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RELATION OF POPULATION SIZE TO MARINE GROWTH AND TIME OF SPAWNING MIGRATION IN THE PINK SALMON (*Oncorhynchus gorbuscha*) OF SOUTHEASTERN ALASKA

By

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INTRODUCTION

In studying the relation of an animal population to its environment it must always be remembered that the population forms part of its own environment. This is due mainly to the influence its size has upon the other elements, both physico-chemical and biotic, of the environment. Allee (1931) in his discussion of the harmful effects of crowding upon growth separates the growth retarding factors into two groups namely, the vague and the definite. Those in the first group consists of such factors as the X-substance of Semper (1874-1881), the autotoxins of the bacteriologists, Henrici (1928), and the growth inhibiting substances of the tissue culturists, Heaton (1926). He refers to this group of factors as being at present unproved but of value as working hypotheses. Those in the second group consist of the more tangible factors such as insufficient aeration, accumulation of excretory products, reduction in available food and overstimulation of the individuals due to increased contacts. Either one or a number of these factors have been shown to be effective in the growth of tadpoles as studied by Yung (1885), Bilski (1921), and Goetsch (1924), in the growth of snails by Willem (1896), Colton (1908), and Crabb (1929) and in fish by Church (1927), Willer and Schnigenberg (1927) and Shaw (1929).

It is to this second group of growth retarding factors that the authors turn for the explanation of the influence of population size on the growth and time of spawning migration of the pink salmon. This study was made in part through the analysis of commercial fishery data and in part through direct observations of the fish populations under natural conditions. Field studies of this kind provide

¹The United States Bureau of Fisheries was combined with the United States Bureau of Biological Survey on July 1, 1940 to form the Fish and Wildlife Service.

opportunity for the application of ecological principles and the theoretical interpretation of biological relationships in the ocean.

LIFE HISTORY OF PINK SALMON

The pink salmon (*Oncorhynchus gorbuscha*) like the other species of Pacific salmon are anadromous. The eggs are spawned in the gravel beds of the streams in the fall of each year and hatch the following spring. The fry after absorption of the yolk sac emerge from the gravel, and migrate directly to the ocean where they feed until the summer of their second year of life. During their 16 to 18 month sojourn in the ocean they make over 95 per cent of their growth. After attaining maturity in the ocean they return to the streams to spawn and die. The adults begin to migrate into the streams in July and continue through August and part of September. By the middle of September most of the salmon have entered the streams and spawning is well under way.

This two-year cycle of the pink salmon has been found by Davidson (1934) and Pritchard (1932 and 1939) to be very consistent. In fact, all evidence thus far available indicates that this species has an invariable two-year life span and is distinctly different from the other species of Pacific salmon in this respect.

PINK SALMON AGGREGATIONS

Although detailed information is not available concerning the habits of the pink salmon while in the ocean, it is known that they migrate seaward in schools of immense size and return in similar aggregations. The fry migrate from the streams almost exclusively at night. Upon reaching the bays at the mouths of the streams they collect into schools of varying size and remain near the shores for a time before migrating into the open channels and seaward. At times the schools of fry from many bays may congregate into vast swarms as they migrate to the open ocean. Dense bodies of these fry have been observed that cover surface areas ranging from 15 to 25 yards in width and from 75 to 100 yards in length. Since the young salmon at this age are not more than 1½ inches long such aggregations are composed of millions of individuals. These symporia or societies are formed during their migration through the larger channels where they are subjected to the inroads of many predators.

At maturity the adult pink salmon appear near the surface in the ocean and migrate shoreward to the streams. Dense schools of these fish have been observed as far as 15 miles offshore covering a surface area from 1500 to 2000 square yards in extent. Similar aggrega-

tions have also occasionally been observed in the larger inside channels. As a rule, however, the adult salmon migrate in schools of a few hundred to ten thousand individuals in the inside channels and inlets.

FLUCTUATIONS IN SIZE OF PINK SALMON POPULATIONS

Any characteristic of an animal population related to its abundance must be studied from a long time standpoint in order to gain a true perspective of the relationship. Since adequate statistics of the pink salmon fishery in southeastern Alaska during the early years of the industry are not generally available it was necessary to select a representative area within the region wherein such statistics could be secured. The Clarence Strait area which includes the waters of Clarence Strait, Behm Canal, and Revillagigedo Channel was selected for this purpose. These waters form some of the oldest fishing grounds in southeastern Alaska and have consistently produced a large part of the total pink salmon packs of the region each year. The statistics of the fishery in this area cover a period from 1895 to 1940. The statistics during the first half of this period were secured from the records of two old-line canneries operating in the area and those for the latter half of the period from the records of a number of the canneries operating in the area as well as from the records of the fish traps in the area.

Although commercial fishing for pink salmon in southeastern Alaska is carried on by means of traps and purse seine boats the traps account for 70 to 80 per cent of the fish caught. The traps are stationary units of gear and are operated along the shores of the larger inside channels where they intercept the salmon on their migration to the streams. If a method were to be devised for sampling the populations of salmon for the purpose of studying periodic changes in their characteristics and habits no better one could be found than that incorporated in the present trap fishery. The average yearly and daily catch records of the traps provide extensive and comparable data on the yearly abundance and seasonal time of the spawning migration of the salmon.

If the number of traps operating in the area had remained constant from year to year then their average yearly catches could have been used directly as a relative index of the yearly abundance of the salmon. Since this was not the case, however, it was necessary to eliminate the influence of competition between the traps created by the yearly changes in their numbers. Owing to the non-linear relationship between average yearly catch per trap and number of

traps operated, and likewise the non-linear regression of both on time (period of years operated) it was impossible to use a correlation analysis to eliminate the influence of competition between the traps by making the number of traps constant and then determining the regression of average yearly catch on time. Hence an empiracle method was employed wherein a regression curve representing the yearly catches of traps of varying numbers from populations of comparative uniformity in size was used as a basis to calculate the relative abundance of each season's populations from the average yearly catches observed. This relative index of abundance was expressed in percentage of the base year 1921 for it was in that year that the populations in the area reached their lowest level of abundance. See Figure 53.

The upper graph in Figure 53 shows the trend in the relative size of the pink salmon populations in the Clarence Strait area from 1895 to 1940. That part of the graph from 1913 to 1940 describes the relative abundance of the salmon as determined from the average yearly catches of the traps operated in the area during the period. Since trap catch records were not available in the area prior to 1913 the data upon which that part of the trend from 1895 to 1913 was determined were secured from the yearly catches of the canneries operating in the area and estimates of the abundance of the salmon cited in the Commissioner of Fisheries reports for these years.

From 1895 to 1911 the pink salmon fluctuated at a relatively high level of abundance with the exception of 1905, which was a comparatively poor year. In view of the statements in the Commissioner of Fisheries reports for these years, it is estimated that the size of the pink salmon populations during that period, although not as great as the peak years of 1934 and 1936, were considerably above the average for the period 1910 to 1940. From 1911 through 1921 there was a steady decline in the abundance of the salmon with the greatest rate of decline occurring just prior to 1921. This decline in abundance of the salmon following 1911, was due primarily to the unlimited exploitation of the resources by the commercial fishery. From 1921 to 1936 there was a decided upward trend in the size of the pink salmon populations and although those of 1937, 1938, 1939 and 1940 fell below 1934 and 1936 they were still above average for this period.

This rehabilitation of the pink salmon populations following 1921 was due to the introduction and enforcement of an adequate conservation policy by the Bureau of Fisheries. The abundance of the pink salmon in southeastern Alaska was not only restored but in-

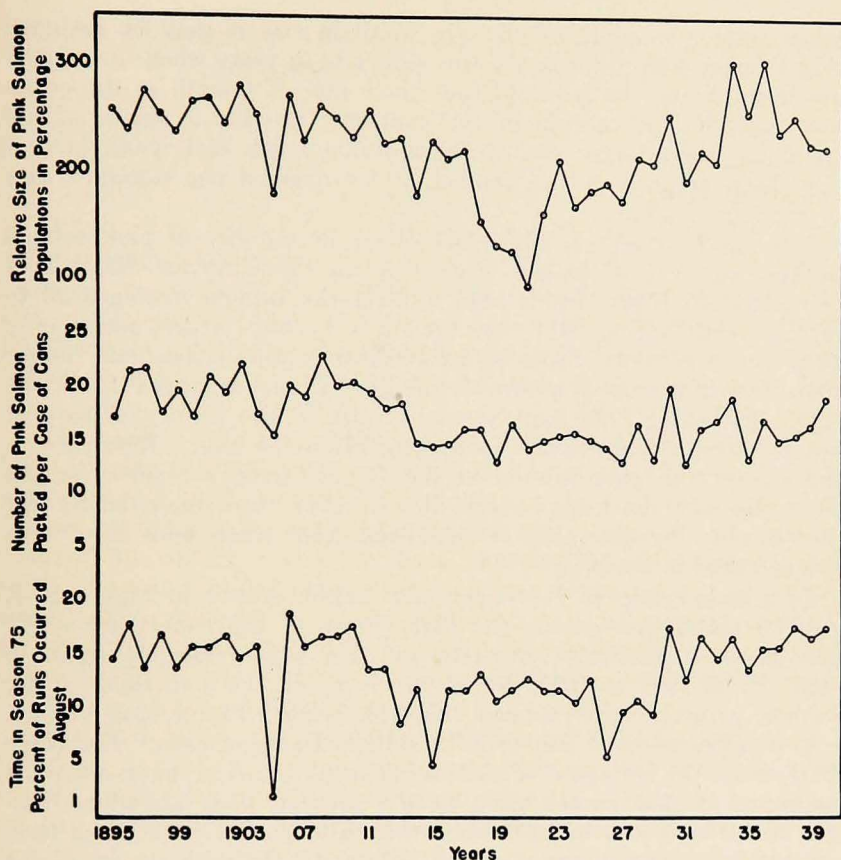


Figure 53. Cyclic changes in the characteristics of the pink salmon populations in the Clarence Strait area of southeastern Alaska from 1895 to 1940. (1) Relative size of pink salmon populations, (2) growth of individual fish as indicated by the yearly number of fish packed per case of salmon and (3) the seasonal time of their spawning migration.

creased under the controlled management of the Bureau of Fisheries. This is a good example of the manner in which our natural resources may be maintained through the application of wise husbandry in their management.

FLUCTUATIONS IN GROWTH OF PINK SALMON

Since the pink salmon have an invariable two year life cycle the size they attain at maturity may be used as a measure of their rate of growth during their sojourn in the ocean. In other words, in

years when the adult salmon are small in size it may be assumed that their growth in the ocean was slow and in years when the salmon are large it may be assumed that their rate of growth in the ocean was rapid.² The records of the canneries provide a means of determining the relative size of the individual fish each year, in that they keep account of the number of fish packed per standard case of canned salmon.

The middle graph in Figure 53 gives the number of pink salmon packed per case of salmon each year in the Clarence Strait area from 1895 to 1940. From 1895 to 1911 the salmon averaged 20 to the case. Following 1911 they tended to become larger, taking only 13 per case in 1919. From 1914 to 1929 they were consistently larger than during the early years of the fishery and averaged 15 to the case. Following 1929 they became erratic in size from year to year but were somewhat smaller averaging 17 to the case. Reference to the size of the pink salmon in the Commissioner's reports for the early years of the fishery show that the fish were small during this period with the exception of 1904 and 1905 when unusually large fish occurred in the runs.

In a comparison of the upper and middle graphs in Figure 53 it will be found that during the early years of the fishery when the salmon were relatively abundant the fish were relatively small in size. From 1911 to 1921, during which period the abundance of the salmon progressively declined, the fish tended to increase in size, i. e. it required fewer fish to fill a standard case of cans. Following 1921, when the Bureau of Fisheries began to introduce more adequate measures for the conservation of the salmon, their abundance began to increase and in 1930 when their abundance reached the level of that in the early years of the fishery the individuals composing the populations tended to become smaller in size, i. e. it required larger numbers to fill a case of cans. In other words, there appears to be an inverse relationship between the size of the pink salmon populations and the size of the individuals that compose them. That is, larger populations tend to consist of small fish with slow growth and smaller populations tend to consist of large fish with rapid growth. A similar relationship between density of population and rate of growth has been observed by Raitt (1939) in the haddock populations of the North Sea, and by Hile (1936) in the cisco populations of Wisconsin lakes.

² Owing to the marked homing tendency in the pink salmon (Davidson, 1934 and Pritchard, 1939) the stream populations are in general highly inbred. Therefore, it is very improbable that the yearly differences in the size of the salmon could be due to chance variations in the genetic composition of the fish.

FLUCTUATIONS IN THE SEASONAL TIME OF SPAWNING MIGRATION OF PINK SALMON

As previously pointed out the adult salmon begin to migrate into the streams in July and continue through August and part of September. However, the numbers that migrate into the streams during each of these months is not the same from year to year. There have been years when the salmon migrated to the streams early in the season and the majority of the fish either entered the streams or collected in the bays at the mouths of the streams during July and early August. On the other hand, there have been years when the salmon migrated to the streams late in the season and the majority of the fish did not appear in the streams or bays until late in August.

The seasonal time of appearance of the runs in the Clarence Strait area prior to 1913 were determined from the date in the season upon which 75 per cent of the pink salmon catches had been delivered to two old-line canneries operating in the area. The time of appearance of the runs in the years from 1913 to 1940 were determined from the dates in the seasons upon which 75 per cent of the pink salmon trap catches in the area were made. Since commercial fishing in the area following 1924 has not been permitted in most years after August 23, all of the data were truncated on this date in order to make them comparable for analysis of time of run.

The lower graph in Figure 53 shows the trend in the time of appearance of the pink salmon runs from 1895 to 1940 as determined by the methods just described. From 1895 to 1910 the runs were as late as they have been in recent years. The statements in the Commissioner of Fisheries reports for these years also indicate the lateness of the runs during this period. The runs in 1905 and 1906 were exceptional in that 1905 was exceedingly early and 1906 exceedingly late. Following 1910 the runs began to appear earlier in the season each year reaching the earliest occurrence in 1915. From 1916 through 1929 the runs were comparatively early, but in 1930 they began to occur later in the seasons again and in some years have been as late as during the early years of the fishery.

RELATIONSHIP BETWEEN CYCLIC TRENDS IN RELATIVE ABUNDANCE, FISH PER CASE AND TIME OF RUN IN PINK SALMON POPULATIONS

In order to secure a quantitative measure of the relationship between the cyclic trends in the characteristics of the pink salmon as described in Figure 53 coefficients of correlation were calculated be-

tween them. These coefficients are as follows: between relative abundance and fish per case, 0.623 ± 0.091 ; between relative abundance and time of run, 0.505 ± 0.111 ; between time of run and fish per case, 0.566 ± 0.101 . These coefficients are all highly significant, their probability values in every case being less than 0.01. Although these coefficients are not very great they indicate the existence of a definite quantitative relationship between the factors considered. Therefore, it may be concluded that when the pink salmon populations were large in size the individual fish composing them were usually small and the majority of the fish migrated to the streams late in the season or migratory period. On the other hand, when the populations were small in size the individuals composing them were usually large and the majority of the fish migrated to the streams early in the season.

Owing to the consistent two-year life cycle of the pink salmon they must, of necessity, migrate to the streams at the close of their second year of life regardless of the growth they have attained while in the ocean. In years when the runs of salmon were early and the fish large in size it appears that the environmental conditions in the ocean were conducive to their rapid development and they attained their full growth early in the second summer of their life cycle. In years when the runs were late and the fish small in size it appears that the environmental conditions were not conducive to a rapid development and the salmon remained in the ocean longer in order to attain their full growth but were forced to migrate to the streams before attaining it. It is possible that there are two internal stimuli which may cause the salmon to begin their spawning migration from the ocean, namely, first, the attainment of physical maturity and second the onset of sexual development.

From 1930 to 1933 inclusive a study was made of the physical characters of the pink salmon entering the stream at Olive Cove on Etolin Island in the Sumner Strait area of southeastern Alaska. A counting weir was operated in the stream which provided opportunity to take samples of the fish as they entered the stream at intervals throughout the entire run. A study was made of the physical characters and degree of sexual development of the fish entering the stream in each of the four quarters of the run. The data describing these characteristics of the salmon at Olive Cove are given in Table I. Since the runs in 1930, 1932 and 1933 were comparable both in seasonal time of occurrence and size of fish the data for these years were combined as a unit and compared to the data of the run in 1931.

The data reported in Table I show that the runs in 1930, 1932

and 1933 were later in time of seasonal occurrence than the run in 1931. The fish composing the runs in these years were significantly smaller than those composing the run in 1931 and showed signs of sexual development earlier in the season than did those in 1931. There was no significant difference in the degree of sexual development of the males in the first and second quarters of the runs but

TABLE I—BODY SIZE AND STATE OF SEXUAL DEVELOPMENT OF PINK SALMON AT OLIVE COVE, ALASKA, FROM 1930 TO 1933

Year ¹	Average body length (millimeters) ²		State of sexual development of males in each quarter of the run (average ratio in percent) ³			
	Males	Females	First Quarter	Second Quarter	Third Quarter	Fourth Quarter
1931	488.5 ± 29.7	482.6 ± 16.1	20.38 ± 1.08	20.61 ± 1.37	20.77 ± 1.14
Average of 1930, 1932 and 1933	446.0 ± 38.4	445.9 ± 26.8	20.20 ± 1.01	20.82 ± 1.27	21.85 ± 1.65	23.55 ± 2.12
Statistics of significance	Comparison of above mean values for statistical significance of differences between 1931 and averages of 1930, 1932 and 1933 data ⁴					
$\Delta_m \pm \sigma$	42.5 ± 3.98	36.7 ± 2.88	0.18 ± 0.22	0.21 ± 0.31	1.08 ± 0.44
<i>t</i>	10.7	12.7	0.828	0.672	2.478
<i>n</i> ₁	112	95	28	22	17
<i>n</i> ₂	337	341	114	81	52
<i>P</i>	<0.01	<0.01	0.40-0.50	0.50-0.60	0.01-0.02

¹ The 1931 data were compared with the averages of the 1930, 1932 and 1933 data combined since the salmon runs in these years were all later in seasonal time of occurrence than the run in 1931. The dates upon which 75 percent of the runs occurred in the Olive Cove area are: 1931, August 11; Average of 1930, 1932 and 1933, August 18.

² Body length is measured from back of head to end of scales on the tail.

³ The head of the males elongates with sexual development and the degree of elongation may be used as a reliable index to the state of sexual maturity. The head length is expressed in terms of the ratio of head length to body length in order to eliminate the size differences in the individual fish. The head length ratio of an immature male is approximately 20 percent and that of a sexually mature male is 24 percent. Owing to unavoidable circumstances the 1931 experiment was discontinued at the end of the third quarter of the run. See Davidson (1935) and Davidson and Shostrom (1936).

⁴ For explanation of methods used see R. A. Fisher (1935).

in the third quarter the males in the 1930, 1932 and 1933 runs were significantly further advanced in sexual development than the males of the 1931 run. The males in the fourth quarter of the 1930, 1932 and 1933 runs were sexually mature. Although unavoidable circumstances made it impossible to measure the fish in the fourth quarter of the 1931 run, general observations showed that they all were not sexually mature and ready to spawn. The degree of sexual development in the female salmon was similar to that in the males

but there are no outstanding changes in their structure accompanying their sexual development that may be used as a measure of it.

In 1931 when the run was early and the fish large in size definite indications of sexual development did not appear in the individuals entering the stream until the last quarter of the run. Thus the majority of the fish left the open ocean long before the onset of sexual development. The large size of the fish in this year may be an indication that upon attaining their full physical growth in the ocean they migrated to the stream regardless of their state of sexual development. In 1930, 1932 and 1933, however, when the runs were later and the fish smaller in size definite indications of sexual development began to appear in the individuals entering the stream in the third quarter of the run and was very marked by the fourth quarter. In fact, in these years the majority of the fish entering the stream in the fourth quarter were sexually mature and ready to spawn. In view of the small size of the fish composing the late runs and their advanced state of sexual development it appears that the onset of sexual development stimulated them to begin their spawning migration to the stream regardless of their state of physical maturity. This relationship between the time of the run and the size of the fish in the Sumner Strait area is not peculiar to these four years only but was also characteristic of the runs during the early years of the fishery. From 1896 to 1926, the coefficient of correlation between time of run and size of fish in this area was 0.644 ± 0.117 , with a probability value of less than 0.01.

As previously pointed out the data for this study, with the exception of those just discussed, were taken from the records of the fishery in the Clarence Strait area mainly because they were the most complete and covered the longest period of time. This relationship of population size to growth and subsequent time of migration of the salmon was also pronounced in the runs throughout all of southeastern Alaska. Evidence of this was found in the marked similarity of data, insofar as they were available, in the other areas to data of the Clarence Strait area, when compared in point of like periods of time. Although there were years when the abundance of the salmon in one or two areas were considerably below the average for the other areas in the region, nevertheless the size of the salmon and their time of appearance in these areas were comparable to those in the other areas with the greater abundance. In other words, it appears that the growth of the salmon and the seasonal time of their migration in the various areas were influenced more by the abundance of the populations as a whole throughout southeast Alaska rather than by the abundance in the individual areas of the region.

BIOLOGICAL EXPLANATION OF RELATIONSHIP

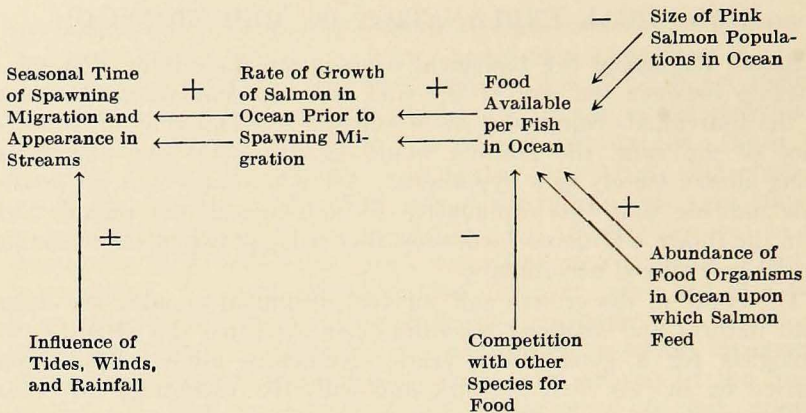
Before discussing the biological explanation underlying this relationship between the size of the pink salmon populations, the size of the individuals composing them and the seasonal time of appearance of the runs, the authors would like to point out that it is being offered merely as a hypothesis. All of the facts thus far available indicate that this explanation is both logical and tenable but if in the future additional facts show that it is not complete or tenable it will be changed accordingly.

The study of the growth and survival of animal populations under both natural and artificial conditions has attracted the attention of biologists for a good many years. Numerous studies have been carried on in this field of work and with few exceptions all point to the conclusion that after a certain limit is reached in the size of an animal population the rate of growth of the individuals composing it decreases. One of the important causes of this decrease in the rate of growth of the individuals, especially in populations of wild animals, is the decrease in the food available per individual which accompanies an increase in their numbers.

As previously stated, although information is not available concerning the size of the pink salmon aggregations in the ocean it is known that the young migrate seaward in schools of immense size and the adults return in similar aggregations. While in the ocean they no doubt feed in schools of varying size as do the king and coho salmon for which there is evidence from the troll fishery. Since the organisms in the ocean upon which the salmon feed tend to swarm as do the salmon it is not entirely amiss to assume that the abundance of the salmon in the ocean brings into play a competition between the individuals for food.

In order to explain how this competition for food, together with other environmental factors, may be responsible for the rate of growth of the individuals and the subsequent time of their spawning migration to the streams, the authors have set up the accompanying word diagram which shows the possible paths of influence of the causal factors involved. In this diagram the double arrows indicate the paths of the most influential factors. The single arrows show the paths of the factors that are as a rule of minor influence but which may at times become paramount in importance. The signs indicate the character of the relationship.

According to this hypothesis the two major factors responsible for the rate of growth of the salmon are namely, first, the size of the pink salmon populations on the feeding grounds in the ocean and, second,



the abundance of the organisms in the ocean upon which the salmon feed. These two factors do not influence the rate of growth of the salmon directly but indirectly through their influence on the food available per individual fish. Furthermore, since these two factors are absolutely independent of each other they may vary together or in opposite directions and may therefore bring about wide fluctuations in the food available per individual salmon, which in turn may bring about similar fluctuations in the rate of growth of the individuals. A minor factor that may influence the food available per pink salmon is the competition these salmon have with other species of fish in the ocean in their search for food. This does not only apply to fish other than salmon, but also to other species of salmon. However, since the pink salmon by far outnumber the other species of salmon in southeastern Alaska, their competition with the other salmon in the ocean may not be of great importance.

The factor that appears to be mainly responsible for the seasonal time of migration of the pink salmon is their rate of growth while in the ocean. Factors of usual minor importance which may influence the time of appearance of the salmon in the streams are tides, winds, and rainfall. The adult pink salmon tend to migrate into the inside channels from the open ocean with the increasing tides. Therefore the occurrence of increasing tides during the migration may tend to speed up the inshore movement of the fish whereas the occurrence of decreasing tides may tend to retard the inshore movement of the fish. Davidson and Christey (1938) have found that offshore and inshore winds have a greater influence on the direction of the migrations than the time of appearance of the runs. The lack of rainfall to maintain the flow of fresh water from the streams along

the shore lines is most effective in retarding the inshore migration of the salmon since they are attracted by fresh water. In years when these three factors have like effects there may be a marked retardation in the time of appearance of the runs in the inside waters and fishery although the salmon may have started their inshore spawning migration from the open ocean early in the season.

In view of the variability the chance combinations of these causal factors may produce in the rate of growth of the salmon and the subsequent time of their spawning migration and appearance in the fishery the authors are of the opinion that the cyclic or long time trend in these characteristics are definitely related to the corresponding trend in the abundance of the salmon but that the yearly deviations from these trends may for the most part be attributed to the influence of the other environmental factors. There have been years when the pink salmon were very abundant, early in time of appearance and the fish comparatively large in size. There have also been years when the runs were small, late in time of appearance and the fish comparatively small in size. These, however, are the exception and not the rule for on the average the size of the fish and their time of appearance may be used at the beginning of each season to roughly predict their abundance.

SUMMARY

In a study of the pink salmon fishery in southeastern Alaska from 1895 to 1940 it was found that:

During the early years of the fishery from 1895 to 1911 there was an abundance of pink salmon in the region which were on the average small in size and late in seasonal time of their spawning migration to the streams.

From 1911 to 1920, during which time the fishery rapidly expanded, the pink salmon declined in abundance, the individual fish increased in size, and the runs appeared earlier in the season.

Following 1921, when the United States Bureau of Fisheries began to introduce more restrictive fishing regulations, the pink salmon increased in numbers. By 1930 they attained their former level of abundance and continued to reproduce near this level through 1940. From 1921 to 1929 the salmon were comparatively large in size and the runs occurred early in the seasons. Following 1929, however, the individuals became comparatively smaller in size, and the runs occurred later in the seasons.

The relationship between these cyclic trends in the characteristics of the pink salmon populations leads to the conclusion that when the

populations are large in size the individuals composing them are usually small and the majority of the fish migrate to the streams late in the season. On the other hand, when the populations are small in size the individuals composing them are usually large and the majority of the fish migrate to the streams early in the season.

The pink salmon have an invariable two year cycle and must of necessity return to the streams to spawn at the close of their second year of life regardless of the growth they have attained while in the ocean. Therefore, a biological explanation of the relationship between population size, growth and seasonal time of the spawning migration of the salmon is hypothesized on the basis of a variable competition between the individual salmon for food in the ocean as their numbers increase or decrease. This in turn directly influences the rate of growth of the salmon and the subsequent time of their spawning migration to the streams.

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