UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

ANADROMY IN NORTH AMERICAN SALMONIDAE

By George A. Rounsefell

FISHERY BULLETIN 131
From Fishery Bulletin of the Fish and Wildlife Service
VOLUME 58

UNITED STATES GOVERNMENT PRINTING OFFICE - WASHINGTON : 1958

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price 20 cents

ABSTRACT

Although there is a considerable range of variation in anadromy between species of the same genus, each of the four genera of North American Salmonidae occupies a different position in degree of anadromy exhibited. Arranged in descending order of degree of anadromy, the genera are *Oncorhynchus*, *Salmo*, *Salvelinus*, and *Cristivomer*.

There is a close correspondence between lethal stream temperatures for the young of certain species and the anadromous habits of those species.

CONTENTS

ANADROMY IN NORTH AMERICAN SALMONIDAE

By GEORGE A. ROUNSEFELL, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

In discussing the anadromous pattern of the salmonids, inevitably the question of landlocked versus anadromous species or varieties arises. Intelligent discussion of this question demands that the terms be at least tentatively defined. The word "landlocked" as it is and has been used is, of course, a misnomer in the majority of cases; only rarely is a population denied access to the sea. Offhand I can recall only two specific cases. One involves the ponds of Cape Cod, many of which lack an outlet, the excess runoff draining into the sandy soil; the other the rivers in Baja California, which for most of the year disappear into their stony watercourses. These rivers of the Sierra Madre of Baja California are the home of the famed San Pedro Martir trout, *Salmo gairdneri nelsoni*.

Of course, many salmonids live above impassable falls. Such fish are not technically landlocked insofar as access to the sea is concerned. However, they are isolated in that any individuals which migrate downstream can never return. Such a situation is favorable to the development of resident races of a species. The more-usual situation is for so-called landlocked races or species to occupy streams or lakes with access to the sea freely traversable in both directions. Furthermore, in many cases both resident and anadromous salmonids, even of the same species, may occupy the same waters for at least part of the year.

The term "anadromous" is likewise difficult to define with a nice degree of exactitude. It is all very well to say that it means "up-running," but before a fish can run up it must first establish residence in the sea. In anadromy, one is confronted with a surprising divergence. The typical life history of the anadromous salmons of the genus *Oncorhynchus*—the five eastern Pacific salmons—includes from less than 1 year to 4 years at sea, with the average probably a little more than 2. The anadromous members of the genus *Salmo*—*salar*, *gairdneri*, *clarki*, and *trutta*, the Atlantic salmon, the steelhead rainbows and cutthroats, and the European sea trout—likewise usually spend about 2 years at sea before reaching maturity.

There is another group of salmonids, the charrs, in which certain stocks usually regarded as anadromous typically spend only a small portion of each season in the sea. These include *Salvelinus malma*, the Dolly Varden charr, and *S. fontinalis*, the eastern brook trout, or more properly, charr, the sea-run members of which are known locally as sea trout or "salters." *Salvelinus alpinus*, the alpine, red lake, or arctic charr, while a freshwater resident in the southern part of its range, also migrates to the sea in the Hudson Bay and arctic regions. Dolly Varden charr of the Karluk River on Kodiak Island, Alaska, were found to spend less than 60 days a year in the sea.

A few species either cannot reproduce, or cannot do so with sufficient success to maintain a natural population, without residing for some time in a marine environment. These species might well be termed "obligatory anadromous." This group includes at least two of the Pacific salmons: the pink, *Oncorhynchus gorbuscha*, and the chum, *O. keta*. The king salmon, *O. tshawytscha*, perhaps should be included. Chamberlain (1907) tells of king salmon being raised generation after generation for 25 years in fresh water at the Trocadero Aquarium in Paris. I have identified as *O. tshawytscha* a salmon fry collected by Dr. Herbert Warfel in Newfound Lake, New Hampshire, from natural spawning. Although there is little doubt that under exceptionally favorable circumstances king salmon can mature and reproduce wholly in fresh water, there is serious question concerning the chances of successful maintenance of a natural population. Commencing as early as 1904 numerous plants were made in many New Hampshire

NOTE.—Approved for publication, March 17, 1957. Fishery Bulletin 131.

lakes, as well as in other New England lakes. Hoover (1936) says, "they have never established a self-sustaining population in fresh or salt water, either in this state or elsewhere in New England." Therefore, I classify the king salmon as obligatory anadromous.

The silver or coho salmon, *O. kisutch*, has shown little tendency to develop natural resident fresh-water populations in North America. Jordan and McGregor (1925) describe a landlocked salmon from Japan, *O. ishikawee*, which is assumed to be a dwarf form of *O. kisutch*. In Montana (U. S. Fish and Wildlife Service, 1951) success has been claimed in holding and maturing silver salmon in fresh water.

In Crater Lake, Oregon, young silvers, *O. kisutch*, were planted to furnish fresh-water angling. Although there are no stream spawning beds available and only steep talus slopes of coarse rubble in the lake, both the silver salmon and rainbow trout reproduced naturally in the lake, according to Hasler and Farner (1942). However, Wallis and Bond (1950) show rather conclusively that although silvers were planted in the lake it was the kokanee (*O. nerka*), the small landlocked form of the sockeye salmon, that actually reproduced. Kokanees were not officially planted in the lake but were introduced, possibly by accidental mixing with silvers in rearing ponds.

Dwarfed, landlocked silvers are reported from Becharof Lake in the Egegik River system of Bristol Bay (personal communication from George J. Eicher, Jr.).

In view of these occurrences in fresh water we believe that *O. kisutch* should not be classified as obligatory anadromous.

The sockeye salmon, *O. nerka*, is the only one of the five Pacific salmons on this continent about which there is no doubt that it can successfully maintain populations wholly in fresh water.

To bring out the differences in degree of anadromy in the Salmonidae, one can compare the pink salmon with the lake charr, sometimes called the togue or mackinaw. At the one extreme, the pink salmon in some localities spawn in the tidal flats off the mouths of streams so that many pass their entire lives without entering strictly fresh water. At the other end of the scale, the lake charr so rarely leave fresh water that the only instances recorded (Ungava Bay and vicinity, Weed 1934) are not established beyond a reasonable doubt. However, Fred Cleaver (personal communication) states that he has a photograph of a lake charr caught in 1939 at the head of tidewater on the Naknek River in Bristol Bay. These two bits of evidence suggest that perhaps *namaycush* is a rare visitor to the sea in the northern part of its range.

Between these two extremes there are several points at which one can draw a line, always bearing in mind that the Salmonidae is an extremely plastic group, so that what we are saying may not always apply to some small segment of a species.

As already noted, the charrs tend to spend only short periods at sea, and furthermore, all the charrs can develop normally without going to sea. In Alaska there are many streams in which most of the Dolly Varden charr go to sea, but at the same time there are populations of stunted Dolly Vardens in many of these same streams living above impassable falls. DeLacy and Morton (1943) found in the Karluk drainage system during the late spring that while the majority of the Dolly Varden charr were making their annual pilgrimage to the sea many could still be found in fresh water in the streams tributary to Karluk Lake. According to Bigelow and Schroeder (1953) the eastern charr, *Salvelinus fontinalis*, seek salt water in the fall after the breeding season and remain there over winter. Speaking specifically of the streams on Cape Cod, they state that the sea trout go down to salt water in November immediately after spawning, to winter there. The charr begin to run again in April, and all of them are in brackish or fresh water by mid-May. The arctic charr, *S. alpinus*, has a more northern range than either *malma* or *fontinalis*, and its habits vary from theirs accordingly; in the southern part of its range the arctic charr tends to be a resident fish, occurring especially in lakes at high altitudes. Even as far north as the Karluk River it is a resident fish. DeLacy and Morton state that only on rare occasions is the arctic charr encountered in the river below Karluk Lake, and specimens are seen in salt water still less frequently.

In the Hudson Bay region, as in central Alaska, the arctic charr occurs at low elevations. Sprules (1952, pp. 11–12) found landlocked charr in a small lake without an adequate outlet, but in general the charr populations in the area visit the sea regularly.

He states that—

> The local inhabitants were questioned and were of one accord in their accounts of the spawning habits of char. They stated that quantities of char were netted along the coast during the early summer but that the catch decreased during August and only an occasional specimen was obtained at later dates. The fish begin to move into the estuaries of the large rivers in late July and early August and are congregated at the head of tide by late August. Evidently some time is spent in this brackish water before the fish ascend the rapids into the fresh-water system. The ascent is made, in general, during a spring [high] tide or during periods of heavy rainfall which swells the rivers.
>
> The adult char leave the lakes as soon as the shore ice disappears. Even before the ice breaks up on the open lakes the char may be seen crowding along the flood waters near the shore in the rivers. The Eskimos did not know how long the young char remained in fresh water, but it is probable that at least one year is spent there prior to their first migration to the sea.

In the genus *Salmo*, which includes the Atlantic salmon, the steelhead salmons (or trouts), and the sea trout (Loch Leven trout), the seagoing habit is firmly established; at the same time, all of these species have forms that are resident in fresh water. Furthermore, the presumably anadromous forms of *Salmo* are all perfectly capable of maturing and reproducing in fresh water. This is true even of the anadromous form of Atlantic salmon, *S. salar*—millions of sea-run young have been stocked in fresh-water lakes, and they mature and grow as well as the landlocked form.

The Atlantic salmon is probably the most truly anadromous species of *Salmo* in that almost all of the young normally make a definite downstream migration. In the other species, many of the young may elect to remain in fresh water, never becoming anadromous. This is well exemplified by the planting in Maine of *S. trutta*. For years many plants were made in the Orland River of so-called Scotch sea trout, supposedly an anadromous form of *S. trutta* sometimes called *S. trutta trutta* or *S. levenensis* by taxonomists. This resulted in the occasional return of a few sea-run fish but also in the establishment of fresh-water angling for brown trout. In other rivers, such as the Sheepscot, the planting of brown trout, sometimes classified as *S. trutta fario*, has resulted not only in fresh-water angling, but in the return of quite a number of fine sea trout. Similarly, on the Pacific coast there are some resident fish in practically all steelhead streams, regardless of whether the species is *Salmo gairdneri* or *S. clarki*.

The fresh-water forms of the anadromous salmonids normally use a lake as a miniature sea, ascending its tributaries to spawn. These adfluvial (see Rounsefell and Everhart, 1953, p. 33) species usually are smaller than their anadromous counterparts on account of the more restricted diet (Blair 1938), but otherwise their life histories are very similar, even to the acquiring in many lakes of the same overall silvery sheen characteristic of salmons at sea. In refutation of this idea some have pointed out the habit of the landlocked salmon *Salmo salar sebago* of often spawning in lake outlets. However, it should be noted that the anadromous salmons and trouts also spawn below lake outlets. This is the usual practice of the sockeye (*Oncorhynchus nerka*) below Chilko Lake on the Chilcotin tributary of the Fraser, and it occurs below lakes in Alaska. The fry upon emerging from the gravels of the spawning redds must swim upstream to reach their nursery lake. This is contrary to their actions in the lake tributaries, and the factors that determine which direction the fry will swim are not yet understood.

This upstream movement of great numbers of newly emerged sockeye fry has been observed as a massed living band moving upstream from the lower Babine River spawning grounds into Nilkitkwa Lake and from the upper Babine River spawning area into Babine Lake (Johnson 1956).

Since in some places the fry move downstream and in others upstream, it is difficult to comprehend how their movement can be wholly directed by any such physical factors as temperature or current. It might be suggested that these newly emerged fry, which must seek food immediately or perish, will move upstream in the usual situation of lake-outlet spawning streams. These outlet streams usually have a gentle current, and just below the lake they would contain sufficient plankton for the fry to commence feeding. Such active movement in hours of light if directed upstream toward the oncoming plankton might overcome any downstream drift during hours of darkness, especially since the fry emerge at a season when daylight hours substantially exceed those of darkness.

Whether the dwarfed, fresh-water forms of the basic species of salmonids are the result of genetic characteristics or of environment has been at least partially answered in the case of the sockeye. There are in reality not two, but three, forms of sockeye, all of which may be present in the same lake. One type is the anadromous form; the second is the dwarfed, landlocked sockeye, called variously kokanee, little redfish, or silver trout; the third type, discovered first in Cultus Lake by Ricker (1938), was termed by him "residual." Presumably these residual sockeye are direct descendants of anadromous parents. The residual sockeye differ from the kokanee in several respects. They remain a dull olive gray at maturity, whereas the kokanee show the bright-red body and green head characteristic of the mature anadromous form. In Cultus Lake, the kokanee spawn early in August and September; the residuals spawn from October to December, like their anadromous progenitors. The residuals are predominately male.

Ricker suggests in a further paper (1940) that the kokanee populations have been derived from anadromous fish in geologically recent times, the residual sockeye representing a step in this process.

The question of whether the kokanee is a separated species or merely a variant of the anadromous form was answered by Foerster (1947). He reared young kokanee and in the spring of 1934, when they were 3 to 4 inches in length, he marked nearly 64,000 of them by removing their pelvic fins. The fish were liberated in Sweltzer Creek, the outlet of Cultus Lake, below the counting fence so that they could not swim into the lake, but would either have to remain in the stream or descend toward the sea.

None of the marked kokanees were recaptured in 1936 when they would have been in their fourth year and were expected to return, as most of the anadromous Cultus Lake sockeye mature in their fourth year. In 1937, however, in their fifth year, examination of 37 percent of the Fraser River commercial catch (756,000 out of 2,225,000 fish) revealed 25 of the marked kokanees had returned from the sea, and 17 more had returned to the counting fence at Cultus Lake. These fish were all fully grown and of a size comparable with that of the usual 5-year-old Fraser River sockeye.

Further experiments on the kokanee were performed as part of the Grand Coulee salmon relocation program on the Columbia River from 1939 to 1943.[1] In a personal communication Hanavan states that Lake Wenatchee, during those years, supported a large population of kokanees uniformly about 7 to 8 inches in length at maturity. Their mature color was a dull olive green, though rarely a red individual was observed on the spawning grounds. None that might be classed as residuals were observed.

In this study of Columbia River salmon, Hanavan and Fulton performed three marking experiments. In the first experiment, 22,000 Lake Chelan fingerling kokanee were marked and released in the Entiat River, resulting in one adult recaptured in the commercial fishery in its fifth year. In the second and third experiments, Lake Wenatchee kokanee were used. The 29,000 marked fingerlings in the second experiment were released in Icicle Creek, a lower tributary of the Wenatchee River, resulting in 79 adults recovered: 3 in their third year and 76 in their fourth. In the third experiment, 60,000 young marked kokanee were released in Lake Wenatchee, their "home" lake. Of these, 302 were recovered as sea-run adults: 3 in their third year, 287 in their fourth, and 12 in their fifth.

Contrary to the Cultus Lake kokanee, the sea-run adults from these experiments were smaller than the normal sea-run stock at maturity. Females averaged 2.4 to 2.7 pounds compared with 3.1 pounds, and males averaged 2.6 to 2.8 pounds compared with 3.4 pounds for marked sea-run stock.

These experiments indicate that the kokanee sockeye have retained the ability to live a marine existence and find their way back to their natal stream. Surprisingly enough, their size at maturity was only slightly less than that of the normal sea-run stocks. Although the difference in size may be genetic, the chief genetic difference between the two forms would seem to lie in the propensity toward anadromy.

There appears, thus, to be some tendency toward lacustrine existence in all anadromous populations and some tendency toward anadromy in all lacustrine salmonids. The presence of adfluvial populations in the headwater lakes of river systems may well be of great advantage to a species by furnishing sufficient seaward migrants to reestablish anadromous populations after streams have been obstructed for a considerable period.

Returns from seaward migrants of the abundant kokanee populations would appear to be the only

[1] Mitchell G. Hanavan and Leonard A. Fulton, U. S. Fish and Wildlife Service, manuscript.

logical source for the large number of adult sea-run sockeye that have attempted at various times to ascend the impassable falls below Lake Chelan or the high dam on the Similkameen River in western Washington. Chapman (1941), who observed these migrations in 1937 and 1938, writes that young, downstream sockeye migrants were reported in an irrigation diversion that takes off from the dam in the Similkameen River. The only source of such migrants is the kokanee population in Lake Palmer, above the dam.

In Maine, occasional Atlantic salmon are found attempting to pass dams that have been impassable barriers for many years. Their source has been disputed, many believing them to be merely strays; however, it is the writer's belief that at least the larger share of such strays are progeny of salmon residing in the lakes upstream from the dam. The fact that for many years young Atlantic salmon of anadromous parentage were stocked in most of the Maine lakes already populated by landlocked salmon may have even intensified the tendency for a small percentage of the young to descend to the sea.

DEGREES OF ANADROMY

Before we can measure the degree to which these different salmonid species are anadromous, we must first establish some criteria. The following six criteria have been used in this analysis:

1. Extent of migrations in the sea.
2. Duration of stay in the sea.
3. State of maturity attained at sea.
4. Spawning habits and habitat.
5. Mortality after spawning.
6. Occurrence of fresh-water forms.

Each criterion has been subdivided into as many categories as appears feasible from our present knowledge. The category signifying the most anadromous condition has been given a weight of 10, the least significant a weight of 0, and the categories between the two have been assigned weights which are, of course, subjective. Although this method can be criticized on the grounds of not being truly quantitative, it does yield a rather satisfactory basis of classification. Perhaps its chief fault lies in the inability to determine the relative merits of each of the six criteria.

The criteria, the categories (with assigned weights in parentheses) arranged in the order of decreasing anadromy, and the species assigned to each category are as follows:

Criterion 1.—Extent of migrations in the sea.

Category *a* (10).—Migrate several hundred miles from their home streams and large numbers occur very far offshore. *Oncorhynchus keta, O. nerka, O. gorbuscha.*

The occurrence of these species in abundance far offshore was demonstrated by Barnaby (1952) and Fukuhara (1953, 1955).

Category *b* (8).—Migrate long distances, but are not abundant far offshore. *Oncorhynchus tshawytscha, O. kisutch; Salmo salar.*

It may be noted that these three species are more piscivorous than the preceding species, which may somewhat affect their remaining closer inshore where more of the smaller pelagic fishes would be encountered.

Category *c* (6).—Migrations chiefly coastwise, somewhat less extensive than in the preceding categories. *Salmo gairdneri.*

The rainbow steelhead is occasionally taken at sea (Fukuhara 1955, Snyder 1921), and they are often captured in salmon traps, even along the outer coast.

Category *d* (4).—Migrations coastwise, chiefly estuarine and usually short. *Salmo trutta; Salvelinus alpinus, S. malma.*

See Grainger (1953), Sprules (1952), and many authors not cited concerning *S. trutta* in Europe.

Category *e* (2).—Migrations in sea very short. *Salmo clarki; Salvelinus fontinalis.*

Neave (1949, p. 21) says of *S. clarki* in the Cowichan River on Vancouver Island, that "In the neighbourhood of the river mouth the cutthroats lead a characteristic estuarine existence moving in and out with the tide. Up-river migrations occur in autumn and spring . . . ."

In southeastern Alaska, the salmon traps take many rainbow steelheads, *Salmo gairdneri*, and often take Dolly Varden charr, *Salvelinus malma*, but cutthroat steelhead, *S. clarki*, are rarely captured even though they may be caught by angling in many southeastern Alaska streams.

The eastern charr, *Salvelinus fontinalis*, likewise is chiefly estuarine. Doan (1948) says that they descend Hayes River into Hudson Bay in the autumn, and in the winter can be caught through the ice at a distance of 7 or 8 miles out from the shore. White (1942) says that some wandered 8 or more miles from their home stream and ascended other streams.

Category *f* (0).—Rarely or never in the sea. *Salvelinus oquassa, S. aureolus; Cristivomer namaycush.*

Criterion 2.—Duration of stay in the sea.

Category *a* (10).—Entire life spent in the sea and intertidal zone. *Oncorhynchus gorbuscha, O. keta* (intertidal populations).

Pink salmon, *O. gorbuscha*, spawn successfully in intertidal gravels in which the salinity in the redds at high tide may reach a maximum of 30 parts per thousand (Hanavan and Skud, 1954). Hanavan stated (personal communication) that chums, *O. keta*, also commonly spawn in intertidal stream areas and live; and that well-developed chum eggs were turned up several times while he was digging in intertidal stream gravels.

Category *b* (9).—All young enter the sea immediately after emerging as fry and remain until mature. *Oncorhynchus gorbuscha, O. keta* (upstream populations).

It is usually considered that pink- and chum-salmon fry commence feeding after they reach the sea, but there must be some doubt on this point. Pink-salmon fry hatching over 250 miles from the sea above the Hells Gate Canyon of the Fraser have a long journey to reach the sea, and presumably would feed en route. The same reasoning applies with more force to some populations of chum salmon. Gilbert and O'Malley (1921) state that chums spawn as far as 2,000 miles up the Yukon. It would seem impossible for the young to make their descent to the sea without feeding. It is well known that chum-salmon fry stocked in a lake will feed voraciously, grow quickly, and furnish excellent fly fishing. In the Egegik River system, chum-salmon fingerlings are reported (personal communication, George J. Eicher, Jr.), which presupposes a long feeding period in fresh water.

That pink-salmon fry do feed in fresh water, even in short streams, is indicated by the observations of Chamberlain (1907), who states that a few have been found to contain remains of insects, larvae, and crustacea.

Category *c* (8).—A high proportion of the young descend to the sea before their first winter. *Oncorhynchus tshawytscha.*

This category applies especially to the fall-spawning king salmon. However, many young kings, especially those hatching from spring-running parents (which usually spawn far upstream) remain in the streams over winter before descending as smolts. These latter populations of kings more properly belong in the next category.

Category *d* (7).—Majority of young migrate seaward following the first winter. *Oncorhynchus tshawytscha, O. kisutch.*

All young enter the sea with the exception of a few precocious males of *O. tshawytscha* that may mature at a very small size in fresh water. This applies both to the silver, *O. kisutch*, and the spring-running king, *O. tshawytscha*. A very small proportion of the adult silvers taken in British Columbia went to sea as fry, only 22 out of 6,312 fish aged (Pritchard 1940); 54 left in their third year, 2 left at some undetermined older age, and all the rest left in their second year. This average age of smolt migrants varies geographically. I am informed (personal communication, George J. Eicher, Jr.) that the average Bristol Bay silver salmon matures in its fifth year and goes to sea in its fourth, i. e., at an age of 5_4 instead of the predominant 3_2 found in Washington and British Columbia fish.

Category *e* (6).—Majority of the young enter the sea after their first winter, but some may elect to remain in fresh water as residuals. *O. nerka.*

These young sockeye of anadromous parentage which elect to remain in fresh-water are predominantly males.

Category *f* (5).—The young normally enter the sea after their first winter and remain there until mature, but some may remain behind in lakes as normal fresh-water residents. *Salmo salar.*

The anadromous form of *S. salar* apparently becomes easily adapted to an adfluvial existence judging from successful rehabilitation of adfluvial populations in New York State using eggs from sea-run parents (Greeley 1955). This, of course, does not mean that *S. s. sebago* may not differ genetically from the present sea-run stocks, but it does indicate that the transposition from sea-run to adfluvial is relatively easy. For the sockeye placed in the preceding category the transposition is obviously more difficult, judging from the differences between the kokanee, *Oncorhynchus n.*

kennerlyi, and the residual sockeye in fresh water which derive directly from sea-run stock. In this category, as in all of the preceding categories, the fish do not ordinarily reenter fresh water until they return as adults on their spawning migration.

Category *g* (4).—The young enter the sea after the first winter and usually remain at sea until mature, which may take from 1 to 2 or 3 years. *Salmo gairdneri*, *S. clarki*.

Anadromy is optional and resident fresh-water individuals occur in practically all streams with anadromous stock. Whether there is any inheritable difference in those that develop at sea and those remaining in fresh water has long been the subject of much controversy. Neave (1944) believes that there are two strains of *Salmo gairdneri* in the Cowichan River, British Columbia, one anadromous and the other resident. However, the existence of two strains of *S. gairdneri* in the same waters may depend largely on there being a sufficiently large lake in a stream system to encourage the development of an adfluvial strain. Shapovalov and Taft (1954, p. 158) state,

While the salmon [*O. kisutch*] go to sea almost immediately, some of the [young] steelhead remain for a whole season in the lagoon or the lower portion of the stream, after which some move out to sea, while others make an upstream migration and then a second downstream migration. While most of the steelhead go to sea before maturing, some fish of both sexes spawn before going to sea, while still others complete their life cycles without going to sea at all.

Briggs (1953) agrees with Neave that two types of *S. gairdneri* occur in the same streams, one anadromous and the other permanently resident in fresh water, basing his conclusions largely on the idea of spatial isolation, since the smaller "rainbows" tend to spawn in smaller tributaries and in shoaler water. No data are given on the age or size of the fish he designated as rainbows.

Experiments to test the pure strain of "rainbow" trout that has been propagated for over 30 years at the Manchester, Iowa, station of the U. S. Fish and Wildlife Service (Ratledge and Cornell, 1953; Carbine 1953) showed absolutely no difference in the migratory tendencies of the Manchester strain compared to nonpure strains from other stations.

Category *h* (3).—The majority of the young enter the sea after the first winter, but some remain in fresh water. A portion of the young that enter the sea may reenter fresh water before maturity. *Salmo clarki*, *S. trutta*.

Category *i* (2).—The majority of the young enter the sea after the first winter, but some remain in fresh water. The young that enter the sea normally return to the stream before maturity, and may visit the sea more than once before they attain maturity. *Salvelinus fontinalis*, *S. malma*, *S. alpinus*.

The annual visit of a portion of the population to the sea is in the nature of a feeding migration. The return migration (usually composed of both immature and adult fish) is often made many months before the spawning period and the adults may continue to feed.

Wilder (1952) has definitely established that in the Moser River, Nova Scotia, the sea trout and fresh-water trout constitute one taxonomic unit. He also found that a much larger proportion of the fish migrated to sea from Mill Brook, which contains a few shallow lakes, than from the main river, which contains several deeper, cooler lakes. This agrees with the findings of White (1941), that *S. fontinalis* moves downstream slowly at low temperatures. With a temperature varying between 0° and 5° C. from April 17 to 28, 1940, only 142 trout moved downstream and of these 36 reversed their direction, while from April 29 to May 11 with the water temperature varying from 5° to 11° C. more than 700 trout descended and only 6 ascended the stream. Wilder concludes that if descending trout encounter cold bodies of water their tendency to migrate is inhibited. This seems to indicate that they are seeking cooler water. If they find a cool lake they may remain instead of continuing to the sea. This behavior is in accord with the comparative upper-lethal-temperature tolerance of *S. fontinalis* and other salmonids discussed in a following section.

According to Bigelow and Schroeder (1953) the eastern charr, *S. fontinalis*, on Cape Cod go down to salt water in November immediately after spawning and return in April, with all of them being in brackish or fresh water by mid-May. However, the same species in Nova Scotia apparently behave in very similar fashion to the Dolly Varden charr in central Alaska. White (1940, p. 176) says,

Smolts, kelts, and nonmature large fish descend in May and early June to the sea, to remain feeding in the estuary or near the shore. They began (1939) to ascend the river in late June, and 93 percent of the "run" was in July.

These trout agree with the local salmon in having smolts that become silvery before migration and that are 2 or 3 years old. Trout smolts and kelts remain in the sea only about two months before returning to fresh water.

Salvelinus malma, the Dolly Varden charr, usually descend to the sea in May and return in July at Karluk, but in smaller streams, especially those without lakes, I believe that both young and adults may spend the winter in salt water. Thus in Ketchikan Creek in southeastern Alaska I have taken immature *Salmo gairdneri* by angling throughout the winter in the deeper holes and log jams but never saw a Dolly Varden. In the early summer Dolly Varden of all sizes can be seen entering the mouth of the creek in advance of the salmon runs. Fred Cleaver (personal communication) quotes Robert Vincent of the Alaska Department of Fisheries as saying that in 1956 on Afognak Island *Salvelinus malma* entered Big Kitoi Creek in the fall, spawned in mid-October, and retreated to the sea before winter. It thus would appear that the season and duration of marine life for *S. malma* is dependent partially on latitude (probably relative and actual sea and stream temperatures) and partially on the size and physical characteristics of any particular stream, since in small streams toward the north winter survival may be difficult unless the stream contains a deep, accessible lake.

Category *j* (0).—This last group comprises species that seem to have become thoroughly adapted to life in fresh water. Rarely, if ever, does an individual visit the sea. *Salvelinus oquassa*, *S. aureolus*; *Cristivomer namaycush*.

Criterion 3.—State of maturity attained at sea.

Category *a* (10).—Maturity of gonads usually very advanced, often before the fish enter fresh water. *Oncorhynchus gorbuscha*, *O. keta*.

Category *b* (8).—Maturity of gonads advanced, as fish enter fresh water. *Oncorhynchus tshawytscha*, *O. keta*.

This category applies to the fall-spawning king, *O. tshawytscha*, and a few of the chums, *O. keta*, that make long migrations.

Category *c* (6).—Gonads maturing as the upstream migration commences. *Oncorhynchus kisutch*, spring-run *O. tshawytscha*.

Category *d* (4).—Eggs usually not in advanced stage of maturity when fish reach fresh water. *Oncorhynchus nerka; Salmo gairdneri*, *S. salar*, *S. clarki*, *S. trutta*.

Egg maturation in fresh water may require a few weeks to as long as several months. For instance, over three-quarters of the Quinault Lake sockeye, *O. nerka*, reach the lake before July 7, and some start ascending the river as early as January (Rounsefell and Kelez, 1938; p. 756) yet they spawn in the fall, after maturing their eggs in the deep, cool waters of the lake. The necessity for cool water in which to mature the eggs may account for the fact that only sockeye running late in the fall usually spawn in rivers below lakes, since the water temperatures below the lakes in midsummer are rather high. Thus the U. S. Bureau of Fisheries placed a weir across the Ozette River, on the outer Washington coast in 1926, to hold sockeye for the hatcheries, but the fish, which practically all ascended the river before July 1, could not survive holding in the river, which derived its flow from the surface waters of Ozette Lake. This stage includes the sockeye, *O. nerka*, which is a lacustrine anadromous form with smaller eggs than the four fluvial anadromous *Oncorhynchus* (Rounsefell 1957).

All of these fish move into streams on a spawning migration even though the gonads are seldom in an advanced stage of maturity during this migration. Thus in the Penobscot River adult *Salmo salar* commence running in late April or May but these early arrivals spawn, together with those ascending later, in the late autumn.

Category *e* (2).—Gonads may vary from immature to slightly mature. The upstream migration may include returning young as well as adults and may bear no relation to time of spawning. *Salvelinus fontinalis*, *S. malma*, *S. alpinus*.

Concerning *S. malma*, Evermann and Goldsborough (1907, p. 266) observed the upstream migration of Dolly Varden charr of all sizes at Pablof Falls in Pablof Creek, Chichagof Island, on July 25. They state that the ovaries " . . . were quite small and immature, and this was evidently not their spawning season."

Category *f* (0).—No adults returning from the sea. *Salvelinus oquassa*, *S. aureolus*; *Cristivomer namaycush*.

Criterion 4.—Spawning habits and habitat.

Category *a* (10).—Spawn successfully in the intertidal zone. *Oncorhynchus gorbuscha*, *O. keta*.

Category *b* (7).—Spawn in streams where there is flowing water. All species of *Oncorhynchus* and *Salmo; Salvelinus fontinalis*, *S. malma*, *S. oquassa*.

Cooper (1940), says of *S. oquassa*, the blueback charr, that "It was seldom seen except when it entered streams in October to spawn."

Category *c* (3).—Lake spawners that construct a spawning redd and bury their eggs in similar fashion to the stream spawners. *Oncorhynchus nerka; Salvelinus alpinus*, *S. fontinalis*, *S. aureolus* (?).

For *S. aureolus* the available information on spawning (Bailey and Oliver, 1939) indicates that they spawn on shallow reefs in Lake Sunapee within the 10-foot contour. There is no information as to whether they construct a redd as do the other salmonids, with the exception of *Cristivomer*.

Category *d* (0).—Lake spawners that do not construct a spawning redd. *Cristivomer namaycush*.

This category differs from category *c* in that the spawning adaptation to fresh water is so complete, and the urge to make an upstream spawning migration so completely lost, that the fish not only spawn in the lakes, but do so without constructing a redd (Royce 1951). Regarding the selection of a spawning site Royce says (p. 66) that as the fish make no attempt to bury the eggs, the bottom must have crevices into which the eggs can roll, and that the location of these suitable areas of bottom in the lake is primarily determined by currents or wave action which keep the bottom swept clean. Quoting from Royce (pp. 68–70),

> The writer has found no evidence that lake trout select a lake bottom supplied with spring water for the deposition of their eggs . . . .
>
> No nest or redd was built. The males spent their time cruising along close to the bottom, occasionally giving the stones a little fillip with their tails . . . . This activity cleaned several hundred square feet of bottom . . . .
>
> No tendency towards oviposition in any definite place on the spawning area was observed. The trout mated at random over the area cleaned off, and there was no attempt by either sex to bury the eggs . . . .

There is apparently at least one race of *Cristivomer namaycush* that is adfluvial. Dymond (1926, p. 68) says,

> It is said that there exists in Lake Nipigon a sort of lake trout known locally as "black trout," which ascends some of the rivers, notably the Sturgeon river, at spawning time. This form . . . seldom attaining more than four or five pounds in weight. . . . It is a fact, however, that very dark trout, all of medium size, do enter the Sturgeon river at spawning time in large numbers. They also spawn earlier than the trout which spawn in the lake, usually beginning about September 20.

No mention is made of the spawning behavior of this group of lake charr, so we can only assume that they spawn without building a redd.

Criterion 5.—Mortality after spawning.

Category *a* (10).—All die soon after spawning, including fresh-water stocks. All species of *Oncorhynchus*.

Category *b* (5).—A few anadromous adults die soon after spawning; subsequent survival of the others is very low. *Salmo salar*, *S. gairdneri*.

Category *c* (0).—Spawning does not have a drastic effect on survival. *Salmo clarki*, *S. trutta;* all species of *Salvelinus; Cristivomer namaycush*.

Criterion 6.—Occurrence of fresh-water forms.

Category *a* (10).—No natural fresh-water populations are known to exist. *Oncorhynchus gorbuscha*, *O. keta*.

Category *b* (9).—No natural fresh-water populations are known to exist, but adults will mature and spawn in fresh water with very limited success. *Oncorhynchus tshawytscha*.

Category *c* (8).—Fresh-water populations are rare. *Oncorhynchus kisutch*.

Category *d* (7).—Fresh-water form is common, but young of anadromous stock remaining in fresh water are chiefly males and differ from fresh-water stock. *Oncorhynchus nerka*.

Category *e* (5).—Fresh-water forms are common; the young of anadromous stock in streams normally enter the sea with the exception of precocious males. Anadromous stock will form normal adfluvial fresh-water populations, but not fluvial populations. *Salmo salar*.

Category *f* (3).—Fresh-water forms are very common, some of the young of anadromous stock usually remain in streams forming fluvial populations. *Salmo gairdneri, S. clarki, S. trutta; Salvelinus malma, S. fontinalis, S. alpinus.*

Category *g* (0).—No anadromous forms. *Salvelinus oquassa, S. aureolus; Cristivomer namaycush.*

It is of interest that when the species of Salmonidae are plotted (fig. 1) according to the six criteria just considered (see also table 1), each of the four genera occupies a distinct area in the degree of anadromy exhibited.

TABLE 1.—*Degrees of anadromy of normal populations of North American Salmonidae*

[According to six criteria, pp. 175 to 179]

Genus and species	Subjective criterion— 1	2	3	4	5	6	Degree of anadromy
Oncorhynchus:							
gorbuscha	10	9–10	10	7–10	10	10	56–60
keta	10	9–10	8–10	7–10	10	10	54–60
tshawytscha	8	7–8	6–8	7	10	9	47–50
kisutch	8	7	6	7	10	8	46
nerka	10	6	4	3–7	10	7	40–44
Salmo:							
salar	8	5	4	7	5	5	34
gairdneri	6	4	4	7	5	3	29
trutta	4	3	4	7	0	3	21
clarki	2	3–4	4	7	0	3	19–20
Salvelinus:							
malma	4	2	2	7	0	3	18
fontinalis	2	2	2	3–7	0	3	12–16
alpinus	4	2	2	3	0	3	14
oquassa	0	0	0	7	0	0	7
aureolus	0	0	0	3	0	0	3
Cristivomer:							
namaycush	0	0	0	0	0	0	0

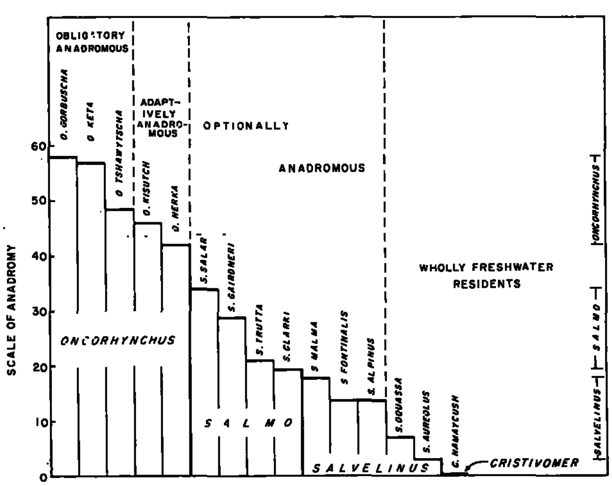

FIGURE 1.—Species of North American Salmonidae classified by degree of anadromy (based on table 1).

The fact that the four genera of North American Salmonidae occupy successive positions in their propensity toward anadromy may be of phylogenetic significance and should not be ignored in any study of their interrelationships.

RELATION OF ANADROMY TO LATITUDE

A rather interesting aspect of anadromy in the North American Salmonidae is the effect of latitude on the degree of anadromy. Different species inhabit different ranges of latitude, but within each species there seems to be a greater degree of anadromy toward the north. Starting with the lake charr, *Cristivomer namaycush*, we find that the only records indicating this species may occasionally visit the sea are for Ungava Bay in the Arctic and Naknek River in Bristol Bay, Alaska.

The arctic or alpine charr, *Salvelinus alpinus*, is known as the sea trout in the Arctic, where most of the populations are anadromous. It has been little studied on the Pacific coast, where it may easily be confused with the Dolly Varden charr; but in the Karluk River, it is lacustrine in habit, only occasional individuals going to sea. On the Atlantic coast also, toward the southern end of its range, the anadromous form of *S. alpinus* is not found, but there are fresh-water groups, such as *S. oquassa, S. aureolus,* and *S. marstoni*, that are either fresh-water counterparts of *S. alpinus* or closely related forms.

For the eastern charr, the northern populations are also more anadromous, since in the southern part of its natural range it is confined to the cooler mountain streams of the southern Appalachians. In New England, anadromous *S. fontinalis* occurs in many rivers on Cape Cod and in Maine. Farther north, on Prince Edward Island and in the southern drainage of Hudson Bay, a large share of the populations visit the sea.

For the genus *Salmo* the evidence is not so clear that latitude affects anadromy. Landlocked *S. salar* occur in lakes in New England, Newfoundland, eastern Canada, and Labrador. That is, the ranges of the landlocked and anadromous forms are similar. The steelhead cutthroat, *S. clarki*, occurs only in the anadromous form in the northern portion of its range in Alaska.

The fact that *Salmo gairdneri* and *S. clarki* have anadromous populations far to the south of any anadromous populations of *Salvelinus* appears to be related to their being definitely more southern in general distribution and thus able to thrive in waters too warm for *Salvelinus*. *Salmo clarki* does not occur in western Alaska, and *S. gairdneri* avoids the colder situations. Thus, *S. gairdneri* is absent from the Egegik and Ugashik Rivers, the coldest of the main Bristol Bay rivers (personal communication, George J. Eicher, Jr.).

It is interesting to note that the kokanee, *Oncorhynchus nerka kennerlyi*, is not recorded from any of the Alaska sockeye lakes. It does occur in Skilak Lake, in Cook Inlet (personal communication, George J. Eicher, Jr.).

The kokanee does occur in a number of the Fraser and Columbia River lakes and even in many of the coastal lakes, both on Vancouver Island and in the Puget Sound region. This poses an interesting question, namely, What are the factors in the environment which militate for or against anadromy? One factor may be temperature. The salmonids as a group are cold-water species. Those that live in the surface fresh waters in the north must, farther south, spend the summer months in the hypolimnion of the lakes. In southern waters, they cannot exist in shallow lakes that lack a thermocline or in deep lakes in which the oxygen of the hypolimnion is largely exhausted during the summer.

Because in the southern part of their ranges some species are unable to tolerate the surface temperatures of the lakes in summer, any spring migration from the lakes must take place before summer stratification develops. There is much variation among lakes in the date of the establishment of a thermocline and in the rapidity with which it forms. Because of this circumstance there is always the possibility of some young of a normally anadromous fish being trapped in the deeper waters of a lake at the time when they should migrate seaward. Such occurrences not uncommonly happen to anadromous sockeye populations in the southern part of their range.

Whether the trapping of anadromous young by a thermocline has any bearing on the existence of fresh-water forms of a species is not yet fully proved; undoubtedly it favors the existence of the residual form of the sockeye discussed by Ricker (1938), but whether these residual populations are the potential progenitors of landlocked forms is uncertain. Ricker points out that such an origin for the kokanees is not only possible but highly probable. He shows several respects in which the kokanees differ from the residuals, one of the most significant being that of their resistance to certain fresh-water parasites. This resistance must be of genetic origin, but if it can be established by selection, rather than mutation, there is no reason to doubt that the kokanee may have originated independently in many different localities.

RELATION OF ANADROMY TO LETHAL TEMPERATURES

The temperature tolerance of young Salmonidae bears an interesting and significant relation both to the degree of anadromy exhibited by the various species and to special adaptations in their life histories. Table 2 and figure 2 show the upper lethal stream temperatures for the young of several species. The data for *Oncorhynchus* (except *kennerlyi*) are from Brett (1952, p. 305) and the temperatures for the other species have been estimated either by the difference in their regression lines from that of *O. keta* in figure 26 of Brett (taken from Fry, 1947) at 1,000 minutes, or from Black (1953).

TABLE 2.—*Upper lethal temperatures for young Salmonidae in fresh water*

Genus and species	Ultimate upper lethal temperature (° C.) [1]	Estimated upper lethal temperature (° C.)
Cristivomer: namaycush	----------	[2] 23.2
Salvelinus: fontinalis	----------	[2] 24.2
Salmo:		
trutta	----------	[2] 25.5
gairdneri kamloops	----------	[3] 25.7
salar	----------	[2] 26.1
Oncorhynchus:		
tshawytscha	25.1	----------
kisutch	25.0	----------
nerka	24.4	----------
nerka kennerlyi	----------	[4] 23.9
gorbuscha	23.9	----------
keta	23.8	----------

[1] From Brett (1952, p. 305).
[2] Derived from figure 26, Brett 1952 (after Fry, 1947) by temperature difference in regression lines at 1,000 minutes from regression line for *O. keta*.
[3] From Black (1953); represents total mortality in 24 hours for fish acclimated at 11° C.
[4] Estimated from Black (1953) as being 0.5° C. lower for 11° C. acclimation temperature and 50% morta ity in 24 hours than for *O. nerka*, as shown in figure 6 of Brett (1952).

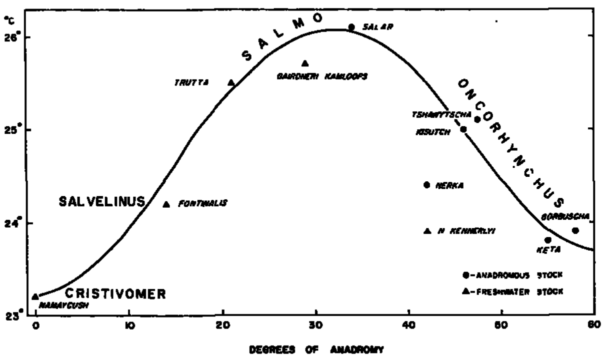

FIGURE 2.—The upper lethal temperatures for the young of certain species of North American Salmonidae in fresh water. (Temperature in degrees Centigrade.)

In those Salmonidae with the lowest upper-temperature limits, *Cristivomer namaycush*, *Oncorhynchus keta*, and *O. gorbuscha*, the young stay in cool water. In *Cristivomer* this is accomplished by keeping in the cool stratum of the lakes, which means retreating to the hypolimnion during summer, especially in more southerly latitudes. In *Oncorhynchus gorbuscha* and *O. keta* the young emerge from the redds quite early in the spring and immediately descend to the sea, thus avoiding high, summer stream temperatures.

It will be noted that although *O. nerka* exhibits a lower degree of anadromy than *kisutch* or *tshawytscha* (fig. 1), the young of *nerka* have distinctly the lower upper-temperature tolerance. This intolerance to higher temperatures fits in with the fact that *nerka* is lacustrine anadromous rather than fluvial anadromous: the young upon emerging from stream redds seek a nursery lake in which to grow. Only lakes that are temperature stratified in summer support runs of *nerka* in its southern range. In the few instances in which young sockeye do not enter a lake, such as the stock spawning in Harrison Rapids in the Fraser River system or the "creek" sockeye found in a few British Columbia streams, the young descend to the sea as fry after the manner of *keta* and *gorbuscha*.

The young of *Oncorhynchus kisutch* and *O. tshawytscha* have a much-higher temperature tolerance than the other members of the genus, as the young of *kisutch* and a fair proportion of those of *tshawytscha* live in the streams during the summer months.

These differences in tolerance of the four fluvial anadromous species of *Oncorhynchus* are reflected in the southern limits of their ranges. For instance, Snyder (1931, p. 16) says,

> Besides the king salmon, three other species enter Klamath River to spawn, namely, the silver salmon (*Oncorhynchus kisutch*), the humpback (*O. gorbuscha*) and the dog salmon (*O. keta*). The humpback and dog salmon are seldom seen and the fishermen are not familiar with them. The silver salmon occur in large nunbers, the migration being later than that of the king salmon.

The king salmon is abundant as far south as the Sacramento River, and the silver salmon occurs in smaller coastal streams south to Monterey. However, the steelhead rainbow, *Salmo gairdneri*, regularly inhabits the coastal streams of southern California—Shapovalov and Taft (1954) say from the United States–Mexico boundary, or possibly even from Baja California northward. This is in keeping with the upper lethal temperatures for the young of *Salmo salar*, *S. trutta*, and *S. gairdneri kamloops*—all of which are higher than for any species of the other genera.

The anadromous cutthroat, *Salmo clarki*, according to Snyder (1940), ranges only as far south as Mad River, north of San Francisco. DeWitt (1954) has extended this range slightly, to the Eel River. This suggests that the upper lethal temperature for the young of *clarki* may be somewhat lower than for the young of *S. gairdneri*. Since the tolerance for the anadromous *O. nerka* is higher than for the adfluvial *O. nerka kennerlyi*, it is probable that the upper lethal temperature for anadromous *S. gairdneri* may similarly be higher than for the adfluvial *S. gairdneri kamloops*.

Brett's regression curve (1952; fig. 26) for *Salvelinus fontinalis* did not parallel regression curves for the other species, in that it had a steeper slope. Therefore, the upper lethal limit could not be obtained with the same degree of assurance. However, the relative position of *S. fontinalis* is undoubtedly correct, since it cannot tolerate midsummer temperatures in the main portions of many streams thickly populated with the parr of *Salmo salar*. In such situations *fontinalis* seeks the cooler, spring-fed tributaries.

The lower limits of lethal temperatures are not so well defined as the upper, but in general there must be some correspondence between them. The only species of *Oncorhynchus* in the Arctic Ocean are *gorbuscha* and *keta*. Thus Dymond (1940) records both *gorbuscha* and *keta* from the mouth of the Mackenzie River. He mentions a notable run of *keta*, some weighing 20 to 25 pounds, in the Mackenzie in 1914, and in 1930 one was captured 5 miles below Fort Smith in the Slave River, tributary to the Mackenzie. Kennedy (1956) reports a chum salmon taken in Great Slave Lake. Dymond also mentions that Borisov (1928) notes a chum salmon taken in the Lena River of northern Siberia.

That members of the genus *Salmo* cannot tolerate as cold situations as the other genera is indicated by their comparative distribution. On the Pacific coast, *S. clarki* does not extend beyond southeastern Alaska and *S. gairdneri* is absent from the colder rivers of Bristol Bay.

On the eastern side of the continent, *Salvelinus alpinus* extends to Baffin Island, but *Salmo salar* only to the Koksoak River in Ungava Bay (Dunbar and Hildebrand, 1952) and in very small numbers in west Greenland.

A most significant feature of the lethal temperature limits found in the various species is the manner in which these limits affect the life histories. For instance, it has already been noted that *Salvelinus alpinus*, *S. fontinalis*, and *S. malma* are all regular visitors to the sea in the northern part of their ranges, but toward the southern end their low upper-temperature tolerance confines them to the cooler waters found at higher altitudes.

SUMMARY

The Salmonidae are very plastic and exhibit all degrees of anadromy. Six criteria have been used to classify them according to degree of anadromy. (1) Extent of migrations in the sea, (2) duration of stay in the sea, (3) state of maturity attained at sea, (4) spawning habits and habitat, (5) mortality after spawning, and (6) occurrence of fresh-water forms.

Gaging the degree of anadromy by these criteria, each of the four genera occupies a different position. *Oncorhynchus* is the most anadromous, following in decreasing degree by *Salmo*, *Salvelinus*, and *Cristivomer*.

In general, within a species the degree of anadromy is greater toward the northern end of the species' range.

The length of time the young of several species are exposed to high stream temperatures is closely related to their upper-lethal-temperature tolerance. This is reflected both in the short stream life of species of lower tolerance to temperature and in the more southerly distribution (except at high altitudes) of *Salmo* and the two species of *Oncorhynchus*—*tshawytscha* and *kisutch*—species which show greater temperature tolerance.

Species with the lowest upper-lethal-temperature tolerance probably have also the lowest lower-lethal-temperature tolerance, since they range farther north—*Oncorhynchus gorbuscha* and *O. keta* into the Arctic Ocean, *Salvelinus alpinus* in Baffin Island, and *Cristivomer* in deep Arctic lakes.

BIBLIOGRAPHY

BAILEY, JOSEPH R., and JAMES A. OLIVER.
1939. The fishes of the Connecticut watershed. New Hampshire Fish and Game Dept., Biological Survey Connecticut Watershed, Survey Rept. No. 4: 150–189. Concord.

BARNABY, JOSEPH T.
1952. Offshore fishing in Bristol Bay and Bering Sea. U. S. Dept. of the Interior, Fish and Wildlife Service, Special Scientific Rept.: Fisheries No. 89: 1–30.

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER.
1953. The Salmons. Family Salmonidae. *In* Fishes of the Gulf of Maine. U. S. Dept. of the Interior, Fish and Wildlife Service, Fishery Bull. 53 (74): 119–133.

BLACK, EDGAR C.
1953. Upper lethal temperatures of some British Columbia freshwater fishes. Jour. Fisheries Research Board Canada 10 (4): 196–210.

BLAIR, A. A.
1938. Scales of Lake Ontario salmon indicate a land-locked form. Copeia 1938 (4): 206.

BORISOV, P. G.
1928. Dog-salmon (Keta) and navaga from the Lena Basin. Materiaux Commission pour l'Étude Republique Autonome Sovietique Socialiste Iakoute, No. 27: 1–15. Yakutsk, Siberia.

BRETT, J. R.
1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Jour. Fisheries Research Board Canada 9 (6): 265–323.

BRIGGS, John C.
1953. The behavior and reproduction of salmonid fishes in a small coastal stream. California Dept. Fish and Game, Fish Bull. 94: 1–62.

CALIFORNIA DIVISION OF FISH AND GAME.
1926. A rare trout from Lower California. California Fish and Game 12 (2): 89.

CARBINE, W[ILLIAM] F.
1953. Further data on the development of a non-migratory strain of rainbow trout. U. S. Dept. of the Interior, Fish and Wildlife Service, Progressive Fish-Culturist 15 (2): 83–84.

CHAMBERLAIN, F. M.
1907. Some observations on salmon and trout in Alaska. Rept. U. S. Commissioner Fisheries for 1906 (Doc. 627): 1–112.

CHAPMAN, WILBERT MCLEOD.
1941. Observations on the migration of salmonoid fishes in the upper Columbia River. Copeia 1941 (4): 240–242.

COOPER, GERALD P.
1940. A biological survey of the Rangeley Lakes, with special reference to the trout and salmon. Maine Dept. Inland Fisheries and Game, Fish Survey Rept. No. 3: 1–182.

DELACY, ALLAN C., and W. MARKHAM MORTON.
1943. Taxonomy and habits of the charrs, *Salvelinus malma* and *Salvelinus alpinus*, of the Karluk drainage system. Trans. American Fisheries Soc. 72 (1942): 79–91.

DEWITT, JOHN W., JR.
1954. A survey of the coast cutthroat trout, *Salmo clarki clarki* Richardson, in California. California Fish and Game 40 (3): 329–335.

DOAN, K. H.
1948. Speckled trout in the lower Nelson River region, Manitoba. Bull. Fisheries Research Board Canada 79: 1–12.

DUNBAR, M. J., and H. H. HILDEBRAND.
1952. Contribution to the study of the fishes of Ungava Bay. Jour. Fisheries Research Board Canada 9 (2): 83–128.

DYMOND, JOHN R[ICHARDSON].
1926. The fishes of Lake Nipigon. University of Toronto Studies, Publ. Ontario Fisheries Research Lab. No. 27: 1–108.
1940. Pacific salmon in the Arctic Ocean. Proceed. Sixth Pacific Science Congress 3: 435.

EVERMANN, BARTON WARREN.
1908. Descriptions of a new species of trout (*Salmo nelsoni*) and a new cyprinodont (*Fundulus meeki*) with notes on other fishes from Lower California. Proceed. Biological Society Washington 21: 19–30.

EVERMANN, BARTON WARREN, and EDMUND LEE GOLDSBOROUGH.
1907. The fishes of Alaska. Bull. U. S. Bureau Fisheries 26 (Doc. 624): 219–360.

FOERSTER, R. E[ARLE].
1947. Experiment to develop sea-run from landlocked sockeye salmon (*Oncorhynchus nerka kennerlyi*). Jour. Fisheries Research Board Canada 7 (2): 88–93.

FRY, F. E. J.
1947. Temperature relations of salmonoids. Proceed. National Committee Fish Culture, 10th meeting, Appendix D.

FUKUHARA, FRANCIS M.
1953. Japanese 1952 North Pacific salmon-fishing expedition. U. S. Dept. of the Interior, Fish and Wildlife Service, Commercial Fisheries Review 15 (2): 1–17.
1955. Japanese high-seas mothership-type drift gillnet salmon fishery, 1954. U. S. Dept. of the Interior, Fish and Wildlife Service, Commercial Fisheries Review 17 (3): 1–12.

GILBERT, CHARLES H., and HENRY O'MALLEY.
1921. Investigation of the salmon fisheries of the Yukon River. U. S. Bureau Fisheries, Appendix 6, Rept. U. S. Commissioner Fisheries for 1921 (Doc. 909): 128–154.

GRAINGER, E. H.
1953. On the age, growth, migration, reproductive potential and feeding habits of the Arctic char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island. Jour. Fisheries Research Board Canada 10 (6): 326–370.

GREELEY, JOHN R.
1955. A streamlined study of New York salmon. U. S. Dept. of the Interior, Fish and Wildlife Service, Progressive Fish-Culturist 17 (2): 89–90.

HANAVAN, MITCHELL G., and BERNARD EINAR SKUD.
1954. Intertidal spawning of pink salmon. U. S. Dept. of the Interior, Fish and Wildlife Service, Fishery Bull. 56 (95): 167–185.

HASLER, ARTHUR D., and D. S. FARNER.
1942. Fisheries investigations in Crater Lake, Oregon, 1937–1940. Jour. Wildlife Management 6 (4): 319–327.

HOOVER, EARL E.
1936. Contributions to the life history of the chinook and landlocked salmon in New Hampshire. Copeia 1936 (4): 193–198.

JOHNSON, W. E.
1956. On the distribution of young sockeye salmon (*Oncorhynchus nerka*) in Babine and Nilkitkwa Lakes, B. C. Jour. Fisheries Research Board Canada 13 (5): 695–708.

JORDAN, DAVID STARR, and ERNEST ALEXANDER MCGREGOR.
1925. Family Salmonidae. *In* Records of fishes obtained by David Starr Jordan in Japan, 1922, by David Starr Jordan and Carl Leavitt Hubbs. Memoirs Carnegie Museum 10 (2): 93–346.

KENNEDY, WILLIAM A.
1956. The first ten years of commercial fishing on Great Slave Lake. Bull. Fisheries Research Board Canada 107: 1–58.

NEAVE, FERRIS.
1944. Racial characteristics and migratory habits in *Salmo gairdneri*. Jour. Fisheries Research Board Canada 6 (3): 245–251.
1949. Game fish populations of the Cowichan River. Bull. Fisheries Research Board Canada 84: 1–32.

NEEDHAM, PAUL R.
1938a. Notes on the introduction of Mexican trout. U. S. Bureau of Fisheries, Progressive Fish Culturist 1938 (37): 1–10. [Memorandum I–131.]
1938b. Notes on the introduction of *Salmo nelsoni* Evermann into California from Mexico. Trans. American Fisheries Soc. 67 (1937): 139–145.

PRITCHARD, A[NDREW] L.
1940. Studies on the age of the coho salmon (*Oncorhynchus kisutch*) and the spring salmon (*Oncorhynchus tschawytscha*) in British Columbia. Trans. Royal Soc. Canada, Ser. 3, 34 (sect. 5): 99–120.

RATLEDGE, H. M., and J. H. CORNELL.
1953. Migratory tendencies of the Manchester (Iowa) strain of rainbow trout. U. S. Dept. of the Interior, Fish and Wildlife Service, Progressive Fish-Culturist 15 (2): 57–63.
RICKER, WILLIAM E.
1938. "Residual" and kokanee salmon in Cultus Lake. Jour. Fisheries Research Board Canada 4 (3): 192–218.
1940. On the origin of kokanee, a fresh-water type of sockeye salmon. Trans. Royal Soc. Canada, Ser. 3, 34 (sect. 5): 121–135.
ROUNSEFELL, GEORGE A.
1957. Fecundity of North American Salmonidae. U. S. Dept. of the Interior, Fish and Wildlife Service, Fishery Bull. 57 (122): 451–468.
ROUNSEFELL, GEORGE A., and GEORGE B. KELEZ.
1938. The salmon and salmon fisheries of Swiftsure Bank, Puget Sound, and the Fraser River. Bull. U. S. Bureau of Fisheries 49 (27): 693–823.
ROUNSEFELL, GEORGE A., and W. HARRY EVERHART.
1953. Fishery Science. 444+xii pp. John Wiley & Sons, New York.
ROYCE, WILLIAM F.
1951. Breeding habits of lake trout in New York. U. S. Dept. of the Interior, Fish and Wildlife Service, Fishery Bull. 52 (59): 59–76.
SHAPOVALOV, LEO, and ALAN C. TAFT.
1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Dept. Fish and Game, Fish Bull. 98: 1–375.
SNYDER, JOHN O[TTERBEIN].
1921. Steelheads caught at sea off the coast near Fort Bragg. California Fish and Game 7 (1): 9–11.
1926. The trout of the Sierra San Pedro Martir, Lower California. University California Publ. in Zoology 21 (17): 419–426.
1931. Salmon of the Klamath River, California. California Dept. Fish and Game, Fish Bull. No. 34: 1–130.
1940. The trouts of California. California Fish and Game 26 (2): 96–138.
SPRULES, WM. M.
1952. The arctic char of the west coast of Hudson Bay. Jour. Fisheries Research Board Canada 9 (1): 1–15.
UNITED STATES FISH AND WILDLIFE SERVICE.
1951. Landlocked silver salmon for Montana waters. Progressive Fish-Culturist 13 (4): 192. U. S. Dept. of the Interior, Washington, D. C.
WALLIS, ORTHELLO L., and CARL E. BOND.
1950. Establishment of kokanee in Crater Lake, Oregon. Jour. Wildlife Management 14 (2): 190–193.
WEED, ALFRED C.
1934. Notes on the sea trouts of Labrador. Copeia 1934 (3): 127–133.
WHITE, H. C.
1940. Life history of sea-running brook trout (*Salvelinus fontinalis*) of Moser River, N. S. Jour. Fisheries Research Board Canada 5 (2): 176–186.
1941. Migrating behaviour of sea-running *Salvelinus fontinalis*. Jour. Fisheries Research Board Canada 5 (3): 258–264.
1942. Sea life of the brook trout (*Salvelinus fontinalis*). Jour. Fisheries Research Board Canada 5 (5): 471–473.
WILDER, D. G.
1952. A comparative study of anadromous and fresh-water populations of brook trout (*Salvelinus fontinalis* (Mitchell)). Jour. Fisheries Research Board Canada 9 (4): 169–203.

U. S. GOVERNMENT PRINTING OFFICE: 1957 O—445841