivers throughout the whole year with their genitalia in all stages of development. His investigations showed that in fish, on leaving the sea the ovaries varied from 121 to 1439 grams per fish of standard length, but the accumulations of solids in their muscles and ovaries together is about the same. So he regarded the 'state of nutrition' as the factor which determines the migration towards the river; when the salmon has accumulated the necessary supply of material it tends to return to its original habitat. Paton regarded the salmon as originally a fresh-water fish which has adopted a sea-running habit. This view concerning the state of nutrition is in accord with the views of other investigators and indirectly conforms to the conclusion of the previously mentioned authors.

As previously remarked, doubtless all of the aforementioned factors, temperature, oxygen, specific gravity, state of nutrition, metabolism, irritability, volume of water in the rivers, and probably many others are operative in one way or another in the anadromous movements of the salmon. It all means, to use the words of Gurley again, that the fish is 'oriented parallel to its environment.' It has been shown that the salmon is restricted to a definite geographic range, which involves temperature limitations (climate). All physical, chemical, and biological elements of this 'life-zone' constitute the salmon's environment. The fact that a salmon is restricted to a particular environment means that it has become adapted, in other words physiologically adjusted to it in the evolution of the species through changes of environment brought about by climatic oscillations during thousands of years. This signifies that conformity to the conditions thus imposed is the price of existence of the species. As the temperature is the index of climates, so it is of the environment of the salmon, as all the other factors are intimately linked with the temperature factor. This latter is the only one requiring further discussion.

In the foregoing consideration of the factors stated to be, or supposed to be, concerned in the reproductive migration of the salmon, it has been seen that each has not been

without apparent exceptions as pertains to their effects, and all of the exceptions have not been shown 'to prove the rule.' But there are no exceptions to the fact that all salmon spawn in a season of falling or fallen temperatures. Gurley was logical in reaching his conclusion that the migration must be 'to-cooler' water. There are apparent exceptions to that, although logically it does not seem reasonable that a fish inexorably compelled by heredity to spawn in cold water should enter from colder into warmer water to attain that end.

As pertains to the salmon which enter a river in summer there can be no question but that in general it is in a season of rising temperature in the river and that the mean temperature of the river water may be no colder and sometimes, no doubt, much warmer than the tidal water. But there may be a question if at the actual time of entrance by salmon, the river water may not be cooler for the time being. It is a well-known fact that salmon do not, as a rule uninterruptedly ascend the river to the spawning places. The winter and spring salmon particularly linger along the river in favorable places until certain changes of conditions induce them to proceed.

It appears as previously remarked, that temperature is not the only factor influencing or governing the ascent of salmon and that many other conditions obtaining in the rivers must be taken into account. Also that rivers, even in the same region may differ from each other in that respect. Concerning this point, Calderwood (1907, p. 139) remarked that it would be entirely erroneous to regard the conditions in Scotland as the same as in a country like Norway. It may be added that it is likely that it would be fully as unsafe to conclude that conditions in New England are the same as those of Newfoundland or Labrador.

So far as temperature is concerned the foregoing evidence points to what seems to be a fact that it is not the steadily lower temperature of the river water that causes the salmon to enter the river and induces ascent after entering, but rather that a favorable change of conditions, heralded by an influx of cooler water, takes place, thus providing the 'stimulus' to which the salmon per force of heredity, is compelled to respond. Salmon hiding in the estuary or pools of a river 'rise' at a certain stage of a rise in the river. A rise in the river is always accompanied by a lowering of the temperature but the initial stages or height of the freshet is usually accompanied by other conditions which are unfavorable for the 'run.' Having started the ascent by virtue of the stimulus of cooler water and other favorable conditions the salmon continues to ascend until unfavorable conditions again inhibit the ascent, to proceed again upon recurrence of a favorable change, or until the end of the journey. Thus, if true, is Gurley's 'to-cooler' migration substantiated. However, there still remains the mystery of the breeding catadromy of some 'landlocked' salmon.

Manner of Migrations from the Sea to Rivers.

'It has long been a vexed question,' says Day (1887, p. 68), 'as to the manner in which salmon enter estuaries and ascend rivers on their arrival from the sea, and although doubtless local circumstances may occasion certain differences, still the mode of migra-

tion would probably in all places be somewhat similar were it unchecked. Mackenzie remarked of the Scottish rivers that the ". . . salmon proceed with the flood tide and rest during the ebb in eddies and in easy water, hence great numbers are always caught in the flood traps of the stake nets placed in their course, while a comparatively few are got in the ebb traps. If the ebb sets in, and the water becomes shallow from the receding of the tide, they drop down with the tide into deeper water, until the return of the flood tide enables them to continue their course, and in this dropping down some fall within the range and are caught in the ebb traps of the engines in question; but it is in the summer season, in dry weather, that by far the greater number are so caught." At this period the water in the rivers is so low that they swim about with the tide, awaiting the flood.'

Day seems to accept the statement as a fact, that the salmon ascend with the flood tide, but he says that it does not disprove that a great many descend with the ebb tide; and cites an instance of several sets of 'puts and putchers' on the right bank of the Severn, all set with the mouths *upstream*. During one visit to these traps he saw seven fish taken all with their head fixed in the puts and directed *downstream*, and therefore concludes that when captured they must have been descending the river with the ebb tide. In a footnote Day says: 'Three views concerning these migrations were held at a meeting of the Dee Conservators at Chester in December, 1884: - - - (1) That salmon run up with the flood tide; (2) That they rest during the flood tide, and run up with the ebb; (3) That they allow themselves to be carried up with the stream of the flood-tide, with their heads toward the sea, and that when the tide begins to ebb they turn, and continue their course against it.'

The latter statement is more in accord with the head-to-current impulse, elsewhere referred to, also with the observations upon the movements of the Sacramento salmon by Rutter and the recent idea advanced by Roule regarding the oxygen 'tropism.' The manner of capture referred to by Day would not appear to conflict with the idea that salmon ascend with the ebb and descend with the flood. If it is a fact, which it seems to be, that in the bays, estuaries, and tidal portions of rivers salmon are feeding during the spring approach to the rivers, and, as it is well established, that most fishes feed against the tide, or current, it is to be expected that the ascent would be on the ebb tide and any descent would be on the flood. But, as Day says on page 69 'the period arrives when these fish consider it necessary to migrate from the tidal portion of a river and ascend into the fresh waters, where, instead of going with the tide, they have to pass on against the stream.'

According to Atkins (1874, p. 333):

'In approaching the rivers, salmon swim near the surface, and are not inclined to leap into the air. In the early part of the season they appear to move at a greater distance from the shores than they do afterward, so that they frequently pass all the pounds and weirs of the estuaries and are first taken in the rivers, where the contracted breadth of the water or some other cause induces them to run near shore. At the height of the salmon season, however, they appear to be coasting along very near the shore, so that

where two weirs are built on the same hedge that near shore takes more salmon than the other.'

Time and Manner of Ascent of Rivers.

By those who have investigated salmon and salmon rivers it seems to be quite generally conceded that in some rivers adult salmon are present at least to some extent every month in the year. If such is the case, the question is why are they there when the spawning time is a comparatively limited period in late fall or early winter?

In connection with this subject the caution expressed by Miescher-Rüsch (1883, p. 462) in referring to other points of discussion, may well apply to the consideration of the present subject. He said: 'In reviewing this whole subject I feel compelled to warn people not to apply the experiences gained in other rivers to the Rhine salmon, and *vice versa*.' And later he remarked that, 'The habits of migration, therefore, seem to vary in the different rivers, perhaps according to the length of the route traveled and the extent of *distribution in the sea* within which certain kinds are found.' He also added: 'From what is known relative to the salmon fisheries of Scotland and Norway, the habits of life of the fish, even, seem to vary.' At about the spawning time of salmon in the neighborhood of Basel, he shows that there are other salmon, which he calls 'winter' salmon, that are not in breeding condition but are fat marketable fish. These fish, he maintains, and presents data in evidence, remain in the river until the next fall.

Miescher-Rüsch did not apply his data to the lower Rhine. As he had not been able to observe the Dutch and North Sea salmon during the season of the year, he could not decide whether, as Barfurth said, numerous large salmon, in almost a mature condition, immigrate from the sea late in summer and during autumn, and all that he maintained was that such belated immigrants, with the exception of a few male fish, did not go up as far as Basel.

Hoek (1910, p. 821–823), however, in 1893 made extensive observations upon the runs of salmon of the lower Rhine in Holland. After referring to the work of Miescher-Rüsch in 1878 and 1879, in which it was demonstrated that three different ages were represented in the salmon of Basel Market and that the difference in age between the youngest and middle-aged salmon was about the same as that between the latter and the oldest fish, Hoek says: 'To check the results arrived at by the Basel professor, I ordered to be measured for me (1893) a large number of salmon caught near the mouth of the Rhine and offered for sale at the Kralingsche Veer market. From March to December 4,653 salmon were measured and the curve constructed with these figures corresponds in the main with that given by Miescher-Rüesch for the Basel salmon.'

Hoek then shows that the salmon of the Rhine present themselves in three sizes: smallest, 54 to 74 centimeters, mean 64 centimeters (2 to 4 kilograms); middle size, 74 to 98 centimeters, mean 88 centimeters (6 to 10 kilograms); largest, 98 to 134 centimeters, mean 106 centimeters (12 to 25 kilograms). Of these fish he says: 'The fishes of different sizes do not enter the river together or in a haphazard way. The different

sizes present themselves in different seasons, but they do in one year exactly as in any other.'

Day wrote (1887, p. 70): 'There is hardly a month in the year when fresh-run salmon may not be found in our rivers, but the main run for spawning purposes occurs as a rule from October to January, or even later. Some of the December and January fish, however, are in that condition, as I have shown, that they could not spawn for many months to come; and I am disposed to think that it is only autumn and winter ascending ones that breed, but experiments are much needed to test this.'

Day (1887, p. 73, footnote) says that Livingston-Stone, speaking of *S. quinnat* says: 'their rate of progress up the rivers varies between very wide limits. The earliest runs are the longest time on their way up the river. The latest runs make the journey more quickly. The fish seem to regulate their speed according to the forwardness of their eggs. While Professor Benecke (*German Fish Assoc.*, March, 1886) could not observe in the Küddow or Rheda during two years' investigations any law governing the migrations of these fishes.'

Perley (1850, p. 57) indicates that the salmon enter the Bay of Miramichi early in the month of June and are generally found in all the considerable tributary streams before the last of the month, where it would appear they remain until the spawning time; and, while it is not directly so stated, it is implied that under certain conditions there are runs at a later period.

Gilpin (1866, p. 78–80) stated that salmon entered Nova Scotia rivers in March at the most southerly and westward ones, and that toward the end of June the run at Halifax is over. The principal run, however, was stated to be in April, May and June. Certain facts inclined him to believe that there was perpetual passing up and down during the summer. In September he stated that gravid fish which one could hardly believe could retain their spawn until November were found in the rivers, and the markets always had a run of November fish, taken outside in the ocean, which were undeveloped as to breeding condition. 'Thus at one point of time,' he wrote, 'we have three sets of fish, one spawning or spawned in the lakes, one running up, and the third ranging the ocean unimpregnated.'

According to Atkins (1874, p. 332): 'Salmon ascend the rivers of Maine in April, May, June, July and August. Arranged according to the comparative abundance of salmon in them, these months would stand thus, *viz.:* June, July, May, April, August; but perhaps in some cases May and July will change places. A great majority, perhaps two-thirds of the salmon, enter the rivers in June. Outside of the five months mentioned there are very few salmon ascending, but, judging from the specimens caught, it seems pretty certain that salmon in prime condition are running in from the sea every month in the year. They have been taken in a gill-net set for them at Buck's Ledge, near Orrington, and the smelt-nets at Bucksport and Winterport take now and then some prime salmon, together with some kelts, in January and February.'

Races of Salmon and Parent Stream Theory.

For many years it was believed to be an absolute fact that salmon invariably return to breed in the rivers in which they were born. Concerning this subject, Day (1887, p. 66) says: 'Salmon appear to possess a homing instinct which induces them to return to the river where they were originally reared.' But he says there are instances occasionally brought to notice where such could not be the case, mentioning the fact that there are almost yearly reports of a grilse or of a salmon being captured off the mouth of the Thames, or Medway, sometimes even attempting to ascend, but from which localities all these fish have long since been destroyed; consequently they could not be descended from eggs hatched in those rivers. In further evidence that the 'homing instinct' could not be so strongly developed that every fish returned to the locality of its birth, Day said that if it were so, attempts to restock salmon rivers, from distant sources, would be useless, but that experiments have demonstrated such procedure to be almost invariably satisfactory.

On the other hand, Gouraud (1902, p. 411) writes that, 'The thraldom of an inherited instinct of direction would go far toward explaining the failure of every attempt to elsewhere establish the quinnat or king salmon of the Pacific' by introduction into streams of the Atlantic Coast of the United States, as well as streams of various foreign countries. 'The Pacific salmon,' he says, 'in habit, in strength, and capacity, is so nearly identified with its Atlantic congener that each should readily thrive in the waters of the other.'

Further on he says: 'Not unlikely the Atlantic salmon possess an inherited cognizance of like oceanic feeding grounds that may be hundreds of miles distant from their native streams; but which would manifestly be unattainable save by fish inheriting an associated instinct of direction.' Gouraud's examples in support of his ingenious argument are apt, but his entire theory is based upon premises which, if not false, are to some extent incorrect and to a large extent uncertain assumptions. Mr. Gouraud's article is referred to here because it is one of the few attempts at an explanation of salmon movements, and while the explanation is in several ways erroneous, it directs attention to the fact that there are doubtless differences of conditions of environment, habits, and instincts among the various species which, when known, will account for the failures of transplanting. That his explanation does not apply in all cases is evidenced by the fact that, although the king salmon has not been established in Atlantic waters, the humpback salmon has to the extent that adult fish appear in streams of Maine in which the young of the species were planted.

Gouraud properly coördinates the feeding and breeding instincts, for they are inseparable, paramount, and the most vital of instincts. They are, however, impelling, not directive. As has been previously indicated, the direction of both feeding and breeding movements is a response to external stimuli. It may be the absence of one or another or all of these stimuli, in other words unsuitable environmental conditions, which accounts for failure to establish the king salmon in Atlantic waters and Atlantic salmon in some Atlantic and foreign waters.

It is manifestly true, as evidenced by many examples and experiments, that many and probably the majority of the salmon do return to the river in which they were hatched. There are many instances of rivers, both in Europe and North America, where the salmon of one differ in size, appearance, or otherwise from those of another. Indeed, there are claims that different tributaries of the same rivers have runs of salmon distinguishable from each other. In North America certain Canadian rivers are noted for having much larger salmon than occur in others, and it has been a long standing belief that the salmon of the South West Branch of the Miramichi differ in size from those of the North West Branch.

I am inclined to the opinion that originally the salmon rivers necessarily were frequented by salmon, the majority of which in one river differed more or less from those of another. This view is supported by historical data and known facts concerning other anadromous fishes. There is evidence that such was the case in certain Maine rivers, once upon a time, but in some of those streams in which the conditions have not otherwise been disturbed, if there are any, the original races have disappeared for various reasons, one of which is that they have been supplanted by transfer of salmon from other waters.

(Kendall, 1895, p. 49) Mr. Benjamin Lincoln of Dennysville, Maine, years ago (1893) stated to the writer that in the early history of the town, salmon were plentiful in Dennys River, but were smaller and of a different shape than at present, having more of a 'mackerel shape,' and not going beyond 12 pounds in weight. In 1845 the ascent of the river by salmon was shut off by a dam, which having been destroyed by fire in 1858, permitted the fish to again ascend the river which they did to some extent. In 1874, Mr. Lincoln began the planting of young salmon in the river, a work which he continued until 1890, obtaining his eggs from the United States Fish Commission. These eggs were from Penobscot salmon. The old run of 'mackerel-shaped' salmon had disappeared and a larger and proportionally deeper fish, true Penobscot salmon, attaining as great a weight as 33 pounds, had taken their place. Furthermore, intensive fishing and reduction in number of breeding salmon tend to reduction in the size of the fish.

Extensive marking experiments in Great Britain and Norway have definitely proved that, while many salmon return to their native rivers, some wander afar, and do not return. This pertains not so much to the first return of salmon from the sea as to fish marked as adult fish and liberated. Dahl remarks that in Norway, of 1000 smolts marked by him after the Scottish method, there were no recaptures in the rivers where they were marked, although several were taken at various distant localities in the sea.

Jordan and Evermann (1902, p. 148) say: 'It is the prevailing impression that the salmon have some special instinct which leads them to return to spawn on the same spawning grounds where they were originally hatched. We fail to find any evidence of this in the case of the Pacific Coast salmon, and we do not believe it to be true. It seems more probable that the young salmon hatched in any river mostly remain in the ocean within a radius of 20, 30, or 40 miles of its mouth. These, in their movements about in the ocean, may come into contact with the cold waters of their parent river, or perhaps

of any other river, at a considerable distance from the shore. In the case of the quinnat and the blueback, their "instinct" seems to lead them to ascend these fresh waters, and, in a majority of cases, these waters will be those in which the fishes in question were originally spawned.'

In comparatively recent marking experiments by J. A. Rodd (1917), Superintendent of Fish Culture, Canada, the fish were all taken as clean-run fish, retained in ponds, stripped, weighed, tagged and liberated. Practically all of the recaptures were in the vicinity of the place where first taken; even those at a distance were in the same general region.

In Maine, notwithstanding the fact that the rivers in which salmon can to any extent spawn and that the only salmon hatchery is in Penobscot waters, for many years occasional salmon have appeared in streams not now usually frequented by them and which they are unable to ascend. Early mentions are of the Saco, Presumpscot, Androscoggin, and Kennebec, where the appearance of an individual below a dam has been noted. In some of the eastern smaller streams a few salmon are taken almost every year.

The foregoing evidence is by no means exhaustive, either way, but it seems sufficient to indicate clearly that naturally each salmon river was frequented by a sufficient number of salmon each year, which were bred in the river, and not enough of migrants from other birth places entered them to prevent the establishment of somewhat differing races, peculiar to their respective streams. In more widely separated regions, as New England and Labrador, for instance, it is quite possible, if not to say probable, that the salmon differ so much physiologically in conformity to the conditions, that those from one locality can not be successfully acclimatized in the other.

Life History of the Salmon.

Methods of Study.

As previously remarked G. Brown Goode (1884, p. 469) wrote, 'At least half of the salmon's life is spent in the ocean.' This is a generalization which does not hold true in all instances, yet the exceptions perhaps may prove the rule. As will be seen later in some localities a great many salmon spend much more than half their lives in the rivers. The life of a salmon begins in the river where as a young fish it remains until it descends to the sea. After residing and feeding in the sea for one or more years it returns to the river with the ultimate purpose of propagation.

In connection with the general phenomenon of the anadromous migrations the seasonal runs of salmon presented a problem to early investigators which gave rise to much discussion and various theories. Rivers were denominated as 'early' and 'late' rivers, according to the time of the year in which the principal ascent of 'clean salmon' took place, and this was associated with time of spawning whether in October, November, December, January, or February. As has been before remarked there are rivers in which salmon appeared to run almost every month in the year, conditions being favorable. Again some rivers appear to have two ascents, one in the spring, the other in the late

fall. In this latter situation the question arose regarding whether spring and fall salmon were always spring or fall fish. In some instances it was thought that tagging kelts might solve the problem.

The earliest attempts to learn something of the life history of the salmon was by marking and by tagging. Fish were sometimes marked by removing a fin or two, or a portion of a fin. Very commonly the entire finlet known as the adipose fin was removed. Tagging consisted of attaching some object to the fish such as a band or metal disc bearing a number corresponding to a numbered record pertaining to the length, weight, sex and condition of the fish when liberated. In later years the tagging experiments were supplemented by 'scale-reading.'

As Calderwood says, the study of scales of late years has been the most important line of investigation. While much regarding the increase in weight and length of time spent in the sea between spawning periods has been learned by tagging, much more of the life-history has been revealed by scale study. It is said that the growth of the scale of the salmon does not begin when the fish is hatched but that there is a period of between two and three months during which the surface of the body has no scales.

Calderwood (1930, p. 53) says: 'As the scales grow from their centres, the surface of the body becomes speckled over with tiny discs meeting at their edges. The material is then laid down so that the scales gradually cover the interstices between the discs, and finally begin to overlap in a posterior direction. I have never seen any report of an investigation into the reason why the overlap arises in a posterior direction, or how the advantage to the fish, as it swims head first, is secured in having the scales arranged as we know they come to be. It would be an interesting study.'

One could imagine that the advantage of such an arrangement to the fish might be similar to that of the arrangement of feathers on the body of a bird when it flies, and that the reverse arrangement would be a decided disadvantage.

The scale of the salmon has been found to indicate its age by lines of growth. It is increased in size by additions of rings of scale substance, each addition making a circular line at its junction with the previously formed ring. If the fish grows fast the lines (sometimes called ridges or 'circuli') are widely spaced. If the growth is slow, the lines are closer together. A well-fed fish grows fast. On the other hand if it feeds but little, the growth is slow. It is believed, with abundance of evidence in support of the belief, that the salmon feeds but little in the winter. Therefore the lines of growth are more or less crowded. These groups of crowded lines form rings known as winter rings or 'annuli.'

Again when the salmon ascends the river to spawn it feeds but scantily if at all, and at spawning time it has lost weight and loses still more after spawning. During this period the scale loses some of its periphery, which gives it an irregular appearance. When the fish resumes feeding in the sea, the more or less ragged scale is mended by scale substance, but a scar is left in the form of an irregular space without lines. This area is known as the 'spawning mark.'

The growth of the young salmon in the river is shown on the scales in the same manner, but the lines are finer and more closely set, so that the duration of the river life of a

salmon is also learned from its scale. Thus by a scale it is possible to determine how long the salmon remained in the river before it went down to the sea as a smolt, how long it remained in the sea until it returned to spawn for the first time, and any further duration between spawning periods that there may be. Then by measurements the increase in length each year is also learned, as well as the probable condition of the fish during any year of its life.

Notwithstanding the early fish cultural interest in the Atlantic salmon of New England, the continued fish cultural propagation of the fish at one federal hatchery in Maine, and its potential commercial and angling value, no attempts to solve the many problems connected with the salmon have been made since those of Atkins over one-half a century ago. But in Great Britain continuous study of the salmon questions have been maintained for years up to the present time.

In previous pages mention was made of the researches of a number of investigators of salmon, among whom were Miescher-Rüsch, at Basel, and Noel Paton in Scotland. In more recent years wonderful advances have been made in the study of the life history of the salmon by numerous workers, such as Johnston, Hutton, Calderwood, Armistead, and others in Great Britain and particularly Scotland; Hoek in Holland; Dahl in Norway; Nordquist in Finland; Rodd, Huntsman and others in Canada.

So much has been learned concerning the salmon through these and other authorities that, in the words of Prof. J. Arthur Thomson (1924, p. vi): '. . . its life-history is known with more precision than that of any other fish, unless it be the eel's.' Basically the life history of all Atlantic salmon, whether of Great Britain, continental Europe, or North America, is the same. But it varies with salmon of different countries with different rivers of the same country, and even with different sections or branches of the same river.

Years in the Sea.

Dahl (1910, p. 39) found that everywhere throughout the country where observations had been conducted, by far the largest majority of salmon examined were fish which had never spawned and had remained in the sea from one to three, and exceptionally four, winters, and which were therefore in their second to their fifth summer after migration to the sea as smolts. He says: 'These fish spawn in the second to the fifth winter after migration, and apparently only a portion of them — chiefly composed of the younger fish — survive the spawning journey and the actual spawning. This little band of survivors returns again to the sea, and some of them after the lapse of one year, others after two years, and very few after three years interval, return to spawn for the second time. Only an infinitesimal portion of these, about one in a 1,000, have shown that they have returned to spawn for the third time.' He further showed (p. 38–39) that, 'it is chiefly the fish which have spawned at an early age that return to spawn for a second time. The great majority of the fish which in the summer are two or three winters old and which spawn for the first time in their third or fourth winter, very seldom reappear in the form of fish with a spawning mark. This, evidently points to the fact that few of the older fish survive more than one spawning.'

From an examination of the scales of 3,350 salmon ascending the rivers to spawn, Dahl (1910, p. 35) found that 964, or about 28.77 per cent, had remained one winter in the sea; 1,712, or 51.10 per cent, had passed two winters; 628, or 18.74 per cent, three winters; 38 or 1.14 per cent, four winters; 7, or 0.21 per cent, five winters; and only one six winters in the sea. Those which had spent only one winter in the sea were grilse, of course, and therefore had not previously spawned. Of those which had spent two winters in the sea, 53, or 3.19 per cent had previously spawned. Of those which had spent three winters in the sea, 95, or 15.13 per cent had previously spawned, and of those which had spent four winters in the sea 32 or 84.21 per cent had previously spawned. Of the whole number examined 188 had spawned, showing a percentage of 94.45 per cent of maiden fish. Thus, only a very small proportion of the whole number had spawned before and were returning to spawn for a second time.

Dahl's (1910, p. 36) conclusions are summed up as follows: 'the salmon does not live many years after migration. Most of the fish have spent from one to three winters in the sea. A salmon, whose scales show more than four winters after migration, is an extraordinary exception. The large majority of the fish, on which our fisheries depend, consists of fish which have not spawned before and which are entering the river for the first time to spawn. It will be noticed that these maiden fish are not all of one age, but may have spent from one to four winters in the sea before they attained sexual maturity.

'This clearly shows that the salmon, which in each year are the material for our fisheries, and which are making their way up to the rivers, are not the whole of the fish in existence. They form only a portion of the various year-classes to which they belong, a portion which is on the point of becoming sexually mature, and which, as it were, has broken away from the rest for the purpose of spawning.'

Calderwood (1907, p. 105–106) says: 'From the evidence at command it appears to be somewhat unusual for a fish to remain till its fourth sea year without spawning, but a few instances are on record. Fish which on recapture are from 30 to 35 lb. show either five or six years' growth on the scales after the smolt condition, and have spawned either once or twice.

Grilse.

The grilse is generally known as a growth stage of salmon which appears in the rivers after having passed one winter in the sea, when, weighing from two to six pounds or more, it possesses certain characteristics that distinguish it from salmon that have passed the grilse stage. The principal external differences are a shorter head, usually slenderer form, color markings, and more easily detachable scales.

They are remarkably active and agile, leaping to considerable heights. Formerly only the male was supposed to be sexually mature and capable of mating with older fish. But from time to time the capture of mature female grilse was reported. These reports were doubted and even disputed and protracted published arguments, pro and con, ensued. However, it has been well established that although male grilse predominate, many female grilse do spawn.

At a meeting of the American Fish Cultural Association, in 1880, a paper entitled, '*Do Grilse Spawn?*' by C. J. Bottemanne (1880, p. 30), Superintendent of Fisheries for the Netherlands, was read by Barnet Phillips. He said, 'Of the entire lot of grilse that enter the Dutch rivers, about seventy-five percent of them, I calculate, are males. All have full milt. By the middle of August the hook (which the male salmon has in spawning time on the point of the lower jaw) is developing fast. The females are always in the minority but in the first part of the season there are more than towards the latter part. All have spawn, and towards the end of October they are so far ripe that when one is lifted by the head the spawn is running out.'

Atkins (1874, p. 331) stated that: 'In our rivers grilse are seldom seen. Three or four per year is the number caught in a weir in the Saint Croix, which takes about 70 adults. In the Denny's the ratio of grilse to salmon caught is not more than one to 500. In the Penobscot they are quite as rare, many a man having grown old in the salmon-fishery without seeing a single specimen.' One old fisherman claimed that at Veazie he had caught, in a dip net, salmon only a foot long, with hooks on their jaws. Such instances Atkins regarded as exceedingly rare.

No opinion has been expressed concerning the reason grilse are so rare in Maine waters, and so abundant in some European and Canadian rivers. In some rivers of Canada grilse formerly occurred in great numbers coming in from the sea at a later date than older salmon, but like them ascending to upper waters mingling freely with them. In Nova Scotia grilse were common in the Shubenacadie River, according to Dr. Gilpin, from August until late in the fall. On the Miramichi, in New Brunswick, they appeared about July 1, and from the middle of that month to the end of August they constituted the main body of salmon entering the river. Their weight was stated to average about three pounds. The principal run in the Nepissiguit, Restigouche, and St. John at Gaspé, was said to be in August and it was stated that they exceeded the older fish in the ratio of 3 to 1.

A series of scores of salmon fishing in the Godbout River, north shore of the Gulf of St. Lawrence, shows that previous to July 15 or 20 the older salmon exceeded the grilse in the ratio of 10 to 1.

Dahl (1918, p. 3–4) says ' . . . the so-called grilse, rarely come before the 24th of June, and form the main bulk of the run in late summer . . . The proportion of salmon to grilse varies greatly in various rivers. Some rivers exhibit a predominance of heavy salmon, while grilse are comparatively few.'

Calderwood (1930, p. 39–40) states that the grilse spawn as the older fish do, but they do not produce as large a proportion of eggs. Also that the grilse eggs are smaller, which has been shown to have an influence on the alevins. He says: 'Grilse appear at a definite time of year. They begin to enter our rivers [Scotland] in early summer, and are most numerous in July.'

Years in the River.

The most obvious external characteristics of the parr are the dark transverse bars and red spots on the sides. Of this stage in our rivers very little has been observed.

When Atkins (1874) wrote his comprehensive report only those caught on a hook and line by anglers and boys had been observed. He stated that when salmon were abundant in Denny's River a good many from four to ten inches long were caught on a hook and line by boys at Dennysville. He wrote that in the course of an inspection tour on the upper Penobscot, from July 22 to 28, 1873, the state commissioners found them rising to the fly in almost every pool from the mouth of the Matagamon [East Branch] to Grand Falls, which, he said, was the upper limit of the ascent of salmon. Atkins must have been mistaken concerning the Grand Falls being the upper limit of ascent, as, even after modification of the falls making them still more difficult to surmount, salmon were known to ascend as far as the dam at the foot of Matagamon Lake, and I myself have caught parr from the dam down to Grand Falls, and in certain localities from Grand Falls to Grindstone.

The age at which parr as smolt descend to the sea has been variously stated. On this point scarcely any observations have been made in this country. Atkins wrote that in the Penobscot, smolts six or eight inches long were taken in some of the weirs near Bucksport in May or early June, almost every year, but they were so rare that many a man had followed salmon fishing for a lifetime without seeing one. In the Miramichi, New Brunswick, Livingston-Stone reported thousands going to sea in July. In Nova Scotia, in the tideway of Bedford River, near Halifax, five young salmon, six to eight inches long, with few vermilion spots, were taken on the 20th of May, 1865. (Some of them were said to have 'spawn' in them.) At Eastport, a number of young salmon, six or eight inches long, were taken in herring weirs every fall, mainly in September. They were supposed to have come from Denny's River. In the East Machias River, at the head of tide, young salmon are often taken in dip nets along with tomcods in December and January. A single specimen from this locality, seen by Atkins, was a smolt. Commenting on the foregoing, Atkins said that the facts were quite insufficient to establish the period of the parr's stay in fresh water.

To Atkins (1874, p. 330) it seemed that the smolt of different rivers did not reach the sea at the same time. In some cases, as at Eastport, they appeared in September, and if they came from Denny's River they may have left in the summer. The same may be said of them if they originated in the St. Croix.

In the East Machias they were found at the head of tide water in the winter, and they reached the mouth of the Penobscot in the spring. In the latter river, Atkins states, the parr observed on its upper waters in considerable numbers late in July were uniformly about six inches long, as estimated from memory by the observers. His opinion was that they could hardly have been less than 14 months old, and that it was quite reasonable to suppose that they should make their appearance at the mouth of the river the next spring, about two years from the time they were hatched.

As determined by scales, Dahl's (1918, p. 11) observations indicated that in Norway the age of smolts at migration varies between two and five winters. He found that in the south the smolts are generally young, but farther north the tendency for them to remain longer in the river before migration was more pronounced.

On October 28, 1900, a single ripe male, 17 cm. to fork of the tail, was found by the present writer on a gravel shoal in the East Branch of the Penobscot. On September 6 to 10, 1901, the present writer also collected 28 specimens of young salmon in a pool immediately below the dam at Matagamon Lake, East Branch of the Penobscot, ranging in length to fork of the tail from 14.5 to 22 centimeters and averaging 17.6 centimeters. The smallest fish was immature, of uncertain sex. One example 14.8 centimeters to fork of tail was an immature male, and one 15 centimeters in the same dimension was an immature female. The balance were males with well-developed milts which would have ripened that fall.

In 1902, eight young salmon from 9.1 to 18.5 centimeters to fork of tail were collected at various places along the East Branch from the mouth of the Wisataquoik to Matagamon dam. They averaged 14.7 centimeters. The smallest was a very immature fish, as was also the 14.8 centimeter fish, both uncertainly males; the others were males with developing milts which undoubtedly would have ripened that fall. These fish were 12.7 to 16.2 centimeters to fork.

The foregoing references to male parrs by no means signify new discoveries for, over 90 years ago, John Shaw called attention to that condition both in parrs which were in retaining ponds and in the river. He wrote (1840, p. 560–561) in 1839, 'All the males [of parrs] at the age of eighteen months, of the several broods in my possession, last autumn (1838) attained a most important corroborative stage [pertaining to the identity of the parr with the salmon] *viz.*, that of showing a breeding state, by having matured the milt, which could be made to flow freely from their bodies, by the slightest pressure of the hands. The females of the same broods, however, although in equal health and condition, did not exhibit a corresponding appearance in regard to the maturing of roe. The male and female parrs in the river, of a similar age, are found respectively in precisely a corresponding state, which may surely be admitted as most important evidence in support of the fact, that all these individuals are, in truth, specifically the same.'

Shaw goes on to say: 'The circumstance of the male parrs with their milt matured and flowing in profusion from their bodies, being at all times found in company with the adult female salmon while depositing her spawn in the river, and the female parrs being in every instance absent, suggested the idea that the males were probably present with the female salmon at such seasons for a sexual purpose. And to demonstrate the fact, I, in January 1837, took a female salmon weighing 14 lb. from the spawning bed, from whence I also took a male parr weighing 1½ oz., with the milt of which I impregnated a quantity of her ova, and placed it in the stream E, pond No. 2, where to my great astonishment, the process succeeded in every respect as it had done with that which had been impregnated by the adult male salmon, and exhibited, from the first visible appearance of the embryo fish up to their assuming the migratory dress, the utmost health and vigour.'

Scale Readings of Maine Parr and Adult Salmon.

Collections of salmon parr which I made in the East Branch of the Penobscot 30 years and more ago, possibly may throw a little light on the smolt migration of that river.

At that time the collections were made it was noted that the parr of the upper river averaged considerably larger than those in that section of the river which came in the lower field of observation. In September, 1901, most of the parr of the collection were taken in an extent of five miles from the dam at the foot of Matagamon, or Grand Lake, down to Stair Falls.

Another small collection was made in August, September, and October, 1902, in connection with tagging operations. A number of parr were measured and tagged but only those injured in the process were saved. This operation was on an extent of about 15 miles from Bowlin Falls to the mouth of the Wissatiquoik River. The same year a few were taken at Grand Pitch, none of which were saved. But they were of the same size-class as those taken up river in 1901. None of the large parrs had any visible parr marks but they had red spots along the sides.

It should be mentioned that 'Grand Pitch' is a waterfall surmountable only by adult salmon. Atkins regarded it as the upper limit for spawning salmon. That salmon did go beyond the falls is proved by the fact that young salmon were found in abundance in suitable places all along the river, and in tributary brooks above the falls up to Matagamon dam, where so far as known no young salmon had been planted. All of the fish cultural operations by the Bureau of Fisheries under Atkins' direction were at Little Spring Brook, some distance down river from Grand Pitch.

In addition to the difference in average size of the young salmon above and below Grand Pitch, a striking difference in their habits was observed. In the river from Bowlin Falls down, the fish appeared to frequent the gravel and shingle shoals where the current was fairly swift but flowed smoothly over broad rather flat areas. In the upper section of the river the fish were always found at the edge of a rapid current where the deep water adjoined the shallower water of a bar or the shore, and particularly where it issued from a pool. Almost all of the fish caught were sexually mature males. All were taken on artificial flies. In the section of the river below Bowlin Falls, evidently there were many parr too small to be easily hooked. In early evening the shallows, above described, appeared to be alive with them at times, where they were leaping and rising for insects.

The difference in average size of parr of the upper waters from those of the lower section is shown by the following figures.

The collection from up river, with which has been included a fully ripe male parr 180 millimeters long, taken October 28, 1900, comprised 29 fish most of which were taken in September, 1901. In total length they measured from 159 to 238 millimeters and averaged 200 millimeters. Twenty-eight parr of the lower section of the river in August, September, and October measured from 135 to 198 and averaged 156 millimeters in total length.

The difference in the averages is plainly due to the facts that from the upper river there were 11 fish which exceeded the maximum size of the fish of the lower river, and 18 that corresponded in size to only nine of the lower section, while of the lower section there were 19 which were smaller than the minimum size of the upper river. These differences are shown in table 3:

TABLE 3.

Size Classes of Parr of the East Branch of the Penobscot, 1901–1902 (one in 1900).

Section of the River	Number of Parr	Total length in mm. Range	Average
Upper	11	200–238	214.27
Upper	18	159–197	192+
Lower	9	160–198	174.0
Lower	19	135–158	149.0

Scales of 29 parr of the upper river, most of which were taken in September, showed that all but three individuals, were in their third year of age, *i.e.*, 2-plus years old. One of these exceptions was 167 millimeters total length and 1-plus years old, and two, taken in October, 231 and 235 millimeters in length were respectively in their fourth year, *i.e.*, 3-plus years old.

Scales of only eight parr from the lower section of the river were examined. In length five fish measured from 136 to 196 millimeters. One other was only 100 millimeters long. The latter and two others, 148 and 174 millimeters in length, appeared to be in their second year, *i.e.*, 1-plus years old. Five of the remainder were 2-plus, and one, 3-plus years of age. The largest fish, a sexually mature male, was the oldest. The ages of all are arranged in table 4 according to the months in which the parr were caught.

TABLE 4.

Age Classes of Parr of the East Branch of the Penobscot.

Months	Number at the age of		
	1+	2+	3+ years
August	1	4	1
September	2	24	2
October	1	1	1
Total	4	29	4
Average lengths (mm.)	146.25	188.4	216.25

The scales of only a few adult Penobscot salmon have been available for examination. In the fall of 1915 three were obtained from the Dead Brook inclosure, used by the Bureau of Fisheries station at Craig Brook for salmon bought of the weir fishermen at Verona Island below Bucksport, in the tidal Penobscot. These fish were usually obtained in May and June, and kept until ripe in the fall, when they were stripped for propagation at the station. The three above mentioned were not weighed but they measured 28, 29, and 29½ inches in total length. The scales indicated that the 28 and 29½ inch

fish had had three years of parr life and one winter in the sea. The parr life of the 29-inch fish was uncertain but it had clearly spent only one winter in the sea. In other words these fish were grilse. The smallest fish was immature or sterile; the largest a ripe male and the other a ripe female.

In September, 1919, three salmon were taken from the fishway at Bangor. One was a female $23^{1}/_{5}$ inches long; the other two were males, each $24^{3}/_{5}$ inches long. The smallest fish had apparently had two years of parr life and one winter in the sea, and was therefore a grilse 3-plus years old. Each of the others had had two years of parr life and two winters in the sea, making them 4-plus years old.

As previously noted, in outer Casco Bay and vicinity salmon are frequently caught in mackerel drift nets and fixed pound nets or traps. Most of the fish taken in mackerel gill nets are small. While some small ones are also taken in the traps, often large ones are caught. Most of the trap fish are taken from June 15 to July 15, but some are caught as early as May and others in the fall months. The trap fishery usually begins in late June and ends early in September. A few of these salmon have come to hand and scales have been obtained from others. It is unfortunate that the data pertaining to all are not complete, but the scales of 41 fish with most nearly complete records have been studied.

There are five records of post-smolts, or smolts which have within the season descended from fresh water. These were taken in July, August, and September. Their lengths ranged from $8^{7}/_{8}$ to $11^{4}/_{5}$ and averaged $9^{3}/_{5}$ inches. All had had two years of parr life and part of the summer in the sea, therefore were 2-plus years of age.

Eleven of the grilse stage taken in May, July, and September, ranged from $19^{2}/_{3}$ to 25 inches and averaged about 21 inches in length. Their scales showed two years of parr life and one winter in the sea, which make them 3-plus years old. Five fish of the grilse stage, taken in May and July, ranging from $19^{4}/_{5}$ to $25^{3}/_{4}$ inches, and averaging $21^{2}/_{3}$ inches, in length, showed three years of parr life and one winter in the sea, making them 4-plus years old. There were also two grilse of three pounds each, accompanied by no other data, which had had four years of parr life and one winter in the sea. They were 5-plus years old.

Thirteen salmon, taken in June and July, ranged in length from $22^{2}/_{5}$ to $35^{1}/_{3}$ and averaging $30^{4}/_{5}$ inches, showing two years of parr life and two years in the sea. They were therefore 4-plus years old. Seven salmon, taken in June and July, ranged in length from 30 to 38 and averaged about 34 inches. Their scales showed three years of parr life and two winters in the sea, which makes them 5-plus years old.

The weights of some of the foregoing were recorded, and the weights but not the lengths of others were given. The weights of the five grilse, above mentioned, ranged from $2^{1}/_{2}$ to four and averaged $3^{2}/_{5}$ pounds. The weights of six salmon all of which had two years of parr life and two years in the sea, ranged from $8^{1}/_{2}$ to 20 pounds and averaged $12^{3}/_{4}$ pounds. The weights of the class which had three years of parr life and 2-plus years in the sea, ranged from $9^{1}/_{4}$ to $19^{3}/_{4}$ and averaged $13^{1}/_{3}$ pounds. None of these fish had spawned and there was nothing to indicate when they would have spawned. Of the 41 fish 29 had had two years and 12 had had three years of parr life.

Relation of the River Life to the Subsequent Life of the Salmon.

The length of the river life, or the period from egg to smolt, of the salmon, is said to react upon the future life of the fish and even affects the fluctuations in the numbers of fish composing the spawning migrations. It will appear later that it not only concerns the individual itself but has its bearing upon its relation to other classes.

Dahl (1918, p. 30) says that the smolts are not all of the same age, nor have they all spent an equal time in the sea when they return for the first time to spawn. Some return sooner, others later quite independently of the age of migration. On the other hand, Calderwood (1930, p. 59–60) wrote that, ' . . . the longer a smolt remains in the river, the shorter time does it spend in the sea, and the converse also holds true.'

Writing of the salmon of the 'Minas system,' near the head of the Bay of Fundy, Huntsman (1931, p. 19) indicates that they are small fish, saying that 79 per cent of those examined had spent two years in the river and 89 per cent were evidently spawning or had spawned as grilse. 'We conclude, therefore,' he says, 'that the small salmon of the head of the Bay of Fundy are fish of which the great majority spawn for the first time as grilse, and, that at that time they are only four full years old from spawning to spawning, as compared with the prevalent five-year old fish in the Saint John, six-year old fish in the Miramichi, and seven-or eight-year old fish in the Grand Cascapedia.'

There are exceptions to the rule as ennunciated by Calderwood and are more in accordance with Dahl's conclusion that when the salmon return for the first time to spawn the time is quite independent of the age of the smolt when it leaves the river for the sea. It would appear that any regularity or irregularity in respect to the age at which salmon first return to spawn may be dependent also upon other factors than the age at which smolts migrate to the sea.

The evidence thus far presented suggests that the phenomena are local and in some instances, perhaps racial as indicated by what Huntsman has said regarding the Minas, Saint John, Miramichi, and Grand Cascapedia rivers. Hutton was convinced that each river had a race peculiar to it. He says (1924, p. 29–30): 'I am firmly convinced that, although all our salmon belong to one species, *Salmo Salar* (the true Atlantic salmon), there are many types, varieties, or "races." ' He goes on even still farther than that saying: 'Admitted, then, that each river has its own type or race, it is only a step further to assume that there may be several races or types in any one river. Probably each tributary will produce its own type. Further, I believe that, generally speaking, each class of salmon will reproduce its own class.'

Gilbert (1918, p. 37) found this to be the case with the Sockeye salmon of the Frazer River, and this is confirmatory evidence even though the Pacific salmons are quite different 'types' of fish from the Atlantic salmon, for as related to the fundamental principles of the phenomenon of an anadromy, the one shows no essential difference from the other. It is clearly evident that, if there is always a preponderance of one certain age-class of parr or smolts in a river, there must be some factors at work which regulates the situation. It is noticeable from what has been stated by various investigators that where only one age class occurs, or it is by far the dominant class, it is likely to be in

relatively small river systems, rather than in the large systems. Might not a relatively large system like the Miramichi, with its numerous tributaries and system, as a whole vary greatly in age classes? May not each of these different age-classes be produced in different tributaries or sections of the river?

Many years ago it was said that the southwest branch of the Miramichi differed from the northwest branch in the size of the salmon. It has been claimed that small salmon produce small eggs and consequently small progeny. Whether this is an individual or hereditary trait, wherever there is a preponderance of small salmon, the result of propagation would be a predominance of small young. If small parr require a longer time in which to grow to the smolt stage the preponderance of three year or older smolts would logically be attributed to a preponderance of small parents. From the 834 Miramichi salmon discussed by Huntsman, even with positive knowledge that they all were fish of that river, it is not possible to tell what section of the river they represent.

There is some evidence, that, if the fish of the two sections are not different hereditary races, they may be regarded as environmental strains. That is, the immediately obtaining environmental conditions determine whether the fish produced there grow fast or slowly and this again determines the time for the migration of the smolt to the sea, which, as has been held, is reflected in the age of the fish when they return for their first spawning. The facts learned concerning 'divided migrations' and alternating 'short' and 'long' periods between spawning migrations do not necessarily oppose such a hypothesis. Rodd's demonstration that fish marked in the fall sometimes return as early fish does not prove that such races, strains, or whatever they may be called, do not exist.

The foregoing discussion pertains to salmon under natural conditions and not to those affected by possible mixtures in fish hatcheries or affected by fisheries.

Huntsman (1931, p. 92–94) writes under the heading *Early Run versus Late Run Fish:* 'The two pronounced "runs" of salmon have been a striking feature of the fishery from the earliest times. In the year 1930 as determined by Messrs. Kerr and Blair, the early run on the Miramichi occurred during the week following June 17, or at least was at its best then. The late run began about the end of September and reached its maximum in the first part of October. What is the explanation of the phenomenon?

'For a very long time it has been claimed by the fishermen that the two runs on the Miramichi represented different kinds of fish and that propagation and protection of the late run was of very little use for the early fish, which alone they caught. It must always be considered as possible that they are racially distinct, for there is the usual difficulty of proving a negative.' Further on he adds: 'We may safely conclude, however, that man's experiment lasting for more than 80 years in restricting fishing to the early run and encouraging reproduction (natural as well as artificial) of the late run has succeeded neither in materially reducing the early run nor in materially increasing the late run. It would, therefore, be most extraordinary if the two runs were found to consist of distinct races.'

Nevertheless they may be racially distinct, for all the salmon taken in the open season are not on their way up river, for it has not been shown that salmon which are to

run late are not caught with the fish which are to run early, and it is known that salmon are in the coastal waters long after the early fish have entered the rivers, and even beyond the season for late runs. It may be asked if the fish taken for artificial propagation are always of the late run. Undoubtedly they are if taken in tide water in the fall. But if taken in the river there might be some doubt about it.

Huntsman's discussion deals with salmon exclusive of grilse. Therefore the ages at which his salmon migrated to sea as smolts do not appear to support the assertions by other investigators, previously quoted, that the three-year old smolt mature and return to breed after a shorter period in the sea than in the case of the two-year old smolt, except perhaps in the same river. Thus, in the Miramichi the dominant class of smolt is the three-year fish, while the predominant period in the sea to the first spawning is 2-plus years, and the dominant age of first returning salmon is 5-plus years. In other words, the period from spawning to spawning is six years, with two, three and five years (4-plus) second in order.

On the other hand in the Saint John in number, the two-year smolt exceeds the three-year smolt, but the predominant period of sojourn in the sea is, like that of the Miramichi, two years, and the age at first return five years (4-plus), with three, one, and six, 5-plus years respectively second in order. In fact no fish showing a 3-plus period in the sea was observed, and the one year period was represented by only 2.1 per cent of the salmon under consideration.

Dahl (1918, p. 30) wrote that there has been a widely spread belief that as the results of a successful spawning year, after the lapse of a definite interval of time, there would be a year of plentiful salmon. But he showed that inasmuch as the runs of salmon resulting from such a successful breeding year are spread over the catches of six or seven years and in such a manner, that to him, it seemed improbable that by means of statistics any remarkable difference in the effect of different spawnings could be shown.

How the results of one spawning season are spread over the catches of several years he showed in the following manner:

'A salmon spawns in the autumn of 1903 —

TABLE 5.

'*Its offsprings migrate as smolts*' After one, two, three or four winters of sea life they return as maiden fish in the years denoted by asterisks.

	1907	1908	1909	1910	1911	1912	1913
The first in 1906	*	*	*	*	–	–	–
Others in 1907	–	*	*	*	*	–	–
Others in 1908	–	–	*	*	*	*	–
The last in 1909	–	–	–	*	*	*	*

'It is obvious,' he says, 'that the results of any one spawning season, whether good or bad, are not restricted to the number of salmon in any single year. The effects are distributed over a long series of years. The fry which are hatched in any particular year may return after their stay in the sea as maiden fish during seven consecutive years, and

this arrangement must undoubtedly be of the highest value as a means of protecting the species. It would indeed be difficult to conceive of any device that is so admirably suited for the distribution and neutralization of the risks to which the individual fry of each year are subject.'

But this 'arrangement' cannot be fortuitous. It must be in conformity to the law of cause and effect. Therefore if there are sufficient reliable statistics it would seem that the fluctuations in the catches of salmon would necessarily be an index to the quantity of salmon present in a given region, and that the quantity present would be a reflection from previous spawnings.

Referring to Dahl's chart, in order to picture the whole situation during those seven years, among other things, the fish resulting from the smolts of the year mentioned will be augmented by fish resulting from smolts of preceding and succeeding years. The chart represents smolts migrating at the ages of two to five years, each returning as maiden fish after one to four years in the sea, in a period of seven years. Each generation expires with the oldest salmon. Assuming that spawning runs of salmon resulting from smolts which had migrated in the four years preceding 1903 were small, and that of 1903 was large and successfully reproduced, naturally it would be expected, other things being equal, that one of the years from 1907 to 1910 would be a good one. If the largest proportion of smolts of a given river were two years old when they migrated and the largest return of maiden fish six-year-old fish, it would seem logical to look for a good run in 1910, and according to the chart that is what would have occurred, for all ages of that generation are represented, and by fish of three other generations as well.

From all that has been learned concerning the life history of the salmon, it is quite evident that the salmon of different rivers differ more or less from each other in that respect, and, as has been said, the river life of the young salmon reacts on the sea life of the adult as to the time at which it shall return to the river. Whatever may be the factor or factors determining the dominance of a particular age-class of smolts, the volume of a salmon return would depend, at least in part, upon age-classes of the fish composing it, for naturally the younger fish would be the most numerous in the aggregate. This is demonstrated in the case of rivers characterized as 'grilse' rivers. Again it has been shown that the greater proportion of returning salmon which have spent more than one winter in the sea is composed of two age-classes or one or the other of two, according to the river.

It, however, has been shown that it does not necessarily follow that all fish which have spent only one winter in the sea return as grilse. Therefore a run of grilse may be of one age-class only, or there may be no grilse or relatively few of them, if any. The age-class which does not return the following year contributes to the 'reserve' stock mentioned by Dahl. But, on the other hand, Dahl's chart indicates that all ages may periodically be present in one year. Therefore, it would seem that there might be periods of abundance or scarcity having origin in a continued dominance of one age-class of smolt. It is only a step further to perceive the possibility of the 'divided migrations' and early and late runs as having some relation to the dominant age-class of parr and smolt.

If each age-class of smolt is wholly or predominately produced in a separate section or a different tributary, as it may well be, the situation would be analogous to separate rivers where only one or another age-class is represented. Any falling off in the runs, as expressed by the fishery, might be due, in part at least, to absence of salmon representing one or the other of the age-classes of smolt rather than to a reduction of all age-classes.

Breeding Habits.

Miescher-Rüsch (1883, p. 432) stated that: 'According to Mr. Glaser's experience, which extends over many years, and which is corroborated by my own observations, extending over a period of eight years, *the normal spawning season* at Basel for the overwhelming majority of all fish may be said to last from the middle of November till the middle of December.' Calderwood (1907, p. 12–13) says that in Scotland there is considerable variation in the limits of the spawning season, varying from a month to two and a half months according to the number and character of the streams taken into account. In the earliest rivers the height of the spawning season occurs about November 7, which is one month earlier than in the latest rivers. For Great Britain generally, Day sets the spawning period between the middle or last week of October and the middle of February or later. Gilpin finds that salmon spawn in the latter part of November in Nova Scotia. According to Livingston-Stone the season commences about the middle of October in the Miramichi River, New Brunswick, although Perley reports that the salmon spawn in the Southwest Branch of the Miramichi in November. Atkins states that in the Penobscot spawning appears to begin during the last week in October and very seldom is delayed until after November 10. But he said a good deal depends upon the stage of water. If the water is low, the salmon will wait until rains raise it. In 1931 the date of fertilization of the eggs in hatcheries on seven Canadian rivers in the Maritime Provinces varied from October 24 to November 15.

In 1839 Shaw (1840, p. 565) wrote: 'The female, regardless of the occasional absence of the males during these contests, and probably satisfied with the presence of the male parrs, proceeds with her operations by throwing herself at intervals of a few minutes upon her side, and while in that position, by the rapid action of her *tail* she digs a receptacle in the gravel for her ova, a portion of which she deposits, and, again turning upon her side, she covers it up by a renewed action of the tail, — thus alternately digging, depositing, and covering ova, until the process is completed by the laying of the whole mass, an operation which generally occupies three or four days.'

Calderwood (1907, p. 14–15) says that he is 'inclined to estimate that on an average the female salmon completes her reproductive functions in a week or ten days. In small streams the time may be shorter.' Atkins says that a female salmon can retain her eggs for three weeks after they are ready to be laid, with little or no injury to them.

In nature all the eggs are not extruded at once, because all the eggs in the ovaries do not become ripe simultaneously. The eggs at the posterior extremity of the ovary be-

come ripe first, and becoming free for extrusion are first deposited. On extrusion they are at once fertilized by the attendant male fish, and then covered by gravel. The female then leaves the redd. As the remainder of the eggs ripen, she returns and repeats the process, for several days, until all the eggs are shed.

Hutton writes (1924, p. 14–15), 'In the majority of our rivers most of the spawning takes place in the upper waters from October to January. In the Wye the bulk of the spawning takes place in November. The operations are usually carried on in strong streams about 2 to 3 feet deep. The fish do not like sand, and they generally select streams with fairly large gravel and stones — say up to the size of large potatoes. A rocky bottom is useless for spawning. The hen-fish does the bulk of the work, as most of the cock-fish spend much of their time in the glorious old game of fighting. It is no unusual thing for one cock to kill another during the spawning operations.

'When the hen-fish is about to spawn she swims up a yard or two and comes up to the surface of the water. She then throws herself on one side and arches her body with the belly curved outwards. Violent convulsions then pass through the whole body of the fish from tail upwards, and this throws up quantities of gravel and silt. It is at that moment the eggs are extruded, and these being heavier than water immediately sink to the bottom and settle in the crevices amongst the stones and gravel. Occasionally the cock-fish sidles up alongside her, but I have never seen the male salmon "throw itself." After these convulsions the lady drops back to the top of the "redd", or spawning bed, where there is usually a hollow or deeper place, which has been cut up by her operations. These convulsions are repeated every three or four minutes, and, as she moves up a little higher each time, she gradually "cuts and covers" a sort of trench up through the gravel. This may go on for about a week or longer, and ultimately she digs up a bed, which is sometimes 3 or 4 yards long.'

The following account of the spawning act of the salmon has been condensed from the recent description of Belding (1934), who definitely differentiates the spawning act from the digging of the redd. The detailed observations on the spawning of the brook, brown and rainbow trout by several investigations during the last four years tend to corroborate his findings.

'The spawning grounds of the Atlantic salmon are scattered along the entire course of the coastal rivers from the upper reaches to just above tidal waters. Here spawning takes place in late October and early November, the season varying yearly with climatic conditions. The spawning grounds are in the shallow, swift-running water. The most suitable soil is a course gravel which contains many stones from two to eight inches in size. While the female salmon may select any position in the river with suitable soil and flow, the majority of the beds are located near the banks of the river, where the flow of the water is broken.

'The redd or spawning bed is easily recognized by the lighter color of the newly exposed gravel and stones. At the upper end is a hollow, usually three by two and one-half feet and some eight inches deep, below which extends a mound of newly turned gravel and stones from eight to 20 feet long and two and one-half to three feet wide, resembling

a newly filled, rounded grave. The fertilized ova lie in the interstices of the stones and coarse gravel at an average depth of ten inches.

'Previous to spawning, the female prepares the initial hollow for the reception of the eggs. Apparently the male has no share in this labor. This preparatory stage usually occurs shortly before the salmon is ready to extrude her eggs, but it has also been observed in females long before their eggs were ripe. The digging of the redd is an operation distinct from the act of spawning. It is not usually accompanied by the extrusion of the eggs, at least not until a suitable hollow has been made. After the selection of a suitable site the female salmon begins the work of excavation by a vigorous action of the tail and body. By powerful movement a column of water is forced against the bottom sufficient to dislodge sand, gravel, and small stones, which are rolled downstream by the action of the current. In this way an excavation is formed. The salmon, by intermittent digging, enlarges the hollow, working on the sides and upstream end.

'*Mating:* When ready to spawn, the female salmon selects a favored male and will aid him in chasing away other amorous males, although she will not go far from the redd. In making her choice she favors the large males and is intolerant of small males and grilse. The favored male takes up his position directly downstream, a few feet below the female, moving occasionally from side to side. The role of favored male is not secure, since he may be supplanted at any time during the season, day, or hour. When there is a surplus of males on the spawning grounds, cruising males are constantly shifting from female to female, awaiting the crucial moment when they may share in the fertilization of the eggs. Not infrequently two and even three males may temporarily occupy secondary positions below a female. Whenever surplus males are on hand, the favored male must share with others the privilege of fertilizing the eggs.

'The favorite time for spawning is at night, but a few female salmon may be found at any time of day digging the redd or, more rarely, depositing eggs. During the spawning season, numerous vacant redds may be seen during the day on the gravel bars.

'The older writers state that in the act of spawning the female salmon digs with her flexed body and extrudes a few eggs, which are swept along with the displaced gravel. The male then takes her place or lies beside her and sheds his milt over the eggs. The alternate extrusion of eggs and milt continues with the digging of the female until a considerable heap of gravel has been formed. The female salmon rests in the pools between the periods of spawning activity and completes her task in from seven to ten days.

'The actual spawning act has seldom been observed, since it rarely occurs during the daytime. The following description appears typical in as much as it agrees closely with that of the spawning of the trout, particularly the rainbow.

'The particular female salmon under observation was accompanied by two males, the larger lying with its head two to three feet below the tail of the female and the smaller some 6 feet below the first male and several feet to one side. Five minutes after several hours of intermittent digging, the female lay extended at the upper part of the redd. Without warning two males rushed quickly alongside, one on each side of the female.

From outside the field of observation a third male came with a quick rush and lay along the side of another male, all four salmon crowding as close together as possible over the hollow bed, bodies parallel, heads on the same level and mouths wide open. The bodies of the males, which remained straight in the axis of the current, were slightly turned toward that of the female and were motionless except for fine muscular quivers. Suddenly the water became densely clouded with the milt extruded from all three males, completely masking the depositing of eggs by the female. The entire procedure was accomplished within 10 seconds and the males then dropped back to their respective positions below the redd. Immediately the female manifested marked activity, digging frantically to cover the fertilized eggs. In the next three minutes she had eight spells of digging, each time making from five to eight muscular "flittings" of the body and tail.

'Fertilization for the most part takes place before the eggs reach the bottom. The spermatozoa are immotile until they come in contact with the water, when they immediately take on a frenzied activity, which quickly diminishes until all movement ceases within 45 seconds. Consequently, fertilization must take place during the first few seconds after the discharge. To be effective the milt should be discharged almost simultaneously with the eggs, since the current rapidly carries the milt downstream below the redd.'

Respiration being as necessary to the developing embryo as to the fully developed fish, suffocation of the embryo by deposits of silt is prevented by the spawning taking place in running water, on a not too fine gravel bottom, where the current brings a constant supply of the necessary oxygen. Among the pebbles and gravel the eggs remain (if not disturbed by predacious animals) until they hatch. In Scotland, Calderwood says hatching may be expected to take place in from 90 to 100 days, in temperatures varying from 40° to 45° Fahrenheit. If the water temperature is kept near 32° Fahrenheit hatching is retarded for about 148 days. In eight Canadian hatcheries in the 1931–32 season at 35–38° Fahrenheit eggs hatched in from 120 to 192 days. Atkins believed that, owing to the fact that in upper Penobscot waters the ice does not leave until May, the eggs do not hatch earlier than that time.

After hatching, the little fish with its attached yolk-sac, which affords its nourishment until it begins to feed by the mouth, continues to grow in the recesses amongst the stones for a period of about 50 days. Towards the end of this period, as the yolk-sac is absorbed, feeding through the mouth begins, and the fish attempts to emerge from its concealment. When the yolk-sac has entirely disappeared, the fish is about an inch long and adopts its free-swimming life. Its habits are then influenced by its needs for food and protection from enemies. The food of the fry is largely Entomostraca and small insects, and larger crustaceans and insects as it increases in size.

In Scottish rivers it is stated that the river life of the yearling salmon is two years, during which period it is known as parr, which when a year old is 3½ inches long. Concerning this phase of the life history of the fish Hutton says (1924, p. 16), 'Shortly before the contents of the yolk-sac are entirely absorbed, the alevin, or rather the fry, commence to feed on tiny insects, I should, however, draw attention to the fact that feeding does

not commence until about five months after the eggs were first deposited in the river. The length of this period depends a good deal on the temperature of the water, and in very cold rivers the length of time before feeding commences will be prolonged. This, again, is a wonderful provision of Nature. If eggs deposited in November were to hatch out, say, in December, and if the small fish required food immediately, it would probably die, for there would be very little food for it. As it is, the eggs do not hatch until February, and no food is required until about April, when food-supplies are more plentiful. Nature therefore arranges matters to suit the food conditions.

The Kelt and Mortality After Spawning.

The term 'kelt,' is the generally adopted Scottish name for the spent salmon. 'The salmon seen on their return to the sea are always in a miserable condition; thin, black, and weak, and poorer than at the completion of the act of spawning,' wrote Atkins (1874, p. 335).

According to various observers kelts are prone to linger in the streams long after breeding, or, at least, very slowly make their way to the sea. Atkins (1874, p. 334–335) believed that having finished spawning a part of the salmon probably immediately drop down to the sea, but he was certain that a part linger in the rivers until spring and then descend. He stated that every year a few descending salmon are caught in weirs on the Penobscot, generally early in May. He mentioned that many of the salmon placed in the pond at Bucksport and not taken out again in the fall remained of their own accord through the winter and only left on occasion of floods in the spring. This is in accord with Day's (1887, p. 74) statement that '. . . when descending seawards, it would appear that the salmon usually pass gradually into salt water, but a heavy flood sometimes carries weak fish down stream.' Atkins said that the salmon kept over winter in the ponds at Bucksport lost weight meanwhile, but had regained, to a great extent, the bright, silvery color of the fresh-run fish.

'After the exhausting labours of spawning,' writes Hutton (1924, p. 43–44), 'the spent fish, or kelts as they are called, drop back into quiet pools where they remain for a long time gradually recuperating. I have known of one case where a fish remained in the same pool for three months. The whole of the functions of the body gradually recover, and the scales again become bright and silvery, and they start on their return journey to the sea, some of them little better than living corpses. This second downward migration generally takes place in February, March, and April. I have never seen a kelt in our water so late as May, but I understand that there are a good many to be found lower down the river, nearer to the sea, in that month. I should think that after May there are very few kelts to be found in the Wye.'

'It is worth noting that kelts show quite visible development of the new ovaries for the next spawning operations, which may not take place for eighteen months, or even more. One also frequently finds several of the old eggs which have not been shed. As far as I can judge, the migration of kelts is only partially affected by floods. They go down when

Nature tells them the right time has come, and not before. For instance, last February (1923) the Wye was in continuous flood throughout the whole of the month, and yet in March we caught just as many kelts as usual.'

Dahl (1910, p. 38) wrote: 'The importance of the spawning journey as a factor of destruction in the life of the salmon is shown more clearly when one takes into consideration the number of fish whose scales show two "spawning marks." In the whole of my material, which consist of 3,350 individuals, I have found only three specimens whose scales showed two spawning marks, that is to say, only three individual fish, which had survived the second spawning.'

Hutton (1922) found that: 'of 883 salmon which returned to spawn a second time, only 74 survived to spawn a third time, and came back with two spawning marks on their scales, and of the 74 only two again survived and came back to the river with three spawning marks on their scales. These two fish, if they had not been caught, might have spawned a fourth time.

'The proportions work out as follows: Deducting the 883 spawned fish from 11,455 — the total number of scales examined — we are left with a net total of 10,572 maiden fish. Out of these 883, 74 or 8.4 per cent (ca. .7 per cent of 10,572) survived to spawn a third time, and only 2 out of the 74 or 2.7 per cent (.02 per cent of 10,572) again returned to the river.

'We can put these figures in a different way.

'Out of every 10,572 salmon which enter the Wye —

'9,689 will die after the first spawning.
'809 " " " " second "
'72 " " " " third "
'2 fish will survive to spawn a fourth time.'

'These figures show quite clearly that the arduous task of spawning has a most serious effect in shortening the life of the salmon, for out of every 10,000 Wye salmon which return to the river as maiden fish, over 9,000 spawn once then die, and of the few hundreds which remain barely 2 (out of 10,000) will survive their third spawning journey.'

In connection with the figures pertaining to the long and short periods of migration Hutton says that the figures show that the long period of migration is much more fatal to the salmon than the short period. Apparently the fish which have suffered least during the spawning operations are the only ones which sufficiently recovered after spending only a few months in the sea, to face another spawning period, and which therefore adopt the short period. Most of the long period fish die after spawning and of the few which survive only a very small number recover sufficiently to be able to spawn again, in the next ensuing season. In other words most of them adopt the long period of migration before they again return to the river.

Hutton attributes the greater mortality in long-period fish to the fact that 'they return to the river in the spring and do not spawn until the following autumn, so that

they have to spend nearly a whole year in the river before they get back to the sea as kelts, during which time they are practically starving.'

Dahl (1910, p. 37–38) evidently did not regard effects of the spawning operation as the only cause of the mortality. He says: 'and this is easily understood when one thinks of all the dangers the fish has to pass through during its spawning journey, and among which by no means the least are the snares and traps of mankind. The violent changes of conditions to which it is subjected during its long journey, during the long fast in fresh water, and during the labours in the actual act of spawning, are bound to be fatal in their effects.'

Duration of Sea Life and Rate of Increase in Weight After Spawning.

In the Scottish, English, and Irish salmon reports, Calderwood (1907, p. 59–66) regarded the demonstration of what was called the divided migration of the salmon, *i.e.*, the habit of the fish after spawning to remain short periods (less than one year), and long periods (one year or over), in the sea, as the most outstanding feature. A summary of these Irish and Scottish reports shows the following:

The Irish short-period fish (from three to eight months, averaging $5^{9}/_{10}$ months) made monthly gains of one-quarter to 2¼ pounds, averaging three-quarter pounds.

The Irish long-period fish (11–17 months, averaging 14 months) made monthly gains from one-seventh to $1^{1}/_{7}$ pounds, averaging about two-fifths pounds.

The Scottish short-period fish (two to nine months, averaging 5.14 months) made monthly gains from one-quarter to nearly two pounds ($1^{24}/_{25}$ pounds), averaging about $1^{1}/_{6}$ pounds.

The Scottish long-period fish (11 to 24 months, averaging about 15.6 months) made monthly gains of $^{4}/_{15}$ to $1^{2}/_{17}$ pounds, averaging slightly over $^{3}/_{5}$ pounds.

Calderwood (1907, p. 71–72) says: 'It may be asked whether grilse kelts, which are subsequently found as summer salmon, continue to be annual spawners, or whether one fish may be at one time an annual breeder and at another a fish of long absence in the sea — a long period feeder. Two Brora records which show remarkably small increase of weight in two years' interval seem to indicate that in both cases the greater part of the time between marking and recapture must have been spent in fresh water, and that annual spawning had prevented any very substantial increase.'

Both fish were kelts when marked and when recaptured. One female, when marked, weighed 5½ pounds and was 28 inches long March 15, 1902. When retaken in the same waters, March 28, 1904, weighed eight pounds and measured 34 inches in length, showing an increase in weight of only 2½ pounds and six inches in length in a little over two years. Another, a female grilse kelt when marked in the same waters (Loch Brora), April 20, 1901, weighed four pounds and measured 25 inches in length. When retaken in the same Loch, March 18, 1903, weighed 6¼ pounds and measured 30½ inches in length, having gained only 2¼ pounds and 5½ inches in length in about one year and 11 months.

On the other hand, Calderwood (1907, p. 73–75) shows records of rapid growth in a

comparatively short time. Thus: a female kelt which, when marked January 18, 1902, in the Tay, weighed 11 pounds and measured 38 inches, was recaptured as a clean summer fish in the estuary of the Tay, August 20, 1902, having gained six pounds in about seven months. As an example of very rapid growth in the Tay, Calderwood cites a record of a kelt of 12½ pounds, which doubled its weight in six months.

The records of five fish could be cited, he says, of 8–12-pound kelts having increased to 19–25 pounds in from a year to a year and a half. One of these records is that of an eight-pound kelt, 38 inches long, marked February 6, 1902, which on August 8, 1903, was found to have gained $12^{3}/_{10}$ pounds and only ½ inch in length in a little over 1½ years.

According to Calderwood the records indicate that there is considerable variation in the matter of short and long periods of absence. That is to say, in some years the short-period fish predominate or are more numerous than in other years. And again the long-period fish are predominant to the extent of an entire absence of short-period fish. Then again they may be approximately balanced. But he discounts the idea that these facts are due to size of the fish.

Calderwood also says that in spawning a female salmon loses approximately one-fifth of its weight. From records of weights and measurements of kelts, Hutton (1922) computed the loss in weight which the fish suffered from the time they entered the river as clean fish to the time they returned to the sea as kelts. He gives the following figures:

TABLE 6.

Weights of Clean Salmon and Kelts.

	Pounds	Per cent
Average weight in April of salmon measuring 30 to 33 inches	11.9	
Loss in weight up to October	1.7	14.3
Weight in October	10.2	
Loss in weight from October to the kelt stage	3.0	25.2
Average weight of kelts	7.2	
Total loss from April to kelt stage	4.7	39.5

'Therefore,' he says, 'In round figures a salmon will lose 15 per cent of its weight between May and October, and a further 25 per cent during spawning, making a total of 40 per cent before its returns to the sea as a kelt.

'Assuming the above is correct,' he continues, 'the question naturally follows — what increase may we expect in a salmon after its return to the river to spawn a second time? This will depend upon two factors — first, the weight of the kelt, and second the period spent in the sea.' Some kelts will adopt what Mr. Calderwood has aptly termed the short-period of migration and will return to the river after spending only a few months in salt water. 'Then again others will adopt the "Long-period", and will spend the whole summer and the following winter in salt water and will return as Spring fish about 12 months after their descent as kelts. . . . We have also a third class, which I will

call the very long-period fish, which remains in the sea for about 18 months before they return to spawn for a second time.'

Out of 10,572 scales examined by Hutton (1922) he found 883 which indicated that those salmon had survived their first spawning period. The number and percentage of those adopting the short, long, and very long periods respectively are stated as follows:

TABLE 7.

Percentage of Short, Long, and Very Long Period Fish.

	No. of Fish	Per cent
Short period	143	11.4
Long period	716	85.6
Very long period	24	3.0

The following survived to spawn a third time.

Short period	51 or 35.7 per cent of 143
Long period	23 or 32 per cent of 716
Very long period	0

He shows that of the 143 short-period fish seven or 4.9 per cent returned to spawn after a short absence, and 44 or 30.8 per cent returned after a long absence. Of the 716 long-period fish, 2 or 0.3 per cent returned as short-period fish again. The above figures show that the largest proportion of the 883 salmon adopted the long period, as did those discussed by Calderwood.

Maine Marking Experiments.

The only marking or tagging experiments of Atlantic salmon in the United States were those of Atkins — from 1872 to 1880 — on Penobscot River fish, in connection with United States hatchery operations near Bucksport, Maine. (Atkins 1885, p. 89–94.) The records thus obtained however are too few to show much of the situation as pertains to Penobscot salmon. Of those marked in 1872 none was recovered. In 1873, 391 fish were later recovered. Because the aluminum plate tags used in the 1873 operations, proved deficient in durable qualities the results obtained were not of marked value. Of 20 recovered in April and May of 1874, all had fallen away in flesh since November. The males had faded in color; the hooks on their lower jaws were still present, but had decreased in size. The females had regained their bright silvery color to a great extent. In the ovaries were the 'germs' of the next litter of eggs, but they were very small. No food was found in the stomachs of either sex. From their condition it seemed to Atkins that these fish could not have been to their feeding grounds during the winter.

Says Atkins: 'In 1875 there were marked and released in tide water at Bucksport, 357 salmon. In the spring of 1876, a considerable number of these were taken in the river, but without exception they were, as in 1874, all poor. In 1877 three specimens were recovered, all in good condition and of larger size than when released. . . . The results

of this second experiment supported the conclusions drawn from those of the first in every particular.

'The salmon marked in 1880, numbering 252 were released in the fresh waters of Eastern river a small branch of the Penobscot. . . . A small reward was offered for the return of fish or tags taken the next spring, and twelve tags were received. Nine of the fish bearing them were weighed and found in every instance to have fallen away in weight since marking. No fully or partially mended fish were obtained or heard of that year, but in June 1882, five prime salmon were recovered bearing the tags affixed in October and November, 1880.' The following table shows the date for each individual:

TABLE 8.

Record of Marking.

No.	Date, 1880	Sex	Length Inches	Weight before spawning Lbs.	Oz.	Weight of eggs Lbs.	Oz.	Weight on release Lbs.	Oz.
1135	Oct. 28	F.	30	9	7	1	15	7	8
1136	Oct. 28	F.	30	9	5	2	1	7	4
1239	Nov. 5	F.	36	17	12	3	8	14	8
1248	Nov. 5	F.	32	10	5	2	5	8	0
1247	Nov. 12	M.	30½					8	8

Record of Recapture.

No.	Date, 1882	Place	Length Inches	Weight Lbs.	Oz.
1135	June 20	Bucksport Center	34½	16	8
1136	June —	Searsport	35½	17	4
1239	June 22	Sandy Point	39½	21	0
1248	June 27	North Bucksport	39¼	21	0
1274 [47]	June 23	Frankfort	—	14	12

Inasmuch as it has been a matter of common observation that all kelts, and particularly those that have been stripped for fish cultural propagation, do not go off immediately to the sea, Atkins was probably correct in his conclusion that his fish did not go to sea until the spring following their liberation as 'artificial' kelts. If so, while the period from the time of liberation would be regarded as a long term of absence, in reality it would be a considerably shorter time in which to attain the weights with which they are credited.

His experiment led Atkins to the conclusion that the salmon were four years old at first maturity and that they were biennial spawners, saying that the results of this third experiment coincide with those of the other two, and they leave little room for doubt that it is the normal habit of the Penobscot salmon to spawn every second year.

It was assumed that the salmon were four years old because it was believed that the smolt migrated to the sea at two years of age, although there was no definite knowledge

on that point, as pertained to American salmon. In those days 'scale reading' was not even thought of. So it was concluded that if the fish went to sea as smolts at two years and spawned biennially the fish would be four years old when they returned to spawn for the first time.

Canadian Tagging Experiments with Spawned Salmon.

Extensive tagging experiments have been conducted for years by the Canadian government. Rodd (1923) in his report as Superintendent of Fish Culture for the Dominion of Canada gives the result of the tagging operations from 1913 to 1923. Previous to 1923 some 6,149 salmon were tagged and liberated after stripping at the hatcheries situated on the Saguenay, Restigouche, York, Miramichi, Margaree and St. John rivers. Of these salmon, 192 or 3.12 per cent were recaptured either as kelt or as clean fish. The data on these fish include: (1) locality of liberation; (2) date of liberation; (3) locality of recapture; (4) date of recapture; (5) weight when liberated; (6) weight when recaptured; and (7) sex. After eliminating the incomplete records and the double recaptures these salmon fall into two groups, (1) 55 kelt and (2) 122 clean or mended salmon. Of the clean fish, 30 or 24.6 per cent were recaptured within one year, 88 or 72.1 per cent within two years, one within three years, and three within four years. From this group 87 salmon with complete and consistent records have been selected for our study.

TABLE 9.

Percentile Distribution According to Month of Recapture.

Month	Percentile Distribution	
	Long absence	Short absence
April	0	5
May	2	40
June	41	20
July	37	20
August	14	15
September	5	0
Total	100	100

Length of absence. The clean salmon may be classified according to the interval before recapture as (1) short-period, (2) long-period, and (3) very-long-period fish. The short period, which indicates an absence of less than one year, includes eight males and 12 females. These 20 fish were recaptured in from $5^{3}/_{4}$ to $9^{1}/_{5}$ months, the average length of absence being 7.6 months. Whether all these salmon were returning for spawning is unknown. The long period, which indicates an absence of over one year in the ocean, includes 16 males and 46 females. These 63 salmon were definitely returning for spawning purposes. The time of absence ranged from 15 to $22^{1}/_{2}$ months and averaged 19.7 months. The very long period also represents a return for spawning, but the four salmon in this group, all females, may have spawned in the interim and may have been on their

third spawning journey. These salmon were recaptured, one in 32 months and three in 43–44 months. The approximate percentage of salmon comprising these groups was (1) short period 23 per cent, (2) long period 72 per cent, and (3) very long period 5 per cent. No special difference was observed between the male and female salmon or whether the first spawning took place after two-winter or three-winter sea life.

Month of recapture. The time of return of the second spawning salmon is of interest. The monthly distribution of the 63 long-absence salmon which were recaptured on their spawning journey indicates that the early run in June and July accounts for most of the salmon. The 20 short-absence salmon were captured even earlier, but whether they were on their way to spawn is unknown.

Locality of recapture. The 63 long-period salmon may be grouped according to the locality of recapture, (1) 28 in the river where liberated, (2) 31 in adjacent coastal waters within 50 miles of these rivers, or (3) four in distant waters. It is interesting to note that about 94 per cent of the salmon were recaptured in or near the river where liberated. However, three salmon from the Margaree River were captured in Newfoundland, and a Saguenay River salmon in the Bay of Chaleur.

Increase in weight. From the Canadian data it has been possible to determine the gross increase in weight, the average increase per month, and the per cent of total increase. The results are summarized in table 10. The actual increase in weight varied greatly, from 0 to 16 pounds for the short period, from two to 27 pounds for the long period, and from four to 16 pounds for the very long period, indicating marked variability in the growth of the individual fish. The average monthly increase was greatest for the short-period fish and least for the very long period. The long-period fish showed the greatest total per cent increase.

TABLE 10.

Increase in Weight During Absence in Ocean.

	Short	Long	Very long
Males			
Number	8	16	—
Kelt weight	10.9	9.25	—
Total gain (pounds)	4.7	11.0	—
Monthly gain (pounds)	0.59	0.57	—
Per cent total gain	43.1	119.0	—
Females			
Number	12	47	4
Kelt weight	10.6	11.8	8.8
Total gain (pounds)	7.6	10.8	7.6
Monthly gain (pounds)	1.04	0.55	0.21
Per cent total gain	71.7	91.5	85.4
Total			
Number	20	63	4
Kelt weight	10.72	11.15	8.8
Total gain (pounds)	6.44	10.851	7.6
Monthly gain (pounds)	0.86	0.5551	0.21
Per cent total gain	60.26	98.48	85.4

Net increase or loss. By applying the methods of Hutton and of Calderwood it is possible to obtain the percentage of net gain or loss in weight for the salmon from the time it first reached the coast for spawning purposes. The salmon loses weight during the pre-spawning fast, at spawning, and during the post-spawning period. Hutton has computed this loss of weight at the completion of spawning and Calderwood has estimated the loss of weight during and after spawning. By these computations it is possible to approximately determine from the known weight after spawning the original weight of the salmon when it reached the coast on its first spawning journey and thus to determine the net loss or gain in weight, since after spawning the kelt must first make up the weight it has lost before it can show a true net gain in weight. The results of these computations are given in table 11.

TABLE 11.

Per Cent Net Gain or Loss in Weight, Computed According to the Methods of Hutton and Calderwood.

Period of absence	Hutton's method					Calderwood's method				
	Number			Per cent change		Number			Per cent change	
	Total	G	L	Av.	Range	Total	G	L	Av.	Range
Short period										
Male	8	4	4	+ 4.9	−39.5 to + 69.6	8	6	2+	24.4	−20.0 to + 89.1
Female	12	8	4	+31.1	−22.8 to + 120.5	12	11	1+	48.7	− 1.8 to + 140.0
Long period										
Male	16	15	1	+84.3	− 8.7 to + 206.0	16	16	0+	103.8	+10.8 to + 225.5
Female	47	44	3	+64.8	−28.3 to + 193.8	47	44	3+	84.3	− 8.8 to + 213.3
Very long period										
Male	—	—	—	—	—	—	—	—	—	—
Female	4	4	0	+39.9	+23.0 to + 74.8	4	4	0+	57.8	+42.5 to + 94.3

G — gain
L — loss

Kelts. Of the salmon recaptured as kelts 19 were males and 36 were females. The recaptures were made both up and down stream from the point of liberation. These salmon were taken in the following months:

TABLE 12.

Salmon Recaptured as Kelts.

Month	Male	Female	Total
December	3	4	7
April	3	2	5
May	11	10	21
June	2	20	22
Total	19	36	55

Of the 19 males the 16 which were gone over winter were absent from four to 7.3 months, averaging a little over 6.2 months. All had lost from one-half to four pounds, averaging slightly less than two pounds. The per cent lost ranged from 8.3 to 38.9 per

cent, averaging 18.4 per cent. Two of the three kelts taken in December showed losses of three-quarters and one per cent, and one a gain of one pound, probably due to faulty weighing.

Of the 36 female kelt, 32 which were gone over winter were absent from 5.7 to 7.7 months, averaging about 6.6 months. The four captured in December showed an average gain of 0.6 pound. Omitting two kelts with impossible gains of ten and 16 pounds, 12 kelt gained from one-half to six pounds, averaging slightly over 2.25 pounds, or a gain of 24.1 per cent, 12 others showed a loss of from one-half to 2.5 pounds, averaging 1.3 pounds, or a loss of 13.2 per cent, and six showed no change. The 30 kelt in all gave an average gain of 0.38 pounds, or 4.4 per cent.

The females which were gone over winter differed from the males in respect to increase in weight, only 40 per cent showing a loss as compared with 100 per cent for the males. They were taken later, 56 per cent being taken in June as against 11 per cent for the males.

SALMON ANGLING.

A Brief History of New England Salmon Rivers.

Atkins wrote that the sea-going salmon of eastern North America was indigenous to nearly every large or small river tributary to the Atlantic Ocean north of the Hudson, and that the only streams of sufficient size to afford full-grown salmon ample room in which to live and move during the summer drought that afforded exceptions to the former universal prevalence of the species in this region were those that do not contain suitable breeding grounds, or those in which breeding grounds are inaccessible to salmon owing to the intervention of impassable falls.

Atkins enumerated 28 'Salmon' rivers from the western border of Connecticut and Massachusetts to the eastern border of Maine, and said that the list would be increased by the addition of quite a number of streams were their history known. Of the 28 streams formerly frequented by salmon, it was stated that there were barely eight in which, at the time of writing, salmon were to any extent regular visitors. The disappearance of salmon from most of these rivers appears to have been entirely the result of artificial causes, chief among which were obstructions of the way to their breeding ground by impassable dams, and pollution.

The New England rivers formerly frequented by salmon listed by Atkins (1874, p. 289–327) were the following, named in order from the south, northward:

Housatonic River. — Salmon disappeared from this river many years ago. There is a record of plenty about 1750; about 1868 one of seven or eight pounds was reported to have been caught below the dam at Stratford.

Quinnipaic River. — It is not known when salmon disappeared from this river. According to Atkins two small fish were taken there in 1872 and 1873 respectively, which were supposed to have been the results of recent introduction of young fish.

Hammonassett River. — Concerning this river there are no definite records.

Connecticut River. — This magnificent stream was formerly one of the best of New England rivers in which salmon are said to have been plentiful up to 1797, after which they disappeared, owing to a dam just below the mouth of Miller's River. In 1866 the four states which are drained by this river made joint effort to restore salmon to the river. From time to time small lots of salmon fry were planted, and subsequently young salmon were taken in the lower part of the river.

In *The History of New Hampshire*, 1792, Belknap (1792, p. 179) says of the salmon that it still ascended the Connecticut to its farthest head.

In an article by Fred Mather (1886, p. 326) it is stated that Professor Baird restocked the Connecticut River until the fish returned to spawn and the fishermen at the mouth of the river sent all of the spawning fish to market and killed the fish which would have laid the golden eggs. He then stopped work on that river, which had not had a salmon in it for some 25 years, but which, five years after planting, sent so many fish to market that 'Connecticut River Salmon' was a regular quotation in the market.

Under the title of *Old Connecticut Salmon Swims*, Charles Hallock (1893, p. 100) writes that in a once abounding salmon swim near Hadley few fish had been caught since 1800. In this locality, he says, in the olden times were located three notable salmon swims. According to Hallock, Sylvester Judd, historian of Hadley, stated that 'Salmon were seldom noticed in records of the seventeenth century. Salmon nets began to appear in 1700, and some Salmon were salted in casks by families before and after 1700. They were seldom sold, and the price in Hartford in 1700 was less than one penny per pound. Fish were so plenty in the Connecticut and its branches that laws were not necessary to regulate fishing for a long time. There was a law in Massachusetts against erecting weirs or fish dams in rivers without permission from the Court of Sessions.'

'Dammed for 100 years,' continued Hallock, 'the Connecticut has been a fruitless stream.' At this time of writing, he said that reports had become current that salmon had been taken in its upper waters, and he prayed that the noblest of New England rivers would speedily become rehabilitated.

Thames River. — Salmon formerly frequented the Thames and some of its tributaries until dams effectually prevented ascent. There are no records of salmon since 1822.

Pawtuxet and Pawcatuck Rivers. — It is stated that salmon were once plentiful in these streams, but there appear to be no available records concerning their abundance.

Providence River. — Atkins did not list the Providence River or its tributaries as a salmon river, and there are no available data concerning these waters in early times.

Merrimack River. — The Merrimack was once one of the best salmon rivers in the United States, but for years after the erection of dams at Lowell, Lawrence, and Manchester no salmon were able to pass them. In *The History of New Hampshire*, Belknap (1792, p. 179) says that salmon still ascended the Merrimack to its 'farthest head.' Later fishways enabled some salmon to pass and the river having received liberal plants of young salmon showed signs of recovery. From time to time adult salmon appeared in the river and were seen in the fishways and occasionally in the upper waters. Subsequently neglected fishways and pollution destroyed the river as a salmon stream. In

1869 the scarcity of salmon is indicated by the fact that the appearance of a single two or three pound salmon, on June 2, at Manchester, was considered of sufficient importance to note in the State Fish Commission report (New Hampshire 1869, p. 646) and that another was caught a short distance below that place in 1870 (New Hampshire 1870, p. 7). But a few years later, improvements in the fishways at the previously mentioned dams having been made, salmon began to appear in the upper waters again, particularly in the Pemigewasset, in considerable numbers.

The report of 1881–1882 (New Hampshire 1882, p. 3) says: 'Your commissioners take satisfaction in reporting that in no year since the opening of the Merrimack river for the ascent of migratory fish have so many salmon passed the fishways at Lawrence and Lowell, and have reached the waters of New Hampshire, as in the past year. Lawrence is the only place at which anything like a fair estimate can be made of the number of fish which pass through the fishways. At this point the water is shut off for about twenty minutes twice a day during the run of fish.'

The Commissioner of New Hampshire in his report dated May 11, 1885 (New Hampshire 1885, p. 3), stated that the spring run of salmon was about the same as that of the year before. The water was again so low in September that none of the fall run, which was usually large, reached Plymouth. The salmon taken this year (1884) were all large fish weighing from 15 to 35 pounds.

The report of Elliot B. Hodge, dated June 1, 1888 (New Hampshire 1889, p. 3–4), says: 'It gives me pleasure to report that there has been a larger number of salmon in the river this season than any year since the Lawrence dam was built. Forty salmon were taken in the fish ponds, from which a large number of eggs were taken. Many more salmon would have been taken had not the heavy July rains kept the river so high that it was impossible to use nets for nearly two weeks during the heaviest part of the run.' 'The largest fish taken was a female, forty inches in length, weight twenty-four pounds; the smallest a grilse, weight four and one-half pounds. This was the first grilse taken in the nets since the station was established.'

For a few years the superintendent of the dam at Lawrence made observations upon the fish occurring in the fishway. The observations are published in the reports of the New Hampshire and Massachusetts Commissions covering the years 1877 to 1887 both inclusive. It is stated that the water was shut off from the fishway, for the purpose of ascertaining what was in it, twice a day up to the 5th of July, and after that but once a day. The closing of the fishway occupied about 15 minutes each time, leaving 23 hours out of the 24 during which nothing was known of the kinds or number of fish passing through it. As the salmon did not loiter but passed quickly over, it was deemed fair to conclude that hundreds passed up unnoticed, and this conclusion was considered to be confirmed by well-authenticated reports of large numbers seen at Manchester as well as all along the Pemigewasset.

In the following table the data regarding salmon observed as reported in the several reports are shown. It was not stated how the weights of the fish were arrived at, that is, whether the fish were weighed or the weights estimated.

TABLE 13.

Salmon Observed in the Lawrence Fishway, May to November, 1877–1887.

Year	1877		1878		1879		1880		1881		1882		1883		1884		1885		1886		1887	
Month	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.	No. fish	Wgt. lbs.
May 30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	10 or 12	—	—	—	—
June	19	177	6	67	12	113	10	111	9	166	4	45	2	35	6	79	3	35	7	82	30	124
	1	no wgt.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	no wgt.	—	—	14	no wgt.
	4	10–12	4	10–12	3	10–12	5	10–12	12	10–20	8	10–15	10	10–20	3	12–20	—	—	—	—	13	6–20
	4	10–15	4	12–15	—	—	3	10–14	19	8–20	—	—	—	—	—	—	—	—	—	—	3	8–20
	—	—	—	—	—	—	5	10–15	5	12–18	—	—	—	—	—	—	—	—	—	—	3	10–20
	—	—	—	—	—	—	3	10–16	—	—	—	—	—	—	—	—	—	—	—	—	—	—
July	2	20	—	—	—	—	1	10	1	10	2	24	—	—	—	—	2	16	—	—	8	87
	2	large	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	8 or 10	—	—	1	no wgt.
	6	no wgt.	—	—	—	—	5	10–12	7	no wgt.	—	—	—	—	—	—	—	—	—	—	3	8–12
	3	8–12	—	—	—	—	3	10–14	—	—	—	—	—	—	—	—	—	—	—	—	8	6–15
	4	10–12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	4	10–15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
August	—	—	3	20	1	16	—	—	—	—	—	—	—	—	—	—	1	10	—	—	3	43
September	—	—	—	—	—	—	—	—	—	—	3	28	—	—	4	52	—	—	4	42	1	12
	—	—	—	—	—	—	—	—	—	—	3	8–15	—	—	—	—	—	—	—	—	—	—
October	—	—	—	—	1	6	—	—	—	—	—	—	—	—	4	48	2	22	2	14	—	—
November	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	8	—	—

It seems that Commissioner Brackett, of Massachusetts, had put the fishways at Lowell and Lawrence in order and the appearance of salmon there instigated observations along the river in New Hampshire. The appearance of salmon at Woodstock, Manchester, etc., resulted in modifying the dams to enable them to pass. In September a storm helped the passage of the fish by carrying away a part of the dam. Those who watched the river estimated that many hundreds must have ascended the river, as many were seen all along up as far as the Profile House. A man set to watch the fish at Livermore Falls stated that hardly a day passed that salmon could not be seen endeavoring to leap the falls.

In 1890 the run of salmon in the Merrimack (New Hampshire 1890, p. 13) was reported as larger than ever before. This was attributed to the unusually high water during the summer. No salmon were taken after September 1, as the water was so high, that the nets could not be kept in place, thus allowing the fall run to pass up the river. As many as 50 salmon were in the large pool below the falls at one time. Many salmon were seen spawning in the river in the last of October. Two years later salmon were still entering the Merrimack in some numbers.

Piscataqua River. — Formerly salmon were very abundant, breeding in the Salmon Falls branch and to some extent in the Cocheco. The rivers have been obstructed by dams for over 200 years. As late as 1830 stray salmon ascended as far as Salmon Falls dam, and in the lower river occasional fish have more recently been taken.

Mousam River. — No salmon have been seen there for many years.

Saco River. — Salmon once ascended the Saco as far as Hiram Falls, and they entered the Great and Little Ossipee rivers. From 1860 to 1873 four salmon were caught in shad nets at the mouth of the river. The latest definite salmon record for the Saco appears to be that of a ten-pound salmon taken in a weir in the summer of 1875 (Anonymous 1875, p. 407). It was said to be the first caught in that river for about 20 years. However, in June, 1894, according to the *Maine Sportsman* (Anonymous 1894, p. 18) 'Four large salmon were seen trying to get over the falls of the Saco River at Biddeford last week. The *Biddeford Journal* says: "Lots of these fish are seen going up river at this season of the year." ' Some have been seen there in recent years and it is said that as late as 1930 salmon were being speared in that place.

Presumpscot River. — This was once one of the finest salmon rivers for its size in the state of Maine, but was early obstructed by dams and only a few salmon have since been taken. Salmon were reported at Cumberland Mills and Sacarappa, in 1873.

Royal River. — Salmon were common in the river up to 1800, and some occurred later. The last salmon seen here was taken in about 1853. For years, owing to the dams at Yarmouth, no fish could ascend the river, and in later years besides the dams, excessive pollution has effected occlusion of fish of any kind in that vicinity.

Androscoggin River. — The Androscoggin and its tributaries were naturally adapted to salmon and were frequented by them until dams prevented ascent. An ineffective fishway, which later by neglect lost even the semblance of such a passage, did not avail to enable salmon to ascend the river farther than Brunswick. Occasionally a salmon has been seen below the dam at that place.

Kennebec River. — In its original condition the Kennebec was scarcely surpassed by any salmon river in the country. Atkins stated that it was the second in the state of Maine in the number of salmon yielded by its fisheries, and in the facilities afforded for their reproduction. No serious natural impediments existed to their ascent of the main river as far as Carratunk Falls, in the town of Solon. At this point there is a precipitous fall, 16½ feet high, which was a serious hindrance to them but not impassable.

In the days of their abundance the main fisheries for salmon were within 20 miles of the mouth of the river, at Waterville 60 miles above, and at Carratunk Falls. At the last place, dip nets were used on the falls and drift nets just below. It was easy for two men to load a boat with salmon here in a day. At Waterville, just below Ticonic Falls, a large number of drift nets were plied every season. As many as 82 have been counted at work at one time; but the average was not over forty. They took several thousand salmon in a season. Other drift net fisheries existed at Augusta and various other points on the river. The fisheries near the mouth of the river were carried on with set-nets and weirs, the former coming into use much earlier than the latter. No exact statistics of their catch have been obtained. The use of nets was not confined to the river. Several were set quite outside its mouth on Hunnewell's Beach. At Cape Small Point, six miles west of the river, there were several nets set, and one trap or ground-net was still in use at Baldhead, for the taking of various species, among which salmon were accounted as of considerable importance.

The salmon fisheries of the Kennebec were in flourishing condition in 1873, when the dams at Augusta were completed. For a few years they continued plenty, and then rapidly declined until they almost disappeared. The drift net fishery at Augusta was for some years abandoned because of the scarcity of salmon. The decade from 1850 to 1860 is generally believed to have been the period of greatest scarcity. In 1866, 1867, and 1868 there was a marked increase, the last year being by far the best since 1850. After that there was another decline, 1870, and 1871 being poor years. In 1872 and 1873 there was another increase which far surpassed that of 1868. It was also remarked on the Kennebec, as on the Penobscot, that the salmon of 1873 averaged uncommonly large.

The *Maine Sportsman* (Anonymous 1894, p. 17) mentioned that a 12-pound salmon, taken near the hospital wharf in Augusta by a drift net in August, was the first salmon taken so far up the river in several years.

A letter dated January 14, 1918, from James Derocher, then superintendent of the Craig Brook salmon hatchery, to the United States Commissioner of Fisheries, in part said: 'I was informed by past Commissioner Austin that a very large school of Atlantic salmon was seen below the tidewater dam in the Kennebec River at Augusta, Maine. This was during July, 1917, and the Commissioner's attention was called to the fact that people were spearing fish in the river. Several arrests were made and it was found that the fish in their possession weighed from 12 to 19 pounds. Mr. Austin informed me that there must have been at least 1,000 fish in the river at that time. He also said that this was the first time in 25 years that Atlantic salmon had been seen in the Kennebec River.'

Sheepscot River. — The Sheepscot was formerly frequented by salmon in great numbers, but the stream was obstructed many years ago. However, occasional salmon have been observed and taken in recent years below the dam at Alna.

Medomac River. — Obstructed for many years, the only salmon taken in recent years have been caught near the mouth of the river. It has been over 100 years since any considerable numbers were taken. In those early days they used to be dipped below the dam at the head of tide water.

Saint George River. — Salmon were plentiful in the river a hundred or more years ago, and considerable numbers were taken 70 or 80 years ago, but have since been rarely seen.

Penobscot River. — At the present time the Penobscot is the only New England river affording any extent of commercial salmon fishery. Atkins wrote that besides being the largest between the Saint John and the Connecticut, it is distinguished from nearly all others within those limits by the manner in which it discharges its waters into the sea, namely, through a large bay or estuary, narrow at its head, where it receives the waters of the river, but widening gradually to its junction with the open ocean. The works of man have interfered less with the migration of salmon in the Penobscot than in any other large river south of the Saint John. Owing to its great volume and other favorable circumstances, dams, quite impassable by salmon, have never been in existence many years at a time. The four points on the lower part of the river at which dams have been built are Veazie, Ayer's Falls, Great Works, and Oldtown.

Of the tributaries, the lower ones were nearly all effectually closed against salmon by dams, and had been in that condition for many years; in few of them, however, if any, was the species ever abundant. In the upper tributaries there were comparatively few obstructions, and there the salmon had access to their original spawning grounds. Of the lower tributaries the finest and most extensive breeding-grounds were in the Piscataquis and its branches, to many of which salmon had access, visiting them yearly and often showing themselves at Brownville on the Pleasant River.

Atkins believed, and in my opinion he was correct in his belief, that the Mattagamon or East Branch, was a better salmon river than the West Branch, and that much greater numbers of salmon resorted to it. Atkins stated that they could ascend as far as Grand Falls, 31 miles from its mouth, but to my personal knowledge they ascended as far as the foot of Mattagamon or Grand Lake, which is a considerable distance further. In the East Branch were extensive spawning grounds, also in the Wissaticook and Sebois streams. The Wissaticook is an impetuous mountain stream, draining the northern and eastern sides of Mount Katahdin. The Sebois traverses a more level district, and is a fine, gentle, gravelly stream, with numerous rapids of sufficient force to form admirable spawning beds. Salmon formerly spawned in all these places.

Up to the time of the establishment of the Great Northern paper mills at Millinocket, salmon continued to ascend the West Branch to some extent, and to a considerable extent the East Branch, including the tributary Wissaticook and Sebois. I observed salmon in the East Branch as late as 1903. In 1904 a visit was made to the East Branch but the water was so low that the stream could not be traversed by canoe.

At that time a visit was made to the junction of the East and West branches to ascertain the conditions exisiting there. It was found that the bottom everywhere, in the main river and the West Branch was covered with waste paper-pulp material, and that the shrubs and bushes on the banks up as high as a previous highwater extended were coated with the same material. It was a substance resembling material of which hornets' nests are made.

It was evident that some time prior to the visit the water had been impregnated with this fine pulp, although it appeared perfectly clear when observed. Whether or not this deposit impedes salmon in their ascent of the East Branch is not known, but is quite positively known that they could not ascend the West Branch. The Great Northern mills are about seven miles up from the mouth of the West Branch. In 1901, 1902, and 1903 young salmon were very abundant in the East Branch from the mouth of the Wissaticook to Mattagamon Lake, and far up the Wissaticook and Sebois. There are no later data concerning these waters, excepting that in the fall of 1916 I visited the Mattagamon Lake and upper East Branch. The water was very low. No adult or young salmon were observed.

An index to the number of salmon ascending the river is in the fisheries. Atkins gave positive data of 13,690 salmon caught in Penobscot Bay and River in 1873, stating that nothing was known of the number of salmon caught above Oldtown. He said that a due allowance for this omission and for certain fishing stations where it was impossible to obtain correct statements, would probably swell the total to 15,000 salmon.

The following statement exhibits the yield of two of the best weirs on the Penobscot as derived from tables given by Atkins for 13 years:

TABLE 14.

Catches of two weirs, time of capture, for 13 years, in the Penobscot, near Bucksport.

Year	Dates	No. of Salmon	Average Weight, Lbs.	Year	Dates	No. of Salmon	Average Weight, Lbs.
1860	Apr. 21–July 11	161	12.3	1867	Apr. 27–July 21	288	11.4
1862	May 5–Aug. 5	165	12.1	1868	May 9–Aug. 12	257	12.1
1863	May 14–July 27	207	9.8	1869	Apr. 17–July 23	151	12
1864	May 9–July 23	111	12.1	1870	Apr. 19–Aug. 18	193	12.5
1865	Apr. 17–Aug. 5	168	11.2	1871	Apr. 17–July 10	112	13.2
1866	Apr. 22–July 25	157	11	1872	May 1–July 20	219	13.2
				1873	May 1–July 31	449	10.5

Smith (1898, p. 116) carries the catches of two weirs from 1874 to 1896. His statistics show considerable increase in 1896 over 1874, but a bigger falling off from Atkins' figures of 1872 and 1873.

The average number taken per annum in the 13 years listed by Atkins was 202.9 and in the 23 years listed by Smith 103.8. The total average weight of Atkins' table is 11.6 pounds; that of Smith's, 13.52. These figures pertained to the same two weirs or

TABLE 15.

Catches of two weirs in the Penobscot, near Bucksport, for 23 years, from 1874 to 1896 inclusive.

Year	No. of Salmon	Average Weight	Year	No. of Salmon	Average Weight
1874	86	14.57	1886	100	16.31
1875	70	12.97	1887	150	13.47
1876	68	15.10	1888	159	13.81
1877	72	13.92	1889	85	14.86
1878	151	13.52	1890	41	15.63
1879	147	11.95	1891	117	10.25
1880	86	12.92	1892	65	15.22
1881	85	17.47	1893	102	13.57
1882	154	11.11	1894	88	13.19
1883	98	16.77	1895	75	15.88
1884	95	9.59	1896	192	13.15
1885	91	12.13			

two weirs in the same locality. Therefore there appears to have been a considerable decrease in salmon up to 1896 when the number exceeded every other year in 36 years excepting 1863 and 1867. Even in 1863 the number was only 15 greater than 1896.

In 1885 a large run was reported, one authority stating that salmon had not been so abundant in the Penobscot for 50 years. The fish were said to run to smalls and mediums. Mr. L. A. Dow, Brigadieis Island, Searsport, was reported high line in that vicinity, his hauls aggregating 507 salmon, averaging 13 pounds each, — a total of 6591 pounds, a profitable season's work.

A letter dated October 17, 1917, from Harry B. Austin, chairman of the Inland Fish and Game Commission, to James D. Derocher, superintendent of the Craig Brook salmon hatchery, said in part: 'I am told by State Warden Frank Perkins more have been seen in the river far up the East Branch of the Penobscot than have been seen for many years, which, inasmuch as this was an off year, is, to say the least, encouraging.'

The *Atlantic Fisherman* (Anonymous 1930, p. 19) under the heading *Penobscot River Sea Salmon Catch Largest in History* has the following note: 'Oscar A. Fickett Company, at Bangor, purchased what is claimed to be the largest catch of sea salmon in the history of the Penobscot River industry. It totalled 1200 pounds.'

Table 16 shows the numbers, weights and average weights of salmon caught in Penobscot Bay and River in 14 years, the first 11 years being consecutive (1895 to 1905 both inclusive). There is then a gap of 12 years for which statistics are not available. Following this are three consecutive years (1918 to 1920).

The catch for three of the first eleven years (1896, 1901, and 1905) amounted to over 6,000 fish each. The largest catch of the three was in 1901, which exceeded that of 1896 by 418 fish. But the catch of 1905 fell short of that of 1896 by only 25 fish. No year of the 11 fell below the 3,000 mark, the smallest catch being in 1898.

The records are too few for positive indication of cycles of abundance or scarcity, but the tables suggest a four or five-year periodicity in the high and low catches. In each of the last three years (1918–1920), the numbers caught fell short of 200, the largest

number being in 1918. The fish averaged largest in 1895 and 1902, but the average in 1903 was not much smaller. The lowest average was in 1905 and the lowest average of the last three years of the table was the lowest for the 14 years. The apparent four or five-year periodicity suggests that, had they lived, the fish would have been five and six years of age in the next spring; which would also suggest two and three years of river life and two winters in the sea. If this be true, it corresponds somewhat with the situation in the Miramichi as indicated by Huntsman.

TABLE 16.

The Commercial Salmon Catch in Penobscot River and Bay, 1895–1905 and 1918–1920.

Year	No. of fish	Weight (lbs.)	Av. weight (lbs.)
1895	4,395	65,011	14.8−
1896	6,403	80,225	12.5+
1897	3,985	51,522	12.9+
1898	3,225	42,560	13.2+
1899	3,515	45,688	13.0−
1900	3,541	44,660	12.6+
1901	6,821	86,055	12.6
1902	3,269	45,782	14.0
1903	4,859	67 470	13.9
1904	4,776	63,395	13.3
1905	6,378	74,158	11.6+
1918	1,653	17,212	10.4+
1919	1,322	13,557	10.25
1920	1,598	15,135	9.50
1930		88,295	
1931		58,012	

Table 17 shows the quantities in pounds of salmon taken by commercial fishermen in Maine waters at irregular intervals in the 42 years from 1887 to 1929 both inclusive; also the catch in the Penobscot Bay and River for seven of the 11 years, with the ratio of the latter to the total Maine catch each year of the seven.

The largest catch in any of the 11 years was in 1888. In 1889 this amount fell off 42,409 pounds. In nine years there was a further loss of 99,418 pounds. In four years there was some increase and still another in three years. This year (1905) the catch for the state was the heaviest of any in the years represented by the table since 1889. There was an increase of 32,976 pounds over that of 1898. Almost 86 per cent of the catch was made in Penobscot Bay and River, which one of the three numerical maxima of that region indicated in table 16. The number was 6,378 fish which weighed 74,158 pounds as indicated. Both tables indicate a decline in the fishery, but the state catch seems to have picked up somewhat in 1929, although it is still below that of 1905 by something over 50 per cent.

TABLE 17.

Salmon Catch for the State of Maine and Penobscot River and Bay for Various Years Between 1887 and 1929.

Year	Total Maine Catch (lbs.)	Penobscot River and Bay Catch (lbs.)	Percentage Penobscot Catch
1887	185,637		
1888	205,149		
1889	152,740		
1898	53,322	42,560	79.81+
1902	60,768	45 782	75.33+
1905	86 298	74,158	85.93+
1908	19,000		
1919	20,920	13,557	64.90+
1924	12,348	9,237	73 18
1928	14,747	12,700	85.59+
1929	43,554	37,215	80.80+

Union River. — Once a productive salmon river, it has not yielded a single salmon for over seventy years. Formidable dams at Ellsworth, within three miles of tide water, effectually obstruct the ascent of fish.

Narraguagus River. — Salmon were plentiful here 90 or 100 years ago and the river afforded a productive salmon fishery. A few salmon even now appear at Cherryfield.

Wescongus River. — Salmon formerly ascended the Wescongus which afforded a limited extent of breeding grounds in the main river and a small tributary. Forty or 50 years ago salmon were caught in dip nets at Columbia Falls and have occasionally appeared there in recent years even as late as the spring of 1932. When Atkins (1874) wrote it was estimated that the annual catch here was about 75 salmon.

Machias River. — It is stated that in olden times salmon were extremely abundant in this river. Something over 80 years ago, it is said, a fisherman with a dip net could take 60 salmon in a day at the lower falls. As in other streams, dams have practically effected extermination so far as that river is concerned, although a few appear at times below the lower dam.

East Machias River. — While in former times Machias River was regarded as the better salmon river, at present and for a long time the East Machias is and has been the better stream. Salmon are now and then taken, and apparently they breed to some extent in Chace's Stream, the outlet of Gardner's Lake. Several salmon were caught with a dip net at East Machias in the latter part of June, 1876 (B.S.H. 1876, p. 319).

Orange River. — It does not appear that salmon ever very numerously frequented this stream, although before dams obstructed it, some entered it for breeding.

Little Falls River. — Salmon ascended this small stream until recent years, and may occasionally do so now. It affords good breeding places.

Dennys River. — Atkins wrote that in its primitive state salmon abounded in this river. In *Notes from Dennysville,* Robert T. Morris (1900, p. 69) under date of July 1,

1909, wrote: 'As a salmon stream the name of the river is Dennys. *Sawmillafecit.* Until very recently the river was full of salmon. There are half a dozen fine pools within the first two miles, and the salmon took the fly freely. They tell of Mr. Prime and Mr. Brackett taking eight or ten salmon a day. Shad came up the river in June in large schools, and furnished an abundance of toothsome fare for the people. Alewives crowded the ripples, and the poorer people laid up barrels of them against a snowy day. But these things are all spoken of in the past tense, because the lumber company has a sawmill at the head of tide water, and the artificial fishway will not allow breeding fish to pass.'

Pennamaquan River. — It appears that salmon occasionally entered this river, which afforded a limited amount of excellent spawning ground. In 1894 (Anonymous 1894, p. 17) 'a fine salmon weighing 20 pounds was caught at North Perry in October, in a herring weir.'

St. Croix River. — The St. Croix by its eastern and western branches respectively discharges the waters of two extensive lake systems, and salmon, once abundant, ascended nearly to the headwaters of both branches. More or less salmon continued to ascend the rivers until recent times, apparently having freer access to the eastern than the western branch. Obstruction and pollution, augmented by poaching, have practically eliminated salmon from the river, excepting the few which yearly, at least up to recent times, appeared in the pool at Calais or Milltown.

In early times the St. Croix River was considered to be one of the most prolific of salmon streams on the Atlantic coast, and during a number of years it yielded a large annual catch, the fish being taken chiefly at and below Salmon Falls, in the upper part of Calais and St. Stephen, as they were making their way up the rapids. It was then the custom for residents of the neighboring country to resort to this favored spot at the proper season for obtaining supplies for their own use, and some market fishing was also engaged in.

In 1850 it was estimated that the catch for the entire river did not exceed 200, and during the next 15 years the quantity taken annually remained very small, amounting in some seasons to only about 100. In 1866 and 1867 an increase was reported. Since then the catch has fluctuated from year to year, but no complete statistics of the same have been obtainable. The run is still so small, however, as to bear no comparison with its condition in the early part of the century. In colonial times vessels were fitted out in Plymouth and Boston to obtain salmon. So great were the quantities known to be in the St. Croix River that they passed by all the other large rivers on the intervening coast, such as the Penobscot and Kennebec and came here to load with this fish.

The total catch of this one weir in 16 years was 1,214, making a yearly average of about 76.

The following table represents the annual catch of one weir in tidal waters at Calais, for 16 years from 1862 to 1877 both inclusive. There are no later statistical data of this kind.

TABLE 18.

Annual Catch of Salmon of One Weir at Calais for 16 Years 1862–1877

Year	Number of Salmon	Year	Number of Salmon	Year	Number of Salmon	Year	Number of Salmon
1862	145	1866	111	1870	36	1874	21
1863	101	1867	104	1871	119	1875	63
1864	30	1868	93	1872	55	1876	89
1865	27	1869	22	1873	84	1877	113

The following accounts of the tributaries of St. John River and the St. Croix River are largely extracted from the report of the Joint Commission relative to the Preservation of the Fisheries in Waters contiguous to Canada and the United States, by Richard Rathbun and William Wakeham, 1897, to which are added some notes taken by the present writer who took part in the investigation by this Commission, in 1893, and in 1909 during inquiries conducted by a later joint commission.

Meduxnekeag River. — This is the lowermost of the international tributaries, joining the St. John River at Woodstock, New Brunswick, and consists mainly of two branches of nearly equal size, which unite about 12 miles above its mouth and only a few miles east of the boundary line. Authentic records show that during the early part of this century salmon entered this river in abundance, more especially in the vicinity of Houlton, Maine, where they continued plentiful until shut out by dams about 1826. During some years, however, it is reported that a few salmon still find their way into the lower part of the river (Rathbun and Wakeham p. 17). There is no recent available information concerning this river.

Big Presque Isle River. — The river is naturally a clear and rapid stream, about 40 miles long, lying between the Meduxnekeag and Aroostook valleys, and reaching the St. John River a few miles below Florenceville, New Brunswick. It was formerly resorted to by salmon, but it has been impossible to ascertain what extent. (Rathbun and Wakeham p. 17).

Aroostook River. — 'The Aroostook empties into the St. John River about six miles above the town of Andover, New Brunswick, and 16 miles below Grand Falls. It is the largest tributary of this system, having a length of 138 miles. Only the last four miles of its course are in New Brunswick. Reliable information respecting the amount of salmon taken annually from the Aroostook is not obtainable, as the fishing is carried on only by sportsmen and poachers, but many relatively large catches are reported from time to time. The species was undoubtedly much more abundant in early times than it is at present, as many if not most of the tributary streams containing the original spawning grounds are now closed by dams or encumbered with refuse. That some spawning places are still accessible, however, is indicated by the continued presence of the salmon in the river (Rathbun and Wakeham p. 17–18).

A Brief History of Salmon Angling in New England.

Fly-fishing for salmon is a time-honored sport and no fish caught in fresh water excels the salmon as a game fish. Taken all in all, it is doubtful if a salmon angler who may have tried all other game fishes of inland waters or of the sea, if restricted to one game fish, would choose other than the salmon, if salmon waters were within his range or his means.

For years salmon anglers of this country, who could afford it, thought they had to go to Canada, Newfoundland, or Labrador, notwithstanding the fact that salmon fishing was almost in their own dooryards. Long after the Connecticut and Merrimack had lost the prestige that they had or might have had, good fishing, although limited in extent, was still to be found in Maine, had the fact been known. It is true one or two local anglers, and perchance some friends from a distance, knew of Dennys River and indulged in the sport there, but they did not advertise the fact.

The history of salmon angling in Maine waters consists of scattered notes in sportsmen's journals. The first salmon taken with a fly in Penobscot waters was landed by J. F. Leavitt and H. L. Leonard of Bangor, Maine, in 1880. The catch was made in the Wissaticook Stream which empties into the east branch of the Penobscot.

It was not until about 1882 that Mr. Fred Ayer of Bangor, who previously made his annual trip to Canadian waters, conclusively demonstrated that the Penobscot, even within the city limits, afforded opportunity for angling previously unsuspected. Later the St. Croix and Aroostook attracted attention, but in each instance the fishing was practically restricted to one pool. In the Penobscot the pool was below the Bangor dam, the lowermost dam of the river. In the St. Croix it was likewise below the Union Mills dam, the lowermost dam of that stream, near Calais; and in the Aroostook it was almost in the 'heart of the city' of Caribou, below the only dam in the main river.

Despite the recorded catch of Messrs. Leavitt and Leonard in the Wissaticook it did not appear to occur to any one that fly-fishing might be found at other places in any one of these rivers, in each of which there were good pools. At the time there were those, knowing that salmon were netted in the vicinity of the Hunt farm, not far from the stated place of capture, who doubted the statement that the fish were taken on a fly. The anglers who brought the fish to Bangor were reputable men, and if they said they caught the fish in the manner and place reported, there seems no justifiable reason for doubting the statement. Furthermore, there is no apparent reason why salmon might not have been taken at many other places in the proper season in the East Branch and its larger tributaries, like the Wissaticook and Sebois.

The following references to angling at the Bangor salmon pool are condensed from various newspapers and sportsmen's journals, principally, *Forest and Stream*, *American Angler* and *Maine Sportsman*. All of the references have not been cited.

1885.

In 1885 more than six salmon were taken in the Bangor pool by Fred Ayer who thus demonstrated that the salmon fishing with the fly is as good on the Penobscot as in any salmon river in the world, according to the *Bangor Whig*, 1885, p. 454. During the same

season, Mrs. George W. Dillingham of New York landed a ten-pounder, thus becoming the first lady to take a salmon on a fly in the Penobscot. The 1885 season accounted for 40 salmon taken at Bangor.

1886.

The 1886 season was a salmon furore at Bangor. Anglers flocked there from New York and Boston to vie with the natives in the exciting sport. The whole town went wild over the sight of big catches almost daily within a mile or so of the civic center. The best catches were made from boats on the Brewer side of the river, the principal fishing ground beginning at a point 300 yards below the Water Works dam. A 24-pounder was credited to Mr. Fred W. Ayer, who also took three more aggregating 51 pounds, all on the fly. He was also credited with another big one, 20 pounds. Jack Guthrie, Henry A. Wing, Dr. Simmons and William Munroe were listed as taking large fish.

1887.

The season opened late in 1887. On April 29 the ice had been out but a few days, while fish were taken on the fly on April 27 in 1886. The situation gradually improved, however, 17 fish being taken at Bangor May 23 with 20 noted sportsmen there. On May 24, 1887, the Fish Commissioners of Maine reported that the fishing below Bangor dam was in full blast. Nine were captured May 23, eight the day before and as many more hooked and lost. The catch ran large in size; from 14 to 25 pounds. They were taking as many on the Bangor side of the river as on the Brewer — something not done heretofore.

The showing of a 21-pound fish in Dame, Stoddard and Kendall's fishing tackle window set all Boston talking salmon, and the interest centered around Bangor. The season had been good there since the late opening, and those high up in salmon lore claimed it was going to hold out well. Mr. Fred Ayer went on record as believing that later there is to be a good run of smaller fish and everybody could take them.

Mr. Ayer's prediction was borne out by a second run of salmon, excellent fish, though smaller than the first run. More fish were caught with hook and line than last season and the captures down river by the market fishermen were also in excess of the 1886 take. Propagation and protection were credited with the wonderful increase of salmon in the river, after the fishery had nearly played out.

1888.

The first take of 1888 was on April 27 — Mr. Fred Ayer again being the lucky man. The river, however, was at full freshet flood caused by rain and warm weather and this caused a lull, when no catches were made. Then came two days of big fishing, 18 fish being taken. The season proved to be by far the most successful since fishing began at the Bangor pool.

1889.

The first Salmon at Bangor, Me. ('H' 1889, p. 271): 'Mr. Fred C. Ayer again, for the third year in succession, landed the first salmon of the season from the pool at Bangor on April 12, almost three weeks earlier than last year.' His fish weighed eight and 12 pounds respectively. For some reason the salmon fishing at Bangor was not as good as in 1888. Although the season opened very early and promised to be unusually good, May and June fishing proved to be very poor. It was said that the acid and refuse from the large pulp mills on the river were driving the salmon out of it.

1890.

'Special' (1890, p. 270) writes: 'The first salmon of the season has been landed at Bangor, but this one has not yet been followed by the good run that the sportsmen are hoping for, though the fish are tried every day. The Boston sportsmen who propose trying for the salmon at Bangor are anxiously waiting for the telegraph to announce that the salmon are rising freely. Somehow there is not much confidence among the sportsmen concerning the run of salmon at Bangor this spring. The fear is that already the extensive pulp mills on the river above — with its many branches also beginning to be lined with pulp mills — are about to show their deadly work upon the salmon of the Penobscot. The chemicals that are discharged into these streams are believed to be death-dealing to the salmon. Last year it was particularly noted that the ascending salmon invariably crossed over to the other shore, where it was possible to avoid the deadly chemicals; and that frequently they were found dead. The great majority of these many pulp mills on that river and its tributaries are the work of a couple of years, and it will be remembered that last year was the first when the great run of salmon at Bangor began to fall off. In fact, the run of last year was practically a failure. Now, this lack of a run last year may be due to other causes; but the theory of those best posted, and who have given the subject the most thought, coupled with a good deal of experience, is that the salmon are either being killed by the pulp mills' chemicals or they are so disgusted with the foulness of the waters of the river they are wont to ascend that they are turned aside into other streams, or else they do not leave the salt water at all. This theory may not be the correct one, but the results of this season will be anxiously watched. It may be that excessive netting, which is permitted at Bucksport and at other points on the river below Bangor, is a great reason why the salmon do not ascend the river. Already a good many salmon have been taken by these fishermen below Bangor and sent into the Boston market.'

The first salmon of the 1890 season was taken at Bangor, April 14, by Mr. E. A. Buck, just below the waterworks dam, and weighed 12 pounds. The following was the result of one day's fishing as near as could be learned: 'Mr. Archibald Mitchell, two fish, 21½ and 22 pounds; Mr. F. W. Ayer, 20 pounds; Mr. H. M. Prentiss, 20½ pounds; Mr. Dodge, 19 pounds; Mr. P. McCarthy, 10 pounds. Dr. Elliot, of Lawrence, Mass., hooked one, but lost it and Mr. McCarthy had the same ill fortune. The fish were

reported rising to the fly in a lively manner, and for some time the fishermen had been enjoying good luck. The water was now getting lower and was favorable for the fishing. The fishing was probably at its best, as the flood was past.

1891.

The early run of salmon in the celebrated pool at Bangor in 1891 was not of any considerable proportions. Following the first one caught, only a few had been taken. In one day, Saturday, April 11, six fish were hooked, but only one was landed. Later the fishing was better at Bangor. F. W. Ayer landed a 27-pound fish and others had been doing well, ten having been landed in one day.

1892.

One hundred salmon, weighing 1,850 pounds were reported as having been taken in the Bangor Pool in 1892. As usual, Mr. F. W. Ayer took the lion's share, he having caught 21 fish, and his nearest competitor eleven. This is not a bad record for a pool that was almost totally exhausted for several years, till restocking and protection brought it up to present proportions.

1893.

The first salmon of the 1893 season was taken from the Bangor pool April 21, nine days later than last year, when the first salmon was taken on the 12th of April. Since the 21st there was a storm and a rise of water, which doubtless hindered the run of salmon, till the water cleared. The salmon caught in the pool, a mile above the city, were the largest on record for this year. The river opened April 5. No salmon were taken with fly until April 21, when Mr. Libbey, an employee of a Bangor shoe factory, landed one that weighed 20½ pounds. Later Dr. Baxter caught one that weighed 23 pounds and P. M. Ayer and several others took fish of 20 pounds or more. The water continued cold and the fish did not bite well.

1894.

Three fish were captured on April 1, and some might have been taken even earlier had it been legal to have done so. The salmon thus far landed were generally of large size, ranging in weight from 20 to 25 pounds each. Fishing was impaired during part of the month because of higher water, but the freshet receded and it became good again. Thursday, April 5 was a lively day at the Bangor salmon pool. Ten fish were struck and three landed as follows: E. M. Hersey, 18 pounds; Charles Foster, 18 pounds; Samuel Atwood of Winterport, 22½ pounds. Mr. Atwood's fish was caught at the highest point of the tide — something very unusual. From 15 to 25 anglers fished the pool daily for three weeks and during the time 20 salmon were killed according to one report. Hon. Charles E. Oak of Caribou, Forest Commissioner took two kelts weighing 14 pounds each and a salmon weighing 23 pounds. E. A. Buck, the shoe manufacturer, caught

two salmon weighing respectively 15¼ and 10 pounds. Seven fine fish were taken on one day. Rev. Newman Smythe caught a 20-pounder; William Hale, two weighing 20 and 21 pounds; John T. Clark, one weighing 18 pounds; Guy Getchell, one weighing 22 pounds; C. P. Hodgkins, one weighing 12 pounds.

1895.

In 1895, one salmon was taken from the pool at Bangor while the ice was not yet out of the river below. The ice moved down from a favorite fishing spot, and a number of fishermen gave the salmon a try March 30. One salmon weighing 23 pounds was taken. Mr. Perley was the lucky fisherman. This was one of the earliest catches on record at that pool.

1896.

April 2, 1896, Frank Cowen, of Bangor, hooked and landed the first salmon of the season at the pool. A few hours after John E. Kent, of Veazie, got another salmon on to the land, that weighed 17½ pounds. The weather was cold, with the river full of floating ice. It was understood that the above fish were both caught with bait, nothing having yet been done with the fly. However, it turned out to be a great year at the pool. The fish were reported as coming up the river in myriads and probably twice as many were caught as during any season in recent years. It was believed the latter part of the run were cultivated fish with which the river had been stocked. They were all young fish, averaging five pounds less in weight than the usual fish and of a different shape, being characterized by a blunter snout.

1897.

The 1897 season started poorly. The ice left the river April 6, four days earlier than 1896. On the opening day, April 3, Charles Bissel of Brewer took a 14½ pound salmon. Rain and roil then spoiled the fishing for a spell, then came improvement and one fish weighing 26½ pounds was taken, among others. The record fish for the pool was 28 pounds, taken three or four days previously. The May run was far from satisfactory at the Bangor pool, but E. J. Hunt was credited with a 27½-pound fish taken the last week in the month. The June run was better than the May run however and J. Henry Peavey of the Bangor Edge Tool Works was reported taking 'a monster,' a 28-pound salmon, on June 28, and was credited therefor with one of the very largest fish ever taken on the Penobscot with a fly.

1898.

On April 1, the opening day of the season of 1898, at the Bangor pool, two fish were taken with flies, George Willey of Veazie landing an 18-pounder; the other, by W. W. Fogg of Bangor, weighing nine pounds. They sold at $1.25 per pound. On April 3, two more were caught. A fish weighing 23 pounds was among the June catch.

1899.

On April 17, 1899, the Penobscot had become free of ice only up as far as Bangor and no salmon reported. The water was four feet over the Bangor dam on April 24; too high for fishing the pool below. There was still a big body of snow in the woods.

New England fishing ('Special' 1899, p. 89), dated Boston, July 22: 'Late Bangor reports say that the salmon season on the Penobscot has been a failure. Very few have been taken from the pool by anglers, and the netters "down river" have not made half their usual catches. Those most familiar with that river and its salmon interests say that the greater need is a close time of from two to three days a week, to allow part of the salmon to reach their spawning beds. During the close time all weirs should be open. The New Brunswick rivers have some protection of this sort, and the salmon are greatly benefited thereby. From July 15 to April 1 all weir and net fishing is closed on the Penobscot, though lead and single line fishing is allowed till September 15. It is contended, however, that the salmon start up the Penobscot early, and that to almost entirely stop them from going up during all the spring and early summer will soon destroy the whole stock.'

1900.

The 1900 season was counted a very poor one. The first salmon of the 1901 season has been taken at the 'Big Pool' by a lady. The fish weighed 18 pounds and sold for $1.25 per pound.

1901.

Up to April 29, the 1901 season at the Bangor Pool did not pan out very well owing to rains and freshet. George Willey had landed two 24-pound salmon and Samuel Drinkwater a 22-pounder. By May 6 conditions were improved and the fishermen were having better sport. Twenty fish were taken for the week weighing from 17 to 27 pounds. Mrs. Wm. A. Munroe took two salmon weighing about 20 pounds each.

New England waters ('Special' 1901, p. 408): 'Boston, May 20. . . The season at the big Bangor Salmon Pool still promises to be a record breaker. An account kept by a Bangor citizen interested in the sport says that sixty salmon have been taken, of a united weight of 1,066 pounds. This shows an average of a little over 16 pounds.'

In a sportsman's journal J. S. Rowe (1901, p. 214) gives us a brief summary of the principal catches of salmon in the pool, for several years prior to 1901, particularly as regards large fish. It is stated that in previous years, the largest fish of tradition were three of 30 pounds each. In 1896, four fish are mentioned weighing respectively 25½, 24, 21½ and 21 pounds. The biggest salmon of 1897 weighed 28 pounds and three others taken by the same angler weighed respectively 25, 20 and 19 pounds. Other large fish recorded in the same year, were seven of specific weights, 27½, 26½, 22, 21½, 20, 20 and 20 pounds. Mention was made of three others aggregating 60 pounds, and two of the combined weight of 35 pounds.

In 1898, specific mention is made of seven fish weighing respectively 30, 24, 21, 21, 20½, 19½ and 18 pounds. In 1899, 12 fish are recorded as follows: 24½, 24, 23, 22, 21½, 21½, 21 and five of 20 pounds each. During the season of 1900, it is stated the most successful anglers of which there were five, killed 34 fish, the largest of which ranged in weight from 25 to 18 pounds, as follows: One of 25, one of 24, two of 23½, three of 23, two of 22, five of 21, four of 20, one of 19 and one of 18 pounds each.

Again in 1901, according to the *Maine Sportsman* (Anonymous 1901, p. 268), the first salmon was taken April 3 and from then to June 30, 109 fish, aggregating 1927½ pounds were killed by 42 anglers. These salmon ranged from 10 to 25 pounds and averaged 17.68 pounds each. The numbers taken by individual anglers ranged from one to 15 fish. The latter number aggregated 232¾ pounds. They ranged from 10 to 21½ pounds and averaged a little over 12½ pounds.

1902.

The first Penobscot salmon of the 1902 season was a 20-pounder, taken in the weirs at Verona, near Bucksport, and selling at Boston for $25. The first fish at the Bangor Pool was taken April 6, also a 20-pounder. Up to April 21 the season was a failure. The weirs below in the river were blamed and the sportsmen predicted the pool would soon be a thing of the past. But on April 29 the pool was cited as affording better sport than last year, with Miss Jennie Sullivan, the first woman to land a salmon last year, capturing the honor again this year with a 20-pound landing. The fish were reported as still rising on May 17, much better on June 30 and fish seen in the pool August 4, also jumping onto the apron of the dam, but not taking the hook. In May Mrs. George Willey was recorded taking three fish aggregating 53 pounds, the largest 23 pounds, and was acclaimed champion woman angler of the Penobscot.

1903.

The season of 1903 must have been very discouraging for weeks, for but two fish were recorded caught up to May 2, the first by Charles Hodgkins, 22½ pounds and the other by Arthur E. Weeks of New York City, 15 pounds. The weirs were barren of catches. On June 20 at the Bangor salmon pool the fishing was slightly improved over the preceding weeks, but even then it was nothing to boast of.

The Maine Season (Rowe, Herbert W. 1903, p. 147): 'Bangor, Me., Aug. 15 . . . The principal surprise of this season has been the catching of salmon late in the season, for until this year no salmon have been taken, if indeed fished for, after the middle of July, when the down river weirs are taken up and the salmon have, for the first time in the season, free access to the river. It has been urged that as salmon can be taken in Canadian rivers until the latter part of the summer, so the Penobscot ought to be able to do as well, but the average angler has not been venturesome enough to face criticism by trying the pool in late July and August. This year, however, several have kept at the sport right along, and to the surprise of most people July and August have maintained

a very fair average in the number of salmon taking the fly, although they have been far more difficult to hook and slower to rise to the fly than earlier in the season. J. H. Peavey, whose expertness in salmon fishery at the pool is well known, has taken eight fish since the fifteenth of July, the date at which the fishing usually ends. . . . This is believed to be the latest date that a fish was ever landed at the Bangor salmon pool since fly-fishing began there.'

1904.

The only records for this year at the pool appear to be those of the *Maine Sportsman* (Anonymous 1904, p. 227) as follows: April 3, May 18, and June 30, total 51 salmon killed by 12 anglers.

1905.

New England Fishing ('Central' 1905, p. 498): 'Boston, June 17 . . . The latest from Bangor is to the effect that all records have been broken at the pool this season, although the best of the sport came late. It is believed that twice as many salmon have been taken this year than there were last year.'

An article in the *Maine Sportsman* (Anonymous 1905, p. 248) entitled *At the Bangor Salmon Pool* gives detailed records of the catch by days of the months from April 11 to July 29 inclusive, by nine anglers: April 11–25, four days, six fish, from seven to 21.5 pounds, average 15.9 pounds; May 3–31, 13 days, 35 fish from nine to 22 pounds, average 11.6; June, 70 fish from eight to 20 pounds, average 10.78 pounds; July, two fish of ten pounds each.

1906.

April 7 opened the 1906 angling season at the Bangor pool, by the capture of an eight pound salmon. Later reports stated that according to the best information obtainable there were about 108 salmon caught at the pool, altogether. The largest fish for the season was landed by Thomas Cannon. It weighed 25 pounds.

1907.

In 1907 considerable newspaper publicity was given to the claim, made by some, that the Penobscot River salmon fishery was doomed. Old habitues of the pool claimed that fish were being freely gaffed in secret spots inaccessible to anglers, that the fishways were inadequate, some improperly constructed, that poaching was rampant and that sufficient efforts were not being made to restock. One dam near Bucksport was mysteriously blown up, the deed being laid at the door of 'suffering fishermen' who had appealed in vain to the powers that be for a proper chance for the fish to pass up over the dam. The claim was also set up urgently that a prime factor in the decrease of catch was that the weir fishermen were allowed to leave their weirs out night and day, on every tide and that it was a miracle that any fish at all got to the pool.

One article (Anonymous 1907, p. 427) stated: 'In common with shad and other dainty fishes it is rather saddening to note that the Penobscot salmon is gradually disappearing from its old haunts. Where thousands used to be taken it is now an event of wide-heralded newspaper notoriety when one fish is caught.' The article then went on to attribute the decrease to pollution, the commercial fishermen and dynamiting. It stated that the supply of salmon was diminishing in spite of the best that the United States fish hatcheries could do.

On the other hand, in the following month, another paper (Anonymous 1907, p. 4) announced the largest catch 'for years,' saying that it was the best fishing there had been at the pool for years and if it would continue for a week or two Bangor might again become the Mecca for fishermen from all New England as it was years ago when the salmon at the pool were as numerous as trout in a brook. In one day ten fish ranging from five to 20 pounds were caught.

And again a week later an announcement under the title *Took seven salmon* (Anonymous 1907, p. 4) stated that the run of salmon at the Bangor pool continued and that the fishermen were having great sport with the big gamy fish. It was reported that the fish were not running large, 12 pounds being a good average, though fish of 20 pounds or better were occasionally taken. The largest of the seven of one day weighed 21 pounds. This comparatively good fishing was regarded as exceptional.

The reported total number of salmon taken at the pool in 1907 was 117, the largest of which was stated to have weighed 23¼ pounds, although it was said that a fish of 24 pounds was killed.

1908.

The following year, *Salmon at Bangor Pool* (Anonymous 1908, p. 7) was the title of another complaint that salmon were decreasing. 'Twelve years ago the salmon, king of fishes, swarmed in the Penobscot River,' said the writer, 'and a man could go up to the pools below Treat's Falls dam, within the city limits of Bangor, and hook a fine big fish before breakfast. Hundreds of salmon were in those days taken with the fly from these pools and thousands were taken in the weirs along the river below Bangor. Now the salmon is so rare in these waters that the taking of a single fish is an event of such interest as to call for mention in the newspapers.'

The principal causes for the disappearance of the salmon were alleged to be the pulp mills and the weirs.

The personal experience of a former State Commissioner of Inland Fish and Game, H. O. Stanley (1908, p. 10), is descriptive and reminiscent rather than pertaining to the salmon fishing of 1908, although it was published in that year. 'My fishing for salmon where I have been successful has been at the Bangor Pool. This pool is within the limits of the city of Bangor, and is at the head of tide water — some eight feet or more tide. It is, as a pool for salmon, magnificent. At this point the river is several hundred feet wide and large enough to accommodate a good many anglers and not interfere with each other.

'It is good fishing from the shore or from boats anchored in the river. It is quite rough water and the current is changing, continually forming new eddies. The most of the salmon are caught from boats anchored in the river. A majority of the fish are not caught by casting as in other pools. Here the angler sits in his boat and lets out his line and guides his fly over any spot below him he desires. The current and eddies do the rest — giving the fly just the right motion. The first thing the angler knows he has a salmon — usually unexpectedly.

'The first salmon caught in this pool was caught by Mr. Fred Ayer of Bangor, who was an expert in that line. It was always thought the Penobscot salmon would not touch the fly until he solved the problem and showed that they were no different from their relatives in other waters.

'I think there are as many salmon come into the river now as there did when I first knew of it in 1872. I understand the catch last year was fully equal to former years. I have no doubt this is due to the splendid work of Hon. Chas. G. Atkins, Superintendent of the U. S. Fish Hatchery at E. Orland, who has been planting thousands of fingerling salmon in the headwaters of the Penobscot River every year for some time. Were it not for this, I sincerely believe there would be but very few, if any, in the Penobscot today.

'The fishing at the pool commences very early — as soon as the ice leaves the river and even before the fisherman down river get their weirs up. I have known of one being caught in the open water below the dam before the ice was out below.

'The first fishing I ever did there for salmon was with my old comrade Mr. Stillwell. I think it must have been early in the 80's.'

The record for the 1908 season was very poor at the Bangor Pool, only 39 fish being taken. The last fish was caught June 12, whereas the fishing usually continues until July, and sometimes into that month. C. S. Bachelder was high line for the season with eight fish, with Charles E. Bissell close behind in a record of six.

1926.

A gap of 17 years occurs in the records at hand. The more or less regular sources of information, one after another, dropped out of existence or for some reason or other failed to report the events at Bangor pool. Doubtless local newspapers and occasionally some others carried notes of the result of fishing there but they escaped our notice for it was impossible to scan them all. However, on June 24, 1926, a 22-pound and a 17-pound salmon were reported caught in the afternoon of June 23. A report on July 3 gave the glad and surprising information that 'all records had been broken this year at the pool, the catch to date on the fly being close to 150 fish. The best previous year in the history of the pool was 1912, when the catch for the season was 160. The season was yet young and it was expected that before it ended the record of 1921 would be doubled. Chief Warden Tom Sullivan, who had been in charge of this pool for a long time said that not in his 30 years of service had the Penobscot been so full of salmon.

1929.

In 1929, there seems to have been some further indications that the forebodings of previous years were not fully fulfilled. It was stated that the celebrated Bangor salmon pool opened for fishing April 1 and four prizes were taken, weighing respectively, 19¼, 15¾, 11¾ and 14¼ pounds. And again a mimeograph sheet of record sized fish issued on April 25, 1929, by the Passenger Traffic Department of the Maine Central Railroad, Portland, Maine, reported that 13 anglers of Bangor and Brewer secured one salmon each weighing as follows: 10, 15, 17, 14½, 7½, 16½, 16½, 17½, 16½, 18, 17½, 17, 13¼ pounds, making in all 17 fish ranging from 7½ pounds to 18 pounds and averaging nearly 15½ pounds.

The Atlantic Fisherman (Fisherman's Doctor 1929, p. 24) is responsible for the following: 'A fine eleven pound salmon jumped into the boat of Lathrop Caldwell on July first. Caldwell hails from Brewer. The fish had not been hooked.'

Again the *Boston Globe* of May 20, 1930, published a dispatch from Bangor dated May 19 concerning a big catch in the weirs. Concerning the fishing at the pool the dispatch said: 'The full force of the run, however, apparently didn't reach the Bangor salmon pool which was densely populated with anglers who made but a few catches.'

Table 19 gives the records of numbers of salmon taken from Bangor pool by a club of anglers of Bangor, each year, for the 40 years from 1893 to 1932, both inclusive. The numbers fluctuate considerably from year to year, yet considered by decades a progressive increase is shown. It is not clear whether this means more anglers, more fish or both.

Table 16 shows that the years of largest commercial catches of Penobscot Bay and river do not correspond with years of largest catches by anglers. Thus 1896 represents a commercial maximum. In the same decade the anglers' maximum was in 1897. Five years later (1901) the largest number was recorded for Penobscot Bay and river. In the same year the anglers catch was only eight below that of their high catch of 1902 in the same decade.

Table 20 shows the number and average weight of salmon taken by anglers from the Bangor pool each month of the fishing season for seven years from 1926 to 1932, both inclusive. As a rule the most salmon were taken in June, although in 1930 the catch in May exceeded that of June by 21 fish, and in 1932 the catch in May exceeded that in June by 26 fish.

Notwithstanding the complaints and lamentations by anglers that the fishing at Bangor pool was being ruined by the commercial fishery down river, the figures indicate that angling has improved, although fluctuatingly, in the last 40 years. On the other hand, the commercial fishery of Penobscot Bay and River appears to have declined. Is this decline on account of decreased intensity of fishing, or are the salmon scarcer than formerly? It is possible that both factors are in effect. That the numerical records for the Bangor pool have increased substantially in the last ten years may be in spite of scarcer fish and may be attributable to the operation of fewer nets in the Penobscot Bay and river.

TABLE 19.

Number of Salmon Caught by a Club of Bangor Anglers at the Bangor Pool, from 1893 to 1932. (Figures Furnished by Walter Higgins, a Member of the Club.)

Year	No. caught	Year	No. caught	Year	No. caught	Year	No. caught
1893	81	1903	39	1913	111	1923	90
1894	51	1904	51	1914	50	1924	111
1895	61	1905	115	1915	72	1925	72
1896	112	1906	111	1916	120	1926	354
1897	125	1907	117	1917	121	1927	112
1898	51	1908	39	1918	52	1928	170
1899	53	1909	37	1919	57	1929	119
1900	57	1910	103	1920	76	1930	111
1901	112	1911	64	1921	134	1931	248
1902	120	1912	153	1922	60	1932	82
Total	723		829		853		1,469

Grand total 3,874

TABLE 20.

Number and Average Weight of Salmon Caught by Anglers at the Bangor Pool, Each Month from April to July[1] Both Inclusive, in the years 1926 to 1932. (Figures Furnished by Walter Higgins, a Member of the Club.)

Years	Months							
	April		May		June		July	
	No.	Av. wgt.	No.	Av. wgt.	No.	Av. wgt.	No.	Av. wgt.
1926	3	—	48	—	290	—	13	—
1927	5	13.85	12	10.98	89	10.56	6	10.17
1928	8	10.81	42	11.42	118	10.57	2	5.00
1929	17	15.24	50	12.24	52	11.21	—	—
1930	—	—	65	10.78	44	10.65	2	7.00
1931	18	8.5	81	10.25	142	9.92	7	10.00
1932	26	12.875	41	11.625	15	12.625	—	—

[1]Fishing season closes July 15.

Denny's River.

The earliest definite reference to the capture of a salmon here is that of one taken on a fly in June 1876. Old residents of Dennysville claim for this river (with the date set as early as 1832), the reputation of being the first river in the United States where salmon were killed on a fly. In 1893 an angler informed me he had taken one or more salmon almost every year. At Dennysville, in 1909, I was told that occasionally a fish was taken but the river was in such bad condition they could not ascend. A July 10, 1924, report credited to a warden, noted a fine run of salmon on the river that year, one fisher having taken 12 sea salmon with fly. In May, 1926, a 19½-pound salmon was reported taken and on May 31, 1928, the weights of three landed were nine and one-half, seven and seven pounds. On June 6 two anglers each landed a salmon weighing seven and 12 pounds. Ralph Bagley was in luck on June 22, 1929. He landed a fish after two hours play, weight 24 pounds.

St. Croix River.

The season at the pool below the Union Mills at Calais, Maine, opened in 1895 with the taking of two fish in May. Local anglers fished the pool several years previously but kept no records. Late in the above noted month Warden Albert French broke the record for this spot with a catch of four fish weighing 17½, 12½, 10 and eight and one-half pounds. In 1896, the June run at the Calais pool was unprecedented, 20 fish being hooked, though but seven were landed. There was good fishing in July and August. The 1897 season must have been most satisfactory, as a July report gives the catch to that time as 105 fish. The 1898 season opened with a landing by Frank Todd of St. Stephen with an 11½-pound fly fish. The record fish for this spot — the Calais Pool — was landed in June, 1898, by Albert French. It weighed 29 pounds, was 38 inches long and 12 inches between dorsal and ventral fins. The 1900 report on May 26 indicated another good season, at last, after several years of poor fishing. Warden French opened the 1901 season in early May by landing a 20½-pound fish.

Aroostook River.

Earliest reports of salmon fishing at Caribou came out in 1890 when an editor caught an eight pound fish in the pool below the Caribou dam, the first fish that season, and taken on a six-ounce bamboo rod with a five cent brown hackle fly after a three-hour tussle. Several others were taken on flies during the summer but none were killed with spears. The state planned a fishway over the dam this year. In 1893 salmon were reported quite plentiful; in 1894 the season opened with the landing of a nine and one-half pounder. In 1895, the new fishway over the Aroostook River dam was completed to the delight of the anglers. Otter River, a tributary, was the scene of the landing of a nine and one-half pound salmon and here too, in 1897, a 16-year-old boy, fishing for trout, is credited with landing a 12 pounder. At the Caribou Pool the first fish of 1898 weighed 16½ pounds.

In June, 1902, the author visited the region and fished the pool. A very few salmon had been caught that season, according to report. The river was low and evidently no salmon were then in the pool. It was alleged by those in position to know that poachers killed about all the salmon down river, practically preventing any from reaching Caribou pool. That salmon spawned to some extent in the river was indicated by the fact that the author caught on a large silver doctor salmon fly a young salmon not much if any over six inches long. The fishway by this dam was in a bad condition, each compartment having been filled with rocks, by some unprincipled individuals of the neighborhood, probably the above-mentioned poachers or some like them. Recent information concerning this river as a salmon stream is wanting.

THE LAKE SALMON (*SALMO SEBAGO* GIRARD).

Plates 5–11.

General Considerations.

Earlier in this memoir reference has been made to 'Landlocked Salmon.' Although this name has long been recognized as a misnomer, it has been quite generally adopted for a salmon which passes its whole life in fresh water. In selecting a substitute name I have followed Herr von Behr (1883, p. 245) in which he says that it seems best to adopt certain names for fish introduced into Germany. For landlocked salmon he uses the name *Amerikanische Seelachs*, which, translated, is American lake salmon. The lake salmon, unlike the marine salmon, are essentially inhabitants of lakes, entering streams, as a rule, to spawn and at times in pursuit of food.

The major amount of information pertaining to the sea salmon is necessarily drawn from foreign countries. On the contrary very little concerning the landlocked salmon is to be learned from European sources. Yet when information is sought concerning the landlocked salmon in this country, it is surprising to find how little is actually known. For many years the lake salmon has been the object of attention by anglers and fish culturists, but it has received scarcely any biological study. Indeed most of the biological consideration has consisted of speculation concerning the *what* and *why* of this fish.

In comparing angling for sea salmon with that for landlocked salmon in this country more than 60 years ago Dr. Hamlin wrote (1874, p. 339): 'But if we cannot boast of our success with the sea-salmon, we may truly exult over the game qualities of the mysterious fresh-water salmon, which inhabits five of our lake systems, and which affords as fine sport as the best fish of the Tweed or the Shannon. This fish is less known to anglers than to naturalists, since the latter have quarreled over its classification and made known to themselves the range of its habitat. But the naturalists have been very careful not to express themselves on paper, and hence the sporting fraternity have not been able to glean much from the scientific reports concerning the disputed fish.'

But the good doctor was wrong: the anglers actually knew more about the fish than did the naturalists. The anglers went astray only when they tried to qualify as systematic ichthyologists, and the naturalists were remiss in that instead of making a biological study of the fish they relied mainly upon the statements and claims of the 'angler-naturalists,' and the examination of a specimen or two, if any at all. So far as the ichthyological systematist is concerned nothing in publication indicates that the situation is much different today than it was half a century ago. Furthermore the original natural situation has been so disturbed by fish cultural operations, that each succeeding year it becomes increasingly difficult to reach any positive conclusions concerning the relationships of the fish.

Names.

'Silfverlax' is the Swedish name for a salmonid of Lake Wenern in southern Sweden, the English equivalent for which is 'silver salmon.' The name, however, does not necessarily signify that the fish is a salmon except in a generic sense. A species of trout is

called by the Swedes 'Grålax,' meaning in English, 'gray salmon.' Yet in all probability the Silfverlax is the fish commonly referred to as the 'landlocked salmon' of Sweden, although the silvery phase of the trout may be confused with it.

In North America the local names for the so-called landlocked salmon are more numerous. The Report of the Commissioners of Fisheries and Game of Maine for 1874 (Stilwell and Stanley 1874, p. 12) says: 'It is known in our State under names so various, that it is almost impossible to recognize the fish saving from one's own personal experience. Salmo Gloveri, schoodic trout, lake shiner, white trout, silver trout, salmon trout, black spotted trout, and landlocked salmon; these are a few of the names by which this fish is known among us.' And on page 16 the report continues, 'We are not ambitious to add another to the numerous "aliases" of this fish, but would it not be better that some order should be attained out of the present confusion of nomenclature by giving it the simple designation of *fresh water salmon?*'

The Canadian fish of the upper Saguenay and Lake St. John region has always been known by the Montagnais Indian name, variously spelled 'wininnish,' 'ouinenish,' Wananish, or more recently 'Ouananiche.' In New Brunswick it bears, or once bore, the name 'shiner.' The Nova Scotian appellation appears to be 'grayling.' Apparently it was always 'salmon' in Lakes Ontario and Champlain.

Many years ago Dr. A. Leith Adams (1873, p. 209–210) gave the fish of eastern Maine the name of 'silvery salmon trout', and stated that old men of the Passamaquoddy tribe of Indians distinguished it by a name that sounded like 'onnenook.'

Atkins (1874, p. 292) concerning the Grand Lake salmon, wrote, 'I have it from an intelligent Indian of the Passamaquoddy tribe, Piel Toma, who lives near Princeton, that fifty years ago they [Atlantic salmon] were caught at Grand Lake stream on the west branch [of the St. Croix River]. The Indians call the sea-salmon Pl-láhm, in distinction from the *land-locked* salmon, which they call *Tag-e-wah-nahn.*'

Both this name and *onnenook* suggest some possible philological relationship with the name *ouananiche.* If ever any distinctive local names were bestowed upon the Green Lake and Sebec Lake fish, there appear to be no available records to that effect. Up to a few years ago, at least, at Sebago Lake the fish was commonly referred to as 'trout' and to distinguish it from the 'brook trout,' which was there called 'redspot,' it was called, 'blackspot trout,' also sometimes 'salmon trout,' by the old inhabitants. Visiting anglers now usually speak of it as 'salmon.' In former years it was possible to catch the fish in the outlet, Presumpscot River, for a few miles down. Small fish with red spots on their sides were called 'Jumpers' by local fishermen. The name is significant and self explanatory. When hooked it spent about as much time in the air as in the water before being brought to net.

In reports of fish cultural operations of the United States Fish Commission, the names at first employed were those derived from the locality where the operations were carried on. Particularly is that true of Grand Lake Stream region where the lakes were designated as 'Schoodic Lakes' and the fish as 'Schoodic salmon.' Sometimes the name, 'Sebago salmon,' was used for the fish of the Schoodic Lakes, as well as for the fish of Green

and Sebec Lakes. In later years the term 'landlocked salmon' came into general use.

Concerning this name Atkins (1884*a*, p. 40) wrote, 'The term "Landlocked salmon," though it may be and probably is, a misnomer so far as it implies any forcible detention of sea-going salmon in fresh water, has come to be generally accepted as applicable to all those salmon of Eastern North America and of Europe that pass their entire lives in fresh water. They are all, according to the most recent conclusions of American ichthyologists, members of the great species *Salmo salar*, the common river salmon of the tributaries of the North Atlantic.'

Geographical Distribution and Habitats.

While waters inhabited by the lake salmon are comprised within the latitudinal range of the sea salmon, their known distribution within these limits is a very disconnected one, and most of the recorded localities of their natural occurrence are in northeastern North America. In Europe the fish have been distinguished from trout in but very few places. The best known European locality is Lake Wenern, in southern Sweden, and this is the principal lake in that country which is supposed to contain them. According to Nilsson (1832, p. 3), who refers to that fish as '*Salmo Salar*,' it occurs also in Lake Siljan. It also is found in Lake Ladoga, an immense lake lying between Finland and Russia.

In Canadian waters the most noted locality for lake salmon is the Upper Saguenay River, Lake St. John, and connected waters, where it is known as 'Ouananiche.' Low (1897, p. 330) says: 'The land-locked variety of *S. salar* or ouananiche, is found in Lake St. John and the tributaries of the Saguenay River, where it has free access to the sea, but as the same fish was found plentifully in both branches of the Hamilton River, above the Grand Falls with its sheer drop of 300 feet it is certainly land-locked there. It is also common in the Koksoak River below Lake Kaniapiskau, above perpendicular falls of eighty feet and sixty feet. Common in Lake Michikamau, on the head of the Northwest River, it is also reported by the Indians as numerous in the upper George River, the Romaine River, the Manicuagan and several others of the rivers flowing into the Gulf of St. Lawrence.'

McCarthy (1894, p. 20–22) says of Lake St. John: 'Bearing the Indian name of Pikouagami, this inland sea measuring fully 30 miles across in any direction, lies deep in the midst of the old Laurentian Mountains, a marvel of beauty to the artist, a paradise to the angler. Tributary to the lake are some eighteen rivers, large and small, flowing from all points of the compass. The most noted are the Ashuapmouchouan from the northwest, the Mistassini from the north, and the Peribonca, from northeast, the Metabetchouan and Ouiatchouan from the south, the Ouiatchouaniche and Iroquois from the west. The three first-named rivers are respectively 300, 350, and 400 miles in length, very deep, and will average from one and a half to two miles wide at their mouths. . . . Ouananiche fishing is found only in Lake St. John, the various rivers flowing into it, and the Grand Discharge. None of the surrounding lakes, unless in direct connection with the rivers, contain them.'

Quoting Dr. Low, Chambers (1896, p. 115–117) writes concerning this fish in Labrador: 'This fish is found in many of the streams that flow from the table-land of the interior, and is not confined to any particular watershed, as it lives in the northern, eastern, and southern rivers. . . . On the eastern watershed we frequently caught landlocked salmon on both branches of the Hamilton River, above Grand Falls, where the sheer fall is three hundred feet. Salmon only ascend the Hamilton River twenty miles above its mouth, where they are stopped by a small fall, which is impassible on account of the peculiar manner in which the water passes over a ledge of rock.

'Ouananiche were taken in the great Lake Michikamou, at the head of the Northwest River, which empties into Hamilton Inlet. . . . No fish were taken in the Romaine River, flowing into the St. Lawrence, but my guide informed me that salmon occurred at the head of that stream and of Natashquan River.

'I do not know what the theories are regarding the occurrence of these fish in inland waters, but of one thing I am certain and that is, they have never ascended from the sea to their present haunts since the close of the glacial period, and I hardly think the conditions were favorable then. My idea is that the salmon was originally a fresh-water fish, and acquired the sea-going habit.

'I have never heard of ouananiche in the waters of the western slope of Labrador — that is, in the rivers flowing into Hudson Bay.'

Halkett (1913, p. 52) refers to the distribution of '*Salmo salar ouananiche*' thus: 'Saguenay River and Lake St. John regions, and lakes and rivers northward to the Ungava region, and eastward to Labrador: occurs also in lakes of Newfoundland — such as Red Indian and Terra Nova Lakes, and lakes at the head of Gambo River.' He lists '*Salmo salar sebego*' as in 'Certain lakes of New Brunswick, such as Loch Lomond and Sciff and Musquash Lakes.'

Formerly salmon inhabited Lake Ontario and Lake Champlain. The question whether these fish were permanent residents of the lakes or ascended from the sea each season was a much discussed question in former years, but it was never decisively settled. The preponderance of evidence, or perhaps it should be said, of opinion, was that they were permanent residents and should be classed as 'landlocked salmon.' Inasmuch as these fish are now extinct in both of those lakes, the question can be settled, if settled at all, only by weighing the evidence and considering such stated grounds for the opinions as may be available.

According to Evermann and Kendall (1902*b*, p. 209) the fish fauna of Lake Ontario comprised 73 species, including the salmon which they list as a *Salmo salar*.

Some 50 years ago, Watson (1876, p. 532) writing of salmon in Lake Champlain says: 'When the writer first became a resident of the district in 1824, many of the original settlers of the country were yet living, who were men of respectability and position, and of undoubted veracity. Their tales of the abundance of the salmon which prevailed at that time demanded for their acceptance an exercise of the strongest faith in the truthfulness of the narrators.' One account was that 1500 pounds of salmon were taken by a single haul of the seine, near Port Kendall in the year 1823. It also stated that in 1838

one man caught 50 or 60 salmon in the Ausable River where no salmon had been seen for 15 preceding years. This appears to indicate that the salmon had ceased to abound in the lake, although more or less sporadic occurrences were afterwards reported.

There is no available information at hand concerning the lakes of New Brunswick and Nova Scotia, other than those mentioned by Halkett, which were naturally inhabited by lake salmon. I have data pertaining to one 'ouananiche' from Newfoundland, which is now in the National Museum of Washington.

Concerning the ouananiche of Labrador reported by Low: if the fish were really salmon, as Low suggests, they must have found their way into those waters through connecting waterways, for they could not have ascended some of those rivers since the last glacial period. With the exception of lakes Ontario and Champlain in the United States no lake salmon of this type has been found to occur naturally in any waters outside of Maine. Originally certain lakes of four river basins contained the fish, which in the order named from east to west are: St. Croix, Union, Penobscot, and Presumpscot. Concerning the natural distribution in Maine, Atkins (1884*b*, p. 342) said that it is singular that they have not appeared all through the Penobscot, as it has many lakes seemingly well suited to them.

Fish culture has extended their range considerably in Maine, where their introduction into some lakes has apparently resulted in a permanent stock. But the results of stocking other New England waters have not been so successful at least in establishing a self-maintaining stock. The same lack of success obtains in other states. Even in Maine attempts to stock small lakes have resulted in failure, owing, no doubt, to some conditions unfavorable to the fish, principally lack of adequate breeding places or insufficient food supply.

There are two branches of the St. Croix River in Washington County. One branch heads in a large lake lying between New Brunswick and Maine, known as Grand Lake, which has a surface area of 23.68 square miles. This lake is the largest of that system. It is said to have once contained resident salmon. Some have been reported as caught in comparatively recent years. But the western branch has always been the most noted for lake salmon. Grand Lake, the largest of the group of lakes on this branch, is the principal salmon lake, although salmon occur in some of the others.

Green Lake, formerly known as Reed's Pond, is one of several small lakes in Hancock County not far from Ellsworth. The lake fills a rather shallow basin among the hills. Green Lake is one of the sources of Union River. Brook trout and smelts of two size-classes are two of the indigenous inhabitants.

Sebec Lake is the largest of a group of lakes which form the source of Sebec River, a tributary of the Piscataquis River, which discharges into the Penobscot. It has a surface area of 10.93 square miles. One or two other lakes contain lake salmon. From Sebec Lake the fish ascend Ship Pond Stream, the principal inlet, and to do so have to leap a considerable fall. Sebec Lake is the immediate source of the Piscataquis River. A dam at the foot of the lake prevents the ascent of fish from the river. Among the various indigenous fishes is the smelt.

Concerning the 'Habitat of Sebago salmon' Atkins wrote (1880, p. 775–776): 'Lake Sebago, the principal haunt of the salmon in this district, is the second largest body of fresh water in Maine. It has an area of about sixty square miles. . . . Sebago Lake discharges its waters into the Presumpscot River, which empties into Casco Bay near Portland. The entire length of this river is about twenty-two miles. It descends rapidly, having a total fall of 247 [now 262] feet between the lake and the sea, yet in its natural condition there was no impediment to the free passage of fish up and down. . . . For many years, however, the river has been obstructed by many high mill-dams, which have entirely prevented the ascent of fish. The descent is of course still open, and the fresh-water salmon are occasionally taken on all parts of the river.

'The principal affluent of Sebago Lake is Songo River, which drains the country lying to the north. The Songo River itself is very short, forming merely the connecting link between Sebago Lake and an extensive chain of ponds (so-called) above. . . . The Songo itself affords no spawning-ground for the salmon. . . . Besides Songo River there is but one other stream known to be a breeding-ground for the salmon inhabiting Sebago Lake, namely, Northwest River. . . . It is also currently reported that the salmon spawn on gravelly bars and beaches in the lake itself. This is not improbable. . . . Besides Sebago Lake itself, the same variety of salmon inhabit Long Pond, the most considerable body of water drained by Songo River, eleven miles long but quite narrow, having an area of nine or ten square miles.'

Since the foregoing was written many changes have taken place in this region, but most of the description of its waters will fit present conditions. The Presumpscot River has been greatly modified in the last 30 years. A high dam prevents a flow of water into the old river bed, the water being diverted into a canal some three miles long leading to a power station. It empties into a pond, a mile long, more or less, with another dam. In several years of observations at Sebago Lake no salmon were even seen spawning on the beaches. But they are known to spawn on a gravelly shoal below White's Bridge. About all the salmon taken for artificial propagation are now netted in a pool in Jordan River, which flows from Panther Pond into the head of Jordan Bay of Sebago Lake. A state hatchery is located at that place, in the village of Raymond. Crooked River, which joins the Songo at Songo Lock, used to be the principal breeding place of the salmon of Sebago Lake. It is said that some salmon still ascend this river, but they are not taken there for propagation as in former years.

Views Concerning the Characteristics and Identity of Lake Salmon.

In a letter to Professor Baird, dated September, 1873, Dr. Hamlin (1874, p. 354) of Bangor, said: 'The *Salmo Gloveri* is nothing but a parr. I examined the fish several years before Girard saw his specimen, and recognized it as the young of the migratory salmon. They have disappeared from Union River since the extinction of the salmon'.

If this were true *Salmo gloveri* would become a synonym of *Salmo salar* and not a name for the Reed's Pond (Green Lake) salmon.

Dr. Adams (1873, p. 216–220) described the Grand Lake Stream fish, which he called the 'silvery salmon trout,' using, however, the technical name '*Salmo Gloveri*' for it, although he regarded it as identical with *Salmo sebago*. His description is detailed and he shows a cut of the fish and figures a gill cover illustrating how that of *Salmo salar* differs from that of *Salmo gloveri*.

He says: '. . . Posterior point of juncture between the operculum and the sub-operculum is about *half-way* between the upper end of the gill opening and the lower angle of the sub-operculum in the salmon, whereas in the silvery salmon trout and sea trouts it is nearer to the *lower* angle of the sub-operculum than to the *upper* end of the gill opening. The operculum is, moreover, relatively larger in *S. salar* than in *S. Gloveri* or *S. Trutta* of Europe, indeed than in any other recorded salmonoid. The maxillary in the adult salmon extends as far back as the posterior margin of the eye, but in Glover's trout it reaches further; and whilst it reaches only to the middle of the eye in the parr and smalt of the salmon, in the same conditions of Glover's salmon trout I found it extending almost to the posterior margin of the orbit.

'The vomer has a double row of small teeth in the young salmon, whereas there is only a single row in the smalt of *S. Gloveri*. The number of vertebræ also differ, being fifty-nine in the former and fifty-seven in the latter; as also the pyloric coeca, which from numerous instances I found to vary from forty-nine to fifty-one, whilst it is well known that the average in the salmon is between fifty-five and seventy-seven.'

'The average weight is from two and a half to three pounds, but individuals are captured of seven pounds, and on reliable authority I know of one caught through the ice on these lakes weighing ten pounds and a half. Even larger fish are mentioned by fishermen, but any weighing over six pounds are uncommon.'

The Maine Fish Commissioners' report (Stilwell and Stanley 1874, p. 14) says: 'We are often asked, "What is the landlocked salmon? Is it what its name implies, an ocean salmon that some accidental circumstance, some convulsion of Nature has barred from return to its ocean home, and thus established a new race; or is it a distinct species?" The year before the death of Prof. Agassiz, we sought from him an answer to these same questions, while on a visit to the Cambridge Museum of Natural History, with our esteemed friend and brother Commissioner, Dr. Hudson of Connecticut. His reply was, "Thirty years since I supposed it to be a *demoralized salmon*, that some cause had prevented from access to ocean; but since then I have changed my opinion, I now think it is a distinct species. I have found it in Sweden" (and we think he added Norway).'

In 1877, Charles Hallock (1877, p. 305–306) discussed the identity of the fish with the true salmon in such an interesting way and, in many respects, so exactly stated the situation as pertains to current popular opinions concerning the identity of the lake salmon with the sea salmon, that it seems worth while to quote from the discussion at some length. Hallock (1887, p. 305–306) wrote: 'Much needless speculation has been indulged in during the past twenty years, and much discussion excited, as to whether this fish was a true salmon, which having been to the sea, preferred not to go there; or that, being a true salmon, and debarred from the sea, he chose like a sensible fellow to

content himself in fresh water; or that by some mischances, he had become "degenerate" in size, beauty, and succulency; and unworthy of his regal progenitors; or whether he was not, after all, truly a variety of lake trout. So much speculation, we repeat, has been indulged in, that it would be a waste of our space to review the *pros* and *cons* of the argument, suffice it to say that one most excellent authority, Dr. A. C. Hamlin, pronounces it identical with the sea salmon, and exhibiting no radical differences, except in the one peculiarity that it does not go to salt water. The bony structure and its fin system are precisely the same as those of *salmo salar*. Therefore we are at liberty to call it a salmon.

'And yet, if we examine its fin system and compare it with that of the togue, we find that the two formulæ vary but slightly; which see:

'Landlocked salmon — Br. 12; P. 15; V. 9; A. 10; D. 12; C. 19.

'Togue — Br. 12; P. 12–13; V. 9; A. 11–12; D. 13; C. 19.

'Now as greater variations are found in lake trout which are declared to be identical species, we are equally at liberty to call the *Salmo sebago* a lake trout, or "*sebago trout*," as some name it. We leave it to those who pay their money, to take their choice, and herewith dismiss the subject. Either conclusion is favored by facts of its biographical history. Within two years we have taken this fish in Canada where there were no obstructions to its passage to the sea; and twenty-five years ago we took the same fish in Maine, where obstructions did not exist but now do. The argument as to its involuntary restriction to fresh water therefore has no weight. *It would not go to the sea if it could; it will not when it can.*' (Italics the present writer's.)

But in 1892, Hallock (1892, p. 25) wrote: 'The Wananishe of the Upper Saguenay River, which were long believed to keep exclusively to fresh water, although they had direct access to the sea, have recently been ascertained to be simply a distinct class of the Sea Salmon, peculiar to its own waters, like all the others, and of precisely the same habits and idiosyncrasies; only the peculiar conformation of the Saguenay region and the extreme depth of the river have hitherto prevented such practical observations as were essential to establish the facts. In places the Saguenay is one thousand feet deep, with an extreme average depth for sixty miles from its mouth, and the Wananishe (*Wa-na-nish*, in the Indian vernacular) are not seen until they reach the riffs of the chute, or Grande Discharge, which constitutes the outlet of Lake St. John'.

In an article entitled *Memoranda on Landlocked Salmon*, in 1884, Atkins (1884*b*, p. 341–342) wrote: 'There have been thought to be several distinct species, or at least several naturalists, finding landlocked salmon in this or that district, have thought them new species and have called them *Salmo sebago*, *S. gloveri*, etc. Within a few years Dr. Bean and others in Washington have carefully compared them with *S. salar* and find no specific differences.'

In 1892 Creighton (1892, p. 81–86) wrote: 'It used to be an article of faith with naturalists and anglers that a salmon — using the word in its everyday sense, not in the technical one of *Salmo*, which generic name includes many very different fish, some of them merely trout — is a salt-water fish which comes into fresh-water rivers to

spawn, and then returns to the sea, or, to use a convenient word, is anadromous. Hence the specific designation *Salar*. Yet nothing in the range of observed facts relating to the *Salmonidæ* . . . is better established now than the existence in certain parts of the United States, Canada, and Sweden of a salmon which inhabits lakes, and is antomically indistinguishable from the salt-water salmon.' He goes on to say: 'The wananishe and the landlocked salmon of Maine are identical, the only observable difference being a slight one in coloration.

Creighton further states (p. 91–92) the characters of the 'Wananishe' as follows: 'As to shape, the wananishe is a perfect salmon, only a dwarf; and the highest ichthyological authorities on both sides of the ocean are agreed that there is no difference of anatomy between *Salmo Salar* and *Salmo Sebago*. I have myself dissected many specimens of sea salmon and wananishe, but can detect no permanent or tangible mark of difference between them.

'The preoperculum, or small bone at the back of the gill cover, has the rounded corner characteristic of the salmon. The system of dentition in the wananishe is precisely that of *Salmo Salar*, but *the teeth are larger and more numerous on the vomer and palatines. This is probably a case of specific adaptation* [Italics the present writer's], as the wananishe lives much on small fish, and unlike the sea salmon when the latter is in fresh water, is continually feeding. In some specimens I have found a few teeth on the hyoid bone, though Jordan and Gilbert ("Synopsis of the Fishes of North America," 1882, p. 311), following Gunther, give the absence of hyoid teeth as a characteristic of the genus *Salar*.

'The number of spinal vertebræ is 59–60; of cæcal appendages, I have counted from 50–60 in different specimens.

'There are 120 rows of scales along the lateral line, 11–12 in a line from the edge of the adipose fin to the lateral line, which, if continued would pass just above the pupil of the eye, and is well marked.

'*The fins are proportionately much larger than in the sea salmon, especially the tail*, which is deeply forked in the young fish, but only slightly lunate in large adults. In a five-pound specimen it will have a spread of seven or eight inches; in a three-pound fish, six inches. The dorsal is high and broad, the pectorals long. The adipose fin is unusually large.' (Italics the present writer's.)

Chambers (1896, p. 16–20) says: 'How the Atlantic salmon, the Canadian ouananiche and the landlocked salmon of Maine appear to the eye of the artist, when compared, is related in the following extract from a letter addressed me by my good friend Mr. Walter M. Brackett, of Boston: "In regard to the ouananiche, or as we call them, landlocked salmon, my first acquaintance with them dates back to 1860 or 1861 (I am not sure which), when I visited Grand Lake stream in the eastern part of the State of Maine, where they then existed in vast numbers; and I have always retained a very vivid recollection of the wonderful sport which I enjoyed. The game character of the fish was a revelation, as up to that time I had not killed a *Salmo salar*. I made several careful studies of them and brought home with me a few specimens, two of which I presented to

Professor Louis Agassiz. They were the first ones he had ever seen. After a careful examination he pronounced them to be landlocked salmon. One of the specimens is preserved in the Agassiz Museum at Cambridge. Several years after, on the occasion of my first visit to the St. Marguerite, I captured two fish which I at once recognized as identical with my earlier acquaintance at the Grand Lake stream. As to the difference between grilse and ouananiche, I can only speak as to their external appearance, never having dissected a specimen of either. This is very marked, as *the eye of the ouananiche is much the larger, the profile rounder, the dark spots larger and much more numerous. The body at the juncture with the caudal is broader and flatter, and the head larger in proportion to the body.* [Italics the present writer's.] In fact, the grilse is much more of an aristocrat than his fresh-water cousin, being finer in his proportions and much purer in color — due, no doubt, to his different habitat and food."

'The above and other variations that have been from time to time reported in either the Canadian or American ouananiche are not sufficient to mark it as a distinct subspecies of *Salmo salar!*'

From the foregoing varied and variable opinions, it is seen that we have a race of fish in certain Canadian waters which has been, for the most part at least, recognized as ouananiche since time immemorial. Also in more recently discovered Canadian waters for some reason the fish still is recognized as ouananiche. As previously stated, the white inhabitants of Nova Scotia to this day designate the fish as grayling. The old white residents of the St. Croix region, there called it 'shiner,' and peculiarly, if not significantly, the Indians of the western St. Croix region in Maine, according to A. Leith Adams, as previously mentioned, called it by a name sounding something like Onnenook, and according to Atkins the same Indians called it tag-e-wah-nahn. Have these Indian names any relation to ouananiche through ouanan and diminutive gutteral such as 'ich' or 'och?'

While the fact that a fish has been described and had a name of Latin form bestowed upon it does not necessarily indicate its identity with, or distinctness from, some other fish likewise described and named, it does indicate that there are recognizable differences from other forms so described and named so far as the individuals observed are concerned. The more individuals there are observed the more likely are the stated differences to be substantiated or to disappear.

Now we have discussed one or more groups of fishes which apparently from prehistoric times have been recognized as so different from another group of fishes as to have had bestowed upon them both by Indian and white settlers, distinctive names. Those people were acquainted with large aggregations of individuals. Then enters the 'trained ichthyologist' who, by observations upon a limited number of both forms, recognizes differences which to him are of specific significance. So Dr. Charles Girard (1854, p. 380) of the Smithsonian Institution, in 1853, described a fish from Sebago Lake ('Southern part of Maine') and named it *Salmo sebago.* For reasons previously mentioned, this fact is principally of taxonomic importance only. To repeat what has been said in other words, if the Sebago fish is absolutely identical with the sea salmon, the name

Salmo sebago becomes a synonym. If it differs from *Salmo salar* by intergrading characters only the Sebago form will receive the trinomial designation *Salmo salar sebago*. If the Sebago fish exhibits only one constant anatomical, physiological, or embryological difference, it is, or ought to be, entitled to the name *Salmo sebago*. By constant difference is meant one that persists under whatever natural condition to which the fish may be subjected and continue to exist. Furthermore, unless such a difference exists the lake-inhabiting salmon is no more entitled to the name, 'ouananiche' than is the Atlantic salmon when caught in fresh water.

While Day maintained that all of the trout constituted a single species, Prof. Smitt regarded the salmon and sea trout as forms of the same species, although using binomials to designate each of them. In fact Smitt's species seem to be what most ichthyologists regard as genera, but he does not follow the usual system of classification.

While Jordan may have compared many specimens of the various geographical forms of salmons, it must be remembered that over 40 years ago, systematic ichthyology was engaged at a somewhat different angle from that of more recent years, at least by some workers. In the old days descriptions of species were more or less stereotyped and made up largely of family or generic characters referring to superficial structures as exhibited by individuals designated as types. On account of the lack of material, it was not possible to observe the variations in proportions of body dimensions exhibited by many individuals of various sizes and ages of each sex from different localities. More obscure anatomical physiological, embryological, and ecological details were lacking. As knowledge increased in the next ten or fifteen years it began to dawn upon some ichthyologists that the labels on some of the 'pigeon holes' of classification did not always accurately designate what should be in them and were somewhat wanting in biological significance.

As has been seen, the lake salmon has been variously regarded as comprising several species distinct from the sea salmon; as one or more subspecies or varieties of the sea salmon, and as specifically identical with the sea salmon. The question here arises concerning what constitutes each of these categories. This has been discussed in preceding pages. As in the case of many other questions, there are two sides to this one. In this instance one side is that of classification or *taxonomy*, and the other is that of nature. Classification is artificial; to a limited extent only it conforms to nature. As Jordan has said, it amounts only to a convenient means of arranging and labelling specimens in collections; and it may be added, of recording them in publication in accordance with structural characters. So far as labelling specimens is concerned, if all lake salmon are specifically identical with the sea salmon, they would properly be labelled *Salmo salar*.

Again, according to the rules of nomenclature, if all the lake salmon are one and the same natural species and specifically distinct from the sea salmon, whether from Lake Wenern, Lake Ladoga, or the lakes of North America, they should bear the name of *Salmo sebago*. If they are all alike and are only of subspecific rank, they must be called *Salmo salar sebago* and not *Salmo salar relictus* as Berg calls them.

Still further, if all the lake salmon independently intergrade structurally with the sea

salmon of the respective regions in a taxonomic sense, they become separate subspecies. If they all differ from each other and each from the sea salmon they must be regarded as distinct species.

According to the rules of zoölogical nomenclature, if they are all entitled to the binomial *Salmo salar*, they should show no permanent structural differences from the sea salmon or from each other.

Before discussing this subject further, attention should be called to one striking fact. That is, according to the authors cited, that at no time in the history of the fish has any one failed to recognize the lake salmon, when caught in the same waters and at the same time, as the anadromous salmon from the sea. Chambers (1896, p. 40) stated that the Montagnais Indians' name for the salmon of the sea is ouchachoumac, or ou-sha-shu-mak, although he adds, that the Indians even now apply this name to particularly dark-colored and extra large specimens of the ouananiche found in certain lakes. Even here, according to Chambers, while the Indian recognized the relationship to the salmon, his statement implies that the large fish were recognizable as ouananiche. There evidently is a distinction. The evidence is that the characters associated with the sea salmon by the Indians were those of size and color. The question then arises, what are the distinctions other than size and color which makes a large, and similarly colored ouananiche recognizable as such? It cannot be perennial habitat alone, for, while those fish occurring in waters inaccessible from the sea could be recognized by that fact, large fish in accessible water also appear to be at all times recognizable.

Some of the previously mentioned authors claim to have recognized the fish even when caught where salmon and grilse were present. Creighton claimed that his guide recognized it as distinct from the grilse, while native Labrador fishermen saw the difference but still recognized it as a salmon. Still it is claimed by some that there are no tangible structural characters by which they can be distinguished. It cannot be color alone, for Chambers stated that a fish from Labrador examined by him, was silvery and had the X-marks, which are characteristic of the salmon. There appears to be a dividing line or line of demarcation of some sort between the lake salmon and the sea salmon, which apparently enables one to say, 'This is a landlocked salmon' or 'That is a sea salmon.'

Of course the two forms are alike in family and generic characters. Several of the authors mentioned have indicated ways in which the two forms differ and no one has shown that those differences do not always exist. In other words so far as observations go, they are constant. According to the rules of taxonomy, as has been repeatedly said, constant differences are specific. No one has ever shown that they intergrade in these characters in which they differ, therefore they cannot be regarded as subspecies. The fact is, as will be seen later, in almost all structural characters, if a sufficient number of individuals are studied, there is scarcely any differential character in which they do not overlap. But such overlapping does not constitute intergradation, for it occurs in fish of different size or age. The differences, such as there are, are constant in fish of the same size, age and sex.

Of course it may be said that the reason that each form is always recognized as such is that if a lake salmon should look just like a sea salmon it would be pronounced a sea salmon and vice versa. Yet no one has ever claimed to have found in waters inaccessible to sea salmon and in which the sea salmon had not been introduced, any salmon that was not recognized as a lake salmon. Furthermore there are lake salmon waters in which sea salmon have been introduced but no salmon has subsequently been caught that was recognized as a sea salmon. For all that each structural character, by itself, is not always diagnostic and some lake salmon so closely resemble sea salmon that it might be difficult to identify a preserved specimen from some unknown locality. Or the locality in which the specimen was caught might admit of the fish being either lake or sea salmon. One such instance came to my attention and is referred to later. It was about the spawning time of both forms. The fish was caught in the outlet of a lake into which lake salmon had been introduced and sea salmon were known to ascend the same stream. Elsewhere Atkins is quoted as saying that the Sebago Lake salmon more closely resemble the sea salmon than did the Schoodic salmon. This remark implies that there was a recognized difference between the Sebago salmon and the sea salmon.

While there are a few single structural characters which will usually enable one to identify his fish, if he knows what those characters are, the real recognition character is the fish itself. The lake salmon embodies a different ensemble of proportions from that of the sea salmon. These proportions are variable in fish of different sizes, ages and sexes. In other words the general make-up of the lake salmon is different from that of the sea salmon. Correlated with that difference is the difference of habits, habitat, and physiology, and these are inseparable in each. These facts taken with other previously mentioned indicate that the landlocked or lake salmon, from egg to adult is always different from the Atlantic salmon, and has been different since it settled in the post-glacial lakes.

Synopsis of The Classification of The Lake Salmon: Technical, Fish Cultural, and Popular.

Fish literature in general pertaining to the Salmonidæ is replete with 'ouananiche,' 'landlocked salmon,' 'Schoodic salmon,' etc. Ichthyological literature designates them either binomially or trinomially, but mostly trinomially. The latter form of name indicates, as previously pointed out, that the fishes are subspecies, or as sometimes called, varieties, of the sea salmon, *Salmo salar*. Some claim that even as a subspecies or variety, the lake salmon is hardly definable; that there are no recognizable structural characters by which one may be distinguished from the other. The 'silfverlax' of Lake Wenern in Sweden has been variously regarded as a salmon and a trout. Popularly it seems that a silvery form of either was so named.

Malmgren (1863, p. 59–60) wrote that in Ladoga occurred a salmon which Dr. Widegren regarded as identical with the Wenern salmon although he did not distinguish it

from the sea salmon or from the trout, *Salmo salar lacustris* of Hardin or *S. lacustris* of Nilsson. With Widegren's conclusion Malmgren did not fully agree, saying in effect that the Ladoga salmon distinguished itself by a number of characters and biological traits, acquired by thousands of years residence in the lake. He therefore regarded it as a 'variety' of 'Trutta Salar,' as he designated the sea salmon (*Salmo salar*) and gave to the Ladoga form the name of '*Trutta relicta*.'

He stated that this fish could be recognized at sight, by its smaller size and different distribution of the black spots on the body; those of *salar* being few and usually situated above the lateral line, while those of *relicta* were rather numerous below the lateral line anteriorly above the pectoral fin, directly behind the gill cover.

In 1866, Günther (1866, p. 107–110) described a salmonid from Lake Wenern, which he supposed was the 'silfverlax,' as a trout and stoutly maintained that it was quite distinct from *Salmo salar*. But it appears, according to some authors, that his trout, which he names *Salmo hardinii* was not the Silfverlax form of the salmon but was really a trout.

Regan (1920, p. 27) refers to two 'fine specimens' of male and female 'Venern Salmon' in the British Museum, under the name of *Salmo salar hardinii*. They were said to be 24 inches long and together weighing 17 pounds; also a female 21 inches long. The fish are said to be deep and profusely spotted and to have 12 or 13 scales between the adipose fin and the lateral line but in other respects typical salmon. The number of scales between the adipose fin and the lateral line is that given by Günther for *Salmo hardinii* and the usual number for *Salmo trutta* or 'Sea trout,' and the species is quite likely correctly identified but probably it is not the 'silfverlax' form of the salmon.

Berg (1916) gives to the salmon of lakes Ladoga and Onega the name '*Salmo salar* L. *morpha relictus* (Malmgren),' and his synonomy of this form comprises:

'*Trutta salar* var. *relicta* Malmgren. Finlands Fisk Fauna, 1863, p. 59 (Ladoga lake, at Kekshalm).

'*Salmo relictus* Kessler [Fishes of St. Petersburg Province], 1864, p. 173 (Ladoga lake, Volkhov, Sias, Svir).

'*Salmo hardinii* Günther. Cat. Fish, vi, p. 107 (Venern L.).

'*Salmo salar* Kessler [Material towards a study of Onega L.] 1868, p. 65, (Onega lake and its tributaries). — Pirshkarev [Fisheries of Onega Lake] 1900, p. 36.'

He says that from Ladoga Lake it enters the rivers Volkhov, Sias, Svir (Paska, Ojat) and from Onega Lake it enters the Shua, Suna, Vodla, Povenchanka, and others.

Berg regards the salmon of Lake Venern and the lakes of Maine, New Brunswick, and Lake St. John of Quebec (*i.e.*, the ouananiche) as entirely analagous to this form.

The Maine fish which appears to have been earliest known to anglers, first to be described, and first to receive a technical name was the Sebago Lake form, to which Girard in 1853 (1854, p. 38) gave the name *Salmo sebago*.

However, the first use of the name *Salmo sebago* was by Henry Williams Herbert (Herbert 1849, p. ix, 18, 21, 22, 23 and 168) who gave it to a 'Sebago Trout' of which he had heard but never seen. In the light of present knowledge and that he was told

that it closely resembled *Salmo salar*, there can be no doubt but that the 'trout' for which the name was intended was the salmon of Sebago Lake.

Girard (1856, p. 85–86) later secured a young salmonid from the Union River, Maine, which he described and named, *Salmo gloverii*.

Concerning *Salmo sebago* Girard says (1854, p. 380): 'Its large scales and fusiform body would undoubtedly recall to mind the salmon, but on more close examination the general shape and outline are far more elegant than in the salmon, preserving altogether better proportions between the different regions of the body. The head forms about a fourth of the entire length, whilst in the salmon it is about the sixth only. The eyes are of medium size, and sub-circular in shape, their diameter being contained about seven times in the length of the head. The posterior half of the maxillary which is regularly and most decidedly curved downwards, gives to the shape of the mouth quite a peculiar aspect. The anterior margin of the dorsal fin is equidistant between the tip of the snout and the base of the caudal. The posterior margin of the latter is regularly crescent-shaped. The adipose is elongated, club-shaped, and situated opposite the posterior half of the anal. The ventrals are inserted under the middle of the dorsal, somewhat nearer the anal than the pectorals. The scales are remarkably large, contrasting greatly when compared to those of *S. erythrogaster*, *S. fontinalis*, and *S. namaycush*, or *amethystus*. There are about a hundred and fifteen of them in the lateral line.

'The color in the female is uniform silvery grey, darker on the back and head. Sub-quadrangular or subcircular black spots are observed upon the sides of the head, behind the eyes, along the back, and half of the flanks, also on the dorsal and caudal fins, to nearly their edge. In the male these same colors exist, but spread all over with a reddish tint, more intense on the flanks and beneath than upon the head, back, and dorsal and caudal fins [?], where the red is sometimes but faintly indicated. The name of *Salmo sebago* is proposed for this species which inhabits the southern part of the State of Maine.'

Girard's (1856, p. 85–86) description of *Salmo gloverii* goes into more detail than that of *Salmo sebago*. It is given here in full for several reasons, one of which is the fact that, by later writers, the name has been variously shifted back and forth from one synonymy to another. At one time it is regarded as synonymous with *Salmo sebago*, at another a synonym of *Salmo salar*, and this apparently quite arbitrarily without examination of the type or reference to the original description. Other reasons will become evident later on. The description is:

'The body of the male is subfusiform and rather slender, particularly in the caudal region; the head being regularly subconical and contained five times in the total length. The maxillaries are gently curved, extending backwards to about the posterior margin of the orbit. The female is stouter, with peduncle of the tail shorter; the head has the same general shape, but is not contained five times in the total length. The maxillaries are less curved, but extend as far backwards as in the male. The eye is very large, its diameter being contained nearly five times in the length of side of head. The caudal is deeply emarginated posteriorly, giving to it a more forked appearance than in either in

Salmo oquassa or *Salmo sebago*. The adipose fin, in the male, is situated opposite the anterior margin of the anal [?], whilst in the female it corresponds to the posterior margin of the same fin.

'The scales are well developed, being somewhat smaller, however, than in *Salmo sebago*, and considerably larger than in either *Salmo oquassa* or *Salmo erythrogaster*. On the dorsal and ventral regions they are considerably smaller than upon the sides and along the peduncle of the tail. They extend, diminishing in size, over nearly the half of the length of the middle rays of the caudal fin. The lateral line takes an almost straight course along the middle region of the flanks. The following is our approximate formula of the rays of the fins:

'D 2. 12. A 1. 9. C 8. I 8. 9. I 5. V 1. 9. P 14.

'There are two anterior rudimentary rays to the dorsal, one or two to the anal, one to the ventrals, eight or ten to the upper lobe of the caudal, to five or six to the inferior lobe.

'The upper surface of the head and dorsal region are blackish brown; the sides are silvery white, and the belly yellowish. The region above the lateral line is densely spread all over with black irregular spots, some of which are confluent; a few scattered ones may be seen beneath that line upon the middle of the abdomen. Four to six of these spots, well defined, are always observed on the operculum, one of which may occasionally reach the preoperculum. A few reddish orange dots, individually situated in the middle of a black spot, are occasionally observed along the middle and upper part of the flanks. Whether these dots are peculiar to the female, or proper to both sexes, I am not prepared to say, from want of sufficient information upon that point.

'This species was first brought to my notice by M. Townsend Glover, of Fishkill Landing, Dutchess county, New York, who caught it in the upper affluent of Union river in the State of Maine, during the middle of September. I propose the name of *Salmo gloverii* as a token of gratitude towards an artist whose labors, if promoted, would contribute so much to popularize natural history, and spread its benefits throughout the country.'

Suckley (1874, p. 143–144) in a paper written in 1861, pronounced Girard's *Salmo gloverii* the young of *Salmo sebago* and based his description of the latter species upon three specimens in the Smithsonian collection, one of which was *Salmo gloverii*.

After giving detailed descriptions of the three specimens Suckley went on to say: 'The young *S. sebago* may be distinguished from the young of any other salmon and trout on the Atlantic slope, by its strongly-marked black spots and coarse scales. The adult male in the collection was 19 inches long. The young of this fish was described as a distinct species, by Mr. Girard, in 1854, and named the *Salmo gloveri*. Upon comparing the types of both, their manifest identity is so apparent, that I have not the least hesitation in making *S. gloveri* a mere synonym of *Salmo sebago*, Grd. Three specimens of the species are in the Smithsonian collection — male, female, and young.'

The three specimens to which reference is made were doubtless those upon which Girard based his descriptions of *Salmo sebago* and *Salmo gloverii*.

The foregoing descriptions alone would be far from sufficient for identification of any eastern salmonid were it not for other known facts pertaining to them. It is quite clear that neither Girard nor Suckley recognized them as salmon. Although Girard remarked a similarity in size of scales and shape of *Salmo sebago* to a salmon, the statement that there were black spots on the tail would be confusing for there were then no eastern salmonid with black caudal spots. However, Suckley apparently corrects that statement in regard to *Salmo sebago* but indicates that there were black spots on the caudal fin of the 'young (*S. gloveri*).' Disregarding the alleged caudal spots, the black spots of the body, large scales, and their location sufficiently indicate a salmon rather than any other salmonid at that time occurring in eastern waters. Both Girard and Suckley regarded the fish as trout as indicated by the use of the term and their comparisons with other salmonids than salmon. The name *Salmo sebago* for a fish with black spots could signify nothing else than the 'landlocked' form of Sebago Lake.

Although Suckley pronounced *Salmo gloverii* the young of *Salmo sebago*, as previously remarked, from time to time in later years, *Salmo gloverii* has been regarded by one or another writer as a synonym of *Salmo salar*, even though recognizing *Salmo sebago* as a distinct species. But inasmuch as early as 1832, at least, history states that there were six mills on the Union River, doubtless with impossible dams, it may be safely concluded that no *Salmo salar* reached the upper waters of that river to breed in those days nor since. Lake salmon are known to have descended outlets to feed and to breed. Therefore it seems justifiable to regard the name *Salmo gloverii* as applying to the salmon of Reeds Pond (now Green Lake).

Jordan and Gilbert (1882, p. 312) regard the lake salmon as specifically identical with *Salmo salar*. Referring to its geographical distribution they say of *Salmo salar*, 'North Atlantic, ascending all suitable rivers in Northern Europe and the region north of Cape Cod; sometimes permanently landlocked in lakes, where its habits and coloration (but no tangible specific characters) change somewhat, when it becomes (in America) var. *sebago*.'

The latest comprehensive systematic ichthyological work is *Fishes of North and Middle America*, by Jordan and Evermann, the first part of which includes the Salmonidæ. It was published in 1896. In this work (Jordan and Evermann 1896, p. 487), after describing *Salmo salar*, the 'landlocked' forms are noticed as follows: 'Represented in lakes of Maine, New Hampshire, and New Brunswick by landlocked *Salmo salar sebago* (Girard) (Landlocked Salmon), smaller in size, rather more plump in form, and nonmigratory, not otherwise evidently different. Sebago Pond and northward, introduced into lakes in various parts of the country; seldom entering streams; reaches a weight of 25 pounds.

'Represented in Lake St. John, Saguenay River and neighboring waters of Quebec by the landlocked.

'*Salmo salar ouananische*, McCarthy, M.S. new subspecies (Ouananiche; Winninish).

'Still smaller, rarely reaching a weight of 7½ pounds and averaging 3½. An extremely vigorous and active fish, smaller and more active than ordinary salmon, but so far as

known not structurally different. Saguenay River, Canada (outlet of Lake St. John), and neighboring waters.'

Six years later (1902) the same authors published a popular work on American food and game fishes. In this the New England lake salmon is referred to as '*Salmo sebago* Girard,' and its characters are stated as follows (Jordan and Evermann 1902, p. 168-169): 'As a rule it differs from the sea salmon in the smaller size, rather plumper form, much harder skull-bones, larger scales and different colouration.'

Strange to say, notwithstanding the fact that for years ichthyologists and anglers alike regarded the Grand Lake Stream fish as specifically identical with the Sebago form, the name *Salmo sebago* was not used for it for a long time, but instead *Salmo gloveri* was adopted. Later, having assumed that the lake salmon was practically identical with the anadromous form of the sea, 'differing only in size and color' from *Salmo salar*, the accepted name for the lake form was attached to *Salmo salar* thus making it a trinomial designation indicating that the fish is a subspecies of *Salmo salar*. Thus the name came to be *Salmo salar sebago*.

Having caught a fish strange to him, it is the desire of the angler to know what to call it. But in the case of the fish under discussion, he has not had much help from the systematist. At one time one authority has told him one thing, at another time another authority has told him something else, and again, one or the other authority has sometimes reversed his opinion, perhaps more than once. However, it is perfectly proper for one to change his mind, if for good and sufficient reasons. If no one ever changed his mind there would be no progress, even in systematic ichthyology. The name does not make the species or subspecies except taxonomically, and this may be a matter of individual opinion. Whatever it is called, the fish remains the same, and whatever number of times its name is changed does not affect its status in its own little cosmorama. The ichthyologist may change his mind as many times as there are herring in the sea, but the fish will not change accordingly. So, when one person arbitrarily says the ouananiche and landlocked salmon of Maine are specifically identical with the sea salmon, citing eminent authorities in support of that statement, and ridicules some other one who claims the ouananiche is distinct from the landlocked salmon of Maine and the sea salmon, both of the subjects of discussion or dispute maintain their respective integrity. Citing authorities and counting fin rays do not settle the question.

The stated desire of the systematist is a stable classification as nearly in accordance with nature as it is possible to make it. To this end from time to time certain rules of nomenclature have been established. But the rules have not always been strictly observed, and even today we find the same author in one publication giving a fish a binomial designation and in another publication designating it trinomially without stating any reason for the change. This is clearly not uniformity, and certainly does not make for stability in nomenclature.

As has previously been remarked, there are other differential characters than those of the conspicuous external structures which should be recognized, although the systematist attaches little importance to them. They may be far more significant of specific

distinction than the characters usually mentioned in diagnosis. To the acclimatist and fish culturalist their recognition is of vital importance, for which reason, when such differences exist they should be recognized taxonomically.

Comparison of Percentile Proportions of Lake Salmon and Atlantic Salmon.

Smitt (1895, p. 830) says that the variability of form within the genus *Salmo* has hitherto rendered it impossible to define with certainty the numerous species that have been adopted. But referring to this variability he again pertinently remarks: 'Still, both from a scientific and economic point of view it is of importance to know the conditions that involve the said inconstancy; and to this end it has been necessary to denote by special names the more or less constant forms that appear under different circumstances and different localities.'

The question as to what constitutes a species has already been discussed at some length. It was suggested that there are two sorts of species. These 'more or less constant forms' which Smitt found desirable to designate by 'special names' constitute one of these two sorts of species. They are the taxonomic species, *i. e.*, forms which in structure conform to certain accepted codes or rules of zoölogical nomenclature. Taxonomic species are not always stable nor immutable, they depend upon the point of view of the taxonomist as Smitt intimated. The other sort of species I designate as natural species. They may or may not constantly differ in visible structure. They may or may not also be recognized as taxonomic species. The greater number of individuals observed the less likely are they to be regarded as distinct taxonomic species, especially if constant or fixed characters are looked for. The variations of proportions complicate the problem of finding in them any distinguishing specific or racial character of taxonomic value.

Certain variations of structure and dimension are regular changes involved in growth. Others are sexual or incident to reproductive development, etc. They are inherent in each and every species.

Some structures and dimensions vary more than others. Salmon of the same age and sex may differ considerably in their proportions even in the same season. For example, of two fish of the same age, caught in the same place and at the same time, one may have spawned in the preceding season and thus have undergone modifications of proportions incident to the breeding season; while the other may never have spawned. At the same time, however, each fish possesses characters which either do not change or else show very little modification. Again the modified proportions exhibited in the breeding season have been acquired by gradual change through the feeding season immediately preceding it. Therefore, through the summer and early fall, salmon which are to spawn that fall may show a wider range of variations than those which are not going to spawn that season. The changes of proportions which accompany the development of the breeding condition are most pronounced in the male, particularly as pertains to the head. One of these is the lengthening of the muzzle, which involves the snout and lower jaw, by actual proliferation of tissue. The proportion of the length of the head to the

length of the fish is increased, but it is a seasonal increase which subsequently may be more or less reduced.

During the growth of the fish certain proportions are increased in *direct* ratio to its length, until they are modified by other factors. Certain other proportions are reduced in *indirect* ratio to the length of the fish, up to a point when they, too, are subjected to modifications. Still other proportions change very little or not at all from parr to adult. Some parts of the fish grow faster than other parts, with consequent increase and decrease in relative proportions. Those structures which develop *pari passu* with the increase in length of the fish retain their relative proportions unchanged.

It seems reasonable to believe that forms which differ in the way that some of the variations are constantly manifested, also differ physiologically. Such differences are phylogenetic and constitute what are here regarded as 'Natural Species' which are often confused with the taxonomic subspecies.

Most of the characters employed by ichthyologists in the classification of salmonids pertain to external countable and measurable structures and dimensions. Occasionally certain internal structures are considered. The external countable structures usually receiving attention comprise fin rays, gill rays (branchiostegals), and series of scales. The internal structures most commonly noticed are the numbers of gill rakers, vertebræ, and pyloric coeca.

While these characters vary to some extent they do not change with the growth of the fish or under other conditions before mentioned. For this reason they have been regarded as some of the most dependable of structural characters and almost always have been used in descriptions.

Measurable characters comprise certain dimensions in relation to each other. These are the characters which give the fish its shape. Some ichthyologists indicate the relation of one dimension to another by stating the number of times the one structure (meaning its dimension) is contained in another. For example, the head is said to be contained so many times in the length of the fish; or, the eye, so many times in the head. Others employ percentile proportions, to indicate this relationship of structures. Thus instead of saying that the head is contained 4 times in the body, it is stated that the length of the head is 25 per cent of the length of the body.

This is the method used in tables 21 and 22, which respectively compare the percentile proportions of non-breeding and breeding salmon. While the number of individuals entering into the comparison are too few and the range of sizes too limited to afford positive conclusions, they serve to indicate, in a measure, the trend of variations; whether they are wide or narrow, and approximately what structures and dimensions vary the most.

The tables show the averages of 25 percentile proportions (fig. 1) arranged in ascending scale according to the average total lengths of eight groups each containing a few individuals of both sexes. The averages of percentile proportions should indicate in a measure, to what factor,— whether age, size, sex, or breeding condition,— these variations are attributable, even though the number of fish in each group is small. In

computing the percentile proportions and their averages, fractions were carried out to two decimal places, then reduced to whole numbers by regarding fractions of 0.5 per cent and up as one per cent and disregarding all fractions below 0.5 per cent. The percentile proportions do not include all that might have been made, but they comprise most of those used in technical descriptions. Three ratios were employed: (1) to length of head, comprising seven dimensions pertaining to the head; (2) to standard length, including 16 proportions, which include the head, fins, and body dimensions; (3) to the length of caudal peduncle, *i.e.*, its least depth to the distances from the adipose fin and anal fin to upper and lower base of the caudal fin, respectively. The percentages of the first and third sets of ratios are naturally higher than those of the others.

The greatest variation is exhibited by those structures and dimensions which undergo the most change incident to growth and the breeding conditions, for the proportions vary according to the changes. Therefore a percentile proportion of one variable to another signifies very little *per se* beyond the fact that the indicated proportion obtains in that particular instance. A difference found by comparison of such a percentile proportion of one individual with that of the same structure in another individual does not necessarily signify that the structure or dimension actually differs in size or extent which a difference in percentile, proportions seems to indicate. For example: given two salmon in which the percentile proportions of the length of the eyes to the length of the head differ by a certain per cent, the difference does not necessarily mean that the eye of one is larger than the other. The eyes may be exactly the same size and still differ in that ratio to the length of the head, due to the fact that the head of one is longer than that of the other. The way percentile proportions vary may be illustrated as follows:

Nall (1930, p. 303) indicates that the maxillary of the salmon increases its proportional length gradually. He says that in a salmon 4 inches long, the maxillary extends back to the middle of the pupil; at 6 inches, it extends to the posterior edge of the pupil; at 2 or 3 pounds, it extends back to the posterior edge of the eye; in larger fish, it extends slightly beyond the posterior edge of the eye. This is a definite comparison of extent in relation to a fixed point. But if the length of the maxillary is considered relatively to the length of the head the percentile proportion may remain the same for the several sizes of fish. Or it may progressively increase in proportion by actual increase of length of the maxillary, the relative length of the head remaining the same. Again the percentile proportion would be greatly increased by growth of the maxillary and a proportional shortening of the head. Or, still again, if, as in the breeding season, the head is considerably increased in length, the percentile proportion of the maxillary would be reduced. Thus the percentile proportions are relative.

The averages of percentile proportions in tables 21 and 22 are of this nature. The increase of one may be reflected in the decrease or even an unchanged proportion of another. Therefore in determining the relative proportions of dimensions, the ratios should be of those dimensions which are modified the least under conditions of growth, sex, and breeding condition, or else of a large number of fish of the same age, sex, season, and breeding condition. The first alternative is out of the question, for it is yet to be

learned what dimensions, if any, do not change their proportions under the aforesaid conditions. The second alternative is impracticable in the present situation since so few specimens have been available and those have lacked uniformity of size and condition. The best that could be done with the material in hand has been to assemble the measurements in groups in such a way as to, as nearly as possible, represent classes of each sex in a number of stages of growth, from parrs to adult breeding salmon.

In tables 21 and 22, the salmon are represented by 78 lake salmon from the Presumpscot River, Grand Lake, and Sebago Lake, Maine, and 65 Atlantic salmon.

It is unfortunate that the purity of the Sebago stock is not positive. Many young Atlantic salmon have been introduced from time to time but the result of the introductions is unknown. It is also possible that some of the Presumpscot fish were affected by sea salmon adulteration. However, the Grand Lake salmon can be depended upon for they were all taken before introduction of sea salmon in those waters. But the Grand Lake fish were all taken in the breeding season, therefore, unfortunately, no summer fish are represented. In table 21 eight length classes are denoted as 1a, 2b, 3c, 4d, 5e, 6f, 7g, and 8h, which represent the average lengths of fish not in the breeding season: 1a, male, Atlantic salmon in parr stage, 214 millimeters (8.4 in.); 2b, Presumpscot male 324 millimeters (12.8 in.); 3c, Presumpscot female 337 millimeters (13.2 in.); 4d, Atlantic salmon male 353 millimeters (13.9 in.); 5e, Atlantic salmon female 413 millimeters (16.3 in.); 6f, Sebago Lake female 416 millimeters (16.5 in.); 7g Atlantic salmon male 533 millimeters (21.0 in.); 8h, Sebago Lake male 556 millimeters (21.9 in.).

While the average proportions of classes of the same length and sex of lake and Atlantic salmon may differ, those of the same sex of different lengths may be alike. In other words there are but few averages of percentile proportions of any length class of the one, which may not be found in a different length class of the other. Again classes of the same length may differ in some proportions and not in others. It is not so much the amount of difference in proportions as it is the way they differ that is the most significant.

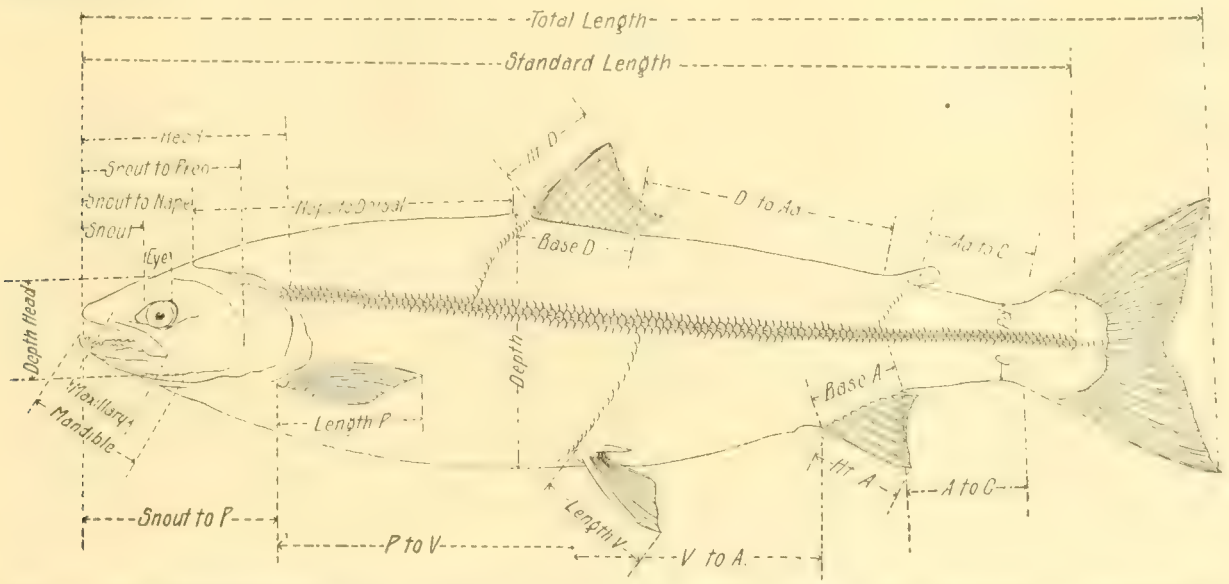

Fig. 1. Key drawing explanatory of proportional and comparative measurements used in discussion of variability and percentile proportions of lake and Atlantic salmons.

TABLE 21.

Comparison of Averages of Percentile Proportions of Atlantic and Lake Salmons Exclusive of Fish in the Breeding Season.

Dimensions	Sex	1a ♂ S. salar	2b ♂ S. sebago	3c ♀ S. sebago	4d ♂ S. salar	5e ♀ S. salar	6f ♀ S. sebago	7g ♂ S. salar	8h ♂ S. sebago
	in.	8.4	12.8	13.2	13.9	16.3	16.5	21.0	21.9
	mm.	214	324	337	353	413	416	535	556
	M.	76	—		75			77	75
Snout to Preo.	F.			77?		75	78		
	M.	48	—					46	
Depth Head	F.			—		54	—		—
	M.	31	35		32			35	33
Interorbital	F.			36		32	34		
	M.	22	17		18			14	13
Eye	F.			18		14	16		
	M.	30	31		32			35	34
Snout	F.			30		32	30		
	M.	35	36		35			35	38
Maxillary	F.			35		34	37		
	M.	53	55		48			55	60
Mandible	F.			56		53	58		
	M.	15	14		14			13	13
Base D.	F.			13		13	14		
	M.	10	10		9			9	9
Base A.	F.			10		9	9		
	M.	15	14		14			11	13
Height D.	F.			13?		12	12		
	M.	13	12		10			9	11
Height A.	F.			11		10	10		
	M.	19	17		16			13	15
Length P.	F.			17		15	15		
	M.	14	12		12			11	12
Length V.	F.			12		11	12		
	M.	25	24		23			20	24
Head	F.			23		21	22		
	M.	17	16		16			14	16
Snout to Nape	F.			15		14	15		

TABLE 21—Continued.

Comparison of Averages of Percentile Proportions of Atlantic and Lake Salmons Exclusive of Fish in the Breeding Season.

Dimensions	Sex	1a ♂ S. salar	2b ♂ S. sebago	3c ♀ S. sebago	4d ♂ S. salar	5e ♀ S. salar	6f ♀ S. sebago	7g ♂ S. salar	8h ♂ S. sebago
	in.	8.4	12.8	13.2	13.9	16.3	16.5	21.0	21.9
	mm.	214	324	337	353	413	416	535	556
	M.	29	29		30			30	29
Nape to D.	F.			30		30	29		
	M.	24	23		26			27	23
D. to Ad.	F.			24		27	25		
	M.	10	9		11			11	10
Ad. to C.	F.			9		12	11		
	M.	23	—		21			19	21
Snout to P.	F.			19		21	22		
	M.	34	31		32			34	33
P. to V.	F.			32		29	21		
	M.	22	22		23			24	22
V. to A.	F.			22		24	22		
	M.	12	11		13			13	11
A. to C.	F.			11		13	12		
	M.	9	9		8			7	8
Cpd.	F.			9		8	8		
	M.	89	94		73			67	87
Cpd.: Ad. to C.	F.			94		65	74		
	M.	76	79		61			56	80
Cpd.: A. to C.	F.			77		54	68		

Likewise the eight length-classes in table 22, which includes fish in the breeding season, are designated as 1 Pr. *M*, 2 Pr. *F*, 3 G. L. *M*, 4 S. L. *F*., 5 G. L. *F*., 6 S. L. *M*., 7 Pt. *M* and 8 Pt. *F*., whereby Pr. signified Presumpscot River, G. L., Grand Lake, S. L., Sebago Lake and Pt., Penobscot River. The *M*. and *F*. denote male and female respectively.

The length classes represented are (1), 37.3 millimeters (14.7 in.); (2), 377 millimeters (14.8 in.); (3) 448 millimeters (17.6 in.); (4), 481 millimeters (18.9 in.); (5), 490.7 millimeters (19.3 in.); (6), 648 millimeters (25.5 in.); (7), 721 millimeters (28.4 in.); (8) 728.8 millimeters (28.6 in.).

TABLE 22.

Comparison of Averages of Percentile Proportions of Atlantic and Lake Salmon of the Breeding Season.

Dimensions	Sex	1 Pr. ♂	2 Pr. ♀	3 G.L. ♂	4 S.L. ♀	5 G.L. ♀	6 S.L. ♂	7 Pt. ♂	8 Pt. ♀
	in.	14.7	14.8	17.6	18.9	19.3	25.5	28.5	28.6
	mm.	373	377	448	481	491	648	721	729
	M.	82		—			80	79	
Snout to preo.	F.		—		77	—			76
	M.			46			—	51	
Depth of head	F.		—		—	49	—	—	46
	M.	34		33			34	35	
Interorbital	F.		34		34	34			36
	M.	14		13			11	10	
Eye	F.		17		14	15			11
	M.	31		37			43	40	
Snout	F.		29		34	34			34
	M.	36		36			36	37	
Maxillary	F.		36		36	37			34
	M.	59		62			67	63	
Mandible	F.		56		56	58			56
	M.	13		14			13	13	
Base D.	F.		14		14	14			13
	M.	9		10			9	9	
Base A.	F.		8		10	10			9
	M.	15		14			?	13	
Height D.	F.		13		11	13			12
	M.	12		12			12	12	
Height A.	F.		11		10	11			11
	M.	15		17			16	15	
Length P.	F.		15		14	16			14
	M.	13		14			13	13	
Length V.	F.		12		12	13			12
	M.	25		27			28	24	
Head	F.		22		23	23			21
	M.	16		18			19	17	
Snout to Nape	F.		14		16	15			14

TABLE 22—Continued.

Comparison of Averages of Percentile Proportions of Atlantic and Lake Salmon of the Breeding Season.

Dimensions	Sex	1 Pr. ♂	2 Pr. ♀	3 G.L. ♂	4 S.L. ♀	5 G.L. ♀	6 S.L. ♂	7 Pt. ♂	8 Pt. ♀
	in.	14.7	14.8	17.6	18.9	19.3	25.5	28.5	28.6
	mm.	373	377	448	481	491	648	721	729
D. to Ad.	M.	22		23			23	25	
	F.		24		24	24			26
Ad. to C.	M.	9		10			10	10	
	F.		9		11	10			11
Snout to P.	M.	—		—			25	22	
	F.		—		21	—			22
P. to V.	M.	32		32			32	34	
	F.		32		32	32			33
V. to A.	M.	22		23			21	24	
	F.		22		23	23			24
A. to C.	M.	11		10			10	11	
	F.		11		12	11			12
Cpd.	M.	9		9			8	8	
	F.		9		9	9			8
Cpd.: Ad. to C.	M.	103		93			83	73	
	F.		99		81	96			69
Cpd.: A. to C.	M.	82		85			82	66	
	F.		83		76	84			66

The object of the tables is to show any variations possibly differentiating lake salmon from the Atlantic salmon. The averages of percentile proportions were derived from a basic table of percentile proportions of individual fish. The ranges of total lengths and percentile proportions represented by the averages in these tables overlap more or less.

Referring to table 21 it is found that the percentile proportions of lake and Atlantic salmon of practically the same average length are divisible into three groups, *i.e.*, (1) those proportions of the lake salmon which are higher than those of the Atlantic salmon; (2) those of the lake salmon which are lower than those of the Atlantic salmon; and (3) those in which the proportions are equal. For example, in female lake salmon of the average length of 16.5 inches (Class 6f) and female Atlantic salmon of 16.3 in. (Class 5e), it is found that the lake salmon differs from the Atlantic salmon in the following proportions:

Lake salmon are higher in: snout to preo. (3%), interorbital (2%), eye (2%), maxillary (3%), mandible (4%), base D. (1%), head (1%), snout to nape (1%), nape to D. (1%), snout to P. (1%), P. to V. (2%), Cpd.: Ad. to C. (5%), Cpd.: A. to C. (26%). In the last two proportions of this table the lake salmon are higher than any Atlantic salmon.

Lake salmon are lower in: snout (2%), D. to Ad. (2%), V. to A. (2%), A. to C. (1%).

The two are equal in: Base A., height D., height A., length P., length V., Ad. to C., Cpd.

Table 21 includes no average lengths of lake salmon as great as the smallest average length of the breeding Penobscot salmon. In table 22, the average of lake salmon of highest length class is 25.5 inches and the lowest of the Atlantic salmon is 28.3 inches. Comparison of the averages of percentile proportions show that they are divisible into three groups: (1) those in which the lake salmon exceeds the Atlantic salmon; (2) those in which the Atlantic salmon exceeds the lake salmon; and (3) those in which the lake salmon and Atlantic salmon are equal. The lake salmon group comprises Sebago Lake fish and the Atlantic salmon the Penobscot fish. Lake salmon are higher in: snout to preo. (1%), eye (1%), snout (0.7%), mandible (4%), length P. (1%), head (4%), snout to nape (2%), snout to P. (3%), Cpd.: Ad. to C. (10%), Cpd: A. to C. (16%).

Lake salmon are lower in: Interorbital (1%), maxillary (1%), D. to Ad. (2%), P. to V. (2%), V. to A. (3%), A. to C. (1%), Cpd. (1%).

The two are equal in: Base D., base A., height A., length V., nape to D., Ad. to C.

The averages of the proportions of two female breeding salmon may be classified in the same way. They are female Grand Lake salmon averaging 18.9 inches in length and female Penobscot salmon 28.6 inches in length. Lake salmon are higher in: snout to preo. (1%), depth head (3%), eye (4%), maxillary (2%), base D. (1%), base A. (1%), head (2%), snout to nape (2%), Cpd. (1%), Cpd: Ad. to C. (12%), Cpd. A. to C. (10%).

Lake salmon are lower in: Interorbital (1%), height D. (1%), height A. (1%), nape to D. (2%), D. to Ad. (2%), snout to P. (1%), P. to V. (1%), V. to A. (1%).

The two are equal in: snout, mandible, length P., length V., Ad. to C., A. to C.

Of the proportions in which the lake salmon exceeds the Atlantic salmon there are six which are common to the three length-groups; they are: snout to preo., eye, head, snout to nape, Cpd.: Ad. to C., and Cpd.: A. to C.

Of the proportions in which the Atlantic salmon exceed the lake salmon, there are only two which are common to the three comparisons, *i.e.*, D. to Ad. and V. to A.

Of those proportions in which the lake salmon and Atlantic salmon are equal, only those of the length V. and Ad. to C. are common to the three comparisons.

A comparison of all these percentile proportions reveals that certain widely different length-classes of lake salmon and Atlantic salmon are alike in some of their percentile proportions. Thus certain length-classes of lake salmon are equal to one length-class only of breeding Atlantic salmon, and in this relation the sexes are sometimes alike and sometimes opposite.

Again the proportions of some length-classes of lake salmon are the same as those of the parr stages of Atlantic salmon. Then again proportions of length classes of lake salmon correspond to no proportion of the Atlantic salmon. When, as is to be seen, the proportion of length classes of lake salmon are exactly the same as that of the breeding Atlantic salmon and the parr also, the fact is probably attributable to the modification of dimension which has taken place incident to the development of the breeding condition of the Atlantic salmon, which raises or reduces, as the case may be the proportion to the level of the parr. In some such instances it is probable that proportion of the lake salmon is to be considered with only one or the other of the stages of Atlantic salmon, *i.e.*, either with the parr or breeding fish; most likely it is with parr.

Some of the relations of length classes, as indicated by the averages, are shown in a different way and by different length-classes of lake salmon of the three locality groups. This fact points to possible differences among them as well as between the lake salmon and Atlantic salmon. These variations of relationship of the proportions as shown by the different length classes of lake and Atlantic salmon in tables 21-22, and of a few other length-classes of Atlantic salmon not included in the tables, are as follows:

Interorbital. — Only breeding lake salmon are not represented in the averages of proportions of the length classes of Atlantic salmon. All of the breeding lake salmon, excepting the 17.6-inch Grand Lake male, have the same proportion, which is intermediate between the proportions of the smaller and larger Atlantic salmon. Thus the breeding lake salmon have lower average proportions for the interorbital than in the breeding Atlantic salmon. On the other hand the smaller length-classes of non-breeding lake salmon have higher averages than the smaller length-classes of Atlantic salmon. In general, then, regardless of sex the average of proportions of interorbital in the lake salmon decrease from the smaller to the larger length-classes, while in the Atlantic salmon they increase. This fact indicates different trends of changes of proportions in the lake salmon and Atlantic salmon.

Eye. — Again it is only by the breeding lake salmon that the Atlantic salmon lacks representation. The proportions of the eye in both lake and Atlantic salmon decrease with increase in length of the fish. All of the proportions of the lake salmon fall within the range of the proportions of the Atlantic salmon. The only difference is that in the lake salmon the average is somewhat higher than in the Atlantic salmon. The females show a greater difference in this respect than do the Atlantic salmon. The 13.2-inch female Presumpscot salmon has exactly the same proportion as the 13.9-inch male Atlantic salmon.

Snout. — Only certain length classes of the Presumpscot and Sebago salmon are not represented in the proportions of the Atlantic salmon and these are not restricted to breeding fish. The proportions of the lake salmon are lower than those of the Atlantic salmon excepting that the 25.5-inch breeding male Sebago fish is three per cent higher than that of the 28.3-inch breeding male Atlantic salmon. The proportions of both male and female Atlantic salmon increase from the smaller to the larger length-classes as do those of the male lake salmon, but the female lake salmon are irregular in that respect.

The 13.2-inch Presumpscot female and the 16.5-inch Sebago female are equal to the

8.4-inch male parr only. The Grand Lake 17.6-inch breeding male equals the 24.8-inch non-breeding female of the Atlantic salmon. The 18.9-inch breeding female Sebago salmon, the 19.3-inch breeding female Grand Lake fish, and 21.9-inch non-breeding male Sebago salmon, equal the 20.3-inch non-breeding and the 28.6-inch breeding females of the Atlantic salmon. The 16.5-inch Sebago female is 2 per cent lower than the 16.3-inch Atlantic female. These proportions for the snout indicate only that the lake salmon, particularly the Presumpscot fish, average somewhat lower than the Atlantic salmon.

Maxillary. — Only the 21.9-inch non-breeding male Sebago salmon is not represented in the proportions of the Atlantic salmon. This average may be distrusted since all the proportions of male lake salmon are alike. However, there are two length-classes of female lake salmon with proportions of only one per cent lower, which equal the proportion of only one length-class of Atlantic salmon, *i.e.*, the 16.5-inch non-breeding Sebago female and the 19.3-inch breeding female of Grand Lake which equal the 28.3-inch breeding male Atlantic salmon.

The proportions of the maxillary of the male Atlantic salmon increases from the parr to the breeding male, which exceeds the male and female parr (which are alike) by three per cent. The proportions of the maxillary of the female Atlantic salmon remain the same from the 6.5-inch Atlantic parr up to, and including the 28.6 inch breeding female of the Atlantic salmon. The 29.3-inch non-breeding female is two per cent higher than the others.

The proportions of the maxillary of the male lake salmon are unchanged from the 12.8-inch Presumpscot male (which is two per cent higher than the 6.5-inch Atlantic parr) up to, and including the 25.5-inch Sebago breeding male, excepting that of the 21.9-inch non-breeding Sebago male above mentioned. The proportion of the latter is higher than any other either of lake or Atlantic salmon. The percentile proportions of the maxillary of the lake salmon average higher than those of the Atlantic salmon in both sexes, even disregarding the 21.9-inch male. The proportional length of the maxillary, then, may be regarded as a distinctive character, at least as far as the present averages indicate.

Mandible. — The proportions of the mandible in the Grand Lake 17.6-inch breeding male, the 16.5-inch and 21.9-inch non-breeding females, and the 25.5-inch breeding Sebago male equal none of the proportions of the Atlantic salmon. But the 13.2-inch non-breeding and the 14.8-inch breeding Presumpscot females, as well as the 18.9-inch breeding Sebago female have the same proportion as the 28.6-inch breeding female Atlantic salmon. The proportion of the 17.6-inch Grand Lake male is one per cent lower than that of the 28.3-inch breeding Atlantic male. The 25.5-inch Sebago breeding male exceeds all the other length-classes of Atlantic or lake salmon, being four per cent higher than the 28.3-inch breeding male Atlantic salmon in this proportion. The proportions of both males and females of Atlantic salmon increase regularly with the increase in length of the fish, but the lake salmon are irregular in this respect. The largest length-class of each sex has a higher proportion than the smallest length-class of each.

Both male and female lake salmon have higher proportions of the mandible than do the Atlantic salmon. The proportion of the mandible of the 12.8-inch male Presumpscot salmon is seven per cent higher than that of the 13.9-inch Atlantic male and that of the 16.5-inch Sebago female is five per cent higher than that of the 16.3-inch Atlantic female.

Base D. — In the proportions for base of dorsal there is very little range in either the lake or Atlantic salmon, but that of the latter is a little greater. While this dimension is not strictly in the categories under discussion since there is only one length class of Atlantic salmon which would exclude a number of length classes of lake salmon from equalling parr only, it is here included.

The single-length class of Atlantic salmon which, in this proportion equals the parr is the 13.9-inch male, which is the highest of the Atlantic salmon excepting the parrs. In the lake salmon there are five length-classes which equal the 6.5-inch male and female parrs. These are the 12.8-inch Presumpscot male, the 17.6-inch Grand Lake male, the 16.5-inch and 18.9-inch Sebago females and the 19.3-inch Grand Lake female. The lake salmon thus averages slightly higher than the Atlantic salmon in this proportion.

Base A. — The ranges of proportions for this dimension are very restricted but that of the lake salmon is a little greater than that of the Atlantic salmon. However, there is a difference shown in that seven of the eight length-classes of Atlantic salmon have the proportions of the base of anal equal to that of the 6.5-inch female parr, while four of ten length-classes have the same proportion and four others are equal to the 6.5-inch and 8.4-inch male parrs only. Yet these proportions seem to have no connection with size, sex or breeding condition of the fish.

Height D. — The proportions for height of dorsal, except for one length-class of lake salmon, are like those of the Atlantic salmon. By them there is nothing shown to distinguish the lake salmon as a whole from the Atlantic salmon. The single exception is that of the Grand Lake breeding male, the proportion of which equals the 8.4-inch male parr only.

Height A. — The ranges of proportions of height of anal are essentially the same in both lake and Atlantic salmon. But the same proportions are somewhat differently distributed in the lake salmon than in the Atlantic length classes. The 12.8-inch non-breeding Presumpscot male, the 14.7–inch Presumpscot breeding male, the 17.6-inch Grand Lake breeding male, and the 25.5-inch breeding Sebago male have the same proportion as the 28.3-inch breeding Atlantic male and the 6.5-inch male parr. Inasmuch as the proportion for the breeding Atlantic male appears to have been increased over immediately lower length-classes incidentally to development of breeding condition, it would seem that the relationship of the above listed lake salmon is properly with the parr of the Atlantic salmon.

Length P. — The 12.8-inch non-breeding male and the 13.2-inch non-breeding female of the Presumpscot have the highest proportion of the lake salmon and higher than any of the Atlantic salmon. The 14.8-inch breeding Presumpscot female and the 18.9-inch breeding Sebago female have the lowest proportion of the lake salmon and lower than any of the Atlantic salmon.

Length V. — The proportion of length of ventral of the 17.6-inch Grand Lake breeding male is higher than that of any length-class of lake salmon or Atlantic salmon other than the parr. It corresponds to the 6.5-inch female and the 6.4-inch male. The proportions of the 14.7-inch breeding Presumpscot male, the 25.5-inch Sebago male, and the 19.3-inch Grand Lake female are equal to that of the 28.3-inch breeding male Atlantic salmon, which is the highest of the Atlantic salmon length-classes excepting those of the parrs. In this proportion the lake salmon average somewhat higher than do the Atlantic salmon which apparently is the only difference.

Head. — The proportions of the head of the Presumpscot 12.8-inch non-breeding male, the 21.9-inch non-breeding Sebago male equal only that of the 28.3-inch breeding Atlantic male, which is highest of the Atlantic salmon length-classes. The proportion of the 14.7-inch Presumpscot male equals that of the parrs, the three of which are alike. The proportion of the 17.6-inch breeding male of Grand Lake is three per cent higher and of the Sebago 25.5-inch breeding male is four per cent higher than that of the breeding male Atlantic salmon, which is the highest of all the length classes.

Snout to Nape. — The proportion of snout to nape in the length classes of the 17.6-inch Grand Lake male and the 25.5-inch Sebago male are equalled by no size-class of Atlantic salmon, the Sebago fish being higher by two per cent than that of the 28.3-inch breeding male Atlantic salmon. The proportions of the 13.2-inch Presumpscot female, the 16.5-inch Sebago female, and the 19.3-inch Grand Lake female are alike and not represented in the Atlantic salmon. The proportion for the 16.5-inch Sebago female is one per cent higher than the 16.3-inch Atlantic female.

Nape to D. — The proportions for the 12.8-inch Presumpscot non-breeding male, the 17.6-inch breeding Grand Lake male, the 21.9-inch non-breeding Sebago male, the 25.5-inch Sebago breeding male, and the 18.9-inch breeding female of Sebago are all equal to the proportion for the 28.3-inch male Atlantic salmon, which is the highest for the Atlantic salmon, excepting that for the 6.5-inch and 8.4-inch male parrs, and which are the same and of course equalled also by the above mentioned lake salmon proportions.

D. to Ad. — In the proportion for this dimension there appears to be a distinct difference between lake salmon and Atlantic salmon, for only one length-class of each has a corresponding proportion, *i.e.*, the 16.5-inch non-breeding female equals the 28.3-inch breeding male Atlantic salmon, which is the lowest for the Atlantic salmon, but is higher than all the other length-classes of lake salmon. The proportions for the 16.5-inch female lake salmon is lower than that for the 16.3-inch female Atlantic salmon by two per cent. The 12.8-inch Presumpscot male equals the 6.5-inch male parr. The 13.2-inch Presumpscot female and the 14.8-inch breeding Presumpscot female equal the 6.5-inch female and the 8.4-inch male parr. The 17.6-inch breeding Grand Lake male equals the 6.5-inch male parr. The 19.3-inch Grand Lake breeding female equals the 6.5-inch female and 8.9-inch male parr. The 21.9-inch Sebago male equals the 6.5-inch male parr. The 18.9-inch breeding Sebago female equals the 6.5-inch female and the 8.4-inch male parr. The 25.5-inch breeding Sebago male equals the 6.5-inch male parr.

Ad. to C. — The proportion for the 12.8-inch Presumpscot male and the 13.2-inch female, the 14.7-inch breeding Presumpscot male and 14.8-inch breeding female have the lowest proportions of the lake salmon length-classes and lower than any of the Atlantic salmon. The 17.6-inch breeding Grand Lake male, the 25.5-inch breeding Sebago male, the 21.9-inch non-breeding Sebago male, and the 19.3-inch breeding Grand Lake female are all equal to the 28.3-inch breeding Atlantic male and the male 8.4-inch parr. The proportion for these is the lowest among the lake salmon. In their proportions, the remaining two, the 18.9-inch Sebago breeding female and the 16.5-inch non-breeding female are like six of the remaining length-classes of Atlantic salmon as well as the 6.5-inch male and female parrs.

Snout to P. — Only the Sebago 25.5-inch breeding male equals no length-class of Atlantic salmon in this proportion. It exceeds the highest of the Atlantic salmon (28.3-inch male and the 28.6-inch female) by three per cent. The length classes, however, are incomplete.

P. to V. — The proportion of the 21.9-inch Sebago female is the highest of the lake salmon length-classes and equals the 28.6-inch breeding female and the 29.3-inch non-breeding female, the highest of the females of the Atlantic salmon. They also equal the 6.5-inch male parr. The 12.8-inch Presumpscot male and 16.5-inch Sebago female equal only to the 6.5-inch female parr.

V. to A. — Here is a continuous series of averages of proportions in which the highest for the lake salmon is like the lowest for the Atlantic salmon, which leaves only one, also the 25.5-inch breeding male Sebago salmon unrepresented in the proportions for the length-classes of Atlantic salmon. But instead of being the highest proportion for the lake salmon, as it is in snout to P., it is the lowest.

In their proportions six of the ten length-classes of the lake salmon equal those of the three parrs, which are alike. They are: the 12.8-inch male and the 13.2-inch female, the 14.7-inch breeding male and the 14.8-inch breeding female, Presumpscot fish, and the 21.9-inch male and 16.5-inch female Sebago salmon.

The proportions for the 17.6-inch breeding male and the 19.3-inch breeding female Grand Lake salmon, also the 18.9-inch breeding Sebago female equal those of the 13.9-inch male and 24.8–inch male Atlantic salmon. The proportion for the 25.5-inch Sebago breeding male is the lowest of the lake salmon proportions and 2 per cent lower than the lowest for the Atlantic salmon.

A. to C.— The ranges of the proportions for the length-classes of lake and Atlantic salmon overlap so that the second and third of the lake salmon correspond with the first and second of the Atlantic salmon, thus leaving one proportion only not represented in those of the Atlantic salmon. This proportion is for the two length-classes of Grand Lake 17.6-inch breeding male and the 25.5-inch breeding male of the Sebago salmon. Nevertheless the lake and Atlantic salmon differ in the predominant proportions of each, in that five length-classes of male and female lake salmon, having the same proportion, correspond to only one in the Atlantic salmon, *i.e.*, the 28.3-inch breeding male, which has the lowest proportion of the Atlantic salmon; and five of the eight length-classes of

the Atlantic salmon, with the highest proportions of all, are not represented in the lake salmon. The proportions for the 16.5-inch non-breeding and the 18.9-inch breeding Sebago salmon equal those of the 6.5-inch and 8.4-inch male parrs and the 28.6-inch breeding female and the 29.3-inch non-breeding female Atlantic salmon.

Cpd.— The ranges of variations of proportions for the length-classes of lake and Atlantic salmon are limited to two proportions each, those of the Atlantic salmon being the lower.

The 12.8-inch male and 13.2-inch female, the 14.7-inch breeding male and the 14.8-inch breeding female, all of the Presumpscot, the 17.6-inch breeding male and the 19.3-inch breeding female, of Grand Lake, and the breeding 18.9-inch female of Sebago are equal to all three parrs which are alike in this proportion and one per cent higher than the highest of the other Atlantic salmon.

The 25.5-inch breeding, the 21.9-inch non-breeding males, and the 16.5-inch non-breeding female Sebago salmon equal to six of the eight length-classes of Atlantic salmon. The two exceptions are the 21.0-inch male and the 20.3-inch female Atlantic salmon which are one per cent lower than the other six. The male and female of lake salmon of the Presumpscot and Grand Lake are exactly the same in their proportions as are also those of the Atlantic salmon. The lake salmon average higher than the Atlantic salmon and clearly show their relationship to the young salmon.

Cpd.: Ad. to C.— The proportions for the length-classes of the lake salmon are all higher than any of those of the Atlantic salmon excepting the parrs, and five of the length-classes have even higher proportions than the parr. The lowest proportion for the parrs is six per cent higher than the highest for the other Atlantic salmon. While none of the proportions for the lake salmon exactly equal those for the parr, the range of the proportions of the lake salmon includes those of the parr.

Cpd.: A. to C.— In this proportion also the lake salmon are higher than the Atlantic salmon and the range of proportions for the length-classes includes the proportions for the parrs, the lowest of which is seven per cent higher than for any other of the Atlantic salmon. Six of the ten length-classes of the lake salmon are higher than any of the parr, but the lowest of these six is only one per cent higher than the 6.5-inch and 8.4-inch male parrs which are equaled by the 18.9-inch breeding Sebago female.

Countable Structures.— The countable structures, to which reference has been made, are shown in table 23, where the ranges of variations of the branchiostegal and fin rays, numbers of scales in a longitudinal count, whole numbers of gill rakers on both arms of the first gill arch, and number of vertebræ are shown. All of the counts, with the exception of the vertebræ, were made on the total number of fish represented in tables 21–22. The vertebral counts are from fewer individuals which comprised none of the Presumpscot River salmon. The variation in any of the structures is slight. The most conspicuous difference between the lake salmon and the Atlantic salmon is in the number of anal rays in which the lake salmon runs a little higher than in the Atlantic salmon.

TABLE 23.

Countable Structures, Usually Referred to in Taxonomic Descriptions, as Derived from Individual Salmon Comprised in the Basic Table from which the Previous Tables were Computed.

	Br.	Fin Rays				Scales	Gill rakers	Vertebræ
		D.	A.	P.	V.			
Atlantic salmon	10–12	9–12	7–9	13–15	9	110–120	17–21	57–59
Sebago Lake salmon	8–12	9–12	8–10	13–15	9	110–116	17–21	57–58
Presumpscot R. salmon	10–13	10–12	8–10	14	9	110–116	17–21	
Grand Lake salmon	10–13	10–12	8–10	13–14	9	106–115	18–22	56–58

Summary.— In a number of the comparisons of averages there is strong evidence of divergence of lake salmon from Atlantic salmon. Atkins mentioned certain characters which indicated the retention of juvenile characters in adult lake salmon such as parr marks. The red spots of the Presumpscot River 'Jumper' is another mark of the same nature. Another strong evidence is that the proportions of so many length-classes, particularly breeding fish equal the proportions of the parrs of the Atlantic salmon.

According to the averages of proportions the lake salmon average a somewhat longer head, longer maxillary and longer mandible, but the most pronounced differences are in that portion of the body back of the dorsal and ventral fins. It is this region of the body of the Atlantic salmon, which Menzies said grows more slowly than the anterior part.

It has been seen that the distance from the dorsal to the adipose fin averages shorter in the lake salmon than in the Atlantic salmon and nearly all of the proportions for the length classes are equal to the parrs of the Atlantic salmon, which is a character of the young Atlantic salmon. The same may be said of the distance from the ventral to anal, excepting that the Grand Lake and Sebago Lake breeding fish do not equal parrs in their proportions.

The averages for the caudal peduncle afford still further evidence in that all but three of the ten length-classes of lake salmon equal those of the Atlantic salmon only in the parrs, which are higher than any of the other length-classes of Atlantic salmon.

The most salient difference between the lake salmon and the Atlantic salmon (exclusive of the parr) is in the ratio of the least depth of the caudal peduncle to its length from the dorsal and anal fins to the upper and lower base of the caudal respectively. This difference may be expressed as follows:

Average for the least depth of the caudal peduncle not over 73 per cent of the distance from the adipose to the base of caudal and not over 66 per cent of the distance from the anal to caudal.....Atlantic salmon (*Salmo salar*).

Average for the least depth of the caudal peduncle more than 73 per cent of the distance from the adipose to the base of caudal and more than 66 per cent of the distance from anal to caudal.....Lake salmon (*Salmo sebago*).

Origin of the Lake Salmon.

Some ichthyologists have regarded this fish as a comparatively segregated sea salmon, *Salmo salar*. Others have stated their views to the effect that the sea salmon is only a sea-run lake salmon. Rarely is it claimed that they should be regarded as distinct species. Once there were those who thought the lake salmon had become adapted to a permanent fresh-water life by having been imprisoned in fresh water by a mechanical barrier which prevented its egress.

Day (1887, p. 104, footnote) says that 'Malmgren believed that anadromous salmon might have had their descent to the ocean summarily stopped and either themselves or their fry, which latter at least must have been in fresh water, had to select between extinction or continuing their race under altered conditions.'

Some of these various ideas that have been advanced concerning the *landlocking* process are more interesting than explanatory. The view that the sea salmon is merely a sea-run race of a fresh-water salmon obviates the necessity of any 'convulsion of nature' to imprison the fish in the lakes, but it does not explain how it has come about that the sea salmon has become so widely distributed, and how it has acquired so many different local hereditary physiological characters, and why it ceased to go into lakes of its alleged origin when it ascended the outlets of those lakes to breed.

A few of the various views mentioned follow: In 1869, Dr. Hamlin (1874, p. 346) wrote: 'The naturalist will ask the question: "Has not the lake-salmon appeared since the erection of dams, and being thus confined and prevented egress to the sea, has it not degenerated into the present variety?"

'The evidence is very conclusive that this fish existed from the earliest times in all the lakes where it is found to-day, and long before the advent of the European on our coasts. The Indians speak of it in their early traditions. The term "land-locked" as applied to it is inappropriate, since the erection of the dams does not prevent the fish from passing to sea during the spring and winter floods.'

Yet only three and one-third years after the foregoing was published Dr. Hamlin (1874 p. 353–354) made the following contradictory statement in a letter to Professor Baird, the United States Commissioner of Fisheries in 1872: 'Since I wrote this article, I have satisfied myself that the non-migratory salmon have been seen in the Schoodic, Penobscot, and Union River waters only since forty years. Concerning the Sebago salmon, I am not so positive, but am quite sure the variety is not one hundred years old, or since the erection of impassible dams on its outlet. The Schoodic salmon are about forty years old, and the old Indian hunters have given me the precise time of their appearance and the disappearance of the migratory salmon, which coincides with the erection of impassable dams.

'Migratory salmon of large size were at that time speared on the same grounds where the small salmon are now taken in great numbers, and which are never over five pounds in weight.'

G. Brown Goode (1884, p. 470) expressed a view regarding the fresh-water origin of salmon as follows: 'I am inclined to the view that the natural habitat of the salmon is in

the fresh waters, the more so since there are so many instances — such as the Stormontfield ponds in England — where it has been confined for years without apparent detriment. The "Land-locked" or "Fresh-water" salmon, known also in the Saguenay region as "Winninish", in the Shubenacadie and other rivers of Western Nova Scotia as the "Grayling", and in different parts of Maine, as "Schoodic Trout", "Sebago Trout", or "Dwarf Salmon", probably never visit salt water, finding ample food and exercise in the lakes and large rivers. In some regions in Maine and New Brunswick their access to salt water is cut off by dams, and some investigators have claimed that Land-locked salmon did not exist there until these obstructions were built, some fifty years ago. This hypothesis, however, is not necessary, for in the Saguenay the Winninish have easy, unobstructed access to the sea. The salmon of Lake Ontario and its tributaries are not thought to enter salt water, and there are similar instances of land-locking in the lakes of northern [?] Sweden.'

In 1884, in answer to a question by Prof. Goode, at a meeting of the American Fish-Cultural Society, Atkins (1884*a*, p. 55–56) said: 'I do not think we have any evidence that the land-locking of the species under consideration has occurred during recent geological periods. There is nothing at present to prevent any of these salmon from going to sea from any of those waters where they are now found. There are obstructions to their coming back, if they once went to the sea, and these same obstructions would hinder the sea salmon having access to the upper waters where the land-locked now live. It is possible that at some very remote period there were obstacles which prevented their descending to the sea. I think it possible, also, that the change in their habits and instincts occurred gradually.'

It was previously mentioned that all of the original salmon lakes, with the exception perhaps of Lake Ontario, are inhabited by smelts. But not all lakes inhabited by smelts contain salmon. In New England these smelt waters are in close proximity to the inland marine clay deposits, which suggests that the smelt may have been one of the factors concerned in the 'landlocking' of the salmon.

The *Salmon and Trout Magazine*, No. 41, October, 1925, p. 309, in 'Editorial Notes' says: 'At this year's meeting of the British Association, at Southhampton, Mr. C. Tate Regan, as President of the Zoölogical Section delivered an address on the subject of evolution, illustrated by instances from the life history of char, upon which, as some of our readers are well aware, Mr. Tate Regan is the greatest living authority. Char, it will be remembered, are believed to have been originally a migratory species, ascending and descending from sea to river as do our salmon and sea-trout, and as char do still at the northern part of their range in the Arctic. But after the last glacial age, with the receding of the ice northwards, the sea water in the Mediterranean and northwards became too warm for char; they could no longer descend and return, and thus became landlocked, remaining now only in lakes, usually but not always deep and with cold water. There each community has been shut up, apart from the others, for thousands of years, and many of these communities, apparently owing to differences in the environment provided by the lake which each inhabits, have developed structural differences

from other communities, such as are sufficient apparently to justify their classification as separate species, or at the least as incipient species. Mr. Regan suggests that the first step towards the formation of a new species is probably the formation of such a community, either with new habits or in a restricted environment, and not as has sometimes been supposed, a change of structure.'

Prior to Regan others have advanced similar theories regarding the char. But each, like Mr. Regan, seems to think that whatever change took place in structure, habits, physiology, etc., happened after being restricted to the lakes. This is not in accordance with a view previously expressed in this memoir to the effect that the evolution was in progress while the fish was an anadromous marine form. The final isolation in lakes retarded evolution, and variation was reduced in proportion to the number of interbreeding individuals in the community.

From preceding quotations and discussions it has been seen that early ichthyologists, but more particularly many anglers, who gave the question any serious consideration, regarded the lake salmon as distinct from the sea salmon. As previously indicated, they believed that the lake salmon was derived directly from the sea salmon by the latter being confined in inland waters by some natural physical obstruction which prevented its return to the sea after spawning, or that young were thus prevented from going to sea. Later, others suggested that the fresh-water forms were unknown prior to the erection of dams which confined the salmon in fresh water. These theories were quickly and easily exploded by showing that the dams did not prevent the salmon from going to sea but did effectually prevent their subsequent access to the lakes.

Furthermore, the case of the Canadian ouananiche, with its always unobstructed access to the sea, was a decisive argument against the physical obstruction ideas but not an explanation of the permanent residence of the fish in fresh water. In explanation of this point G. Brown Goode, and later Samuel Garman (1896) expressed their opinions to the effect that the lake salmon was the typical salmon and the marine, anadromous fish, only a sea-run form. In other words the process was reversed and the taxonomic type — *Salmo salar* — was supposed to have had its origin in a natural type of *Salmo* normally residing in fresh water. The 'sea-run' salmon was not regarded as specifically distinct from the fresh-water form although the 'sea-run' form apparently never reverted to its lake habitat and habits.

Opposed to the fresh-water origin of the sea salmon is the fact that the lake salmon naturally occurred only in a relatively few, fairly deep, cool lakes out of many in which they did not occur although these apparently afforded similar conditions. It would hardly seem that the sea salmon could be merely sea-run forms, as the lake salmon waters afforded only a limited number of relatively small nurseries to yield such an abundance of sea-run salmon, unless the sea-running habit had been acquired at an earlier geological period when the fresh-water distribution of the salmon had been much greater but had been reduced in a later period.

It seems impossible to accept the latter alternative owing to the ease with which inland waters, other than those at present naturally occupied by the lake salmon, are

stocked with salmon and smelts. If both of these fish had formerly been more generally distributed, in view of the fact just stated, it is hard to conceive of any reason for their disappearance from waters which evidently were perfectly well adapted to their continued existence. Furthermore, there has never been any evident attempt of transplanted lake salmon and smelts to go to sea. The occasional occurrence of both young and adults in outlets is plainly explainable on other grounds.

Atkins believed that the fresh-water salmon was derived from the sea salmon, and suggested that it was possible that the change in their habits and instincts occurred gradually. Doubtless that is a fact, and a theory once suggested to me, was that the 'land-locking' of the sea salmon was a voluntary process on the part of the salmon, and that conditions satisfactory to the salmon, particularly those of food supply and water temperature, were the principal factors concerned. The considerable individual variations of salmon in the same lake were accounted for by assuming that the 'land-locking' process had continued for a very long period, even from the time that the salmon first ascended into those waters. Those adult individuals, which exhibited the most pronounced differences from the sea salmon were supposed to be descendants of the earliest individuals to breed in those waters. It was assumed that as long as the sea salmon had access to the lakes, there were some of the offsprings which annually remained and matured there. A part of these interbred with the older inhabitants, a portion bred with contemporary broods, and others perhaps, interbred with matured offsprings of subsequent additions from the sea salmon runs, etc.

This idea was supposed to account for the fact that there were individual lake salmon so markedly different from the sea salmon that they could consistently be regarded as distinct species, while others were hard to distinguish. While to some extent satisfying the requirements of explanation, this theory possessed one serious defect in that it did not explain why all of the old strain and all of the subsequent crosses remained in fresh water, while only the broods of the pure strain of sea salmon went to sea, which it seems must have been the case, for the sea salmon never appear to show any similar individual variations when fresh from the sea.

If none of the theories that have been advanced are tenable, what can be offered as an excuse for the existence of the so-called landlocked salmon or lake salmon? It seems to me that the question can be answered with some degree of plausibility by adopting some of the ideas expressed in our previous discussion concerning the evolution of the Salmonidæ. However, it should be said that without further research such an answer is of necessity fully as theoretical as any of the foregoing, but it appears to me to afford fewer vulnerable points. Such a theory differs in but few essentials from that of the voluntary landlocking process just mentioned. Thus instead of the lake salmon being merely the sea salmon, which, as Dr. Hamlin's (1874, p. 341) Indian guide said, 'forgot to go to sea,' it is a divergent from a common ancestral or primitive stock, as Goode says. But this primitive stock was a marine, not a fresh-water fish.

One conceivable way to account for the divergence of the lake salmon and its adaptation to fresh water is that the divergence culminated since the last glacial period. It is

self-evident that the lakes now inhabited by the lake salmon were not inhabitable by any fish until long after the ice sheet had receded. In fact most of the lakes were the result of the glaciation.

In North America, it is said, the post-glacial sea extended up the St. Lawrence and included Lake Ontario and Lake Champlain. But so far as known there was nothing to prevent salmon ascending into those lakes in more recent years. Their recent occurrence there was not necessarily associated with the inland extension of marine conditions. The same may be said, perhaps, of Lake St. John. The occurrence of the ouananiche in other waters of that same drainage is not remarkable, but if it has extended its range into other more eastern drainages, it would seem that it must have been by the way of inter-communicating inland waterways, as suggested by Dr. Low, for it hardly seems possible that a cataract like Grand or McLean Falls could ever have been surmountable in any post-glacial time.

All of the original landlocked salmon lakes were in close proximity to the inland extension of the sea, so close indeed, that sea water may have extended into them. However, none of the lakes inhabited by the salmon was obstructed by impassible falls at any time. Many other lakes, earlier or later, became accessible but apparently were not occupied by the salmon. This appears significant from the fact that as previously mentioned, some of them appear to be suited to the salmon, as evinced by results of artificial stocking. It seems probable that the reason they were not naturally stocked was due to the fact that at the time the salmon lakes were first occupied by salmon, other lakes were still unfavorable and, assuming that the salmon had become adapted to certain conditions, later natural stocking was prevented by intervening unfavorable conditions. This view receives support from the fact that although all of the rivers of Maine, in fact all of any considerable size in New England, have been ascended by sea salmon until prevented by man-made obstructions, and no landlocking has taken place.

It has been stated that all lakes inhabited by lake salmon also contained smelt, excepting perhaps Lake Ontario, and possibly it once existed there. But there are many lakes inhabited by smelt, some of them above waterfalls and rapids at present impassible by any fish from below. There are 'landlocked' chars in water not now accessible from the sea, as Regan stated. A few are found in New England, particularly New Hampshire and Maine, and many in Canada. In fact we find in certain inland waters, both associated with the salmon and in waters containing no salmon, species similar to those named by Nordquist as relics of the Yoldia Sea, *i.e.*, coregonids, smelts, sticklebacks, etc. This fact indicates that similar conditions existed in both countries when these fish were distributed. The chars, smelts, and sticklebacks are undoubtedly of marine origin, and they were doubtless landlocked prior to the salmon. In other words the salmon were the last to reach the region of recent occurrence.

This is in accordance with a previously stated zone theory (p. 11); also it is in accord with 'Jordan's Law' (1929, p. ix) which is: 'Given any species in any region, its nearest related (geminate or twin) form is not to be found in the same region or in any remote

region, but in a neighboring district separated from the first by a barrier of some sort, or at least by a barrier of country, the breadth of which gives the effect of a barrier.'

As I understand it this does not signify that two closely related species never occur now in the same locality but that they were evolved under somewhat different conditions through isolation, and when found in the same locality it is due to the later advent of one of them. As the Law indicates, the barrier may be one of distance, and Jordan (1929, p. ix) has also said that 'most of our species are plainly related to geographical influences, or rather obstacles. The presence of barriers of mountain, sea, prairie, or desert, or of climate, food, or enemies, limits the range of forms.'

As has been previously suggested, the barriers or obstacles effecting the divergence or separation of the closely related chars, trout, and salmons, were largely climate, and distance, with attendant conditions. A theory previously advanced was to the effect that chars, trouts and salmons were not evolved under the same conditions or in the same latitudinal range. Without entering into a prolonged repetition of the theory, it may be said that the chars are the result of adaptation to more rigorous changes of conditions than were the trouts and salmons as indicated by their present distribution and the conditions of their habitats. In their structure and distribution, the trouts appear to have been subjected to less rigorous conditions and the salmons to have been the least affected, and these later were the latest to attain their present distribution.

As pertains to the evolution of the chars, trout, and salmons there seems to be no necessity for regarding the trouts and salmons as having been governed by natural laws different from those affecting the chars. The factors concerned differed only in degree. This is implied, although not definitely so stated, in the suggestion offered by the editor of the *Salmon and Trout Magazine*, previously quoted. It is a logical conclusion that the 'landlocking' of the salmon occurred in something the same way as of the chars and trouts. All three forms originated in somewhat different environmental conditions. And if Jordan's Law holds with the fish in the sea, they could not have originated in the same region, and the same may be said of the sea salmon and lake salmon.

Doubtless, during the glacial period the range of the primitive salmon stock was much farther south than that of the char stock, and broadly speaking, the trout stock was intermediate in its range. With the recession of the ice the ranges moved northward, each became adapted to the particular conditions within its range, and in the case of the salmon, the most northern section came in contact with the greater amount of cold, fresh water, which they frequented for food and reproduction. To repeat, they became adapted to those particular conditions. With the elevation of the land the expanses of brackish and fresh water contracted and the fish were isolated by force of their adaptation and the 'barrier' of warmer and more saline waters of the sea. There they had to remain, not on account of dams, natural or artificial, not because they 'forgot to go to sea,' as Tomah, Dr. Hamlin's Indian guide said (Hamlin 1874, p. 341), but perhaps, to paraphrase the words of Hallock (1877, p. 306) it could not go to sea if it would. Through physiological adaptation and heredity they had become fresh-water salmon.

The 'landlocking' process was not synchronous in all lakes inhabited by the fish in recent times, but in general, *pari-passu* with the changing conditions northward following the recession of glacial conditions. Probably not all of recent natural salmon lakes were stocked in this way, for there are some localities where it seems that they must have spread by way of inland water routes.

That the lake salmon were relatively late arrivals in fresh water is indicated by the fact that in some instances chars and smelts occur in waters above waterfalls which are now insurmountable by any fish and where they could not have gained access at any other time than when the falls were not as formidable as at present. But when salmon appear above such falls possible routes of dispersal are evident.

If the immediately foregoing theory is in accord with the facts, the nearest to a marine prototype of the lake salmon would be those now found in the most northern regions, as for example the White Sea, Iceland, Greenland, and Ungava Bay, if the salmon actually occurs in the latter locality. Smitt in 1886 recognized the White Sea salmon as different from the Baltic salmon and gave it the name of *Salmo brevipes*.

Of course it is recognized that this hypothesis is mostly speculation, but it must be admitted that many facts warrant it. To repeat: it is manifestly impossible that the fish should have originated in those fresh waters, which they now inhabit, for the region was once covered by a field of ice thousands of feet thick over a period of thousands of years. The fact that Lake salmon now flourish only in certain cold 'glacial lakes', indicate that their present physiological requirements are the culmination of thousands of years of adaptation to changing conditions since their preglacial progenitors roamed the seas.

Since the foregoing was written Dr. Henry B. Ward (1932) has advanced a theory of 'The origin of the landlocked habit in salmon' in which he regards temperature as the principal factor. His theory is based largely upon his observations on the effect upon sockeye salmon (*Oncorhynchus nerka*) produced by a dam erected comparatively recently in Baker River at Concrete, Washington. Although most of the evidence in support of his theory pertains to apparent results of a recent restriction of sockeye salmon to the lake produced by the dam, and the waters above it, Ward extends the theory to apply to landlocking of salmon in general.

Ward's idea of the landlocking process will be made sufficiently clear by a quotation from what he says under the heading 'Origin of a natural race of Landlocked Salmon' (p. 577) and of his conclusions (p. 578–579). He says: 'The question now arises — how do conditions in nature resemble those which were artificially created by the erection of the dam, and do somewhat similar influences ever interfere to prevent the young salmon from completing the journey to the sea? Earlier in this paper attention was called to the fact that landlocked salmon planted in certain lakes tend to desert those waters. One will naturally assume that in such cases some influence is lacking which in other localities inhibits the fish from deserting the lake. I am of the opinion that temperature is the ruling factor and that changes known to have occurred in the recent geological history of the northern hemisphere are calculated to afford an adequate explanation of the formation of landlocked races of salmon in widely scattered lakes.'

In his conclusions he writes: 'In the light of all the evidence one may conclude: The landlocked salmon in a lake were not influenced or held in restraint by the formation of any mechanical barrier that cut off access from the ocean but by some factors within the lake itself which changed primitive conditions. Some change brought about the disappearance of the current stimulus that would have led them on down-stream to the ocean. These new conditions caused them to hesitate and finally to abandon their journey to the sea. In the Baker River it was the erection of the dam which created a great body of quiet water and thus eliminated the current stimulus. Following that it was the warming up of surface waters which led the young fish to seek deep, cool waters. One should recall also that when in the old unmodified river the migrators had reached the sea, the next move of the young fish was to turn there into deeper, cool waters. The succession of responses is the same in both cases. The changes brought about by the erection of the dam were rapid and the results immediate.'

If Ward's interpretation of the situation at Baker River is correct, other things being equal, any obstruction happening at any time in a sockeye salmon stream, which produces an area of deep quiet water having the surface warmer than the river water was prior to the intervention of the obstruction, would result in the landlocking and dwarfing of the salmon. Accordingly like conditions might have the same effect on Atlantic salmon. Thus it would be possible for the salmon to have become landlocked at any time, since the glacial period up to the present time, or to become landlocked in the future if subjected to those conditions. But from the author's argument it is to be inferred that he regards some cases of the 'landlocked habit', especially in the older landlocked fish, as having become hereditary and non-reversible.

A specific instance may be cited in support of the view that the 'landlocked' habit is hereditary. In 1897 I was privileged to spend several months at Wallowa Lake, Oregon. In this lake was a permanently resident 'dwarfed' Sockeye locally known as 'yank.' The migratory sockeye, there called 'redfish,' ascended to that lake to spawn. Many of the former and a few of the latter were collected, also young of the large form were collected for me, as they were descending the Wallowa River below the lake. If the resident little redfish originated in any such way as Ward suggests, when the passage again became clear, the fish had lost the impulse to go to sea and the migratory fish returned to the lake to spawn and its young retained its sea going habit.

Many generations of the 'Quinnat' or 'king salmon' were retained and propagated at the Trocadero Aquarium at Paris, France. Apparently no one has regarded them as landlocked salmon. The same species has been introduced into several lakes of New England, where it grew up and in some instances attained breeding condition. But lacking suitable conditions they never reproduced.

Ward is doubtless correct in regarding temperature as one of the determining factors in the natural landlocking of salmon, but it was probably only one of many. The phenomenon at Baker River is merely suggestive of that fact and has no other significance in its relation to the natural 'landlocked habit'.

Habits.

Concerning the Swedish lake salmon, which he calls '*Salmo salar*', Nilsson (1832, p. 3) says that it spends the winter in certain lakes, Wenern and Siljan, whence in late spring it ascends the rivers. Therefore, in winters, he says, it uses the lakes as its sea, never entering salt water.

Atkins (1880, p. 777–778) says: 'The habits of the Sebago salmon are identical, so far as observed, with those of other fresh-water salmon. They dwell and feed in the lakes, occasionally running into the larger streams after food, and at spawning time, which begins the last of October, they seek the gravelly rapids of the streams and there excavate nests, in which they deposit their eggs. The old fish abstain from food at spawning time, but young males are taken with eggs in their mouths and stomachs. The males are found frequenting the spawning beds when only 6 inches long, retaining still the dark bars and red spots on the sides, and these little fish yield milt abundantly. The females, however, are not found till well grown up. At the feeding season both sexes take bait and rise to the fly, and are taken in Songo and Crooked Rivers and in Sebago Lake. In Long Pond they are never taken except at the spawning season, while ascending the stream or near its mouth.'

Food and Feeding.

The lake salmon occurs naturally in no lake, unless it contains smelt, unless it be in some inland waters of Labrador where it is claimed the ouananiche has been found, or, again in Lake Ontario. Lake Wenern in Sweden and Lake Ladoga in Finland and Russia contain smelts. It seems to be a fact that the best known lake salmon waters are also smelt waters. As pertains to the lakes and streams of Maine, it has been quite generally stated that the principal food of the 'landlocked salmon' is the fresh-water smelt. Indeed, it has been found to be a fact that salmon introduced into new waters where there are no smelt, do not thrive unless smelts are also introduced. This pertains to adult fish, for it is well known that the young salmon subsist largely upon insects, either in the aquatic larval state or such as fall upon the water.

The stomachs of a great majority of the many Sebago Lake salmon that from time to time I have examined in 16 seasons from April to October, between 1898 and 1916, both inclusive, contained smelts when they contained anything at all. The smelts were always the small form and translucent young. Rarely some other fish, such as a perch or a cyprinid, was found. A 10½-pound salmon caught June 13, 1901, contained four smelts, four or five inches long, and one yellow perch (*Perca flavescens*) about seven inches in length. Another about 16¼ inches long contained 33 young yellow perch from a little over an inch to about two and one-eighth inches in length, also two nymphs of some insect and one grasshopper.

During the summer months salmon frequently contained a number of species of insects in varying quantities, sometimes insects only, at other times smelts also. The insects were obtained from the surface of the lake where they had been blown by the

wind. On some days the surface of the lake would be covered locally by a variety of forms upon which the salmon appeared to feed indiscriminately; sometimes some particular insect would predominate, or perhaps it would be the only insect present. But the salmon gorged themselves on them. At this time it is impossible to enumerate all the forms that have been found in the salmons' stomachs. But I recall various beetles, including June bugs and potato beetles; various winged insects such as flying ants, bumble-bees, mayflies, moths, grasshoppers, and various others, including spiders.

In the Presumpscot River the resident salmon appeared to subsist largely upon the aquatic stages of various insects such as caddis fly larvæ, stonefly and mayfly nymphs, alderfly larvæ and nymphs. Frequently the fish would be gorged with these bottom forms, but often they would take the adult insect at the surface and even leap from the water for the flying insect. Adult stone flies (locally called 'millflies') were excellent bait for the so-called 'jumpers' of the Presumpscot. Occasionally the larger salmon contained one or more fish, such as a small perch, a shiner, or young sucker. In the early spring, when the smelts were ascending in the streams to spawn, the salmon pursued them up the larger streams and about the mouths of the smaller ones flowing directly into the lake.

After the breeding season of the smelt, dead and dying smelts occurred in numbers at the surface of the lake where the salmon would pick them up. The only means of learning where salmon occur when not observed at the surface, is by fishing. By this means it has been found that they may be caught in water as deep as 70 feet but more often nearer the surface, even where there were 70 or 100 feet of water. While some anglers still-fishing for salmon and the large smelt at the same time, which is usually in about 70 feet of water, fish near the bottom, others, while fishing for smelt near the bottom have out only about 30 feet of line for salmon. This indicates that the salmon vary the depths at which they feed as well as the food which they eat. I have caught a salmon on a fly at the surface near where others were getting them in 60 or 70 feet of water.

During midsummer the salmon is not so frequently caught by trolling as in the spring and early summer, but the largest salmon that I ever caught, a 16-pound fish, was taken by trolling with smelt bait on the first day of August, 1907, while on the same day the largest salmon ever taken on a hook, a 22½-pound fish, was caught by still-fishing in deep water, with red-fin shiner bait.

The salmon used to begin to ascend the Songo River on the breeding migration in September. Apparently they then practically ceased to feed, for seldom would one take a bait or a fly, although in the river they would be seen rising to the surface as though getting something there in the way of food.

However, even in October I have caught 'jumpers' on artificial flies and bait, and the stomachs of these fish, which had well developed reproductive organs, sometimes contained insects.

The young, after they have attained the parr stage, while in the streams subsist largely upon insects, both those in the aquatic stages and such various forms as fall

upon the water. If they have the opportunity they will eat the eggs of other fishes. They have been seen lying below the redds of brook trout and as the spawn was emitted by the trout they would dash in and help themselves to the eggs.

Spawning.

The anadromous habit is not restricted to the sea salmon for the lake salmon also usually ascends affluents of lakes to breed. But, curiously enough, in some instances, it may be said to be catadromous in that it descends outlets. Facts and theories have been advanced to explain the anadromy of the sea salmon. Some of these have been previously discussed in this memoir. It is difficult to apply these beliefs to the lake salmon. There are no spring and summer migrants of the lake salmon homologous to those categories of the sea salmon, although the fish enter both inlets and outlets in the spring, presumably to feed. The movement associated with the 'breeding impulse' occurs in the fall, although it may begin a month or two before the spawning time. But the requisite conditions for spawning are precisely the same as in the case of the sea salmon, relatively cold-running water and a gravelly bottom. It may be imagined that the advanced development of the reproductive organs initiates the movement for reproduction, and it is conceivable that the fish are so sensitive that they quickly detect the inflowing or outflowing currents, with, perhaps, cooler water and increased content of dissolved oxygen. It is noticeable, too, that in the stream which they ascend, the run is more likely to occur after a rise of water following a rain. How a rise in an effluent could induce a downward migration is not quite so clear. However, it is possible that the increased current of the outflow is felt in the lake. At Grand Lake Stream it has been observed that salmon would linger in deeper water until a gate in the dam was raised sufficiently to cause a more rapid outflow, when they would come down close to the dam. Thus by this means they are induced to enter the trap-net set to take them for propagation.

Of the 'Silfverlax' of Lake Wenern, 'Rudge' (1909, p. 378) says: 'About the middle of May it begins to ascend the Klar Elv (and in smaller numbers the Gullspångs Elv), and continues to do so until the middle or end of July, the run being generally at its height about Mid-summer Day. By the way of this stream and its continuation northwards, the Trysil river, it has reached Osterdal in Norway, where it is now found in several lakes. In September and October it spawns, after which it returns to the Venern remaining there throughout the winter.'

Of the Lake St. John fish, Creighton (1892, p. 87) says: 'The rivers which flow into Lake St. John all contain Wananishe, which, however, do not ascend them in any great number till the autumn. The ova are well developed at the end of September, and the fish are then on their way to the spawning-beds, which are, as in the case of the salmon proper, gravelly shallows with a steady current over them. The spawning season is at the end of October. The spring movement of the fish from Lake St. John down into the Grande Decharge, and the autumn movement up into the rivers flowing into the

lake, correspond with the spring and autumn migrations observed at Schoodic Lake by Mr. Atkins. A number of the fish, however, remain in the Grande Decharge and evidently breed there and in its small tributary streams, for the adults can be caught through the ice, and I have taken parr and smolts at almost every part of the Grande Decharge. These, however, may possibly have come down with the spring freshets. On the other hand, I have repeatedly taken adults there in September with milt and ova well developed; the change of coloration, hooked lower jaw, indifference to food, sluggish movements, and all the other characteristics of salmon near spawning-time, were well marked in them.'

Concerning the habits of the 'landlocked salmon,' in 1884, Atkins (1884*a*, p. 42–43) wrote that it never visits the sea except accidentally, and makes its home in the freshwater lakes. 'It has its feeding grounds in the lakes and rivers, and instead of fasting six months or a year at a time, curbs its ravenous appetite for but a few weeks at the spawning season. My observations on the date of spawning lead to the conclusion that it is a week later with the land-locked than with the anadromous salmon. In approaching the spawning ground the landlocked salmon move up into an affluent stream or down into an effluent stream, being governed so far as I can see, by the peculiar circumstances of each case.'

The spawning season, or at least egg-taking season, at Grand Lake Stream in 1878 extended from November 1 to December 2, males usually predominated up to the middle of the month, from which time the proportion of females to male rapidly increased. The females predominated until the 26th, although the numbers of both fell off considerably in the few days previous. After that the males again predominated, but only a few fish were taken. In fact, on the night of November 30 only six fish were taken, of which five were males.

Again in 1879, the males exceeded the females from October 30 to November 6, from which time until November 12 the females usually preponderated over the males, although on one date (night of November 7–8, an equal number of each were taken, and, on the night of November 11–12, the males exceeded the females). The total catch of spawning fish in these two seasons was 4,422 of which 1,934 were males and 2,488 were females. One small mature male 9½ inches long weighing 7 oz. is mentioned in the report.

Size Attained by Lake Salmon.

The lake salmon has been said to differ from the sea salmon chiefly in size. It has been regarded as a dwarfed salmon and has been frequently referred to as such, even by comparatively recent writers. The belief that the 'landlocked salmon' were dwarfed salmon originated with the small race of 'Schoodic salmon' but the belief has been perpetuated to this day, in most fish literature notwithstanding the many records of much larger fish from other fresh waters. There is nothing to indicate that the salmon of lakes Wenern and Ladoga were greatly undersized. Malmgren stated that in Lake Ladoga it

attained a maximum weight of 18 pounds and the usual weights were ten to 16 pounds. These weights compare very favorably with those of sea salmon in many rivers on both sides of the Atlantic.

There have been many reports of salmon from Sebago Lake, Maine, weighing from ten to 20 pounds and of a few still larger. For this lake the largest on record are two, taken during fish cultural operations, which according to B. B. Jones (1908, p. 8), 'Were respectively of the following dimensions and weights: 39 and 35 inches long; 11 and nine inches deep; 35½ and 31¼ pounds in weight. The largest taken by an angler weighed 22½ pounds. Such sizes do not support the generalization that lake salmon are dwarfed fish. However, there is no doubt but that in some waters there are races of salmon which do not attain a large size and may be regarded as dwarfed in those particular instances.

The Lake St. John, or Saguenay fish, or ouananiche, average a little over two and one-half pounds, according to Creighton (1892, p. 90–92). 'Four-pound fish were numerous enough a few years ago, but anything over that size is large, and only occasionally will a six-pounder be found. Out of many thousands I have seen but one seven-pound fish; it was twenty-seven inches in length, and a very lank specimen. If properly filled out, it would have weighed nine or ten pounds. This solitary instance gives one some faith in the stories of the large size of the Wananishe when the region was first settled, forty years ago. Occasionally very large ones are seen feeding by themselves, but they are extremely wary, and there is no authentic record of one above seven pounds, though the late Senator David Price, of Chicoutimi, is said to have caught one of eleven pounds in weight.'

Grand Lake Stream. — Dr. Adams (1873, p. 202) stated that he, with a friend, visited the region in August, 1866, to verify the reports that stunted salmon, averaging about three pounds and rarely attaining seven pounds, existed there.

Atkins (1884*a*, p. 43–44) says that at Grand Lake Stream, according to Norris, anglers' scores of years ago were as follows:

June, 1856,	634	fish	averaged	1.38	pounds each
" 1857,	452	"	"	1.49	" "
" 1858,	575	"	"	1.42	" "
May, 1865,	379	"	"	1.33	" "

Atkins again states that the average weight of some hundreds each of males and females taken at the spawning time in 1875 and 1876 was:

	Males	Females
1875,	1.6 pounds,	3.1 pounds
1876,	1.8 pounds,	3.08 pounds

That such great differences of average weight of the sexes did not always obtain is shown by these figures given by Atkins:

TABLE 24.

	Males	Females
1878	2.3 lbs.	2.2 lbs.
1882	3.1 "	3.08 "
1883	3.2 "	3.0 "
1884	4.0 "	4.11 "
1885	3.65 "	3.61 "

Concerning these figures Atkins remarked that they applied only to the salmon of Grand Lake Stream and that in other parts of the Schoodic waters the fish were of various sizes; in some places larger and in other places smaller. He cited specific instances of great differences of size of fish of different lakes of the region.

Such diversity of size is not remarkable nor peculiar to this particular fish. The same phenomenon is exhibited by the 'brook trout,' the 'lake trout,' and various other fresh-water fishes. Furthermore there are often considerable variations in size of the Atlantic salmon in different sections of the same river basin. There are doubtless periodical fluctuations in size of fish in the same body of water as suggested by the following data of Grand Lake salmon, giving the average number of eggs to a female.

In 1878, 1,785 females averaged each 965 eggs. The average weight of 280 of the fish was 2.2 pounds. In 1882, 1,004 females yielded an average each of 1,674 eggs. The average weight of 308 of these females was *3.08* pounds. In 1883, 661 females, averaging 3.4 pounds each, yielded 1,618 eggs. In 1884, 808 females, of which 768 averaged 4.11 pounds each, yielded an average of 2,253. This was the largest average number of eggs per fish from 1875 to 1923 inclusive (none taken from 1891 to 1896 inclusive), therefore it may be inferred that in all these years the females did not average over 4.11 pounds in weight. In 1885, 611 females yielded each 1627 eggs and averaged 3.6 pounds in weight. The average yield of eggs per female in 1884, was exceeded only in 1924, 1925, and 1926.

According to the anglers' records as reported by bulletins of the Maine Central Railroad: in 1924, 35 fish ranged from three to 6½ pounds and averaged 4.65 pounds; in 1925, 15 ranged from one to 6¾ pounds and averaged 4.16 pounds; in 1926, six fish ranged from three to 7½ pounds and averaged 4.91 pounds. Thus there appears to have been some fluctuations in average sizes of fish from 1875 to 1930, but on the whole a slight increase. According to the Maine Central Railroad records more relatively large fish were taken than in the earlier years. The records also show that the fish taken by anglers in the last few years at Grand Lake average from three to five pounds according to the season, with apparently more large fish than formerly.

In as much as practically all the salmon angling at Grand Lake Stream is now done on the lake instead of in the stream as in former years, it might be thought that the apparent increased size of fish, or rather the more numerous relatively large fish, could be accounted for by that fact, since it was seldom that the larger fish of any lakes made

their way into the outlet except in some instances, as at Grand Lake Stream, to spawn. However, except in the first few years of fish cultural operations at Grand Lake Stream, the fish collected for fish cultural propagation were intercepted and taken above the dam at the foot of Grand Lake, in the fall of the year. Since Grand Lake Stream was the principal breeding place for the salmon of Grand Lake, doubtless during the operations there, all sizes of salmon were taken.

Perhaps some light may be thrown on this point by the following fish cultural records for Grand Lake Stream which were compiled from the annual reports of the superintendents of the Federal hatchery at that place. The reports show the actual average weights of the fish only in a few of the earlier years of the operations there under Atkins. But the average number of eggs per female each year gives some idea of how the fish averaged in size.

If the records are arranged in periods of years they show that in the first three periods of five years each from 1876 to 1890, both inclusive, there was a decline in the total number of fish taken but an increase in the average number of eggs per female, indicating some increase in the average size of the female.

At this station after 1891, fish cultural operations were suspended for five years. They were resumed in 1897, but records for 1903 are not available. However, in the two-year period of 1904 and 1905 there was some increase in the number of fish and a corresponding decrease in the average number of eggs per female over the four-year period from 1897 to 1900 inclusive, which indicates a decrease in the size of females.

In the period of five years from 1906 to 1910, there was the largest take of salmon, with the exception of 1876–1880, in the whole history of the station. There was also some increase in the average number of eggs per female over the preceding three periods.

In each of the succeeding four periods of five years each, while the number of fish caught was somewhat lower than in the preceding period, the number was maintained about the 4000-mark and the average number of eggs per female, on the whole, increased somewhat. In the last five-year period from 1926–1930, both inclusive, the 1980 females yielded an average of 2043 eggs per fish.

If a curve were constructed showing the annual variation in the yield of eggs as related to the total number of females, it would indicate, as a rule, that the larger numbers of fish averaged smaller in size than the smaller numbers of fish. The yearly list of these statistics, which follows, reveals a varying number of years when the fish apparently run relatively large or small with considerable fluctuation in that respect. An arrangement in periods, as previously discussed, would level the curve somewhat, yet it is apparent that in later years there has been a general increase in size of the female of Grand Lake salmon or else more efficient fish cultural methods have been attained.

Doubtless periodical fluctuations in size of fish always occur naturally. But in the case of Grand Lake it is easy to see that, since the stock is dependent upon artificial propagation a survival of a large number of planted fish, in a few years, would increase the number of spawning fish by a preponderance of small breeders. This would be augmented by any considerable mortality of larger or older fish through capture or other causes.

TABLE 25.

Records of Salmon Taken for Fish Cultural Propagation at Grand Lake Stream, Compiled from Reports of the Superintendents of the Federal Fisheries Sub-station at that Place, in the Period from 1875 to 1930.

Year	Total salmon	Total males	Total females	Females spawned	Average number ova to ♀
1875	2626	1055	1571	1569	680
1876	1021	272	749	670	810
1877	4148	1776	2372	2372	910
1878	2907	1122	1785	1785	965[1]
1879	2022	938	1084	1084	1027
1880	2171	698	1473	1427	1638
1881	1022	370	652	652	1452
1882	1604	600	1004	1004	1674[2]
1883	1014	295	719	661	1618[3]
1884	1186	378	808	808	2253[4]
1885	810	199	611	611	1627[5]
1886	754	249	505	505	1847
1887	906	339	567	567	1527
1888	974	487	487	487	1979
1889	870	313	557	557	2182
1890	510	139	371	371	2099
1891	579	199	380	380	1650
1897	337	129	208	208	1345
1898	866	358	508	508	1224
1899	627	256	371	371	654
1900	819	322	497	497	824
1901	3210	1464	1746	1746	830
1902	1127	545	582	582	809
1904	1325	605	720	720	760
1905	2160	843	1317	1317	728
1906	1058	500	558	558	479
1907	1633	874	759	759	804
1908	2657	1166	1491	1491	1341
1909	1265	488	777	777	1934
1910	904	386	518	518	1475
1911	731	323	408	408	1635
1912	860	421	439	439	998
1913	363	670	693	693	1564
1914	916	396	520	520	1306
1915	844	396	448	448	1511
1916	1084	476	608	608	1776
1917	1003	420	583	583	1286
1918	680	381	299	299	1060
1919	957	446	511	511	1769
1920	333	143	190	187	1696
1921	451	259	192	188	1340
1922	1241	818	423	417	1379
1923	1225	685	540	540	1823
1924	782	336	446	444	2470
1925	603	264	339	336	2379
1926	671	423	248	245	2420
1927	685	566	345	340	2175
1928	973	450	523	506	1928
1929	930	566	364	314	1739
1930	1176	595	581	575	2070

[1]The average weight of 280 females was 2.2 pounds, ranging from 1 pound 6 ounces, to 4 pounds 3 ounces.
[2]Average weight of 308 females was 3.08 pounds, ranging from 1.3 to 4.9 pounds.
[3]Average weight of females 3.4 pounds, ranging from 1.8 to 4.8 pounds.
[4]Average weight of 768 females, 4.11 pounds, ranging from 2 to 6.2 pounds.
[5]Average weight of 577 females, 3.6 pounds, ranging from 1.5 to 6.2 pounds.

On the other hand, if for any reason the plants of fish resulted in a small proportion of fish to reach maturity, the average size of them would apparently be increased, although all along the range of sizes might be practically the same.

But when the fish increase both in number and size, where the size depends upon artificial propagation, it indicates improved conditions in fish culture. This seems to be what has happened at Grand Lake Stream in recent years.

Green Lake. — (Stilwell and Stanley 1874, p. 13). 'About 12 miles from Bangor, on the Calais road, is a lake known as Reed's pond. It is of some eight or nine miles in length, extending to the city of Ellsworth, and emptying into Union River. This is the lower link of a chain of these ponds containing these fishes, of a size like those of Sebago lake in Cumberland county, that compare with the Schoodic and Sebec salmon, as does the huge Rangely trout with our ordinary brook trout. They are the same fish, only developed to a greater size by the superior range and purity of water, and greater supply of feed for both the young fry and the growing fish. The Reed's pond salmon have in the past, been caught of great size and weight, viz., 22, 15 and ten pounds.'

The Maine Central Railroad bulletins from 1915 to 1930 give the records for Green Lake for only two years as shown by the following table.

TABLE 26.

Year	Period	Number of anglers	Number of salmon	Average weight	Number of individual weights recorded	Range of weights	Average weight
1921	April 20–29	34	61	3.17+	13	2–6¼	3
1922	April 20	2	2	4.25	2	4–4½	4.25
1927	April 25	Details are lacking but about two good salmon a day reported.					

Sebec Lake. — The Maine Fish Commissioners' report for 1874 (Stilwell and Stanley 1874, p. 13) says of the salmon of the Sebec region: 'They are all similar in size and general appearance to the Schoodic shiner or salmon.'

Records for ten years from 1915 to 1929 (lacking those for 1923 and 1928) reported in the multigraph bulletins issued by the Maine Central Railroad, show that the smallest salmon caught weighed two pounds and the largest 8⅓ pounds. The averages of those for which individual weights were given range from about two to about 3⅜ pounds.

Sebago Lake. — As stated elsewhere, Sebago Lake has long had a reputation for large salmon. Possibly the earliest mention of the size of a Sebago salmon occurs in an apocryphal diary attributed to Hawthorne in his boyhood, sometime prior to 1825, while he resided with relatives in the vicinity of the village now known as South Casco. The statement (Pickford 1897) is as follows: 'On the way from the Island to the Images Mr. Ring caught a black spotted trout that was almost a whale, and weighed before it was cut open, after we got back to uncle Richard's store, eighteen and a half pounds. The men said that if it had been weighed as soon as it came from the water it would have been nineteen pounds.'

More authentic early records of size appear in a magazine article descriptive of fishing expeditions on Sebago Lake in 1830 ('M' 1832, p. 526–529). The author said that the salmon trout, as he called it, varied from two to 14 pounds. His records are: one upward of 6 pounds, several largest 8 pounds, two, male and female, the first a little under and the second a little over 8 pounds. He said, 'The Transcript notices the appearance of a 18 lb. trout from Sebago pond in the Boston market.'

In 1833 Dr. Jerome V. C. Smith (1833, p. 334) says of a trip by a party of which he was a member: 'On this occasion the average number taken in a day, by the party of four, which ransacked the lake in a boat, was near twenty-five, the weight being from about two to five pounds each.

'Very erroneous opinions are formed of the weight of these trout. They are generally exaggerated; and this may be said of them whenever they are found, but as it respects this pond, though it is not uncommon to take them of six, and occasionally of twelve pounds, yet it was the opinion of the celebrated Mr. White, which has been confirmed by our own observation, that considering the prevailing number of small fish, they do not average over a pound and a half each through the season of fishing. This remark may strike some with surprise, who have told a very different story, founded perhaps on their individual good success. The truth is, they have degenerated not only in size, but in numbers, owing to various causes, unnecessary to detail.'

The foregoing was written over 100 years ago, but in recent years the same statement has been made of Sebago salmon.

From sportsmen's journals and papers, largely *Forest and Stream and American Angler*, it has been possible to present a few records of weights of salmon taken in Sebago Lake, for 28 years out of over 40 years from 1875 to 1917 inclusive. Similar records condensed from reports in bulletins issued by the passenger department of the Maine Central Railroad from 1915 to 1930 are also briefly given here.

Supplementing these is table 27 compiled from data furnished by the Maine Commissioners of Inland Fish and Game, during those years.

In the sportsmen's journals probably, as a rule, only the largest fish were reported and many smaller ones caught were never mentioned. Only in a few instances are there sufficient numbers of fish to make the average mean much. The greater the number of fish in any year the smaller the average seems to be. Thus: in 1886, 10 fish averaged 11.2 pounds; in 1896, 26 fish averaged 6.2 pounds; in 1905, 39 fish averaged 8.37 pounds; in 1909, 164 fish averaged 5.5 pounds; in 1917, 176 fish averaged 3.5 pounds. The largest fish of each of the 28 years represented, *i.e.*, 27 fish range from six to 22½ pounds, and averaged about 12½ pounds.

Better averages are reached in the Maine Central's records. The averages of those for which individual weights are given range from two to 5.43 pounds. The most common averages are between four and five pounds. The fish recorded as largest range from 1½ to 11½ pounds and average from 3.8 to 6.39 pounds. The records suggest some decrease in size in the most recent years.

A falling off in size is also indicated by the data from the Raymond Hatchery. The

largest fish taken each year becomes progressively smaller, from 18 pounds in 1916 to eight pounds in 1930. There is also a decided falling off in average yield of eggs per female in the last five years.

TABLE 27.

Records Pertaining to Sebago Salmon Netted for Artificial Propagation in the Pool of Jordan's River at the State Hatchery, at Raymond, Maine, from 1916 to 1930, both Inclusive.

Year	No. of salmon	Size compared with previous year	Weight of largest fish	No. of males	No. of females	Average no. of eggs per female
1916	1120	little smaller	18	560	560	1607
1917	855	smaller	18	373	482	1319
1918	1775	smaller	16	1093	682	1466
1919	1700	larger	16	700	1000	1250
1920	1482	larger	16	682	800	1520
1921	855	larger	16	295	560	1785
1922	1214	smaller	14	477	737	1036
1923	725	larger	12	365	360	1666
1924	1213	smaller	14	578	635	1377
1925	1584	larger	12	578	906	1324
1926	1440	smaller	10	548	892	708
1927	2200	av. 3½ lbs.	9	1000	1200	625
1928	3000	" 3½ "	8	1470	1530	693
1929	1600	" 3 "	8	950	750	707
1930	2800	" 3 "	8	1390	1410	692

THE PRESUMPSCOT RIVER 'JUMPER.'

Plate 9.

Since the 'Jumper' is now extinct and since salmon of similar peculiarities have been described from no other waters, it has seemed desirable to write a separate brief history of the fish.

In the Presumpscot River, which is the outlet of Sebago Lake, the Sebago salmon used to breed and in the spring of the year, large well-conditioned salmon were found in the stream. Later they disappeared. Prior to the erection of the dam at the head of the river, and later while the fishway was effective, most, if not all, of the salmon returned to the lake. In later years, the fishway having become impassible, some of the fish continued to disappear, where to, no one knows. If they went to sea they doubtless would have been noticed at the dams and mills lower down the river. However, small salmon resided in the river the year around. Until the new dam was built at the head of the river and the water diverted by a canal these smaller salmon, known as 'Jumpers' were found in the upper part of the river wherever there were waterfalls or rapids. After this the fish were still inhabiting the river below the dam at North Gorham.

The large salmon were always distinguished from the so-called 'jumper.' The local name 'jumper' was given to a small but very active fish of peculiar coloration, which attained a weight of at least three or four pounds, and which were also usually distinguished from the lake salmon of like size occurring in the river at the same time.

Adolescent salmon, with their bright silvery scales, more pointed snout, subequal jaws, more forked tail, black crescentic and X doubled-X spots, and with or without red spots, caught in the same locality were regarded as lake salmon. The 'jumper' was more trout-like in form, had a blunter snout, included lower jaw, scarcely crescentic tail. It usually had no black spots but had dark brown, chocolate-colored and brick-red or brown spots surrounded by brick-red on the body, and always red spots along the side. The sides of the abdomen were usually brassy yellow. There were doubtless old fish of long-time residence in the river. They appear now to be extinct, the locality below the North Gorham dam having been more recently ruined by the erection of a dam farther down which backs the still water nearly up to North Gorham dam.

Hamlin (1874, p. 349–350) fished the Presumpscot River before there was any dam at the foot of the lake, at least his description of the locality leads to that assumption. Hamlin's narrative of his experience with the salmon of the Presumpscot indicates that at that early date, even with free communication with the lake, the 'jumper' was already established in the river.

After describing his own loss of a fish, he goes on to say: 'My companion, however, was more fortunate, and landed a two-pound fish. The first glance at this fish indicated a distinct variety from the salmon of the Schoodic and other lakes; for its sides were very much spotted, even below the lateral line, and some of the spots were underlaid with deep crimson, which appeared in rich contrast with the black and pearl of the sides; the dorsal fin was also very much checked with large and distinct black spots. It would remind the angler of the *Salmo trutta marina* and the *hucho* trout of Europe, so distinctly marked was the dorsal fin. But the examination of five other specimens at a later day proved that the spots were not constant; for not one of the five exhibited more spots than the fish of the Schoodic, and some of them not so many. The appearance of the dorsal fin was also much changed, and in some fish the spots had quite disappeared, which leads me to believe that the excess of spots is due to food and locality.'

Probably the fish caught by Dr. Hamlin's companion, of which he (Hamlin) describes the colors was a typical 'jumper,' but some of the other five might have been juvenile lake salmon.

SUPPLEMENTAL NOTES TO PART 1.

Anatomy of Salmonidæ. — The salmons, trouts, and chars are essentially alike in their visceral structure and arrangement.

All species possess a dorsal mesentery which connects the middle line of the air bladder and the intestine, extending from the diaphragm anteriorly to within a short distance of the posterior end of the abdominal cavity in the female and quite to the end in the male. Another mesenteric fold connects the air bladder and the upper or esophagal limb of the stomach. All species have a ventral mesentery connecting the lower surface of the intestine and the ventral abdominal wall, extending from just posteriorly to the pelvic region to the posterior end of the abdominal cavity.

Gravid ovaries are never of the same length, one, usually the left, always the longer. Each ovary is suspended by a mesovarial fold extending from its respective side of the aid bladder somewhat inward and downward to the inner surface of the ovary whence it forms the walls of a somewhat boat-shaped ovary with obliquely crosswise ovigerous laminæ, from which, when ripe, the ova, escaping from the enveloping capsules, lie in the groove formed by the inclined edges of the laminæ and the mesovarium within.

The line of the air bladder attachment of the mesovarium extends gradually inward until it joins that of the dorsal intestinal mesentery near its posterior terminus. The ovarian covering continues on each side as a troughlike fold until it unites with its opposite and forms a common trough on the upper surface of the intestine, extending from the posterior terminus of the mesentery to near the genital pore, where it widens and becomes attached to each side of the abdominal wall.[1] This arrangement forms a troughlike oviduct from each ovary open above save for the peritoneal covering of the air-bladder. Consequently the ova do not 'fall into the abdominal cavity before extrusion.'

Genus *Cristivomer* is restored to the lake trout which was called *Salvelinus namaycush*. While the vomerine character alone does not always distinguish it, the forms of the mesethmoid and maxillary bones do. The mesethmoid is comparatively long and narrow, scarcely at all fan shaped, while in all other salmonids it is comparatively short and more or less broadly fan shaped. (Kendall 1919, p. 78–81.) The maxillary is relatively long, and subcylindrical and flattened only near its posterior end. The supplementary maxillary bone is also long and narrow. These characters appear to be of generic value, particularly when taken in combination with other usually distinguishing characters.

[1]This is the 'peritoneal trichter' of Weber (1886).

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EXPLANATION OF PLATES.

PLATE 1.

Atlantic salmon, *Salmo salar* Linné. Male, 29.5 inches long, from Penobscot River, Maine. Breeding fish, stripped Nov. 5–7, 1914.

PLATE 2.

Atlantic salmon, *Salmo salar* Linné. Female, 20.5 inches long, grilse, taken off Cape Elizabeth Lightship, Maine, July 11, 1922.

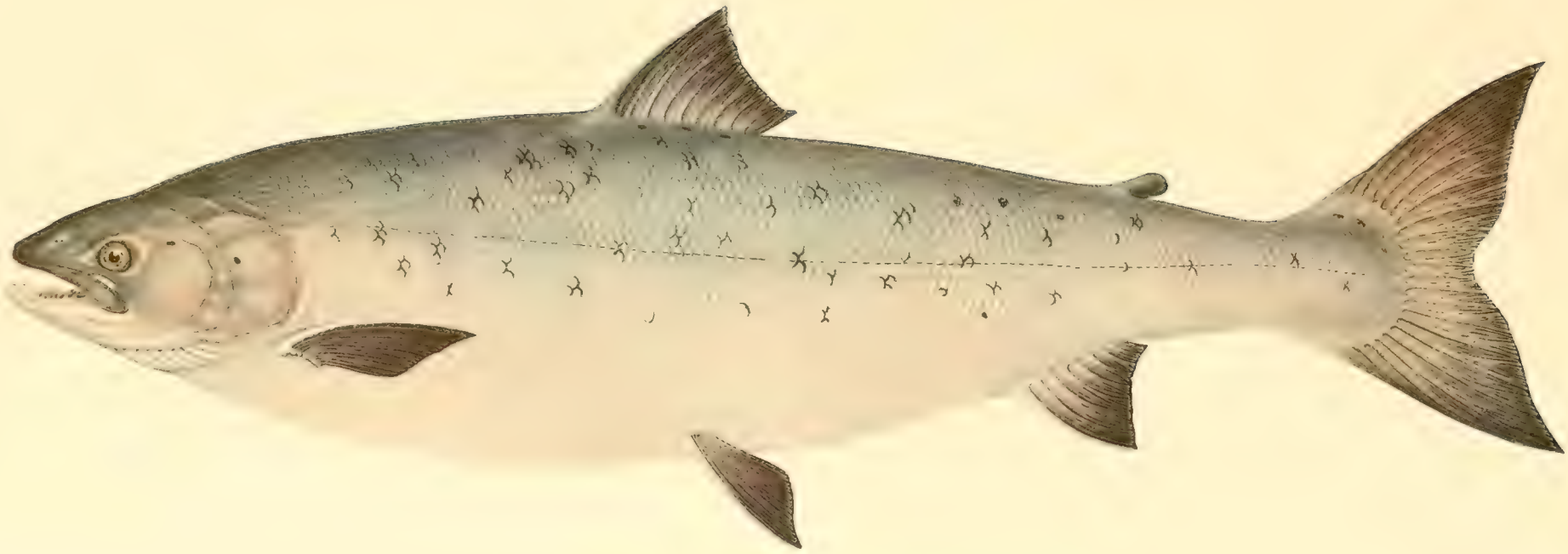
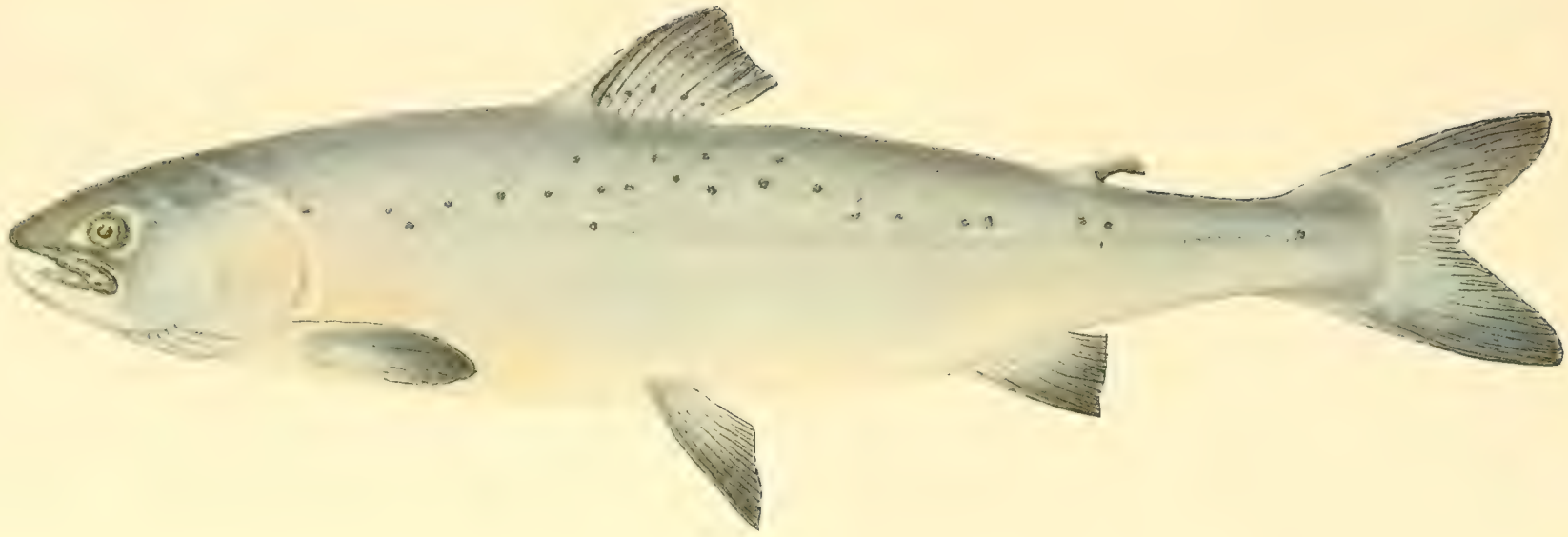


PLATE 3.

Atlantic salmon, *Salmo salar* Linné. Male?, 8.5 inches long, 'post smolt' from Richmond's Island off Cape Elizabeth, Maine. Taken in 'trap' July 12, 1922.



Kendall on New England Salmons.

PLATE 4.

Atlantic salmon, *Salmo salar* Linné. Female, 29 inches long, from Penobscot River, Maine. Breeding fish, stripped Nov. 5–7, 1914.

PLATE 5.

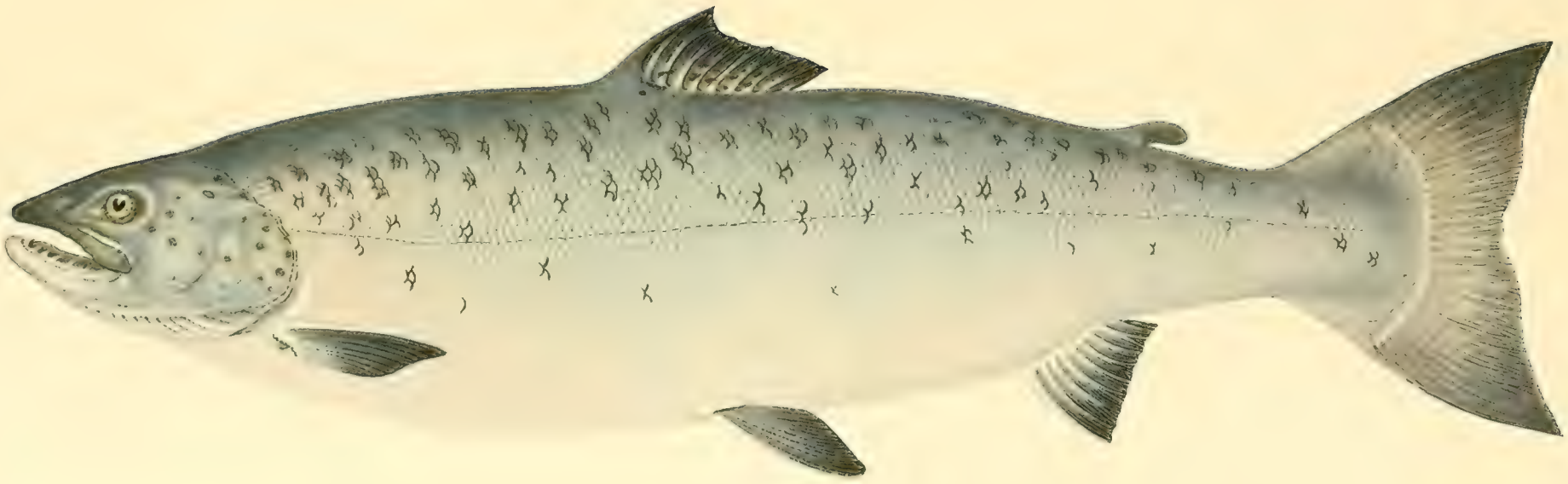
Sebago Lake salmon, *Salmo sebago* Girard. Male, 25.5 inches long, in breeding condition. Taken in Jordan River, tributary of Sebago Lake, at the State Fish Hatchery, Raymond, Maine, November 9, 1912.

PLATE 6.

Sebago Lake salmon, *Salmo sebago* Girard. Female, 21.75 inches long, in breeding condition. Taken in Jordan River, tributary of Sebago Lake, at Raymond, Maine, November 9, 1912.

PLATE 7.

Sebago Lake salmon, *Salmo sebago* Girard. Female, 18.66 inches long, taken in Sebago Lake, Maine, May 31, 1915.



DALL ON NEW ENGLAND SALMONS.

PLATE 8.

Sebago Lake salmon, *Salmo sebago* Girard. Male, 21.33 inches long, taken in Sebago Lake, Maine.

PLATE 9.

'Jumper,' *Salmo sebago* var. Female, 14 inches long, near breeding condition. Taken in Presumpscot River, outlet of Sebago Lake, at North Gorham, Maine, September 25, 1907.

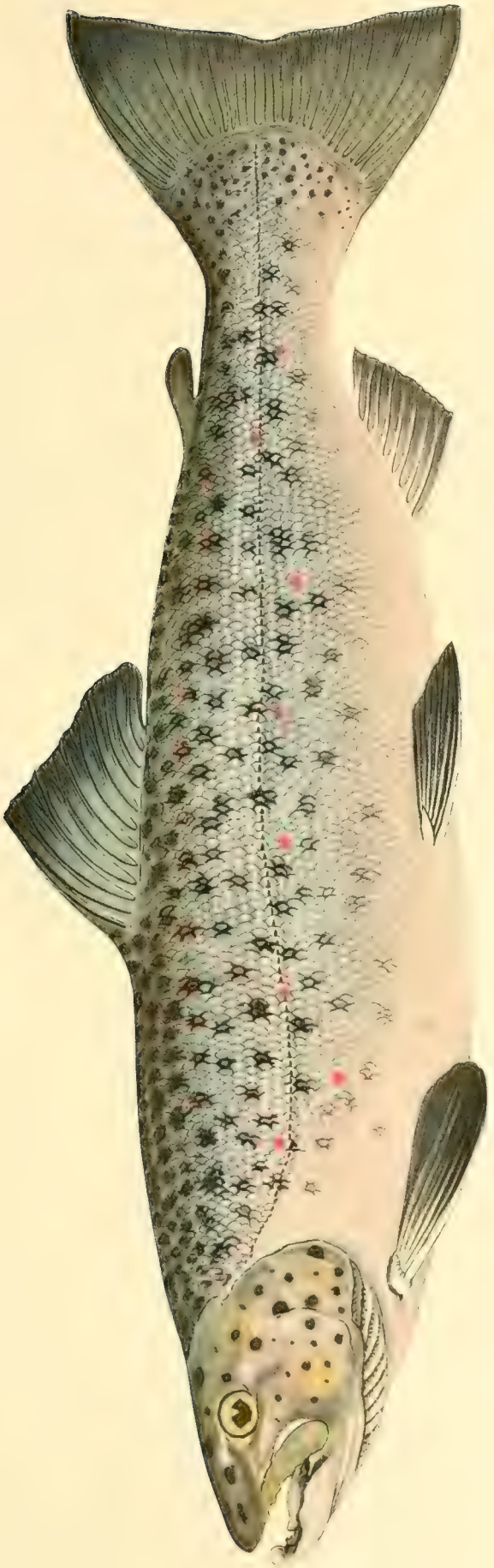


PLATE 10.

Grand Lake salmon, *Salmo sebago* var. Male, 14.25 inches long, in breeding condition. Taken in Grand Lake at Grand Lake Stream, Maine, November, 1915.

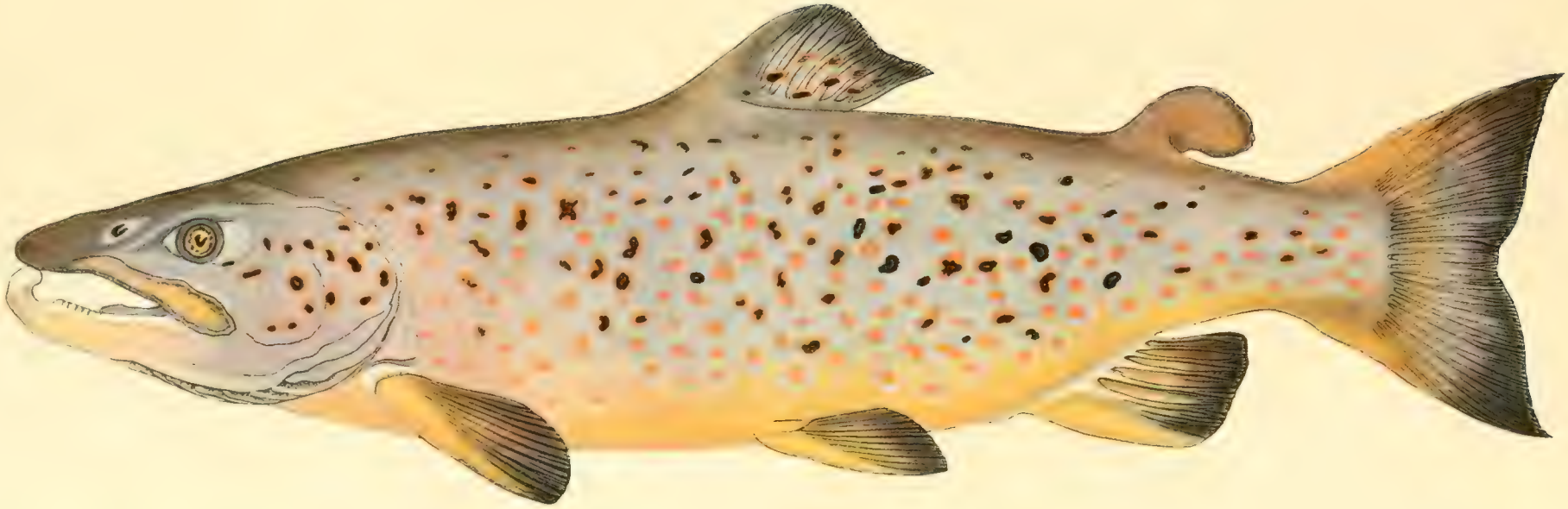
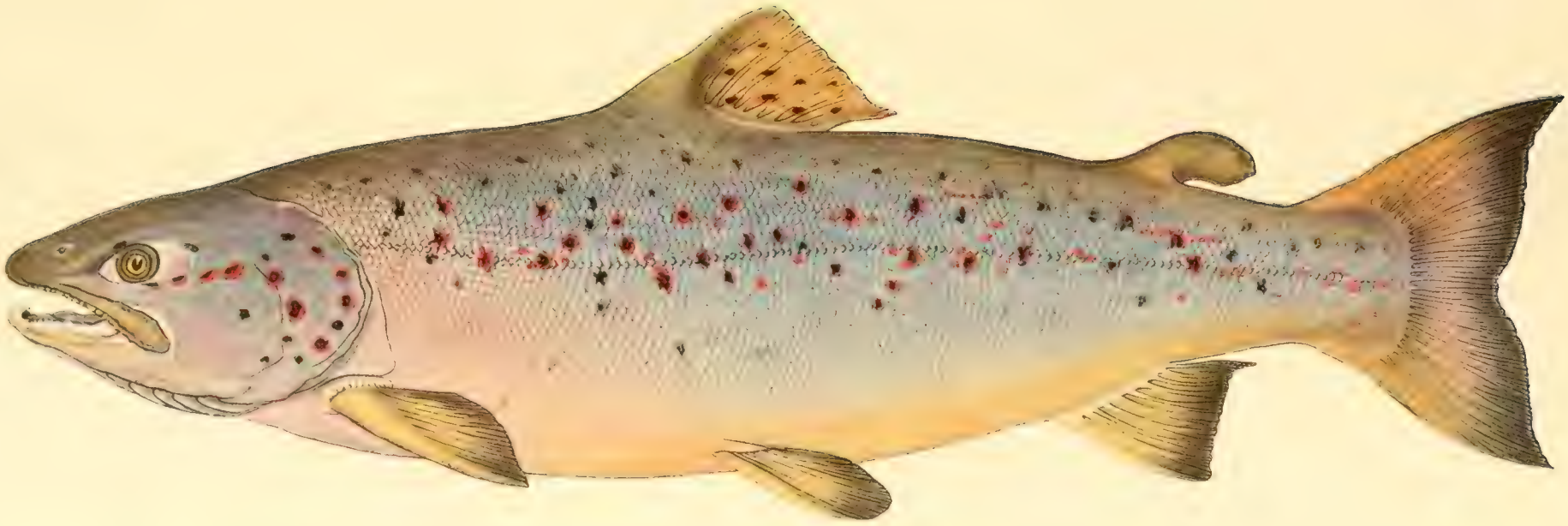


PLATE 11.

Grand Lake salmon, *Salmo sebago* var. Female, 13.5 inches long, in breeding condition. Taken in Grand Lake at Grand Lake Stream, Maine, November, 1915.



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