ON THE ORIGIN OF KOKANEE, A FRESH-WATER TYPE OF SOCKEYE SALMON

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THE sockeye salmon (*Oncorhynchus nerka* Walbaum) of the north Pacific region is typically an anadromous fish, whose young usually remain in a fresh-water lake for at least a year before migrating to the ocean. In a great many lakes, however, there occur populations of *O. nerka* which are not anadromous, but live and reproduce entirely in fresh water. Such fish have been given the varietal name *O. n. kennerlyi* Suckley, and are variously known as kokanee, kickaninnies, land-locked sockeye, little redfish (when mature), and silver trout (immature).

Kokanee are found both in lakes which are, or have been recently, occupied by anadromous sockeye, and in lakes which today lack sockeye. Of the British Columbia lakes listed by Dymond (1936) as containing kokanee, the following are of the first-mentioned kind: Adams, Burns, Chilliwack (Chiloweyuk), Francois, Fraser, Shuswap, and Stuart Lakes in the Fraser River drainage; Osoyoos in the Columbia drainage; Cowichan and possibly Nanaimo on Vancouver Island. Those which are said to lack anadromous sockeye are: Canim, LaHache and Niskonlith in the Fraser drainage; Arrow, Blue, Christina, Kalamalka, Kootenay, Missezula, Okanagan, Round, Skaha, Slocan, and Woods Lakes in Columbia drainage; and Cameron, Horne, Shawnigan, and Sooke Lakes on Vancouver Island. Nicola Lake may be listed as doubtful in this regard, while Seton and Anderson Lakes are omitted because there is some doubt that the fish reported were true kokanee (Ricker, 1938, p. 213).

Kokanee and anadromous sockeye are very closely related, the only known morphological difference between them being the much smaller average size of the kokanee. There is no reasonable doubt that the two forms have diverged from a common stock in recent geological times. Either anadromy or lacustrine life must be the primitive, and its opposite the more recently acquired, habit of the species. The typically anadromous habits of other species of the genus, and the continuous distribution and probable intermingling of the anadromous sockeye populations in the ocean, as compared with the isolation of various kokanee stocks, present overwhelming evidence that kokanee populations have been derived from anadromous fish in times geologically recent. Information and speculation concerning the probable course of this evolution are presented in this paper.

Difference between Kokanee and Residual Sockeye

The discovery of another kind of sockeye salmon, the *residual sockeye* has thrown some new light upon the interesting process of evolution of kokanee from anadromous sockeye. Residual sockeye were described from Cultus Lake, where they are not an uncommon fish (Ricker, 1938). In a sense they are intermediate between the other two kinds of sockeye. Although the progeny of anadromous fish, they are not themselves anadromous; yet they were found to differ from kokanee in the following respects:

Characteristic	Residual Sockeye	Kokanee
Sex ratio	Predominantly male	Normal
Age at maturity	Males: II, III, less often IV Females: III and IV	Males: III and IV(?) Females: IV(?)
Size at maturity	16 to 38 cm.	22 to 41 cm.
Colour at maturity (males)	Dull olive-grey	Green head, red body
Absorption of scale margins at maturity	Little or none	Always advanced
Infestation of *Salmincola*	Usually heavy	Light or none
Time of spawning	October to December	August and September
Parentage	Anadromous sockeye	Presumably other kokanee
Abundance	Usually common	Scarce

From this it is clear that in Cultus Lake the immediate progeny of anadromous sockeye do not develop into typical kokanee, if they fail to migrate to sea. Since they live in the same small lake as do the kokanee, reaction to different environments is not a possible explanation of the differences between them. There must exist certain genetic differences between the two stocks, whose phenotypic expression is in some of the characters listed. Further, the process of the formation of kokanee from the residual offshoots of the anadromous stock must have involved modification of the genetic elements controlling these characters, and has been therefore a true evolutionary process.

It is not necessary to assume that, in all lakes where they may be found, kokanee and residual sockeye will differ in exactly the same respects as at Cultus Lake. It seems likely, however, that they everywhere do differ in some respects—for it is *a priori* highly improbable that natural selection, acting on *anadromous* fish, would develop the maximum number of favourable adaptations for *fresh-water* life. For optimum adaptation to lake conditions, a period of strictly lacustrine existence would seem essential.

Two stages may therefore be distinguished in the formation of kokanee from anadromous sockeye: (1) the production of residual offshoots of seagoing sockeye, and (2) a period of genetic evolution among the progeny of these residuals, during which better adaptation to lake life is attained.

Factors Affecting the Occurrence of Residual Sockeye

How widespread is the occurrence of residual sockeye among anadromous populations under natural conditions is a matter of conjecture. Apart from Cultus Lake, there is a somewhat doubtful record of their occurrence in Seton and Anderson Lakes of the Fraser River system; and Mr. J. T. Barnaby has informed the writer that, in the course of his investigations of Karluk Lake, Kodiak Island, Alaska, he has obtained three specimens of residual sockeye. It should be noticed, however, that before gill-nets were used in 1932, their existence in Cultus Lake was not suspected; and since very few sockeye lakes have been explored in this manner, it may even be that they occur naturally wherever there is an anadromous stock.

The occurrence of residual sockeye under conditions not strictly natural has been described in several papers by Ward (1929, 1930, 1932). On the Baker River in Washington a high power dam was erected in the stream migration route of a sockeye salmon run. At the time of their downstream migration, the smolts encountered an artificial lake with surface temperature much higher than the natural lake they had left, and which, in some years at least, had no surface overflow, except when gates were opened at intervals to allow such smolts as had collected to go out. In the years following construction of the dam, mature "land-locked" (i.e., residual) sockeye appeared above it. Of several features of the changed environment which might account for the sudden appearance of residual fish (or at least their sudden increase in numbers, for there is no certainty they did not exist previously) Ward places most emphasis upon the high surface temperature of the reservoir. As an accessory factor is cited the simple fact of its existence, which introduces a new and strange body of nearly stagnant water in a migration route where normally the first quiet water to be found had been the ocean. The lack of a continuous surface overflow in some years may also be influential in stopping the migration.

That high surface temperatures terminate the downstream migration of young Cultus Lake sockeye, leaving a certain number "trapped" in the lake each year, was the belief of Foerster (1937b) from his study of the migrations over a number of years. Of the yearlings so held, some migrate a year later, others never do; and the segregation into the various classes was shown (Ricker, 1938, p. 205) to be in a peculiar manner correlated with sex and rate of growth.

Granting that a *sudden* increase in temperature, owing to change in environment such as occurred at the Baker River, may make residual sockeye out of a large fraction of what would normally have been migratory smolts, it is not necessary to conclude, with Ward, that a *gradual* change of the same magnitude would produce the same effect. For if the increase were spread over several hundreds, or thousands, of years, as in the case of a lake warming up after the retreat of the glaciers of the last ice age, the sockeye population would have many generations in which residual types could be weeded out by natural selection, and kept down to a small fraction of the total. Thus at the end of the temperature increase the stock might be producing a fraction of residual fish little or no greater than at the beginning.

It is possible that some lower limit of environmental temperature

Lake	Anadromous sockeye	Residual sockeye	Kokanee	Epilimnial temperature	Authority
Cultus......	Abundant	Common	Very scarce	Warm (20-22°)	Ricker, 1938
Cowichan ...	Very scarce	?	Abundant	Warm (20-23°)	Carl, 1938 and MS.
Washington .	Few or none	?	Abundant	Warm (21°)	Schultz, 1935 Kemmerer, 1923
Shuswap....	Abundant	?	Abundant	Warm (19-22°)	Clemens et al., 1938
Chilliwack...	Fairly common	?	Abundant	Cool (16° on July 1/26)	Foerster, MS; verbal reports
Harrison....	Abundant	?	None*	Cool (up to 17°)	Foerster, 1925
Karluk......	Abundant	Rare	None*	Cold (maximum usually 11-13°)	Barnaby (letters)

*A record of absence of a fish from a lake is, of course, always subject to correction by a subsequent discovery. In the case of Karluk Lake, extensive observations of spawning beds, and gill netting over several years, have not discovered any kokanee (Barnaby). On Harrison Lake, hatchery operators who have searched the lake and its tributaries for salmon for three decades (Messrs. A. Robertson, W. F. Baxter, G. G. Thompson) are unanimous in affirming their absence. This is significant in view of the fact that, scarce as are kokanee at Cultus Lake, one or two had been taken there by fish culturists prior to their capture in our nets.

exists below which all young sockeye go to sea, and no residuals at all will be produced. But of its existence there is as yet no evidence. Sockeye lakes are varied as to temperature. In the schedule on p. 124 some examples are listed, with a note concerning the presence or absence of residuals and kokanee in them. In view of our scanty knowledge concerning the occurrence of residuals, the presence of the derived kokanee may be taken as an indication that residuals have occurred in the lake at some time in the past, provided the hypothesis of separate origins of kokanee populations be accepted (cf. p. 134). The presence of residuals in Karluk Lake—much the coldest of the series—is itself enough to show that most sockeye lakes offer no *temperature* barrier to occurrence of this type of fish. In another cool lake they have apparently occurred sufficiently commonly to give rise to a kokanee population.

The Evolution of Kokanee

A review of the differences, given earlier, between residual and kokanee sockeye in Cultus Lake reveals some whose development must have involved true genetic modification, others which arise from extraneous or "accidental" causes. In the latter category may be placed the abnormal sex ratio of residuals—this has been shown to occur in the course of the segregation of residuals from smolts at migration time. Part of the tendency toward precocious maturity among residuals, particularly the fast-growing fish which mature in their second year, appears to arise from the same cause.

The other known differences between kokanee and residual sockeye appear to be the result of genetic modification of the residual stock. They may be discussed in the light of a picture of a process of evolutionary change by natural selection of favourable genes, so that increasingly close adaptation to lake life ensues.

(1) *Susceptibility to Salmincola.* Vulnerability to the attack of these copepod parasites may well be a variable character among sockeye, just as men differ in susceptibility to disease organisms. Anadromous sockeye are not so much affected by them as are residuals, for they lose them on entering salt water. Residuals, however, are exposed to attack for their whole life, and at Cultus commonly bear heavy infestations, which result in considerable damage to the gill filaments. Hence greater immunity to *Salmincola* attack would almost certainly be of greater survival value to a lacustrine than to an anadromus fish, and Cultus Lake kokanee are, in fact, almost immune.

It should be noticed that the survival advantage need not be great to accomplish this result. According to Fisher's (1930, p. 76) calculation, if the survival advantage conferred by a given increase in immunity were even as little as 1 per cent, the genes responsible for it would pervade the population within a few generations after the hazards of initial establishment were overcome.

The process of change might even take place without new mutations in genes affecting this character, if the original anadromous stock exhibited sufficient genetic variability in this respect. If not, improvement would have to await the occurrence of favourable mutations in sufficient numbers to allow of a reasonable chance of the ultimate survival of one or more of them.

(2) *Colour at maturity.* The dull colour of residual sockeye, and the failure of their males to absorb the scales and toughen the skin at maturity in anything like the same degree as anadromous males (their parents) are facts not readily explained. Possibly some substance or stimulus is needed which would normally be obtained principally in salt water, or in the course of their homeward migration. On this view, the high colour and associated skin characters of kokanee must have been reacquired by them in the course of their evolution, through a process of selection which has favoured those able to react more strongly to small quantities of the substance, or to different stimuli. Whatever may be the exact factors selected, there is an excellent case for the existence of selection; for the end result is very similar to anadromous fish, which may be presumed to have attained an optimum as regards breeding adaptations under their particular conditions of existence. The survival advantage in this process would presumably be in the nature of sexual selection—the brighter and tougher males being more successful in obtaining mates and warding off attacks. Any who have watched the vicious biting and shaking which mark the struggles between mature male Pacific salmon (most easily observed among the chum salmon, *Oncorhynchus keta*), will have no doubt that a tough skin is one characteristic which favours success in reproduction. Whether colour plays an independent role, or is simply a by-product of the other changes, could only be determined by experiment.

(3) *Anadromy.* A possible genetic factor on which selection would act most powerfully, in the development of a kokanee stock, is that (or those) which governs the tendency to migrate seaward. It seems likely that the progeny of residuals would be mostly migratory, since they have the genetic constitution of anadromous fish, with perhaps a slightly greater proportion remaining in the lake than is the case with the progeny of the latter. From this condition to that of the kokanee, where few or none are supposed to go to sea, represents a

great change in genetic character. A study of the percentage of anadromy among the offspring of kokanee and of residuals in the same lake would be most interesting in developing this point.

Foerster (1937a) had no success in his attempt to make kokanee become anadromous by denying them access to a lake and liberating them in a stream at one year of age with year-old sockeye migrants. Nevertheless it is *possible* that even the best-adapted kokanee populations naturally produce a few migratory smolts annually, just as anadromous populations produce a few residuals; and exceptional climatic conditions might even send a large number to sea, in an unusual year. It is improbable, however, that there is normally any great number of such migrants, for if so, it would reduce the ability of the kokanee to compete with anadromous fish in the struggle for survival, as described below.

(4) *Time of spawning.* The process of change in the above three respects would be accelerated and made more permanent if, after it had proceeded a certain way, the new kokanee types could be prevented from breeding with the residual fish. This fact would confer a survival advantage upon the offspring of kokanee which spawned at a different place, or time, than the residuals. In this way the earlier spawning of Cultus Lake kokanee may have been evolved, while at Chilliwack Lake kokanee are said to spawn *in streams* at about the same time as the anadromous fish lay their eggs on gravel beds *in the lake.*

With or without acceleration from these or other methods of segregation (e.g. hybrid sterility resulting from gene translocations, etc.), in time all types intermediate between the residuals and the better-adapted kokanee would be rendered scarce by selection, and the door almost closed to continuation of contributions from the residual to the kokanee population. For now any fresh-water progeny of residuals must meet the competition of the better-adapted kokanee, and will have small chance of ultimate survival. The residuals themselves may continue to appear, and may even increase in numbers, as they spring each year anew from the anadromous stock and need disappear only when it does.

Competition between Kokanee and Anadromous Sockeye

Competition between and selection among the progeny of residual sockeye may reasonably be held to account for the evolution of kokanee. It does not follow, however, that in every lake where residuals are found there will necessarily appear a kokanee population.

For as well as competing with the residuals in the course of their evolution, the kokanee must meet the competition of a much more numerous brood spawned by anadromous parents. On the ground of structural similarity, and the food study of Clemens (1939) it is clear that the principal food of kokanee is the same as that of young sockeye, i.e., pelagic plankton. In an earlier paper (Ricker, 1937) evidence was presented that in Cultus Lake competition for food is so acute among the large sockeye populations that the average rate of increase in weight is reduced to less than half of what is usual. Hence there will also be intense competition for food between the fresh-water and anadromous stocks, in an environment filled to near capacity with fish of this type.

The larger Cultus Lake residual sockeye eat a few small fish, including newly-hatched sockeye, and the larger kokanee may reasonably be supposed to do the same. We judge this, however, to be a minor phase of the competition between the two forms, as it is doubtful if a distinction could be drawn between young sockeye and young kokanee, by any kind of predator.

Since they consume identical foods, it might perhaps seem that both kokanee and sockeye could not continue to live side by side in a lake where the food available was being exploited to nearly its fullest extent. For, as Gause (1934, p. 109) found with two species of *Paramoecium* growing at near-maximum abundance, the one having the greatest potential rate of reproduction should gradually exterminate the other. This may in fact be what has happened in accessible lakes, like Lake Washington, which sockeye no longer frequent; and it suggests the interesting possibility that if the kokanee could in some way be controlled (reproductive rate reduced), the sockeye might still be able to maintain themselves. Naturally this could only be determined by experiment, for there are causes of the extermination of anadromous runs which have nothing to do with kokanee competition.

At the other extreme are lakes which have no kokanee. If Karluk and Harrison Lakes, for example, really lack kokanee entirely, it may be because the anadromous fish there have been at such an advantage in survival rate that no progeny of residuals have been able to survive permanently, to develop into a kokanee stock. Here again, however, an alternative hypothesis is possible—viz. that residuals, particularly females, have always been so scarce that purely accidental, as opposed to differential, mortality among them and their progeny has been sufficient to prevent the evolution of kokanee.

Finally, there are lakes where both kokanee and anadromous sockeye are found. For these it must be postulated that each type of fish has a higher reproductive rate than the other, when relatively scarce, the actual numbers of each found being that representing an equilibrium position where net survival rates are equal. It is perhaps unnecessary to add that such an equilibrium, determined over a period of years, might include considerable accidental or periodic fluctuation in the numbers of both types, from year to year.

To make the argument more concrete, examples of factors which would favour both kinds of fish may be cited.

A. Factors favouring kokanee:
  (1) Ability to spawn in shallower water, owing to smaller size.
  (2) Possible lesser hazards of lacustrine life, as compared with ocean life.
  (3) Obstacles to the return of sockeye from the sea, including human fishing, which decrease survival rate among sockeye.
  (4) Partial prevention of seaward migration of the anadromous stock by means such as the "temperature-blanket" of Ward. (This involves the additional assumption that the resulting residuals are of less reproductive value to the anadromous stock than the survivors of a similar number of migrant smolts.)

B. Factors favouring anadromous sockeye:
  (1) Larger size, enabling them to exclude kokanee from favourable spawning grounds.
  (2) Possible greater egg production per fish.
  (3) Possible better survival of eggs in the redds, owing to deeper excavation of nests.
  (4) Possible lesser hazards of ocean life, as compared with freshwater.
  (5) Possible anadromy among part of the progeny of kokanee, which in effect would reduce the survival rate of the kokanee stock.

Several of the points mentioned are of such a nature as would be most favourable to a *small* population, and hence taken together could easily result in a balance between sockeye and kokanee. For example, the ability of kokanee to spawn in shallower waters might permit them to maintain a population of such a size as fully used the available shallow redds, but increase beyond that would be impossible if the deeper redds were monopolized by sockeye. Expressed otherwise, the "ecological niches" occupied by the two forms, during one part of their life cycle, would be sufficiently different to permit the survival of both.

The suggestions above could be extended indefinitely, but will not become particularly significant until data are assembled relating to them. Two, however, run counter to currently accepted theories of kokanee formation, and will merit further discussion.

(1) The formation of a warm-temperature "blanket," which might prevent the seaward migration of a part of the progeny of anadromous sockeye, has been suggested by Ward (1932, p. 575) as the "ruling factor" governing the appearance of kokanee. It has been shown above, however, that kokanee have appeared in a relatively cool lake (Chilliwack Lake), hence it cannot be that warm temperatures have been essential to their evolution. This is not to say that the fact of the warming of our lakes following the ice age *may* not have been influential in producing residuals in sufficient numbers to permit of the survival of their progeny, and hence the evolution of kokanee; but on this subject there is little information. What is clear, is that the absolute level of temperature attained does not need to be very high.

Considering that many lakes having warm surface water today contain abundant anadromous sockeye runs, it is difficult to imagine that under natural conditions high epilimnial temperatures alone would ever be responsible for their extermination, by presenting a physiological barrier to downstream migration. Since all sockeye lakes cool off in winter, to obtain suitable temperatures for migration, the smolts would merely have to shift the time of migration earlier in the year—a thing which they do very readily today in response to differences in temperature between years (Foerster, 1937b); and in the course of the many years over which warming has taken place, natural selection could if necessary easily effect an adjustment in the norm of the population's temperature-migration reaction. Individual smolts, for example at Cultus Lake, are very variable in respect to the time and temperature at which they migrate (Foerster, 1929), so that there should be ample genetic variability on which selection could operate.

(2) The formation of waterfalls or other obstacles to migration of adult salmon has often been suggested as a possible cause for the evolution of kokanee. Ward (1932, p. 575) rightly points out that such obstacles do not prevent the downstream migration of smolts. Hence they cannot be responsible for the first stage in kokanee formation—the appearance of residual fish. But in a lake where residuals already occur, and where exceptionally great survival advantage of the anadromous fish successfully prevents the permanent survival of the residuals' lacustrine progeny, the appearance of an increasingly serious obstacle to migration might well provide the necessary condition of reduced anadromous survival rate which would permit the evolution of a kokanee population. Hence obstacles to the migration of parent

salmon should not be too readily dismissed as of no importance in kokanee formation.

If already established, kokanee would in such a case increase in numbers, as percentage return from the smolt migrations diminished and the kokanee's "biotic potential" increased relative to that of the sockeye. It is perhaps suggestive in this connection that the lakes of the lower Fraser region, lying at or near sea-level (Coquitlam, Pitt, Alouette, Harrison, Lillooet, and Cultus) appear to have had few kokanee or none, while lakes of the upper Fraser, beyond the difficult canyon rapids, frequently contain them in abundance.[1] Another lake of the lower river, Stave Lake, though at no great elevation, had a difficult or perhaps impassable waterfall at its mouth, and in historic times has always contained numerous kokanee.

Discussion

The picture of the process of kokanee evolution presented above is largely based on the postulates of the "genetical theory of natural selection"; which, as far as the writer's reading goes, has been most clearly and completely described by R. A. Fisher (1930). These place emphasis upon the occurrence of small gene mutations as the basic units on which natural selection works, and discount the importance of the larger "saltations," such as those whose effect, if morphological, is likely to be distinguishable by casual inspection.

It has been suggested to the writer, however, that if the differences between kokanee and residual sockeye could be the effect of a single major gene mutation, explanation would be had for the peculiar fact that the kokanee stocks of different lakes are in general quite similar in appearance. Whereas it is almost an axiom of evolutionary theory that isolation makes for divergence, kokanee from the various lakes of such widely separated localities as the North American coast, Vancouver Island, Kamchatka (Krokhin and Krogius, 1936), and Hokkaido (Oshima, 1934) show no obvious peculiarities, as far as can be ascertained from the meagre descriptions at hand, except in average size attained and to some extent in colour.[2] If a mutation resulting in

[1]Chilliwack Lake on the lower river may perhaps be considered an exception, for it has numerous kokanee; and no very difficult rapids in its outlet at the present time. The lake is, however, at an unusually high elevation (660 metres) and for some distance the gradient of the outlet is steep—suggesting that at some time in the past it may have been more difficult of access.

[2]The suggested similarity may be more apparent than real. A study of the body proportions, number of fin rays, etc., of a large series of specimens has been made in only one case—the Lake Washington kokanee described by Schultz (1935)—so that comparisons of these characters are not possible.

the definite variant "kokanee," fixed in its phenotypic manifestations to the degree that are some of the *Drosophila* mutations, occurred in sockeye stocks with some frequency, it would be unnecessary to look farther for explanation of the similarity between various kokanee stocks. The objection to be made is, of course, that, between the sockeye's genetic constitution and that of the kokanee there are differences which make the latter better adapted for lake life in at least three respects (restriction of anadromy, ability to develop complete secondary sexual characters in fresh water, relative immunity to *Salmincola* attacks). While single gross mutations usually have multiple effects, it is seldom indeed that even one of them is of a positive adaptive character; while for one mutation to have several such adaptive effects exceeds all bounds of probability and of experience.

The same fact—the similarity of diverse kokanee stocks—led the writer to wonder if the various points of difference between residual sockeye and kokanee might all be closely related to a single character having survival value. In earlier drafts of this paper it was suggested that susceptibility to the parasite *Salmincola* might be such a character; the stunted growth and lack of breeding colour of residuals being considered as possible effects of loss of vitality or actual injection of poisonous substances by the parasites. But such observations as are available do not bear out this view—for example, there was no correlation between size, colour, or apparent vitality, and the number of parasites on individual fish.

There seems no necessity, however, for considering either of the hypotheses put forward in the last two paragraphs. Adaptive interpretations are evident for all of the known differences between kokanee and residual sockeye, so that a picture of gradual evolutionary modification along the lines suggested by Fisher must be considered decidedly probable. If the end products in different lakes are similar in these respects, it need only be a reflection of the obvious fact that, in changing from an anadromous to a lacustrine way of life, there are a number of adaptations which will everywhere be useful.

A final point may be considered—that of the independent versus common origin of the various kokanee stocks known today. In his several papers, Ward appears to have assumed an independent origin for most or all of the present-day kokanee stocks, and the same view underlies the argument of the present paper. One of our consultants, however, has very properly enquired whether it is not superfluous to postulate an independent evolutionary process for each individual lake. He believes that the lakes of the American, Siberian, and Japanese coastal drainages may have been populated by kokanee from a single source following the ice age. No information at our disposal can be said to preclude this possibility entirely, and the reader may, if he prefers, revise and criticize the argument of this paper on the view that the evolution has occurred only once.

But if once, why not many times? No new principle is involved except the explanation of a general resemblance between the different stocks, which was done (we believe adequately) above. The common-origin view, on the other hand, would in some instances at least involve assumptions that the other does not need. Immature kokanee normally frequent lakes only, not rivers. The adults often ascend streams to spawn, and in places where a low divide separates two rivers or tributaries, the possibility of a water connection in earlier postglacial times must be considered. In other cases, including Chilliwack Lake which is ringed by high mountains, and the various island kokanee populations, the pioneer kokanee arrivals must have made an atavistic seaward migration, followed by return to the new lake at maturity. It must be assumed in these latter instances that (1) there was somewhere a lake from which an appreciable number of young kokanee went to sea each year, or at least in some years, (2) on returning some of them did not go to their native waters, but reached new areas; (3) since the Fraser and Columbia flow from the north, and the colonization of these rivers would be from the south, the new colonists among the wanderers must have passed the mouths of their "home" streams and proceeded on upstream with an energy and persistence that took them past rapids which prove difficult even to native anadromous sockeye; (4) arrived in the new region, any survivors were able to breed with the native sockeye run (the chance of two fish of kokanee origin pairing off together seems negligible), and sufficient of the hybrid fry must have had the non-migratory kokanee habit to establish a lake population from which a new stock of kokanees was selected.

Nothing in this train of events is inherently impossible, but none has been proven to occur, and that described under (3) at least must be a rare occurrence. Because of the homing tendency, the establishment of even the anadromous sockeye in new areas presents certain difficulties, and judging by the failure of most artificial transplantation experiments, must be in nature a haphazard and tedious process. How much less frequently could the sequence of exceptional events described above come to fruition!

Summary

1. In discussing the evolution of kokanee, two stages must be considered: (*a*) the occurrence of "residual" or lake-type offspring among

the progeny of the anadromous stock; (*b*) the modification of the progeny of such residuals into the typical kokanee. Discovery of differences between the residual and kokanee types living in the same small body of water, demonstrates the necessity for postulating a period of evolution in fresh water during which typical kokanee characteristics are developed.

2. Little is known concerning the conditions which conduce to non-anadromy among the progeny of anadromous sockeye. Certain observations of Ward and Foerster suggest that abnormally high water temperatures during or toward the close of migration time may lead to increased production of residual fish. That some residuals are produced when temperatures are quite low is, however, shown by Barnaby's observation of their occasional occurrence in a cold Alaskan lake. Rather complex effects of sex and of rate of growth upon failure to migrate have also been established.

3. The process of evolution of kokanee from residual stock, considered as the change from one type to the other as they now occur at Cultus Lake, would involve (1) acquiring greater resistance to the attacks of a lake parasite; (2) development of more intense colour and skin modification at breeding season; (3) suppression of anadromy; (4) advancing the time of spawning by about two months. All of these may readily be interpreted as adaptations to lake existence, number (4) resulting from the survival value of keeping the others undiluted from interbreeding with residual or anadromous fish.

4. Following establishment of kokanee in a lake, there is reason to believe they will seriously compete for food with the anadromous sockeye. Such competition will of necessity have an effect in regulating the relative and absolute numbers of the two kinds of fish. It may hasten the decline and extinction of the anadromous form when and if the latter's total environment deteriorates relative to that of the kokanee, as for example, by excessive fishing or other mortality during the non-lacustrine part of its life cycle.

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