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AGE AT MATURITY OF THE PACIFIC COAST
SALMON OF THE GENUS ONCORHYNCHUS



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AGE AT MATURITY OF THE PACIFIC COAST SALMON OF THE GENUS ONCORHYNCHUS.



By CHARLES H. GILBERT,
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INTRODUCTORY.

During the past two summers (1910 and 1911) the writer has been engaged on behalf of the United States Bureau of Fisheries in determining the age at maturity of the five species of Pacific coast salmon, together with such other facts of their life history as can be inferred from the structure of their scales. The problem has a peculiar interest as concerns these species because of the fact, now sufficiently demonstrated, that all individuals perish when they have attained sexual maturity. They spawn but once and then die, whatever the age or size at which sexual maturity has been reached^a and whatever may be their physical condition at the time of spawning. This peculiarity in their life history renders the question of their age at maturity an unusually important one, both from the scientific fish cultural and the purely economic standpoints.

Many attempts have been made to solve the problem for the two species commercially most important—the king salmon and the sockeye—usually by marking the artificially reared fry by clipping one or other of their fins before they are liberated, in the hope of recognizing the adult fish on their return at maturity. Unfortunately, these important experiments have lacked adequate supervision, and have furnished somewhat discordant and uncertain results. These have been supplemented, however, by the experiments in Tomales Bay, Cal., and in New Zealand, where fry were planted in streams not frequented by the species in question and the return of the adults was noted. Also, in the case of the sockeye, we have had as additional evidence the quadrennial increase in the Fraser River, which has been very generally accepted as demonstrating a four-year cycle for this species.

All the evidence available was considered by F. M. Chamberlain, in his highly valuable "Observations on Salmon and Trout in Alaska" (Bureau of Fisheries Document No. 627, 1907), with the resulting conclusion (p. 66):

There seems to be sufficient reason for believing four years to be the usual term of life for the sockeye and the king salmon, but experiment has pretty conclusively shown that they may mature in less time or may be retarded beyond that term.

^a With the possible exception of certain male king salmon fingerlings, which mature precociously in the streams during their first year, at a length of 3 to 7 inches. The fate of these has not as yet been determined.

This may be accepted as an adequate statement of our belief respecting these species up to the present time. It has lacked in definiteness and in detail. No conclusive evidence has been presented concerning the age of the markedly undersized fish or "grilse," which are conspicuous parts of the king salmon and sockeye runs. We have no knowledge concerning the extreme age which any species may attain, nor concerning the proportions in which different ages are represented in the spawning run. Furthermore, the question of size with relation to age has been wholly undetermined, the belief being yet widely entertained that no such relation exists, size being solely dependent on richness of feeding in the sea.

There remains to be noticed a recent attempt by Prof. J. P. McMurrich^a to solve these problems by a consideration of scale and otolith markings. The figures of scales and otoliths presented in this paper show sufficiently that these structures present seasonal markings which when correctly interpreted will afford reliable indication of age. It is to be sincerely regretted that Prof. McMurrich's interpretations have been based on inadequate data, and these have misled him into announcing a series of conclusions so largely erroneous as to confuse rather than clarify the questions at issue. A further discussion of these matters will appear under each of the species considered below.

The present paper contains a purely preliminary statement of certain facts in the history of our salmon which can be substantiated through a study of scale structure. This method offers certain obvious advantages over that of determining the age by marking the young, although the latter method should be employed and rigidly supervised in corroboration of the former. But the scale method is of unlimited application. Any desired number of individuals can be investigated in connection with size and sex and other modifying factors. It thus becomes possible to analyze an entire salmon run into its age components, and each of these can then be the subject of further investigation and analysis. We can thus determine the range in size of each group and of the males and females separately for each age, and when definite events in the life history of the fish record themselves upon the scales—as we believe to be the case—corresponding categories can be formed and the possible effects of these events on growth and period of maturity can be determined. A very wide usefulness, therefore, attaches to this method, and for its proper elaboration discriminating study of many thousand specimens must be made.

While the method is new as regards Pacific salmon, it has been experimentally tested and fully approved by the Fisheries Board for Scotland in the case of the Atlantic salmon, and is now universally accepted as furnishing reliable data as to the age and many other facts in the life history of that fish. It has been shown to be applicable also to various species of trout, and its value has been demonstrated in fishes as widely divergent as the carp, the eel, the bass, the flounder, and the cod. Descriptions of this scale structure and its significance have appeared in a large number of papers, both scientific and popular. It will suffice here to repeat that the scale in general persists throughout life, and grows in proportion with the rest of the fish, principally by addi-

^a The life cycles of Pacific coast salmon belonging to the genus *Oncorhynchus*, as revealed by their otolith and scale markings. Transactions Royal Society of Canada, 1912.

tions around its border. At intervals there is produced at the growing edge a delicate ridge upon the surface of the scale, the successive ridges thus formed being concentric and subcircular in contour, each representing the outline of the scale at a certain period in its development. Many of these ridges are formed in the course of a year's growth, the number varying so widely in different individuals and during successive years in the history of the same individual that number alone can not be depended on to determine age. For this purpose we rely upon the fact that the fish grows at widely different rates during different seasons of the year, spring-summer being a period of rapid growth and fall-winter a season when growth is greatly retarded or almost wholly arrested. During the period of rapid growth the ridges are widely separated, while during the slow growth of fall and winter the ridges are crowded closely together, forming a dense band. Thus it comes that the surface of the scale is mapped out in a definite succession of areas, a band of widely spaced rings always followed by a band of closely crowded rings, the two together constituting a single year's growth. That irregularities occur will not be denied, and this is natural, inasmuch as growth may be checked by other causes than the purely seasonal one. Also a considerable experience is requisite for the correct interpretation in many cases, and a small residue of scales of doubtful significance has always remained. This element is too small to affect the general results, and further investigation will almost certainly eliminate the doubtful cases altogether.

SOCKEYE OR RED SALMON (*Oncorhynchus nerka*).

[Pl. I-III; fig. 14, pl. VIII; fig. 22, pl. XII.]

The sockeye, red salmon, or blueback, as it is variously known, has been assumed to mature principally if not wholly in four years, on the basis of the constant four-year periodicity in the magnitude of its run in the Fraser River. Richardson is reported as having marked young sockeye at Karluk, Alaska, and observed their return at four years on the average. Chamberlain marked young hatched from 1902 eggs and planted the marked fry in the Naha River, Alaska. The return of adults bearing the appropriate mark was reported in 1906 and 1907, and has continued to be reported for each year since that date, including the summer of 1911. If these results are accepted, individuals may even reach the age of 9 years before maturing; but this is a conclusion so at variance with other evidence and with general probability that complete corroboration is required.

Finally, on the basis of scale and otolith structure, McMurrich announces 4 years as the age of adult Fraser River sockeye and 2 years for the undersized or grilse form. But as he frankly bases his investigation upon the a priori assumption that Fraser River sockeye must be 4 years old, and interprets scale and otolith structure in accordance with that assumption, it can hardly be claimed that his conclusion adds anything to our previous knowledge. This becomes the more apparent upon an examination of his figures, which indicate that he unfortunately chose for examination certain large specimens which were in reality 5 years old and not 4. Forced by this method to make an erroneous interpretation of the central area of the scale, all his conclusions are vitiated which

deal with the sockeye, the king salmon, and the coho. Thus the sockeye grilse is a 3-year and not a 2-year fish, a fact which we learn with some relief, in view of the very large numbers of grilse which regularly make their appearance three years after each quadrennial big run in the Fraser and the small numbers which can be observed in the intervening years. For reasons which will appear later, McMurrich's initial error did not to the same extent affect his interpretation of the scales of the humpback and dog salmon.

Our knowledge of the life history of the young sockeye is founded first on the important researches of Commissioner J. P. Babcock for the Fraser River (Report Fisheries Commissioner for British Columbia, 1903), and later of Chamberlain, for certain streams in Alaska. These investigators agree that in the early spring two sizes of young sockeye may be found together in the streams on their downward migration to the sea. The smaller of these comprise fry of the year hatched from eggs of the preceding fall, and are then about $1\frac{1}{2}$ inches long. Those of larger size are yearlings, which instead of running out to sea the previous spring as fry, have remained in the lake during their first year and have grown during that time to a length of 3 or 4 inches.

The relative proportions of fry and yearling migrants in such streams as the Fraser and the Karluk are unknown. More fry have usually been captured in the fine-meshed nets employed for the purpose, but the superior strength and wariness of the larger yearlings have doubtless affected the result. It is also unknown whether in the same stream these two groups remain relatively constant in size or fluctuate widely from year to year in accordance with changing conditions of unknown nature. Chamberlain has pointed out that in the Naha River, Alaska, all the young remain in the lake during their first year, and migrate in their second spring as yearlings. It seems very probable that the chances of survival of yearling migrants is better than that of the fry, in which case a larger proportion of adults might be derived from that group, even in streams where considerable numbers migrate as fry. As will be shown below, the scales develop differently in the two groups. The history of each group can therefore be traced and the proportions which attain maturity can be determined.

In his interpretation of the sockeye scale McMurrich assumes that 13 of the 14 specimens which he examined belonged to the group which migrated as fry, the central close-ringed area of the scale having been formed during their brief life in fresh water. But, as a matter of fact, at the time when young fry migrate no scales whatever have made their appearance. In this group, therefore, the adult scales contain no record of life in lake and stream, even the innermost rings having been formed under marine or estuarial conditions. The close-ringed area which forms the center of the scale in McMurrich's specimens, as well as in the great majority of Fraser River sockeyes (pl. II, fig. 4), designates members of the second group, which have remained in their native stream or lake until their second spring. It presents, therefore, such record as we have of approximately the first year and a half of their life cycle. Plate III, figure 5, represents a scale, enlarged 40 diameters, of a yearling $3\frac{3}{4}$ inches long, taken in the Fraser River in April, 1903, by J. S. Burcham, working under instructions of Commissioner J. P. Babcock.

The scales in different yearlings captured at the same time and place differ considerably in size of scale and in the number of rings which they contain. Precisely similar variations are found in the nuclear areas of the adult scales, these being larger in some individuals than in others, and containing more numerous rings. Every variety of scale from migrating yearlings can be matched in the close-ringed centers of adult scales, both as regards actual size and in the number and arrangement of the rings. We can entertain no doubt, therefore, that the two have had an identical history. (See pl. II, fig. 4, with center of adult scale enlarged 40 diameters.)

The peripheral part of the scale seldom offers any difficulty. After life has begun in the sea, a regular alternation occurs of bands of widely spaced and of narrowly spaced rings, as shown in plate III, figure 6, the widely spaced rings representing the vigorous growth of spring and summer, the narrow rings the retarded growth of fall and winter. Finally, at the margin of the scale of the mature sockeye about to enter the Fraser are found a few widely spaced rings, indicating that the rapid growth of the summer in which maturity is attained early comes to an abrupt conclusion. This is true in the sockeye in greater degree than in other species of the genus, and may have its explanation in the earlier date at which mature sockeye discontinue feeding. All species of Pacific salmon (the steelhead is not here considered) cease to feed on entering fresh water at maturity, but the sockeye is extreme in this regard. Those bound for the Fraser are already fasting when first encountered along the Vancouver Island shore at the entrance to the Straits of Fuca, where other species are feeding greedily. The sockeyes are then over 100 miles from the mouth of the Fraser and are assuredly at that time not under the influence of fresh water. Fishermen are well acquainted with the fact that the sockeye, unlike the king salmon and the coho, are not to be taken by trolling, even when first they strike the coast.

With these facts in mind, we turn to plate II, figures 3 and 4, which represent a scale typical of a majority of the sockeyes of the Fraser River run. The nuclear area of finely crowded rings contains no record of the first winter after the eggs are laid, but represents the first summer and second winter which were spent in the lake. The broad band of widely spaced rings surrounding the nuclear area was formed in the sea and represents the second summer, thus completing the second year of the cycle. Then follow a narrow winter band of closely spaced rings and a second distinct summer band, constituting the third year of the cycle, and another winter band and the short marginal summer band of the fourth year.

While the majority of the Fraser River run are in their fourth year as shown by the evidence here adduced, a considerable number of them, including all the larger individuals, are just as evidently in their fifth year. The 4-year fish show, outside the nuclear area, three summers' growth and two winters' growth in the sea. The 5-year fish, as shown in plate VIII, figure 14, have just as distinctly, outside the nuclear area, four summers' growth and three winters' growth in the sea. As is given in a later table, there is a wide overlapping in size of the 4 and the 5 year fish, but all the smaller specimens are 4 years and all the larger are 5 years old. The specimens examined and

figured by Prof. McMurrich unfortunately were chosen from among the larger of those to be found on the cannery floor.

The great majority of the Fraser River sockeyes have scales of the type above described, the nuclear area being small, of crowded rings, and sharply set off from the widely spaced summer rings which surround them. As we have shown, these have all developed from fish which migrated seaward as yearlings. A different type is represented by plate XII, figure 22, in which it is seen that the nuclear area is much larger, the rings less closely crowded and widening gradually outward, until in extreme cases they merge almost imperceptibly with the succeeding summer rings. A scale of this type is figured by Prof. McMurrich (pl. III) and is interpreted by him as indicating a fish "which went to the sea as a yearling in the second spring after hatching." But the very reverse would seem to be the case. The large size and more widely spaced rings of the nuclear area indicate that growth in those individuals which spend their first year at sea is much more rapid than in those which remain in fresh water, and this is in accord with the few experiments which have been made with king salmon to determine that point. But more conclusive evidence of the history of these fish is found on comparing their type of scale with the scales of the humpback and dog salmon, which always migrate seaward shortly after hatching and while still in the fingerling stage. The nuclear area of humpback and dog salmon is exactly similar to the sockeye type last described, being comparatively large in size and of widely spaced rings. Furthermore, the king salmon, which migrates seaward partly as fingerlings and partly as yearlings, exhibits the same two types of scale shown by the sockeye, one with a small nuclear area of crowded rings, formed as can be demonstrated during the first year in fresh water, the other similar to the "sea type" of the humpback and dog salmon. While therefore we lack such direct demonstration as could be obtained by marking sockeye fingerlings on their seaward migration and observing on their return that the scales exhibit the "sea type" of nuclear area, there is yet sufficient evidence for the correctness of the theory to warrant us in accepting it.

The possibility of distinguishing throughout their lives those individuals which passed to sea immediately after hatching from those which migrated as yearlings has opened up a wide field of investigation, upon which we have thus far barely entered. A certain practical difficulty is encountered at the outset. In the majority of cases there is no question to which type a given scale belongs. But among those of undoubted "sea type," including humpbacks and dog salmon, as well as certain sockeyes and king salmon, there is found a tendency to the narrowing of a few of the rings immediately surrounding the nucleus, forming a sort of core to the nuclear area. (See pl. x, fig. 17.) The significance of this is in question, but we may perhaps hazard the conjecture that in such a case the individual tarried in fresh water or played back and forth on the tides for an appreciable time, during which growth was less rapid than in the majority which passed directly out to sea. Whatever the cause, this tendency to a slight central narrowing of rings of the nuclear area is of not infrequent occurrence in scales of the sea type, and is occasionally so pronounced as to simulate the smaller and least typical of what we may call for purposes of distinction the "stream nucleus." In a small proportion of

cases this may be the source of genuine doubt as to the early history of the individual and incidentally as to its age. For, if the nuclear narrowing be interpreted as indicating the first year spent in fresh water, the age will be greater by one year than if it be interpreted as the central narrowing of a large nuclear area of the "sea type." It is believed, however, that all doubt of this character can be removed by further investigation. For purposes of a preliminary discussion, like the present, as the doubtful cases are few in number, they can be omitted from consideration.

There is a fair indication—not to be taken as conclusive—that those individuals among the sockeyes which proceed to sea shortly after attaining the free swimming stage experience a mortality far in excess of those which pass to sea as yearlings, but that those of the first class which survive grow much more rapidly the first year than they would have done had they remained in fresh water. To a certain extent they seem to maintain this preponderance in size during succeeding years. In the Fraser River, as already indicated, only a very small proportion of adult fish have developed from young which sought the sea during their first year. Thus out of 625 individuals taken at random, without selection, from the cannery floor, only 35 belong to this group, while 590 had spent their first year in their native waters. So limited a number as 35 forms a wholly inadequate basis for generalizations, but it is worthy of note that 3 of these were grilse, maturing in their third year, 30 were in their fourth year, and only 2 in their fifth. If a larger series shall verify essentially the proportions here indicated it will demonstrate that early migration of the young accelerates growth and also the early coming to maturity, producing a larger proportion of grilse which mature in their third year, and a much greater preponderance of fourth to fifth year fish than occurs among those which migrate as yearlings. The increased size at the same age becomes evident on comparing the three "sea type" grilse above mentioned with "stream" grilse taken on the same date. The former were respectively 23, 23½, 23½ inches long and weighed 4¾ to 5¼ pounds. Sixteen grilse of the stream type taken on the same date (all that were secured) show the following lengths in inches: 17¾, 18, 18, 18½, 18½, 18½, 18½, 19, 19, 19¼, 19½, 19½, 19½, 20, 20½. Three of these, 18½, 18½, and 19½ inches long weighed each 2¾ pounds. It is further noticeable that 2 of the 3 grilse of the sea type were females, while among Fraser River grilse of the stream type females are so rare that we have thus far discovered but one among over a hundred grilse examined. This is a matter, however, which may be subject to wide variation in different streams. In the Columbia River, for instance, in 1910, grilse were numerous, and males and females in approximately equal numbers.

In discussing the commercial value of a run the grilse may be omitted from consideration, as ordinarily they are few in number and so small as to have practically no value. The valuable elements of the run are fish which are maturing in their fourth or in their fifth years. It was attempted during the season of 1911 to determine the relative proportions of these two generations, their range in size, and their average weight. In order to simplify the problem as much as possible we have omitted from our list the comparatively few individuals of sea type. In 500 fish of stream type, taken at random from the cannery floor, 271 were 4-year and 229 5-year fish. Of the 271 4-year

fish, 126 were males, 145 females; of the 229 5-year fish, 129 were males, 100 females. The total number of males (255) was but slightly in excess of the total number of females (245). Among 4-year fish the females were decidedly in excess, among 5-year fish the males.

As regards weight, 113 4-year fish taken without selection aggregated 709.25 pounds with an average of 6.27; 104 5-year fish weighed 776.25 pounds, with an average of 7.46. Extremes of weight among 4-year fish were 4.75 and 8, among 5-year fish 5.75 and 8.75.

The following table gives distribution in accordance with their length of the 500 individuals of the stream type in which age was determined, the 4-year males being compared with the 5-year males, and the 4-year females with the 5-year females.^a At the time the measurements were taken the jaws in the males were seldom strongly hooked, but a preorbital elongation was apparent which accounts in part but not wholly for the greater length of males than of females. The fish were measured over the curve of the body from the end of the rostrum to the tips of the middle rays of the caudal fin. It will be noted that the range in size of the 4 and 5 year fish overlap widely, but the curves are characteristically distinct, the 5-year fish averaging at least 2 inches longer, out of a total range of 5 inches in length for each group. Examination of a larger series of individuals would unquestionably extend the limits of each group by the addition of the exceptionally large and the exceptionally small, but the table as presented doubtless gives correctly the range in size of the vast majority at the time the examination was made. It will be of great interest to compare similar curves prepared for the same river basin in successive years; also curves of the sockeye run in different basins.

FIVE HUNDRED FRASER RIVER SOCKEYES WHICH HAD MIGRATED TO SEA AS YEARLINGS, GROUPED BY SEX, AGE, AND SIZE.

Length in inches.	Males.		Females.		Length in inches.	Males.		Females.	
	4 years.	5 years.	4 years.	5 years.		4 years.	5 years.	4 years.	5 years.
21					26	21	25	2	27
21½			1		26½	11	22		15
22			1		27	4	15		12
22½	2		2		27½		15		4
23	4		11		28		12		2
23½	5		19	1	28½		2		
24	13		49	2	29				
24½	20	4	27	3	29½		1		
25	23	13	22	13					
25½	23	20	11	21	Total.	126	129	145	100

Three-year fish, or grilse, were not included in the above table. During the summer of 1911 they were not numerous. Only a few (perhaps 3 or 4 on the average) could usually be found in each 1,000 fish brought in. It is the current belief among those who handle Fraser River sockeyes that all the grilse are male fish. As previously noted,

^a Measurements were made August 2-4, 1911, in the cannery of the Pacific American Fisheries at Bellingham, Wash. To the management of this concern we desire to express our grateful appreciation of their uniform courtesy.

all those examined by us were males, with one exception, a female with well-developed ova. Examination of the scales (see pl. I, fig. 1) shows that the final summer's growth is more extensive in grilse than in those which mature at 4 and 5 years, and the narrowing of the marginal rings to form the third winter band has often begun.

Much larger specimens than those included in the table were selected for examination in an attempt to find individuals older than 5 years. Several were found over 30 inches long, weighing 12 pounds, but all were 5-year fish. Examination of a larger number may possibly bring to light a rare individual which has not matured until its sixth year. Even this is doubtful and we assuredly do not anticipate finding older than 6-year individuals among the Fraser River sockeyes. The significance of the marking experiments of the Bureau of Fisheries in the Naha River, with the reported recovery of marked specimens up to 9 years old, remains to be determined.

If it be true, as indicated in our table, that relatively so large a proportion of Fraser River sockeyes mature in their fifth year, it may appropriately be asked how the enormously increased run every fourth year can be maintained in that river without its benefits becoming gradually distributed through five-year individuals over the intervening years. The great run of 1909 must have developed as 4-year fish from the superabundant eggs deposited by the great run of 1905. But if an almost equal proportion of those eggs should fail to mature until their fifth year, as was true in the 1911 run which we investigated, we should have expected a second great run, characterized by their relatively large size, in 1910. Such increased runs in the fifth years do not occur, and of this we have as yet no explanation to offer. There is some evidence that the fifth years of the cycle are characterized by fish of somewhat larger size than the other "off years," indicating, if true, a larger proportion of 5-year fish, but the total run is not appreciably increased. Certain it is that the fish of the big runs average smaller than those of the intermediate years. This might conceivably be explained by a limited food supply and sharper competition among the enormous schools of that year, but it is more probably due to the practical elimination of 5-year fish. Those 5-year fish present would have developed in their due proportion from the few eggs of an "off year," and would be too scattered to produce any effect among the vast hordes of 4-year olds. But these are matters for further investigation.

KING SALMON, OR CHINOOK (*Oncorhynchus tshawytscha*).

[Pl. IV-VII: fig. 15, pl. VIII: pl. IX; fig. 18, pl. X; fig. 25, pl. XIV.]

Speculation concerning the age of the king salmon (also called spring salmon, tyee, Chinook salmon, Sacramento salmon) has been encouraged by the enormous range in size which is exhibited by spawning fish. Adult females have been reported as small as 5 pounds, and adult sea-run males much smaller than this, while individuals of from 80 to 100 pounds weight occasionally are seen. No answer has heretofore been given to questions concerning the total range in years represented by these various sizes, nor as to the exact relation of age and size.

A detailed experiment to determine these points was undertaken by Superintendent Hubbard of the Clackamas (Oreg.), station, in 1896. Five thousand young, hatched

fish eggs of the preceding fall (1895), were marked by removing the adipose fin, and were then liberated. In 1898^a Columbia River cannery men reported the capture of some 375 of these marked fish, indicating their return in their third year. Thirty-two are reported, with details of sex and weight. Nineteen of these were females, ranging from 10 to 35 pounds; 13 were males, from 19 to 57 pounds in weight. The average for the 32 is 27.69 pounds, about 5 pounds above the average of all Columbia River salmon of this species.

The following year^b between 40 and 50 were reported, the average weight said to be nearly 10 pounds greater than of those taken in 1898. And in 1900, by offering a small reward for marks saved and sent in, the Oregon commissioner received 72, with no indication of weight. No further record of the capture of marked fish is contained in the Oregon reports. According to this experiment, it would appear that both males and females may mature in their third year, and that very large fish (57 pounds) may appear among those returning thus early. These results have been accepted by Rutter and others, the evidence appearing on its face unimpeachable, but they are so wholly at variance with results obtained through a study of the scales that we have scrutinized the records with some care. Certain minor inaccuracies are obvious, but the dates are well attested, and the only criticism which seems pertinent is that the commissioner apparently relied wholly on reports from the canneries, and did not personally inspect any of those specimens reported in 1898 and 1899.

Other marking experiments on the Columbia River, made by the Washington Commission at Kalama and Chinook, indicate 4 and 5 years as the age of returning fish, none being recorded in the third year. In the well-known planting experiments in Tomales Bay, Cal., and in New Zealand, both of which resulted in establishing spawning runs in streams which hitherto had not possessed them, no run was reported until the fourth year. In view of these facts and others, we must hold in question the report of the Oregon experiment of a considerable return in the third year of both males and females of large size, in spite of a certain appearance of conclusiveness in the report itself.

The history of the king salmon is known principally from the work of Rutter and Scofield on the Sacramento River, and of Chamberlain in Alaska. The fact is well attested that large numbers of fry pass into salt water in spring or early summer as soon as possible after the absorption of the yolk. Many others, but in unknown proportion, remain behind in the streams and migrate the following spring as yearlings. Whether any of these, which have been somewhat unfortunately termed "summer residents," pass out during the late summer or on the high water of the fall remains unknown, but many if not all of them remain during the following winter. The center of the king salmon scale, which records their early history, is subject to more variation than in the sockeye, and will require longer investigation in connection with young salmon of known history.

^a Sixth Annual Report Fish and Game Protector of State of Oregon, 1898, p. 48.

^b Annual Report Department of Fisheries, State of Oregon, for 1899 (1900), p. 15.

In general, king salmon scales exhibit the same two types characteristic of the sockeye—a stream type, with close-ringed nuclear area, sharply set off from the enveloping wide-ringed summer band (pl. IV, fig. 7), and a sea type, of large nuclear area, with less crowded rings, which widen outwardly and usually pass gradually into the rings of the second summer (pl. VII, fig. 13). The nuclear area of the close-ringed stream type agrees with the entire scale of a yearling on its seaward migration in its second spring, and can be safely so interpreted. The nuclear area of the sea type is here interpreted as in the sockeye, as indicative of an early passing to salt water, on the part of those individuals which migrate as young fry. A more extended inquiry into this matter must be made before offering data with full conclusiveness, but it may be offered in evidence that young king salmon about 4 inches long taken in Puget Sound in mid-summer exhibited the wide-ringed sea type and were in their first year (pl. VII, fig. 12). It may also be noted that on examining a series of larger king salmon ($9\frac{1}{2}$ to $17\frac{1}{2}$ inches long) taken in late summer in Puget Sound, all were found to be in their second year, the smaller individuals ($9\frac{1}{2}$ to $11\frac{1}{2}$ inches) exhibiting the stream type of nucleus (pl. IV, fig. 7), and the larger members of the series ($13\frac{1}{2}$ to $17\frac{1}{2}$ inches) the sea type (pl. VII, fig. 13).

Conspicuous in every spawning run of king salmon are the numerous undersized males, known locally as grilse, jack salmon, or sachems. Two theories have been held regarding these, according to which they have been considered either stunted individuals of equal age with the larger salmon, or younger fish which have matured precociously. The theory of precocious development has had wider currency of late, and is in entire agreement with the evidence from the scales, according to which the individuals are always in their second or third year. The mature second-year fish are smaller than those in their third year, and are usually little in evidence, as they escape readily through the meshes of the nets. None which were mature at this age have been taken by us in Puget Sound. But on the Columbia River, a considerable series of mature males in their second year, 9 to $18\frac{1}{2}$ inches long, were secured from the seines and fish wheels. It will be noted that this range in size agrees with that already given for immature second-year fish from Puget Sound. It is further significant that in the Columbia River series, also, the smaller individuals, 9 and $9\frac{1}{4}$ inches long, are of the stream type, and the larger, 13 to $18\frac{1}{2}$ inches, are of the sea type.

The larger grilse (19 to 26 inches) are in their third year (see pl. IV, fig. 8; pl. VII, fig. 11), and among them, again, the smaller individuals of the series are preponderatingly fish of stream type and the larger of sea type. But in the third-year fish there is more overlapping of the two types, as though subsequent inequalities in growth had partially concealed the initial advantage secured by those which had early sought the sea. This is a question which merits further investigation on a much larger series than has thus far been examined.

From salt water in Puget Sound we have secured immature third-year fish, both males and females, and also matured third-year males, taken by purse seines from the same school, and both feeding voraciously and equally on small sand lance and young

herring. There was no difference in size between the mature and the immature individuals, nor could they be externally distinguished, unless by a certain distention of the abdomen in mature specimens, due to the developed testes. It became evident from our observations: (1) That a very small proportion of the males of a given year develop precociously; (2) that precocity is apparently not caused by the influence of peculiar external conditions operating upon the individuals thus affected, but by some unknown factor; (3) that precocious development does not stunt the growth. No mature female king salmon less than 4 years old have thus far been encountered.

The commercially valuable portion of the king salmon run consists mainly of 4 and 5 year fish, with less frequent 6-year individuals. Plate v, figure 9; plate x, figure 18; and plate vi, figure 10, represent these three ages. On the Columbia River they are roughly grouped at the canneries as "half salmon" and "full salmon." The half salmon consist very largely of 4-year individuals and the full salmon those 5 and 6 years old, although there is a certain amount of overlapping, as in the sockeye. The 4-year fish include more females than males, and the 6-year fish are males in even greater proportion. It is thus seen that the females are much more uniform in the age at which they mature than are the males, being practically limited to their fourth and fifth years, while males may develop precociously at any age before the fourth year, or may be retarded beyond the usual period. A single male, weighing 67 pounds, observed by Mr. N. B. Scofield in the Sacramento River, was in its seventh year. None larger than this have been examined, although such are known to occur, so the total range of the species may even include 8 years. Anything beyond seven is problematical and beyond eight must be considered highly improbable.

Among the king salmon taken by purse seines in Puget Sound and those taken by trolling in the salt water of Monterey Bay, Cal., are found 4-year-old male and female individuals which are mature, and others of the same size and age which show no activity of the gonads and would not mature until a later year. The same is true of the 5-year-old fish, but the undeveloped individuals of this age are more largely males. It seems evident that the maturing individuals feed together in the same schools with those which are undeveloped and become segregated only when the period arrives for them to seek their spawning stream.

Prof. McMurrich announces, in the recent paper already referred to, that scale and otolith structure indicate mature king salmon to be always 4 years old and the grilse 2 years old. Such a conclusion is on its face highly peculiar and improbable. That certain males should mature in their second year as grilse and all others unanimously pass their third year without precocious development would be highly remarkable. Fully as improbable would be the corollary as regards size in relation to age. As is well known, the larger grilse equal or very slightly exceed the smaller salmon of the regular 4-year series. Prof. McMurrich's contention is again based on his erroneous interpretation of the nuclear area of the scale, taken in connection with the very limited amount of material which he examined. Plate v of his paper indicates a typical 5-year scale of the stream type, the nuclear portion which he designates fresh-water being

correctly so interpreted, but representing the first year and a half of the life cycle and not the first few months only. Plate vi, figure 1, is also a 5-year fish of similar type. Plate vii represents, however, a 4-year scale, the second summer showing an "intercalated check" wholly similar to that characterizing the sockeye scale represented on plate ii. But whereas the sockeye scale presents three winter bands outside the "intercalated check," the king salmon scale presents but two, hence the necessity for the author's interpretation of the same structure in two opposite ways, in order that both may appear 4 years old. As already indicated, the sockeye scale presents five years' growth and the king salmon four.

We shall not here enter upon a detailed discussion of accessory bands formed by checks in growth during the summer, especially during the first summer in the sea. Such have been demonstrated by Johnston to occur in the Atlantic salmon and are abundantly represented in any series of Pacific salmon or steelhead scales. Their true nature can usually be recognized without difficulty—as in the specific cases mentioned—by the proportion of the bands in which they occur and often by a wide variation in their appearance in different scales from the same fish. Occasionally, however, they so closely simulate genuine winter bands as to occasion some difficulty and doubt, and may then constitute one of the more troublesome features in the interpretation of large series of scales. But the proportion of doubtful cases is very small and such can be eliminated from the series without danger of affecting disastrously the results.

McMurrich's plate vi, figure 2, represents a grilse in its third year. Here the nuclear area of the scale is abnormal and does not give satisfactorily the history of the first year. Other scales from the same fish would have given this in all detail. But we have to do apparently with a fish of stream type, which spent its third winter (marked second winter) in the sea, and was therefore toward the close of its third year. Its length (approximately 20 inches) is that which we have found uniformly characteristic of third-year grilse of stream type.

SILVER SALMON, OR COHO (*Oncorhynchus kisutch*).

[Pl. xi; fig. 21, pl. xii.]

The coho agrees with the sockeye and king salmon in having a dual habit during its first year. Certain of the young migrate to sea as soon as free-swimming, others, in unknown proportion, remain in the stream until their second spring. Fingerlings are present in all streams visited by this species throughout the summer, fall, and winter of the first year. If a seaward migration occurs in the fall, it has so far not been demonstrated. In the latitude of San Francisco yearlings are very numerous in all the smaller streams as late as March and April, and are often caught by trout fishermen during the early spring months. They remain in evidence several weeks after the appearance of the fry of the year, and may then be 3 to 4½ inches long, being of the same size and general appearance as yearlings artificially reared in aquaria. Rather suddenly, on some spring freshet, they disappear from the stream. Some in their downward migration are often left stranded in overflow pools along the lower course of the stream.

A scale taken from a migrating yearling (pl. XI, fig. 19) is entirely similar to those of the stream type in the case of the sockeye and king salmon. A few widely spaced rings in the center, representing the late spring or early summer growth of the fry, are followed by closely crowded rings of fall and winter. The outermost of these are often very slender and broken. The number of rings formed during the first year varies widely, perhaps from 10 to 25, the larger number being found in general in individuals of larger growth. In many migrating yearlings the more rapid growth of the new year is apparent around the edge of the winter band (pl. XI, fig. 19), but the rings thus formed in the stream are not nearly so wide as those formed during the same season after reaching the sea. There is thus, surrounding the first year's growth, often an intermediate zone which, together with the surrounding band of very widely spaced rings, represents the second summer's growth. (Pl. XI, fig. 20.) The outer rings of the intermediate zone may even be narrowed, as though a check to growth was experienced at the migrating period. Such an intermediate zone is by no means of universal occurrence.

The further fate of the stream type yearlings is well shown in a series secured in Puget Sound in the month of August, 1910 (pl. XI, fig. 20). These range in size from 6 to 14 inches and wholly parallel the series of yearling king salmon of stream type, $9\frac{1}{2}$ to $11\frac{1}{2}$ inches, with which they were found associated. As they were taken with purse seine in the open sound, the greater number of individuals were sexually undeveloped, but a few males were developed precociously. The precocious males later join the spawning run and have been found associated with it.

We are unable to give any satisfactory account of the fry which run to sea soon after hatching. Chamberlain has reported these in Alaska waters as more numerous than those which descend as yearlings. By analogy we should expect the same to be the case in Puget Sound and California. But neither among the yearlings of Puget Sound nor the adults of this and other regions do we find scales of the sea type in any considerable numbers. Three alternatives seem to confront us. Either (1) the young do not proceed to sea as fry in the southern part of the range of the species, or (2) the fry do not survive in salt water, or (3) unlike the sockeye and king salmon there is no difference in growth during the first year between those which proceed to sea and those which remain in the streams. As bearing on this last point it must be stated that a very few individuals of undoubted sea type have been examined. The matter is one in need of complete investigation. We are of the opinion that the spawning run in Puget Sound and in California is composed of those individuals which spent their first year in the streams, with exceptions so few as to possess no practical significance.

The spawning run has been examined by us in numerous individuals covering the range in size from 17 to $30\frac{1}{4}$ inches. All of these have been fish in their third year, the scale being shown in plate XII, figure 21. The closely crowded nuclear area represents here as elsewhere the first year and a half spent in fresh water. Outside this are seen the parts representative of the life spent in the sea, consisting of the bands of the second summer, the third winter, and the third summer. Larger specimens should be

examined than any to which we have had access in search of 4-year-old individuals, but such may not be found.

Experimental evidence is thus far largely lacking in Pacific salmon to corroborate inferences we draw from scale structure. But in the coho we have one piece of evidence conclusive as far as it goes. In the midwinter of 1910-11, with the assistance of Superintendent Frank A. Shebley and Mr. W. H. Rich, we marked a certain number of yearlings in Scotts Creek, Santa Cruz County, Cal., by excising both ventral fins. In the spawning run of the winter of 1911-12 several of these returned to the same stream as mature male grilse, with scales clearly in agreement with their known age, having formed a single summer band outside the close-ringed nuclear area and a marginal narrowing for the fall growth. Full-grown fish differ from these only in having completed the winter band and one additional summer band. A more detailed account of this experiment will be given later.

Prof. McMurrich announces the coho adult to be 2 years old. He has here again underestimated by one year the significance of the nuclear area.

DOG SALMON (*Oncorhynchus keta*).

[Pl. XIII; fig. 26, pl. XIV; pl. XV and XVI.]

Less is known of the life history of the dog salmon than of any of the species thus far considered. Our knowledge of the young is entirely due to Chamberlain, who secured them on their seaward migration as fry, some with remnants of the yolk still attached. They were not associated with larger individuals which could be considered yearlings. As stated by Chamberlain, "records of the occurrence of larger individuals in streams have not been authenticated, and, so far as known, all leave the fresh water as soon as they are able to swim." Records of yearling dog salmon have been made by the writer and by others in the streams of Washington, Oregon, and California, but all such have been founded on incorrect identification of the coho yearlings.

At the time of the seaward migration of the fry no scales have been formed. It is therefore obvious that even the inner rings of the nuclear area give the history of life in the sea and not in the fresh water.

In late April, 1911, we found the fry of this species about 1½ inches long, very numerous about the wharves and shores at Seattle, vigorously feeding on ostracods to the exclusion of other food. In midsummer, fingerlings are to be seen abundantly in the Puget Sound traps. In common with the young of other species they pass along the lead and into the heart of the trap, where they remain until forced to pass through the coarse meshes of the webbing.

The fingerlings of the dog salmon are then conspicuous among the others by their slender, graceful form, the dark blue of the back and the conspicuous black margins of the tail. Plate XIII, figure 23, represents the scale of such a specimen, 6 inches long, taken August 2, 1909, from a trap in the Gulf of Georgia. It will be noted that the rings are widely spaced, indicating much more vigorous growth than is commonly shown by such young of other species as spend their first summer in fresh water. The rings are

slightly narrowed from the center outward to about the twelfth, the outer rings showing again a decided widening. The significance of this midsummer check in growth during the first year is unknown. It is frequently wholly absent, may be present as a bare trace, or may become so well marked as to simulate the nuclear area of an individual of other species which spent its first year in the stream.

But little is known concerning the dog salmon in their second year. Fine-meshed purse seines in Puget Sound, which take so many 2-year-old coho and king salmon, are said now and again to capture dog salmon also, but none have been seen by us. A single mature male in its second year, 21 inches long, was secured at Bellingham August 3, 1910. As the habit of the species is to mature about equally during the third and the fourth years, this young male is properly to be designated a "grilse," precociously developed a year in advance. Plate XIII, figure 24, presents the scale of this specimen. The run of dog salmon has not been adequately observed, as it occurs late in the fall, when most investigators have left the field. Examination of a larger series may well show that precocious individuals (grilse) are as numerous in this species as in the others thus far considered. Whether females as well as males mature in the second year remains to be ascertained.

The series examined by the writer, exclusive of the fingerling and the grilse given above, consists of 58 mature individuals obtained at Bellingham August 2 and 3, 1910, ranging in length from 23 to 35 $\frac{1}{4}$ inches. They are so distributed as completely to cover this range in size. From the following table it will appear that the spawning fish are almost equally in their third and in their fourth years; or if there be any preference it is in favor of the third year. The two years overlap from the 26th to the 30th inches, inclusive, a size which seems to include the greater number of males in their third year and of females in their fourth. But the limited number of examples investigated is inadequate to decide this point. A single large male, 35 $\frac{1}{4}$ inches long, the largest specimen secured, was in its fifth year.

DISTRIBUTION OF MALES AND FEMALES, BY AGE AND SIZE, IN A NUMBER OF DOG SALMON, CHOSEN AT RANDOM.

Length in inches.	Third year.		Fourth year.		Fifth year.	
	Male.	Female.	Male.	Female.	Male.	Female.
23	1	3				
24	1	0				
25	2	4				
26	5	2	2	0		
27	3	0	0	4		
28	2	0	3	4		
29	5	1	2	1		
30	2	0	2	0		
31			4	0		
32			1	0		
33			3	0		
35					1	0
Total . . .	21	10	17	9	1	0

AGES AND LENGTHS OF A NUMBER OF DOG SALMON, TAKEN AT RANDOM WITHOUT SELECTION.

Years.	Length in inches.												
First.....	6												
Second.....		21											
Third.....			23 $\frac{3}{4}$	23 $\frac{3}{4}$	23 $\frac{1}{2}$	23 $\frac{3}{4}$	24	25	25	25	25 $\frac{1}{4}$	25 $\frac{3}{4}$	25 $\frac{3}{4}$
Fourth.....													
Fifth.....													

Years.	Length in inches.												
First.....													
Second.....													
Third.....	26	26	26	26 $\frac{1}{4}$	26 $\frac{1}{4}$	26 $\frac{1}{2}$	26 $\frac{1}{2}$	27 $\frac{1}{4}$	27 $\frac{1}{4}$	27 $\frac{1}{2}$	27 $\frac{1}{2}$	27 $\frac{1}{2}$	27 $\frac{3}{4}$
Fourth.....			26										
Fifth.....													

Years.	Length in inches.												
First.....													
Second.....													
Third.....				28 $\frac{1}{4}$		28 $\frac{1}{2}$		29		29 $\frac{1}{2}$	29 $\frac{1}{2}$	29 $\frac{1}{2}$	29 $\frac{1}{2}$
Fourth.....	28	28	28	28 $\frac{1}{4}$	28 $\frac{1}{4}$	28 $\frac{1}{2}$	28 $\frac{3}{4}$		29 $\frac{1}{4}$				29 $\frac{1}{2}$
Fifth.....													29 $\frac{1}{2}$

Years.	Length in inches.												
First.....													
Second.....													
Third.....	29 $\frac{3}{4}$	30	30 $\frac{1}{2}$										
Fourth.....	29 $\frac{3}{4}$		30 $\frac{1}{2}$	30 $\frac{3}{4}$	31 $\frac{1}{4}$	31 $\frac{1}{2}$	31 $\frac{3}{4}$	31 $\frac{3}{4}$	32 $\frac{1}{4}$	33	33 $\frac{1}{2}$	33 $\frac{1}{2}$	
Fifth.....													35 $\frac{1}{4}$

In the above table fractions of inches are included with the whole numbers. While the number of individuals under consideration is too limited for safe generalization, it may yet be noted that both third and fourth year females average distinctly smaller than the males of their own age.

In plate XIV, figure 26, and plate XV and XVI, figures 27 and 28, are presented scales respectively of 3, 4, and 5 year fish. The scales of the dog salmon are broader than in any other species, the rings being approximately circular, or even broader than long. The nuclear area is always large, as in the sea type generally, comprising roughly half the diameter of the scale in 2-year-olds. The central portion of the nuclear area is usually of the open wide-ringed type, the outer portion dense (especially so laterally) and ending in a perfectly defined margin, with abrupt transition to the summer growth which follows. Considerable variation is found in the outer half of the nuclear area, but seldom any which could cause confusion. The size of the area is little variable. Only in cases where it presents a double outer band can any question arise. A slight narrowing of rings in the middle of the nuclear area is not infrequently present. Occasionally this is emphasized until the median and the marginal nuclear bands are about equal in development. In such cases irregularities and fusions can usually be found, and the size of the total nuclear area and the subsequent growths can be relied on to determine.

There is usually no narrowing just outside the nucleus to form a "core," but this may be present in a faint form, or occasionally be more pronounced.

Subsequent years' growths are usually about equal, the well-formed winter bands about equally spaced and very strongly marked. Occasional exceptions occur, in which the second summer's growth has been unusually wide and the third summer's growth much less so, with the result that the second and third winter bands are more closely apposed than usual. Such cases must be distinguished from others in which a double second winter band occurs, or an "intercalated check," during the latter part of the summer. In instances of the latter class there are usually irregularities in the development of the redundant band in different scales, also fusions of the two bands here and there. There is also a lack of any very sudden break or change in character of the rings outside a redundant band, and no unconformity in the rings, characters which very generally accompany the new year's growth.

At the 1st of August, when our series of scales were taken, the rings of the outer summer zone had in all cases begun to narrow into the winter band. The great thickness of the winter bands in this species may be in part thus explained. They may represent more than half the year's growth, beginning perhaps in July and continuing until the new year's growth commences at some period in the spring. Material collected at Seattle the last of April, 1911, did not include this species, but in the king salmon smaller individuals had then produced from two to six broad rings of the new growth, and larger ones (from 18 inches up) contained usually no new growth. If this holds also in the dog salmon, the winter bands represent growth at ever-decreasing rate from July to May of the following year, the few wide summer rings representing sudden vigorous growth for but two or three months. This is of course insufficiently established.

Taking the great majority of specimens (in at least 90 per cent), the scales are perfectly typical and schematic, a glance with the aid of a simple lens being adequate to determine the age. This regularity and simplicity is also evident in the humpback salmon, and is in both species to be attributed to the fact that the young all have the same history, proceeding at once to sea, whereas in the other species, as has been shown, a dual habit is found.

Prof. McMurrich's contention that the dog salmon is a 4-year fish, with a nuclear area representing life in fresh water, has already been sufficiently answered. Plate VIII of his article has unfortunately the nuclear area so blurred in reproduction that its character can not be positively determined. If, however, this area was close-ringed "as in the sockeye and spring salmon, a central nucleus surrounded by a zone of fresh-water lines," the scale could hardly belong to the dog salmon. Such a description could not apply to plate IX, which represents obviously a 3-year-old scale, with the medial portion of the first winter band very narrowly divided but the two portions wholly fused at the sides. The significance of the so-called "spawning mark" we do not here discuss.

HUMPBACK SALMON (*Oncorhynchus gorbuscha*).

[Fig. 17, pl. x; fig. 29, pl. xvii.]

Available data concerning the habits of young humpbacks are derived almost wholly from Chamberlain's observations in Alaska. Like the dog salmon, the humpback young seek the sea as soon as they are able to swim. No yearlings have ever been reported from fresh water. In accordance with this habit, the nuclear area is consistently of the sea type, as in the dog salmon, being large in size and consisting for the most part of rings widely spaced. An inner nuclear core or region of narrowed rings is not infrequently present, and may here also simulate a close-ringed small nucleus of stream type. But the examination of a large series, taken in connection with the known history of the young, satisfies that such is never the correct interpretation.

No young humpbacks in their first year have come under our observation. Those listed by Chamberlain (op. cit., p. 55 to 57) were taken during the summer months and ranged from about 40 to 115 millimeters, the larger individuals being those of late summer. All were undoubtedly in their first year, and would yield interesting results on examination of their scales.

The possibility that the humpback salmon reaches maturity in less time than other species is considered by Chamberlain, who states: "The rapid growth of the young and the biennial occurrence of the species in Puget Sound may be noted in behalf of this belief." This suggestion that the species matures in its second year is wholly substantiated by the evidence of the scales (pl. x, fig. 17 and pl. xvii, fig. 29). A wide-ringed nuclear area of sea type, with its outer portion consisting of a definite winter band, is followed by the band of widely spaced rings representing the second summer's growth. Numerous individuals have been examined, representing all sizes readily secured in a spawning run, and all were uniformly in their second year. Statistics containing sizes of males and females have not been prepared.

Prof. McMurrich's inference from the humpback scales is correct, except perhaps that portion which recognizes in the central area of the scale a record of life in fresh water.

SUMMARY OF RESULTS.

The following conclusions can be drawn from data here presented:

1. The sockeye spawns normally either in its fourth or fifth year, the king salmon in its fourth, fifth, sixth, or seventh year, the females of both species being preponderantly 4-year fish.
2. The young of both sockeye and king salmon may migrate seaward shortly after hatching, or may reside in fresh water until their second spring. Those of the first type grow more rapidly than the second, but are subject to greater dangers and develop proportionately fewer adults.
3. Coho salmon spawn normally only in their third year. The young migrate either as fry or yearlings, but adults are developed almost exclusively from those which migrate as yearlings.

4. Dog salmon mature normally either in their third, fourth, or fifth years, the humpback always in their second year. The young of both species pass to sea as soon as they are free swimming.

5. The term "grilse," as used for Pacific salmon, signifies conspicuously undersized fish which sparingly accompany the spawning run. They are precociously developed in advance of the normal spawning period of the species. So far as known, the grilse of the king salmon, coho, and dog salmon are exclusively males, of the sockeye, almost exclusively males, except on the Columbia River, where both sexes are about equally represented. The larger grilse meet or overlap in size the smaller of those individuals which mature one year later at the normal period.

6. Grilse of the sockeye are in their third year, of the king salmon in their second or third year, of the coho and the dog salmon in their second year.

7. The great differences in size among individuals of a species observed in the spawning run are closely correlated with age, the younger fish averaging constantly smaller than those one year older, though the curves of the two may overlap.