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PRINCIPLES AFFECTING THE SIZE OF PINK AND CHUM
SALMON POPULATIONS IN BRITISH COLUMBIA

by

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ABSTRACT

Changes in population size are governed by the birthrate, the sex ratio and the deathrate.

In pink salmon the average egg-production per female is about 1700 and variations from this average are insufficient to account for observed changes in adult populations. The sex ratio is approximately 50-50.

Survival during the freshwater phases of the life cycle has been found to vary from approximately 1% to 24%, the average survival being significantly different in different streams. Variation is relatively greater in streams in which average survival is low.

Natural survival in the ocean is considered to average about 5% of the number of young fish reaching the sea.

In the central region of the British Columbia coast the annual catch averages about 60% of the adult fish, this percentage being relatively constant for both small and large runs.

Pink salmon maturing in "even" and "odd" years represent separate populations. These populations vary in size independently but may maintain a relatively constant ratio for a series of generations. This ratio varies from near equality to extreme disparity. Marked changes in the level of abundance may occur suddenly.

Three types of mortality are recognized: (a) mortality which becomes relatively heavier as populations increase in density (compensatory) (b) mortality which becomes relatively heavier as populations decrease in density (depensatory) (c) mortality which is independent of density (extrapensatory). (a) is especially identified with the period of spawning and incubation; (b) is considered to occur mainly during the period of fry migration and to be due to predation; (c) may occur at any stage but is probably most variable during the period between entrance of the adults

into fresh water and emergence of the fry.

Population changes initiated by extrapensatory factors, among which stream-flow conditions are considered to be important, are exaggerated by depensatory factors (notably predation on fry) but tend to be resisted by the compensatory influences which operate during the period of spawning and incubation. Stabilization of a level of abundance depends on a balance between these processes.

In general, freshwater mortality is more variable than ocean mortality and plays a greater part in inducing population changes.

It is suggested that the average freshwater survival of an unfished population would approximate 2.4% and that this efficiency must be raised to about 6% to permit a sustained catch of 60% of the adult population. A lower freshwater output is likely to result in a reduction in size of the stock.

Large runs in both even and odd years are not fundamentally incompatible. The possibility of promoting a low-level stock to a persisting higher level of abundance is indicated.

Chum salmon are subject to the same types of mortality as pink salmon but the results are modified by the higher average egg-production (ca. 2700) and the variable length of the life cycle. The species tends to occupy streams in which physical conditions are less stable. Compensatory influences are frequently obscured by these conditions, resulting in irregular fluctuations in abundance.

In the application of remedial measures similar principles apply to both species.

The Thesis of Mr. Ferris Neave
entitled
"Principles Affecting the Size of Pink
and Chum Salmon Populations in
British Columbia"

is accepted:

Dean Angus

Clemens

Cameron

Hoar

Hutchinson

Robbins

Sage

Spencer

Warren

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INTRODUCTION

The various species of Pacific salmon (Oncorhynchus spp.) exhibit changes in abundance which may be of an annual character or may be associated with longer time periods. Such changes are of general interest because they represent phenomena which in some form and at some time are common to all species of animals and indicate the terms on which populations continue to exist. They are also of specific practical interest because the fortunes of a large industry depend upon both the short-term and long-term abundance of these fish.

The present study represents part of a broader investigation undertaken under the auspices of the Fisheries Research Board of Canada, with the general object of acquiring information necessary for (a) the prediction of changes in abundance of Pacific salmon (b) the maintenance or increase of the stocks of these fish available for sustained exploitation.

The purpose of the account presented herewith is to examine the general factors determining population size in two of the five species of Pacific salmon occurring in British Columbia, with particular reference to the above-mentioned problems of prediction and practical remedial action. These two species (the pink salmon, Oncorhynchus gorbuscha, and the chum salmon, O. keta) are sufficiently similar in life history and distribution to facilitate a common investigation. At the same time they exhibit certain differences in the details of behaviour, life history and fecundity which help to elucidate general principles applying to both species.

In attempting to reach conclusions which may contribute to an understanding of the general processes governing population levels and changes, data have been assembled from various sources. The investigations at Nile Creek and Hooknose Creek, to which frequent reference is made, were

initiated by the present writer and have been carried out under his direction since their inception. He has also directed ocean tagging operations on both species and has conducted widespread observations on their numbers, distribution and general ecological relationships in fresh water. For the purpose of reaching general conclusions, however, he has not hesitated to use and interpret additional data for which he was in no way personally responsible. The sources of such information are acknowledged in the text.

PINK SALMON

(Onchorhynchus gorbuscha (Walb.))

The pink salmon is generally distributed throughout the length of the British Columbia Coastline. In fresh water it is scarce in certain areas of both the east and west coasts of Vancouver Island. Elsewhere, the numbers of adults in alternate years may be small. With these provisos it is the most abundant salmon in British Columbia.

The adults enter fresh water mainly in August and September, utilizing both large and small streams. In moderately large unobstructed rivers such as the Bella Coola they may travel upstream for as much as 50 to 70 miles, while in the Skeena watershed many thousands annually ascend the Babine River to a distance of nearly 400 miles (by water) from the ocean. In general, however, a great part of the spawning takes place close to salt water, sometimes beginning within the limits of tidal influence. Deposition of eggs occurs mainly in September and early October. In observed instances the hatching of the alevins is completed during February and the emergence of the fry from the gravel, followed by their immediate migration to salt water, reaches a peak at the end of April or early in May. The young fish can be observed feeding in schools at or near the surface of the sea in May and June, when they may already be found at a distance of many miles from their presumed source of origin. With the advancing season they appear to disperse somewhat and to descend to a depth which, combined with their increased size and activity, makes capture difficult (Observations of writer and others in Strait of Georgia). Their subsequent marine distribution is not ordinarily witnessed until the following summer, when the maturing fish begin to be taken in July by the fishery,

So far as is known, the total life cycle invariably occupies two years.

EGG-PRODUCTION

Since changes in the size of any population are determined by the birth-rate and the death rate, the number of eggs produced is of basic importance in the present study. Total egg-production is obviously a product of the average egg-production per female and the number of females in a population.

Egg-production per female

Available data on the average production of eggs by female pink salmon are shown in Table I.

From these figures it appears that (1) the general average egg-production per female in pink salmon is about 1700, which is lower than that of any other species of Pacific salmon (2) differences in average number of eggs occur between different localities and in the same locality in different years.

The first point carries the obvious implication that if the species is to maintain itself the mortality occurring during the life cycle (from egg to spawning adult) must be less than in the other species of Oncorhynchus. If we assume an average egg-production of 2700 per female chum salmon (see Page 42), with equality of sexes, then a total mortality of 99.93% applied to the product of a spawning pair would just permit replacement of the parents. The application of the same mortality rate to pink salmon eggs (taking an average of 1700) would reduce the spawning stock to less than one quarter of its original size in three generations. To maintain stability it would be necessary to apply a mortality rate of 99.88% to the pink salmon. This latter rate would permit a chum salmon spawning stock to triple itself in two generations. A steady state would of course be represented in either instance by: $M = \frac{100(E-2)}{E}$, where M is percent total mortality and E is the average number of eggs per spawning female.

It does not follow that if the average egg-production of either species were changed, the mortality rate at present characteristic of the species would remain unaltered. It does follow, however, that if average egg-production remains constant, a change of a fraction of 1% in the total mortality rate would quickly

produce a spectacular increase or decrease in the spawning stock. Hence the average egg-production per female of a population which is maintaining a fairly constant level over a prolonged period, must be a very sensitive measure of the mortality which is actually prevailing.

While these considerations can be applied to long-term averages, considerable variation in egg-production is apparent from generation to generation and from place to place. In so far as topographic differences remain constant, they must reflect local differences in mortality rate or active changes in population size. Variations in fecundity from generation to generation may, however, merely represent fluctuations around an average. Pritchard's (1948a) figures for average egg counts in a series of consecutive generations of a pink salmon population range from 1535 to 1899. This represents a fluctuation of about 11% above or below the overall mean of 1718. Such a variation is certainly far from insignificant but it is evident that other major factors must be found to account for the much greater variations which occur in pink salmon populations.

The extent to which egg-production is controlled by hereditary factors is unknown. Presumably certain limits are so determined. Well-marked and persistent differences in fecundity between widely separated sockeye populations of the Fraser River system and also between the various stocks of the Skeena watershed are known to exist. It can readily be supposed that such differences are genetically established, although the effects of external conditions have not been experimentally excluded. ¶ We can concede the possibility that genetically controlled changes in fecundity may take place at times. Such occurrences, however will not account for the fluctuating type of variation which is observed in a

¶ At Port John, where pink salmon runs of the genetically well-segregated "even" and "odd" year cycles both occur, no significant difference in egg-production is yet apparent (data supplied by J.G. Hunter).

series of generations of a given population. It is assumed that such deviations can be ascribed to external conditions such as food supplies or selective fishing.

SEX RATIO

The sex ratio should be considered in attempting to define the factors which may affect population size, since any continued inequality between the sexes would have to be taken into account in determining reproductive efficiency.

The percentage of each sex recorded in the spawning escapement to various streams is shown in Table II.

These figures do not vary consistently in one direction and for the most part the deviation from equality is small. The tabulated values refer to populations remaining after the operation of a fishery which has been thought to be sometimes selective in respect to sex of fish caught. The above figures do not indicate any marked selectivity unless the latter has acted in such a way as to balance an initial inequality in the production of the sexes. However, Robertson (1951) in a sample of 232 migrating pink salmon fry at Hooknose Creek, found 52% males and 48% females, -- a difference which is insufficient to suggest a general departure from a 50-50 ratio.

The presence of females in excess of 50% might represent either a potential wastage of eggs or an increased efficiency per capita of population, according to the spawning habits of the fish. On this point Shuman (1950) reports "a definite tendency towards monogamy". He adds: "While it is probable that a male occasionally will attend more than one female, either because of the early death of the first mate, or because he has been driven from her by a stronger and more pugnacious male, the effectiveness of multiplicity of service must be demonstrated conclusively before it can be

Table I. Average egg content of pink salmon

Locality	Year	No. of fish	Average no. of eggs	Authority
McClinton Creek	1930	97	1535	Pritchard (1948a)
" "	1932	73	1758	" "
" "	1934	165	1799	" "
" "	1936	91	1899	" "
" "	1938	40	1698	" "
" "	1940	41	1619	" "
Morrison Creek, V.I.	1943	38	1779	" (unpub.)
" " "	1945	27	1862	Neave "
Namu	1934	41	1841	Foerster & Pritchard (1936)
Fraser River	1934	48	1755	" " " "
Port John	1947	38	1520	Hunter (unpub.)
" "	1950	20	1593	" "

Table II. Sex ratio (percent) of pink salmon escapements

Locality	Year	No. of fish	Males	Females	Authority
McClinton Creek	1930	66,153	49.8	50.2	Pritchard (1948a)
" "	1932	15,600	51.3	48.7	" "
" "	1934	155,196	49.9	50.1	" "
" "	1936	52,312	46.3	53.7	" "
" "	1938	10,577	52.5	47.5	" "
" "	1940	35,521	53.7	46.3	" "
" "	1942	36,893	47.6	52.4	" "
Morrison Creek, V.I.	1943	15,755	48.6	51.4	" (unpub.)
" " "	1945	13,411	52.0	48.0	Neave "
Hooknose Creek	1947	5,576	47.1	52.9	Hunter "
" "	1948	1,160	48.5	51.5	" "
" "	1949	1,173	55.4	44.6	" "
" "	1950	1,857	44.7	55.3	" "

considered an important factor in salmon propagation under natural conditions". However Cameron (1939) found that there was no permanent pairing of the sexes and that "males varied their attentions between adjacent females". In view of his definite observations, it may be concluded that a deficiency of males, to the small extent noted above, is unlikely to reduce the reproductive efficiency of a population.

On the assumption that extra males produce no benefits, the appearance of an excess of this sex in a previously equally divided population would necessitate a reduced mortality rate or an increased egg-production to maintain a constant population. Fig. 1 shows the adjustments which would be required in either of these directions at various levels of male preponderance, as compared with a standard of 1700 eggs and a 50-50 sex ratio. Fig. 2 shows the percent decline of the population on the assumption that 1700 eggs continued to produce an average survival of two fish, unequally divided as to sex.

Since a marked preponderance of males on the spawning grounds appears to be infrequent, this factor is not considered to be generally important in determining population levels. Although selective fishing may introduce local inequality at times, it is provisionally assumed that both the young fish and the spawning populations tend to have an equal division of the sexes. The complications introduced by the presence of "jacks" (precocious males) do not arise in the case of the present species.

MORTALITY

Since the birthrate can be regarded as relatively constant, major changes in population size must be ascribed to changes in mortality.

It is convenient to divide the total mortality which attends the life cycle into three categories, namely:

Fig.1. (1) Total mortality required to maintain constant population, with egg production of 1700 and varying preponderance of male fish. (2) Egg production required to maintain constant population with mortality rate of 99.8824% and varying preponderance of male fish.

Fig.2. Decline of population with egg production and mortality rate constant and increased proportion of male fish.

Freshwater Mortality
Natural Ocean Mortality
Fishing Mortality

For practical purposes these categories correspond to consecutive portions of the life history, since pink salmon fishing is almost entirely confined to a short period at the close of the ocean phase of existence.

MORTALITY AND SURVIVAL IN FRESH WATER

1. Total freshwater survival

Counts or quantitative estimates of the number, sex ratio and egg-content of adult pink salmon migrating up certain streams, and of the number of young migrants subsequently descending to the sea, have been made at several localities over varying periods of time, utilizing weirs and pens for trapping the fish. The total number of eggs carried upstream by a given spawning run has been estimated by sampling an appropriate number of females throughout the period of the upstream migration and has usually been termed the "potential egg deposition". The number of young fish recorded as sea-going migrants has been expressed as a percentage of the potential egg deposition, thus representing the "reproductive efficiency" or percentage survival between these two points in the life cycle.

The operation of counting weirs is attended by difficulties, most of which are connected with sudden large increases in the volume and speed of the water flow. Enforced suspension of counting for short periods has been a not infrequent occurrence in the history of some installations of this kind, necessitating a certain amount of interpolation. The possible errors resulting from such lacunae have been discussed by Pritchard with reference to the series of experiments conducted by him at McClinton Creek. Somewhat similar considerations apply to certain other cases. The figures obtained by careful and competent investigators are accepted here as being the best possible estimates and as being very close to the true values.

They are basic to the consideration of factors causing changes in abundance of pink salmon.

From published records and through the courtesy of investigators in making their unpublished results available, the figures presented in Table III have been compiled.

Table III. Freshwater survival of pink salmon. Fry entering the sea expressed as percentage of potential egg deposition.

<u>Locality</u>	<u>Brood-year</u>	<u>Survival (%)</u>	<u>Authority</u>
McClinton Creek	1930	10.6	Pritchard (1948a)
" "	1932	17.4	" "
" "	1934	9.0	" "
" "	1936	6.9	" "
" "	1938	23.8	" "
" "	1940	19.0	" "
McClinton Creek	Average	14.45	
Morrison Creek, V.I.	1943	4.7	Pritchard (unpub.)
" " "	1945	6.7	Neave "
Hooknose Creek	1947	0.87	Hunter (1948)
" "	1948	8.02	" (1949)
" "	1949	6.24	" (unpub.)
" "	1950	14.76	" "
Hooknose Creek	Average	7.47	
Sashin Creek, Alaska	Average (1940-50, 11 years)	1.93	U.S.Fish & Wildlife Service ^x

^x The writer is indebted to M.G. Hanavan, Acting Chief, Alaska Fishery Investigations, for these figures which are of great interest for comparative purposes.

The average recorded freshwater survival in the three streams for which several years' data are available is as follows: McClinton Creek, 14.45%; Hooknose Creek, 7.47%; Sashin Creek, 1.93%. These differences are large and can be considered to be statistically significant ($P < .05$). Evidently these populations are not being subjected to the same conditions of environmental pressure.

These different average survival rates may have a profound effect not only on the absolute number of sea-going migrants but also on the magnitude of the fluctuations between different generations of such migrants. Evidently if a population is subject to an average freshwater mortality of 86%, a variation of as much as 7% in either direction (79% to 93%) will only increase or reduce the output by 50%. On the other hand, with an average mortality of 98% a shift of only 2% in the mortality rate would double the output or eliminate it entirely. The following comparison shows the effects of the recorded ranges of freshwater mortality as applied to the offspring of a pair of fish producing 1700 eggs.

Stream	Observed mortality range (%)	No. of migrants produced		Ratio of (a) to (b)
		(a) Maximum	(b) Minimum	
McClinton	76.2 - 93.1	404	118	3.45:1
Hooknose	85 - 99.1	255	15	17.00:1
Sashin	95.6 - 99.8	109	3.4	32.00:1

It appears that a much greater range of fluctuation (as measured by the reproductive success of individual pairs of fish) can be expected in streams in which the average survival rate is low.

2. Immediate causes of death

Many more or less specific causes of loss can be recognized as contributing to the total mortality experienced in the freshwater phases.

These can be listed by periods, as follows:

A. Period preceding burial of eggs

- (1) Predation on adult unspawned fish.
- (2) Death of adult unspawned fish through other causes, notably as a result of barriers or insufficient water.
- (3) Losses of eggs through retention in the body or failure of fertilization.

B. Period of incubation and alevinage

- (1) Erosion or scouring, i.e., removal of gravel and contained eggs or alevins by flood, with resultant death by mechanical injury, exposure to predation or deposition in unsuitable situations.
- (2) Asphyxiation. Mortality caused by insufficient exchange of gases with the environment, due to unsuitability of the original location or to subsequent deposition of silt, etc., resulting in reduction of the water supply or reduction of the dissolved oxygen content of the water.
- (3) Unfavourable temperature for development.
- (4) Freezing of eggs or alevins by coincidence of prolonged cold weather with exposure of spawning beds to air.
- (5) Reduction of water level, resulting in death by desiccation or prevention of the emergence of fry from the gravel.
- (6) "Superimposition" or "overdigging". Mortality of the same type as in (1) but caused by the operations of fish which have occupied spawning sites already containing the developing eggs of earlier-spawning parents.
- (7) Killing of eggs or alevins by fungus.
- (8) Predation. (Not usually regarded as serious during this period).
- (9) Exposure of eggs to salt water in tidal areas.

C. Free-swimming period

- (1) Predation.
- (2) Trapping of fry in pools or backwaters.

Breakdowns of total freshwater mortality by assigning percentage losses to such categories as the above have been made in specific instances by Hobbs (1937) for Oncorhynchus tshawytscha and Salmo fario and by Cameron (1941) for the present species. Two main difficulties are encountered in

attempting to reach general conclusions as to the relative importance of such individual factors in determining the final output. The first lies in the absence of quantitative data indicating the variation which undoubtedly exists in different streams and different years. The second difficulty is connected with the fact that many of the factors recognized are interrelated in such a manner as to make the assignment of losses an arbitrary matter. For example, the losses among pre-spawning fish may be assigned largely to a biological factor, predation. The extent of this predation, however, may depend to a large extent on a non-biological factor, namely the prevailing water level (the writer has observed rather heavy predation by bears on unspawned pink salmon which had been prevented from surmounting a waterfall by low water conditions: later, an increase in stream flow largely eliminated the losses at this spot). On the other hand, to isolate and emphasize such factors as scouring and silting as being the chief causes of mortality during the period between deposition and fry emergence may underemphasize the part played by biological factors in producing the result. The size of the run may determine the proportion of the fish which are forced to select less desirable sites. Again, a comparatively small difference in high water levels might greatly alter the ratio of losses between "siltling" and "scouring" without producing a corresponding effect on the total mortality.

3. General conclusions

While mortality will be discussed further, on a different basis, on later pages, the foregoing brief review of the extent and nature of freshwater losses favours the following preliminary conclusions:

Freshwater mortality is always heavy, accounting for a large majority of the eggs or young fish present.

Large fluctuations in the percentage output of fry are generally caused not by major variations in the total mortality rate but by small

variations which are large in relation to the very small percentage of fish which normally survive.

While considerable annual variations in percent survival are evident in a given stream, there are also significant average differences in the mortality rates of populations inhabiting different streams.

Populations having a low average freshwater survival are likely to show large relative differences in efficiency of reproduction from year to year.

The immediate causes of death are interrelated. Specific factors are not necessarily additive in effect but act reciprocally to some extent. Total mortality may therefore be expected to vary relatively less than mortality from a particular cause.

MORTALITY AND SURVIVAL IN THE OCEAN

As indicated previously, the mortalities which take place in the ocean can conveniently be referred to two categories, - Natural mortality and Fishing mortality^x. Before attempting the segregation of these it is convenient to establish a basis for estimating their combined effect on the young fish which have escaped from fresh water.

The number of adult fish entering a given stream from the sea will represent numerically the survival of the young migrants leaving the stream in the appropriate previous season(s) if (a) all the survivors return to the parent stream, or (b) the number of survivors which do not return to the same stream is balanced by an equal number of fish which originated elsewhere.

With regard to (a), reference may be made to marking experiments

^x In the largest rivers, i.e. the Fraser and the Skeena, some commercial fishing takes place in fresh water. Since, however, this fishing is a direct continuation of operations which for the most part are prosecuted in the sea, the distinction is not recognized in the present account.

reported by Pritchard (1939). This investigator found that in the year for which the most reliable data were available, 90% of the recoveries were from the "home" stream and only 0.2% were recovered in areas and at times which appeared to preclude their return to McClinton Creek. He concluded on the basis of all the evidence "that some of the pink salmon in the natural run may wander from the parent stream but the numbers so doing are not economically significant". Also, "For all the marking experiments on pink salmon it can be stated that in the case of natural runs the majority of fish returned to the parent stream". In a later paper Pritchard (1948b) supported his conclusion by reporting the results of an examination of pink salmon carcasses in streams other than the parent creek. He found only two marked fish in 5922 examined, whereas McClinton Creek showed a proportion of marked fish equivalent to 131 in 5922.

(b) Even with respect to the small minority of fish which undoubtedly "wander", it may be presumed that such wandering is not in one direction only but that there is a tendency for absentee fish to be replaced by individuals which originated in other streams.

It is therefore concluded that the escapement of adults to a stream usually represents very closely the numerical survival from that stream's output of young fish.

In the instances for which data are available, the percentages of returning adults in relation to outgoing fry are given in Table IV.

These survival figures represent the adult population after it has been subjected to both natural ocean mortality and fishing mortality. For practical purposes these two factors can be considered to operate consecutively, not concurrently. The fishing for this species takes place during such a relatively short period at the end of the ocean phase that natural ocean mortality can be regarded as having ceased when fishing mortality begins.

Fishing mortality therefore is added to natural mortality without reducing the latter to an important extent.

Table IV. Marine survival of pink salmon. Adult escapement expressed as percentage of outgoing fry.

Locality	Brood-year	No. of experiments	Range (%)	Average (%)	Authority
McClinton Creek	1930-40	6	0.29-6.75	1.71	Pritchard (1948b)
Morrison Creek	1943	1	-	2.10	Neave (unpub.)
Hooknose Creek	1947-48	2	2.7 -3.7	3.20	Hunter "
Sashin Creek	1940-45	6	0.6 -3.5	1.93	U.S.Fish & Wild-life Service ^x

^xThe writer is indebted to M.G. Hanavan, Acting Chief, Alaska Fishery Investigations, for these figures which are of great interest for comparative purposes.

So far, it has not proved feasible to separate natural mortality from fishing mortality in the case of individual streams. The reasons are mainly connected with (a) the difficulty of obtaining a complete, or reasonably complete, recovery of marked fish from a fishery which is prosecuted to a large extent with purse-seines and which delivers catches at widely separated points (b) uncertainty as to the relative effects of natural and fishing mortality on marked and unmarked fish (c) the heavy differential mortality which is believed to follow the marking of fish which must be operated upon when only 30 - 40 mm. long.

It is possible, nevertheless, to reach certain general conclusions as to the order of magnitude of the two types of mortality to which fish are subjected in the ocean.

The average survival represented by the final escapements (Table IV) is about 2%. Evidently the survival from natural ocean mortality must be sufficiently greater than 2% to account for a fairly intensive fishery. At the same time we might expect that the average survival would be considerably

less than the 9.9% which Foerster (1936) estimated as the ocean survival for sockeye. Although the latter species commonly spends a year longer in salt water than the pink salmon, this factor in the opinion of the writer, would by no means offset the vulnerability associated with the very small size at which pink salmon reach the sea.

The most obvious source of information on the point at issue is a comparison between the catches and escapements of certain areas. For such comparisons to be valid, the fish caught must be proceeding to the streams with the spawning populations of which they are being compared. In many areas there is no certainty whatever that the fish caught are related to the spawning streams of the same area. This is particularly true of the fish which enter the straits between Vancouver Island and the mainland which, as tagging experiments show, may be proceeding to any of a wide variety of localities from Queen Charlotte Strait to Puget Sound. There is, however, a large region of the central part of the British Columbia coastline, corresponding with the Department of Fisheries Statistical Areas 6, 7 and 8, which can reasonably be considered as a self-contained unit in respect to catches and escapements. Taggings carried out under the direction of the writer at the south and north ends of this region in 1947 and 1948 showed little migration to other areas (only about 3% of the tags recovered came from "outside" districts (unpublished data)). A comparison is accordingly presented (Table V and Fig. 3) between catches and escapements reported for this region by officers of the Department of Fisheries. "Catches" were reported in hundred-weights and have been converted to approximate equivalent numbers of individuals. The escapements quoted have been arrived at by summing the estimates of spawning populations made by inspectors on about 180 individual streams and rivers (I am indebted to Mr. J.G. Hunter for this compilation). Estimates have usually been recorded by observers by means of letters indicating that

the population was within certain limits, e.g. "H" = between 5000 and 10,000 fish. In order to obtain numerical totals the mid-points of the indicated ranges were assigned to the estimates.

Table V. Reported catch and escapement of pink salmon in the central region of British Columbia

<u>Year</u>	<u>Catch</u>	<u>Escapement</u>	<u>Total run</u>	<u>% caught</u>
1934	2,250,000	2,046,675	4,296,675	52
1935	1,682,000	1,205,875	2,887,875	58
1936	3,502,000	2,577,500	6,079,500	58
1937	1,841,000	909,050	2,750,050	67
1938	1,619,000	1,512,425	3,131,425	52
1939	2,800,000	970,800	3,770,800	74
1940	663,000	622,875	1,285,875	52
1941	1,073,000	916,250	1,989,250	54
1942	1,175,000	1,045,600	2,220,600	53
1943	5,250,000	1,805,150	7,055,150	74
1944	2,510,000	856,400	3,366,400	74
1945	6,900,000	2,517,275	9,417,275	73
1946	1,685,000	724,775	2,409,775	70
1947	2,076,000	662,275	2,738,275	76
1948	2,834,000	985,100	2,835,100	74
1949	3,233,000	1,720,350	4,296,675	65

The difficulty of estimating accurately the salmon population of a stream on the basis of, at most, a few visits during the spawning season is well-known and fully admitted. The totals, however, represent a very large number of individual estimates by various observers. In general, the catch seems to constitute a rather constant percentage of the run, whether the latter be large or small, although the degree of exploitation appears to have been maintained at a higher level since about 1943. Accepting this evidence of a rather constant relationship between catch and escapement^x, we may defer acceptance of actual figures until another clue has been considered.

^x Such a relationship might well be expected, in view of the efficiency of the fishing fleet and the measures adopted by the Department of Fisheries to ensure the escape of a proportion of the run.

The taggings to which reference has been made yielded total returns from the fishery of about 30%. In both instances tagging was carried out over a period of several weeks which, however, did not include the earliest stages of the fishing season. The recoveries of tags applied during the latter part of the fishing period will certainly tend to be below the general fishing mortality rate (returns from the first week of tagging were 40% and 33% respectively from the two operations). Even these figures are undoubtedly too low. Non-return of recaptured tags is believed to be a far from unimportant source of loss and, in addition, even the earlier fish tagged had been available to the fishery for various lengths of time and represented a population which had undergone some depletion.

On the other hand, the fishing mortality deduced from the comparison of catch and escapement is probably somewhat high. Not all salmon streams are inspected in each year. A fraction of the escapement is thus unrecorded. The evaluation of runs in streams on which counting weirs are operated leads to the conclusion that stream patrol observations usually underestimate the populations which actually enter.

With these limitations in mind, the writer believes that the average fishing mortality in this region in recent years can be placed with some assurance at between 50% and 70% of the adult run: 60% would seem to be a reasonable working figure. If we accept 2% as representing an average survival after the operation of the fishery (p.14), this would imply a survival from the natural hazards of ocean life of 5%, i.e. a natural ocean mortality of 95%^x.

^x The acceptance of a 95% natural ocean mortality and a 60% fishing intensity would require a freshwater survival of about 6% for maintenance of the population level (see p.34) in this region. This is in good agreement with the average recorded survival (7.5 ± 2.9) of Hooknose Creek, which is situated in this district. The fish of the Central region appear to be at least maintaining their abundance (Fig. 3).

How far these conclusions can be applied to other districts is uncertain. The size and mobility of the present day salmon fleet is such that a heavy fishery can quickly be brought to bear on a run of fish appearing in any section of the coastline. Pressure of fishing gear thus tends to be distributed according to the numbers of fish available anywhere. Certain runs, however, are undoubtedly vulnerable for a longer period than others, due to their long migrations through confined straits and channels. Tag returns of 40% were obtained from taggings carried out at Sooke and in the Alert Bay area in 1943 and 1945 (Pritchard and DeLacy, 1944; DeLacy and Neave, 1947). These figures imply a somewhat higher fishing mortality among salmon which travel to "inside" waters via Juan de Fuca and Johnstone Straits than among the fish of the central region.

While 5% is considered to be an approximation to the average natural ocean survival, there is no good evidence as to the range of variation. In only one of the recorded cases (Table IV) does the return to a stream exceed this figure (the 6.75% observed in one year at McClinton Creek), indicating that natural survival must have reached this level even if fishing mortality was nil. The lowest recorded return (0.29%) would imply a natural survival of less than 5% unless the fishery took 94% of the adult fish. This seems unlikely, although it is obvious that the average fishing mortality for a large district cannot be expected to hold good when applied to the run of a particular stream in a particular year. Further speculation on the limits of variation of natural ocean mortality would seem to be unwarranted until more data are available.

CHANGES IN ABUNDANCE OF ADULT PINK SALMON

Fig. 3, to which reference has already been made, may be cited as an example of changes in abundance when a large area is considered. Since the pink salmon has a constant life span of two years the "even" and "odd"

Fig.3. Reported catch and escapement of pink salmon in the central region of British Columbia. (1) Total run (2) Catch.

year runs represent different stocks and can be treated separately in considering changes in population levels. Fig. 4 shows the same data segregated into the two components.

Figures for the number of pink salmon caught annually in the traps situated near Sooke may be presumed to reflect with considerable accuracy the relative magnitude of the runs entering Juan de Fuca Strait, since this gear is nearly constant in quantity and position from year to year and takes its toll at an early stage in the passage of the fish through the fishery as a whole. Since the difference in size between the "even" and "odd" year catches is so great as to make graphical representation inconvenient, the figures are tabulated (Table VI).

Table VI. Numbers of pink salmon caught annually in traps at Sooke, B. C.

<u>Year</u>	<u>Number</u>	<u>Year</u>	<u>Number</u>
1938	1472	1939	169,018
1940	328	1941	55,503
1942	116	1943	33,699
1944	605	1945	221,871
1946	110	1947	168,284
1948	214	1949	109,304
Average	474	Average	126,280

The evidence (discussed previously) that the annual catch made by other types of gear is closely related to the size of the run, makes it legitimate to use catch figures alone as indices of relative abundance in certain areas. Fig. 5 shows annual catches reported for the Skeena River area over a lengthy period.

From these examples, which apply to large areas and do not necessarily reflect the course of events in individual streams, the following inferences can be drawn:

Fig.4. Runs of pink salmon in the central region of British Columbia.
(1) Even years (2) Odd years.

(1) Changes in abundance between one generation and the next do not usually exceed a two- or threefold increase or decrease (unless the numbers are very small, as in the "off" years of some areas). This is in spite of the fact that the rigid life span of the pink salmon precludes any buffering effect which might be introduced if fish matured at different ages.

(2) Occasionally a larger "jump" or "crash" takes place, as is exemplified by the big difference between the 1930 and 1932 catches of the Skeena area.

Actually this occurrence took place over a much larger area than that to which the graph refers, being a conspicuous feature of catch records for northern and central British Columbia.^x A similar failure in the recurrence of the big "odd" year run to the central region appears to have occurred in 1919.

The sudden upswing of this stock in 1943 and the sharp recession in 1947

(Fig. 4) are further examples of these discontinuous changes in abundance.

An upward jump of similar relative magnitude is shown by the Sooke trap catches in 1945 (Table VI).

(3) After one of these major changes the population is apt to remain near the new level for at least a generation and sometimes for a prolonged period.

(4) The "even" and "odd" year stocks fluctuate independently, neither small nor large changes in one cycle being necessarily reflected by similar tendencies in the other cycle. The average level of abundance of the two cycles may be quite similar, as in the central region from 1934 to 1949 and in the Skeena area from 1931 to 1949, or the two stocks may exist for long periods on a totally different scale, as demonstrated by the runs at Sooke, where the odd-year fish exceed the even-year fish in a ratio of more than 250 to 1.

^x The possibility that the low catches of 1932 merely reflected economic conditions is considered by Hoar (1951). The continued low level of the catches provided by this stock in the face of the high market demand of the last 15 years, together with the existence of a reasonable alternative explanation, seems to the writer to constitute convincing evidence that such a "crash" actually occurred. Moreover, chum salmon production, which should have been at least equally affected by economic conditions, showed a marked increase in this area in 1932 (see fig. 8).

Fig.5. Pink salmon catches reported from Skeena River area. (1) Even years
(2) Odd years.

THE MECHANISM CONTROLLING POPULATION LEVELS

In seeking to understand the above-mentioned features of population levels and population changes it is necessary to conceive a mechanism which will permit the occurrence of seemingly contradictory results. On the one hand we are confronted with the fact that the pink salmon has successfully withstood a heavy fishing mortality for many years. Since this fishery, if it had been merely added to existing mortality, would have wiped out the commercial importance of the species in a very few generations, it is evident that the reduction in the number of adult fish has been accompanied by an increase in the reproductive efficiency of the escapements. On the other hand, the evidence is equally plain that two stocks can exist for prolonged periods in the same area at very different densities, with no tendency to reach a common level. Furthermore, when a large stock suffers a major "crash" it may remain for many generations near the new level with no apparent tendency to regain its former numerical status unless or until some equally sudden "jump" takes place.

In considering this problem it is necessary to distinguish between three "types" of mortality, namely:

- (1) Mortality which becomes relatively heavier as populations increase in density (and vice versa), thereby tending to stabilize the prevailing population level.
- (2) Mortality which becomes relatively heavier as populations decrease in density, thereby tending to exaggerate fluctuations initiated by other causes.
- (3) Mortality which is independent of population density, that is, taking a given percentage of the population whatever the density of the latter may be.

Mortality of the first type has long been recognized as being the ecological basis on which the maintenance of intensive long-term fisheries depends. One of its effects, that is, the tendency for a reduced population *to* show an increased reproductive efficiency, has been termed "resilience" by some

authors (Thompson, 1944, 1950; Pritchard, 1948a). The present writer does not find this term particularly attractive. It appears to emphasize only half of the process, namely the decreased mortality which takes place at low levels of population. The increased mortality which attends high population levels is of course equally characteristic. In other words the relationship is, or can be, continuous over a very wide range of population density. It is not an innate power to respond to a condition of depression but merely an expression of the fact that changes in population density necessarily entail changes in the death-rates ensuing from certain causes. The term "density-dependent mortality" has been used in other fields, particularly in entomological studies (see Solomon, 1949). This accurately designates the relationship but seems cumbersome particularly when it becomes necessary to recognize "inversely density-dependent mortality", that is, the type of mortality referred to in category (2) above. The present writer suggests "compensatory mortality" as a convenient term for the relationship now under discussion.

This kind of mortality appears to be highly characteristic of the period from spawning to the emergence of the fry. It might be supposed that physical factors such as flood, drouth and silting would tend to have the same effect on a population whether the latter be large or small. This is indeed the case to an important degree (see p. 27) but these factors do not act in this way alone. In practice the spawning sites available in the limited environment of a stream appear to vary considerably in favourability. With increasing numbers of spawners a larger percentage of the fish are compelled to make their redds in marginal or unfavourable positions. This condition, coupled with the increased "superimposition" and perhaps the mutual interference between individuals of a dense population, tend to produce a lower average efficiency of reproduction.

Over the whole period of freshwater existence Pritchard (1948) at

McClinton Creek observed a general inverse relationship between number of adults and percentage output of fry migrants. Certain anomalies were apparent, however, especially at the highest population level encountered. These are discussed below.

The importance of mortalities which become relatively greater with diminishing density of population (and vice versa) seems not to have been appreciated by fishery biologists. Quite evidently, however, there are influences which frequently prevent the effective operation of compensatory mortality, since otherwise the large and small populations of an area could not indefinitely preserve their respective numerical positions. There would be a constant tendency to converge. Such influences ~~cannot~~ be merely neutral; they must actively oppose the compensatory process, since the existence of the latter is beyond dispute. Actually, as we have seen, pink salmon populations can be relatively stabilized for considerable periods at a wide variety of levels. The anti-compensatory influences must accordingly act over a wide range of densities. The term "depensatory mortality" is proposed for the type of mortality which is inversely related to population density. The identification of the factors which work in this way, and the period in the life history when they operate, are obviously matters of vital importance to our study of population changes.

A specific example of depensatory mortality appears to be provided by the observations of Davidson and Hutchinson (1943). These authors reported that in January 1942 a wholly exceptional flood caused extremely heavy losses among pink salmon eggs and alevins in the lower reaches of Sashin Creek. Surviving fry migrants came mainly from the upper reaches, an area which usually receives little seeding, being relatively rocky. Owing to the population pressure produced by an exceptionally large run of adults in the fall of 1941 an unusually large number of adult fish had utilized this upstream area.

Such occurrences are probably relatively infrequent and certainly cannot provide the constant counterbalance to the compensatory process which seems to be demanded by the observed maintenance of diverse population levels. Fishing undoubtedly could be prosecuted in a depensatory mannery. The taking of a fixed quantity each year would mean that small runs would be heavily exploited and that large runs would be relatively lightly fished. But as we have seen the fishery does not seem to operate in this way at the present time, since closures are applied with a view to permitting the escapement of a relatively constant proportion of the run.

Actually, the only form of depensatory mortality which is adequate to account for the observed facts appears to be associated with the period of fry migration. This period, although short in duration, is a peculiar and critical phase in the life-cycle. It represents the precipitation of a large and very vulnerable population into the community of stream-dwelling organisms. The transience of the situation precludes the establishment of any long-term balance between predators and prey. The migration is merely an exodus in which heavy losses are/sustained without any significant compensatory growth or development on the part of the survivors.

In his study of the McClinton Creek fry run of 1941, Cameron (1941) tentatively estimated a 60% overall mortality among fry passing to the ocean from a spawning area which extended for a distance of two miles from salt water (or a 32% mortality based on the potential egg deposition). The mortality, however, varied with the distance which the fish had to traverse and also increased during the week by week progress of the run. He pointed out the probable advantages to the fry of an early, compact migration in reducing mortality during this period.^W

General observations indicate that the predators mainly concerned with fry mortality are other fish, resident in the same stream or themselves migrating seaward at the time. In the localities investigated trout, coho, [?]smolts, and

^W It is possible, although unverified, that earlier entrance into the sea might bring corresponding disadvantages if the seasonal increase of marine zooplankton were less advanced. - F.N.

sculpins are important. The small size and nocturnal habits of the fry-migrants appear to prevent major inroads by terrestrial predators. Losses are therefore largely determined by the number and activity of the local aquatic predators. Even in years when production is relatively low, fry-migrants will ordinarily constitute a large and readily available food supply during the short period of their downstream migration. Hence the predators will tend to take a fixed number rather than a percentage and the mortality will be of the depensatory type. The total number of predators present from year to year will presumably vary less than the number of pink salmon fry, since several species are involved and various age-groups are represented.

The data provided by Fritchard and by Cameron for McClinton Creek may be re-examined in the light of this viewpoint. Cameron's estimated 60% mortality represents 7,590,000 fry lost in 1941. Assuming predation to be constant from year to year, this figure may be added to each year's recorded fry-migrant output to obtain a theoretical figure for the number of fry escaping from the gravel. A comparison between Fritchard's figures for migrant output and these hypothetical figures for fry emergence is presented in Table VII.

Table VII. Effect of predation on the fry-migrant production of pink salmon at McClinton Creek.

<u>Potential egg deposition</u>	<u>Fry Migrants</u>	<u>% efficiency</u>	<u>Hypothetical fry emergents</u>	<u>% efficiency</u>	<u>% predation</u>
8,500,000	2,020,000	23.8	(9,610,000)	(110)	(86.2)
13,200,000	2,300,000	17.4	9,890,000	75	57.6
26,600,000	5,060,000	19.0	12,650,000	48	29.0
50,800,000	5,384,000	10.6	12,974,000	25	14.4
53,200,000	3,675,000	6.9	11,265,000	21	14.1
139,500,000	12,600,000	9.0	20,190,000	14	5.0

As might be anticipated, the calculated values for emergence produce an obvious absurdity at the lowest level of population, when the predators could hardly be expected to obtain the maximum number of fry which they are capable of devouring. In spite of the crudeness of the procedure, however, the adjustment produces a better relationship (inverse) between the size of the spawning population and the percent efficiency of reproduction, every value now appearing in its proper sequence in the series. In particular, the anomaly of a higher percentage output from a deposition of 139,500,000 eggs than from one of 53,200,000 and the similar discrepancy between the efficiency at the 27,000,000 and 13,000,000 levels are eliminated. The reduction in the effectiveness of predation with increasing fry production is well illustrated in the last column of Table VII.

It may therefore be inferred that compensatory mortality prevailed over the whole size range of the spawning populations observed at McClinton Creek up to the time of emergence of the fry. Subsequent predation, on the other hand, introduced compensatory effects which in some instances caused a transposition of the final results.

Recognition of these different kinds of mortality permits a reasonable explanation of the problems posed on a previous page. With other conditions constant, a reduction in the number of spawners (by fishing or other cause) will be followed by increased survival up to the free-swimming stage. The absolute number of fry produced may not be very different from the previous average (cf. the relative uniformity of "hypothetical fry emergents" from depositions of different magnitude) and fluctuations of the population will remain within moderate limits. If, on the other hand, the number of emergent fry is drastically reduced (as could happen through unusually unfavourable physical conditions or through the reduction of spawners below the level which could produce a large fry emergence even with the decreased mortality) the predators will

take a larger relative toll and the population will be depressed to a new level. At the other extreme, a particularly abundant fry emergence may "break through" the control imposed by predators and enable the population to reach a level at which predation takes only a small percentage and control is effected mainly by compensatory mortality.

The depensatory part of the mechanism tends to resist a return to the former level. This would account for the apparent fact that pink salmon populations can become stabilized for long periods at very different levels and that new levels are sometimes reached by sudden "steps" rather than by gradual transitions. The term "level" is used of course in a comparative sense, to denote a period of relatively minor fluctuations. These, too, are presumably accentuated by predation but not to an extent which precludes rectification by ordinary climatic variations or other factors.

It is evidently the role of depensatory mortality to exaggerate changes and, by opposing compensatory mortality, to stabilize these changes when they become great. Since, however, neither compensatory nor depensatory influences can initiate changes we must recognize the existence of a third type of mortality which is independent of population density. In conformity with the other terms suggested herein, this may be called "extrapensatory mortality".

As already pointed out, certain physical factors in the freshwater environment may act to some extent in a compensatory manner, that is, they constitute an immediate cause of death, although their effectiveness is determined by the density of the population. There can be no doubt, however, that numerically similar spawning runs can show great variation in efficiency of reproduction. Favourable and unfavourable conditions of stream flow and temperature can operate at all levels of population density. The general effects of stream flow are discussed by Neave and Wickett (1949). In this

publication Wickett has also shown a significant degree of correlation between the July - August precipitation and the number of adult pink salmon returning in the next generation in the central region of British Columbia.

Fishing mortality (as applied at the present time) seems to be mainly extrapensatory in that it operates with fairly equal intensity on large and small runs - at least in the area for which comparisons have been made (p. 16). Since, however, it appears to take an approximately constant percentage every year, it merely conforms to population sizes which have been determined previously and cannot be regarded as a potent source of year to year fluctuations. A sufficiently intensive fishery could undoubtedly produce a declining trend, or a drop to a new level, by drastically reducing the number of spawning fish.

On the other hand, natural ocean conditions could act in a manner similar to the freshwater conditions mentioned above, - for example, temperature and the quantity or availability of food supplies could produce variations which are unrelated to the size of the population. Further reference to this point is made in the following section.

RELATIVE EFFECTS OF FRESHWATER, NATURAL OCEAN AND FISHING MORTALITY IN DETERMINING POPULATION LEVELS

Although a large majority of the total losses attending the life-cycle takes place in fresh water, it does not follow from this fact alone that fluctuations in population size are determined in this medium. Variation in mortality, rather than its total magnitude, will be important in this connection. Actually, since the individuals (or potential individuals) entering either environment commonly suffer a mortality exceeding 90% before concluding the phase, it is evident that a small change in mortality rate in either instance would exert a profound effect on the end result.

Pritchard (1950) found that at McClinton Creek the total ocean survival showed greater relative variation (that is, ratio between highest and

lowest recorded values) than the freshwater survival (Freshwater survival, 23.8% to 6.9%, ratio 3.5:1. Ocean survival, 6.75% to 0.29%, ratio 23:1).

There are reasons, however, for believing that this is not a representative comparison between the variability of freshwater and natural ocean survival.

Corresponding figures for other localities are:

	% freshwater survival	freshwater ratio	% ocean survival	ocean ratio
Sashin Creek	6.4 - 0.2	32:1	3.87 - 0.74	5.2:1
Hooknose Creek	15.0 - 0.87	17:1	2.7 - 3.7	1.4:1

The combination of McClinton Creek data with these other records gives a total freshwater ratio of 119:1, without extending the McClinton Creek range for ocean variability.

The small degree of variation in the freshwater survival at McClinton Creek is evidently due to the absence of the low values which have been found elsewhere. The relative stability of the stream conditions at McClinton Creek during the period of the investigations is attested by the good relationship (already discussed) between the size of the spawning population and the efficiency of fry production. Evidently no drastic extrapensatory factors intervened to upset this relationship. Under such circumstances it is quite likely that changes in population size can be determined in large measure by natural ocean conditions. However, it should be noted that the figures given are the net result of natural and fishing mortality. Although we have found reason to believe that fishing mortality takes a relatively constant percentage from year to year when a large area is considered, such constancy cannot be expected to prevail for the run to an individual small stream. Pritchard himself considered that the intensity with which the McClinton Creek run was fished varied a good deal. The low ocean survival observed in most years at McClinton Creek, contrasted with a very high survival in one year, suggests the possibility that this run is usually fished heavily but can on occasion escape major exploitation.

As regards natural mortality, the present writer thinks that major importance in determining changes in population size can usually be assigned to freshwater factors, in view of the following considerations:

(1) On general grounds, physical conditions such as water volume, temperature and available space are more variable in fresh water than in the ocean.

Moreover, the eggs or alevins, unlike the ocean fish, are unable to seek optimum conditions but must experience the full impact of environmental changes.

(2) According to the view expressed on previous pages, variations in fry production imposed by such changes are reinforced by the depensatory effect of predation on the outgoing fry.

(3) The apparent independence of even and odd year stocks in respect to fluctuations suggest that these originate in fresh water, which is the only phase in which these two populations are completely separated.

(4) A significant correlation has been found between a meteorological factor affecting spawning conditions and variations in the sizes of resulting runs.

(5) The output of fry-migrants from fresh water is at times so low that a reduction in the adult population must necessarily result unless ocean survival is raised to a level which seems unreasonable in the light of existing information (see Fig. 6).

(6) At each of the localities for which several years' data are available (McClinton Creek, Sashin Creek, Hooknose Creek) there appears to be a relation between the efficiency of freshwater reproduction and the direction of size change in the resulting adult escapement. The most striking instance has been the change from a larger odd-year run to a larger even-year run, observed at Hooknose Creek. This reversal in the relative size of the two stocks was clearly initiated in fresh water.

In only one important respect does ocean life seem to offer opportunity for greater variability in natural mortality than freshwater existence.

This is in the availability of food supplies, a problem which is of relatively small importance in fresh water. The appreciable differences in average size of individual pink salmon in different years (see Hoar, 1951) may reflect feeding conditions. It is reasonable to suppose that variations in mortality can also be due to this cause. Incidentally, the growth of the females in the ocean may also affect the number of ripe eggs produced, thereby introducing a factor into the production of the next generation. This factor, however, appears to be small in relation to observed changes in population size (see p. 3). It will, moreover, tend to be offset by the compensatory mortality attending incubation and alevinage.

The role of marine conditions in determining population size cannot be dismissed as insignificant, although the writer believes that their effects are usually much smaller than those of freshwater factors.

A question of some interest and importance is whether or not ocean mortality tends to be compensatory, - that is, whether it tends to offset the numerical variations in the fry populations which enter the sea from year to year. Any such tendency would of course limit the effectiveness of remedial measures based on increasing the output of sea-going migrants. If the reasons already advanced for considering freshwater factors to be largely responsible for determining fluctuations are valid, then compensatory influences in the sea, if they exist, must be small, since on average they do not obscure the effects attributed to fresh water. Davidson and Vaughan (1941) have, however, hypothesized the existence of intraspecific competition in the sea as a factor affecting the average size of individual pink salmon of the Clarence Strait area of southeastern Alaska. This view was based on an inverse relationship between size of populations and size of individuals of the adult runs.

It can be maintained on general grounds that pink salmon, however numerous, constitute but a small element in the complex economy of the sea. It cannot be supposed that there is a special limited and relatively constant food supply exploited only by pink salmon. If other species are involved (e.g. herring, chum salmon and the various other vertebrates and invertebrates which feed on the same kinds of zooplankton) the degree of competition should be determined by the total population of this association of species, not merely by the fluctuating abundance of pink salmon. The effects would also be distributed. In other words, the rather moderate changes in pink salmon abundance reported by Davidson and Vaughan would have to alter the relation between the available food supply and all the animals using it before specific effects on pink salmon became apparent. Ordinarily, the chances that such an interaction would be detectable in the face of annual changes in food availability wrought by such factors as water temperature, amount of sunlight or prevailing wind, would seem to be small. Perhaps a degree of such competition may occur in areas where the output of young pinks is very high and the fish tend to remain within restricted ocean areas. On the British Columbia coast Hoar (l.c) found no inverse association between body size and population size. He noted, however, that changes in body size are in the same direction over the whole British Columbia coast and that odd-year fish tend to be larger than even-year fish, in spite of the fact that in some districts they are far more abundant. Since the even- and odd-year stocks are effectively segregated as regards interbreeding, the possibility of a genetic factor may be entertained.

The idea of compensatory size adjustment is more or less opposed to compensatory mortality. The occurrence of the latter would, of course, tend to eliminate the differences in abundance with which Davidson and Vaughan associated large and small fish. As mentioned, the evidence at present

Fig.6. Relation between freshwater survival of pink salmon and size of spawning stock at various levels of fishing intensity. An average natural ocean survival of 5% is assumed. F.M. = fishing mortality.

available indicates that on the British Columbia coast neither the mortality of a year-class nor the individual size of its members is determined to an appreciable degree by its own abundance. Perhaps the most convincing argument against the general occurrence of compensatory mortality in the sea is to be found in the large and long-continued disparity in the numbers of even- and odd-year stocks which has already been mentioned as characteristic of certain areas. A mechanism for establishing and maintaining this disparity has been suggested on previous pages. Such a condition could not be maintained, however, if ocean mortality tended to favour small populations and reduce large ones.

By accepting the view that freshwater and ocean mortality vary independently and that fishing mortality tends to remove a fairly constant percentage, certain effects of varying these elements can be noted. The calculations presented represent averages which might be expected to prevail over a period long enough to eliminate the effects of annual fluctuations. Fig. 6 shows the effect on the spawning stock of various rates of fishing intensity and freshwater survival, on the basis of an average egg-production of 1700 eggs per female and a natural ocean survival of 5%, which has been considered (p. 17) to represent an approximate average for this phase. A 50-50 sex ratio is assumed. The percentage freshwater survival required to keep the population constant at various levels of fishing intensity is indicated by the "level of maintenance".

It can be seen that under the postulated conditions the average freshwater survival of an unfished population must be quite low (2.35%) if the population is not to keep on increasing. The addition of a 40% fishery would require an increase of 67% (i.e. to about 4%) in freshwater survival. A freshwater survival of approximately 6% (i.e. about 150% greater than the survival indicated for an unfished population) would permit a fishing

mortality of 60%. This is approximately the condition (both of freshwater survival and fishing intensity) which is indicated by the data at present available for the central region, if Hooknose Creek figures can be taken as a guide (p.). Fig. 6 shows the great increase in reproductive efficiency which is required to offset still higher levels of exploitation. Whereas a rise in fishing intensity from 40% to 60% demands an increase of 33% in freshwater survival, a rise from 40% to 80% would demand a 200% improvement in the efficiency of fry output. Although compensation on this scale seems startling it has possibly been accomplished at McClinton Creek. The high average freshwater survival (14.45%) is accompanied by a low return of adults and it would be unnecessary to revise our working figure of 5% natural ocean survival if fishing mortality amounted to 80% or 85%. Such a fishing intensity would not be out of line with the known exploitation of Fraser River sockeye runs and could perhaps be readily achieved where large populations are funnelled into a restricted area such as Masset Inlet. It may well be, of course, that average ocean survival varies in different areas. If the marine habitat of McClinton Creek fish is less favourable than that of central region fish, it is not necessary to assume such a high fishing mortality.

Obviously, however, the ability of a population to sustain a fishery will depend upon the extent to which compensation is possible. With increasing exploitation a premium will be placed on stocks which reproduce under such favourable external conditions that, in the absence of a fishery, their continual increase is largely prevented by factors associated with their own density. The prevalence of compensatory mortality over a wide range of population levels has been indicated at McClinton Creek and under such conditions a high rate of exploitation is possible.

It may be confidently expected, however, that in many streams the efficiency of fry output is determined to a much greater extent by extra-pensatory or depensatory factors. The physical conditions may be so rigorous

or so variable that differences in population size do not produce corresponding changes in reproductive efficiency. Under some conditions a small population may be nearly as vulnerable to flood or drouth as a large population, in addition to suffering relatively heavier losses through predation. The imposition of even a moderate fishery on such a stock will produce a decline, whatever the total initial size of the population may be.

At the risk of repeating an obvious proposition, it may be emphasized that the effect of a fishery is to reduce the mortality which is directly related to population density. As we have seen, much of the mortality which attends the life cycle is not of this nature and will be unaffected or even actually increased by a fishery. We have also expressed our belief that the compensatory potentialities are wholly or mainly located in that part of the life cycle which occurs between spawning and the emergence of the fry from the gravel. On this view, the average maximum fishery which a stock can sustain (in the absence of artificial control) is determined by the degree of adjustability of the mortality during this relatively short period, -- which also happens to be a period when another type of mortality (extrapensatory) may produce important effects.

The left-hand side of the following tabulation gives a generalized representation of the manner in which we might expect mortality to be distributed in the progeny of a pair of fish belonging to a stable, unfished population.

	<u>Unfished</u>	<u>60% fishery</u>
Parents	2	2
Eggs	1700	1700
Emerging fry	100	250
Fry entering sea	40	100
Mature fish	2	5
Escapement	2	2

To provide a stable population at the 60% fishing level the distribution of mortality must be altered in some such manner as is suggested in

the right-hand column. This scheme applies only to the offspring of individual pairs of fish and leaves out of account the total size of the population. If compensatory influences are so strong that after subtraction of 60% of the adult population the remaining 40% can produce the same total number of fry (that is, the required increase in reproductive efficiency per pair of fish can be realized immediately), then the average size of adult runs should not decline, in spite of the reduced escapement. If, on the other hand, the reduced escapement cannot make good the losses caused by fishing there will be a tendency for the population to fall until a level is reached at which the individual pairs of fish can attain the required reproductive efficiency. Probably some adjustment along these general lines can frequently be made. However, a marked lowering of the total fry population, as we have seen, is attended by the danger that predation will become relatively more intensive, so that increased percentage survival up to the time of emergence is offset by reduced survival of migrating fry.^x There seems to be no inherent reason why a crash should not be prolonged into a further decline (that is, a stabilized level might not be reached in one generation) but under the mechanism envisaged the initial drop is likely to be sudden and severe. Similarly the building up of a population might continue after a sharp rise. Some evidence of this can perhaps be seen in the Skeena and Central Region graphs. The further increases could, however, merely represent seasonal deviations from an established "level".

CONSERVATION PROBLEMS

In spite of the indicated possibility of continued declines, the writer sees no convincing evidence of gradual long-term decreases in the existing populations, when large areas are considered. Reference has already

^x Suppressive effects of this kind might of course be less pronounced if certain predators (e.g. coho, trout) were themselves declining at the same time.

been made to the occurrence of jumps or crashes, followed by the establishment of a new level. A "trend-line" covering a period in which such a "step" has occurred will slope upward, or downward but such a line may give a false impression of gradual change. As indicated previously, the current "decline" of the Skeena and Nass areas appears in the main to represent a change in level which appeared in the odd-year stock in 1927 and in the even-year stock in 1932. There is some indication that a further drop in the odd-year stock may have taken place in the 1945-47 cycle (Fig. 5).

The general association between fluctuations in abundance and physical conditions in fresh water has been indicated (p. 27). There is evidence that crashes are the result of the same factors operating with exceptional severity, although it is not always possible to be dogmatic about the specific causes of events which happened many years ago. Very low water-levels were faced by the parents of the 1932 fish when entering streams in northern and central British Columbia in 1930. The August rainfall in these districts was about 76% below the mean (Dept. Marine & Fish. 1932). In 1945 there was an August rainfall deficiency of similar magnitude, with September precipitation also well below normal. The abrupt drop in population size from 1945 to 1947 affected not only the Skeena fish, which were already at a relatively low level, but also the Central region fish, which were at a peak of abundance in 1945 (Fig. 4). In 1925, climatic conditions in the Skeena area at spawning time do not appear to have been unfavourable but an extremely heavy precipitation which occurred in the lower Skeena valley in February 1926, accompanied by unseasonably high temperatures, may well have produced a destructive flood. The failure of the pink salmon run of the Central region in 1919 followed wholly exceptional floods in that region in the autumn of 1917.

Sudden failures can thus be logically attributed primarily to physical conditions experienced in fresh water. There remains, however, the

possibility that intensive fishing may keep populations down to a level at which they are more susceptible to natural disasters. It may also tend to prevent a low population from reaching the numerical strength necessary to "break through" and achieve a higher general status.

While it is beyond the scope of this paper to deal with specific cases and treatments, certain general conclusions or opinions are implicit in the foregoing discussions which might influence the approach to conservation problems and can be expressed briefly as follows:

Freshwater and natural ocean survival are largely independent of each other, with freshwater survival showing the greater range of variation. Therefore improved output of migrants from fresh water will on average be reflected in larger runs of adult fish.

Under intermediate conditions of fishing intensity a total freshwater survival of 5% or less is likely to produce a reduction in size of the spawning population. A freshwater survival of 2% or less will on an average reduce the population, even if no fishing takes place.

Large runs in both even and odd years are not fundamentally incompatible. (The Koeys River may be cited as an example of a stream which has heavy runs of adults in both cycles.)

The general objective of remedial measures should be to change natural extrapensatory mortality into fishing mortality, while keeping total mortality (on a percentage basis) constant. In effect, this means the promotion of the most favourable physical conditions for spawning, incubation and alevinage. In the absence of lethal factors which are density-independent, compensation can exert its full effect in making good the losses inflicted by the fishery. At the same time, remedial measures should aim at producing a large total emergence of fry (not merely a high efficiency of individual reproduction) since a large fry population will suffer relatively less predation

than a small population. A stock should be large enough to produce a maximal emergence even at the risk of some loss of individual efficiency.

From the point of view of conserving pink salmon alone, it may be better to ameliorate physical conditions merely at the places and times at which incubation takes place, rather than to effect general and permanent stream improvements which may have the effect of also raising the stocks of predators.

Predation is believed to be a major factor in keeping stocks at a low level. The elimination of predators (or the protection of fry from their attacks) should greatly increase the contribution to the fishery of stocks which are in this condition and should tend to prevent further drops. The effect on stocks which are at a high level of abundance would be much less pronounced. It may be argued, however, that certain predators (e.g. coho, trout) are more valuable than pink salmon.

The persistence of a low level of abundance (in the absence of a marked change in the condition or accessibility of spawning grounds) means that the total fry emergence is not large enough to escape excessive depensatory mortality, in spite of the increased reproductive efficiency of individual fish. The spawning stock should therefore be increased to the greatest possible extent, even if no current "decline" is evident. In thus attempting to establish a higher level, a brief total closure of the fishery would seem to be sounder conservational practice than the institution of a reduced fishing rate over a longer period. While even a total escapement of the adult run might not suffice to make the "jump", it would offer a chance of success, especially if it happened to coincide with favourable climatic conditions. A successful result would enable fishing to be continued at the same percentage level but on a larger stock.

The maximum sustained fishery which can be imposed on the existing runs of different streams varies widely (not improbably from 80% to zero), hence an escapement which is adequate for a particular area should not be presumed to be equally applicable elsewhere.

In general, light runs should be little fished, in view of the danger that the cycle will be pushed to a persisting low level. The operation of the present protective measures, which tend to promote equal pressure on large and small runs, is however definitely preferable to a fixed annual quota or to an attempt to pack the same quantity of fish each year. Such an attempt would defeat its own ends by reinforcing the compensatory processes which tend to exaggerate large and small runs.

In attempting to establish a run in a new locality or in a cycle which is not represented by existing populations, a satisfactory result would be unlikely unless (a) predators are not numerous or (b) the number of eggs or fry introduced is great enough to be equivalent to the product of a large natural escapement.

CHUM SALMON
(Oncorhynchus keta (Walb.))

The chum salmon is as widely distributed as the preceding species in the coastal waters of British Columbia and is common in certain streams, notably in the Vancouver Island district, from which the pink salmon is virtually absent. In some years it provides a larger catch, by weight, than any other species of Pacific salmon.

In certain glacier-fed streams of central and northern British Columbia in which a good flow of relatively cold water is maintained during the summer, some chums spawn as early as August 1st. Usually, however, the main runs enter fresh water somewhat later than the pink salmon, the most intensive spawning taking place between the end of September and mid-November. In some streams even later runs also occur, with fish still arriving in late December and January. In small coastal streams spawning usually takes place within a few days after entering fresh water. Although an occasional chum salmon reaches the upper Babine River, the species shows less inclination or ability than pink salmon to surmount obstacles and travel for long distances up streams. Much spawning takes place very close to salt water. In conformity with the spawning habits the downstream migration of fry may extend over a somewhat longer period than that of pink salmon and the peak of this run is frequently reached about the middle of May. The habits of the young fish in salt water, so far as these have been observed, are similar to those of pink salmon, the two species being frequently found in company.

The length of the life cycle varies. While a majority of mature fish are usually four years of age, 3-year old and 5-year old fish are commonly represented. In commercial catches third-year fish occasionally constitute nearly or quite 50% of local catches.

Since the problems and factors relating to the population sizes and changes of chum salmon are in many respects similar to those which have been

discussed in connection with pink salmon, they will be presented here in the form of a comparison with the latter species.

EGG-PRODUCTION

Egg counts for chum salmon in British Columbia have been reported as follows by the investigators whose names are associated with the same localities in Table I.

<u>Locality</u>	<u>No. of Years</u>	<u>No. of Fish</u>	<u>Average No. of Eggs</u>
Namu	1	21	2760
Fraser River	1	51	2943
Nile Creek	3	47	2726
Hooknose Creek	4	114	2254

Average of all localities - 2671

The general average of roughly 2700 represents about 63% higher numerical production than that of pink salmon. As already pointed out (p. 2) this implies a different total mortality rate during the life cycle. Otherwise, the abundance of the two species would diverge very rapidly.

SEX RATIO

The numbers of each sex recorded in spawning escapements to Nile Creek and Hooknose Creek are given in Table VIII.

It will be seen that the deviations from equality are small and it seems fair to assume that a 50-50 ratio represents an average condition, as in the case of pink salmon.

MORTALITY

MORTALITY AND SURVIVAL IN FRESH WATER

1. Total freshwater survival

Quantitative records for the efficiency of reproduction during the freshwater phase in British Columbia are available only from Nile Creek since 1945 and Hooknose Creek since 1947. The estimated potential egg deposition and the recorded output of fry migrants at these two localities are given in Table IX.

Table VIII. Sex ratio (percent) of chum salmon escapements

<u>Locality</u>	<u>Years</u>	<u>No. of Fish</u>	<u>Males</u>	<u>Females</u>	<u>Authority</u>
Nile Creek	1945	3,062	49	51	Neave (1947)
" "	1946	1,861	51	49	Wickett (unpub.)
" "	1947	986	52	48	" "
" "	1948	386	54	46	" "
" "	1949	933	48	52	" "
Hooknose Creek	1947	10,106	48	52	Hunter (1948)
" "	1948	1,014	51	49	" (1949)
" "	1949	705	51	49	" (unpub.)
" "	1950	2,362	50	50	" "

Table IX. Freshwater survival of chum salmon

<u>Locality</u>	<u>Brood- year</u>	<u>Potential Deposition</u>	<u>Fry Migrants</u>	<u>Survival %</u>	<u>Authority</u>
Nile Creek	1945	3,540,000	138,388	3.90	Neave (1947)
" "	1946	2,115,000	8,319	0.40	Wickett (unpub.)
" "	1947	1,276,000	4,808	0.38	" "
" "	1948	385,000	23,188	6.03	" "
" "	1949	1,022,000	782	0.08	" "
Hooknose Creek	1947	10,977,000	108,746	0.99	Hunter (1948)
" "	1948	1,055,000	77,497	7.37	" (1949)
" "	1949	714,000	44,463	6.22	" (unpub.)
" "	1950	2,859,000	431,349	15.09	" "

The effect of the recorded outputs, in terms of the average number of fry migrants produced by a pair of spawning fish with a potential deposition of 2700 eggs, would be as follows:

<u>Stream</u>	<u>Observed mortality range</u>	<u>No. of migrants produced</u>		<u>Ratio of (a) to (b)</u>
		<u>(a) Maximum</u>	<u>(b) Minimum</u>	
Nile Creek	93.97 - 99.92	163	2.2	75:1
Hooknose Creek	84.90 - 99.01	410	27.0	15:1

While the ratio between highest and lowest recorded efficiency at Hooknose Creek is approximately the same as that of pink salmon in the same stream (see p. 8), much greater relative variation is evident at Nile Creek. At both localities, however, it is obvious that great variations in population size can be initiated in fresh water.

2. Immediate causes of death

All the specific causes of freshwater losses listed for pink salmon (pp. 4-10) can be regarded as potential sources of mortality for the present species. The variability and interrelationship of these factors have already been emphasized but there appear to be certain quantitative differences in their effects on the two species although these differences cannot be measured accurately from existing data.

At the time when chum salmon enter fresh water the run-off in coastal streams has usually increased considerably from the low flows which prevail in August and September. Hence certain forms of mortality at this stage of the life cycle are likely to be smaller than for pink salmon. The losses which may thus be in varying degrees avoided might be more directly due to the impassability of falls; predation; exclusion from spawning areas by lack of water; unfavourably high temperature.

On the other hand, the less compact spawning run which frequently characterizes chum salmon increases the danger of superimposition by the later arrivals, which are frequently observed to select the same sites as earlier

fish. Moreover, despite the larger number of eggs, chum salmon, owing to the much larger size of the fish and the space required for redds, probably cannot seed a limited area as efficiently as pink salmon. Overcrowding effects may thus appear at a lower population level, particularly since chums are apt to remain in the lower portions of spawning streams instead of distributing themselves throughout the accessible portions of the water-system.

Many of the streams utilized by chum salmon show extreme seasonal or irregular changes in run-off. Losses due to erosion can therefore be severe. The very low percentage of fry-migrants in certain years at Nile Creek appears to be associated with the incidence of floods in association with an unstable stream bed. Serious losses are also caused at times in Vancouver Island streams by the drying up of spawning beds in spring, thus preventing the emergence of fry, or by the trapping of the latter in pools before they can reach the sea (Neave 1949).

3. General conclusions

In Hooknose Creek, where sizable runs of both species occur, the percentage efficiency of fry-migrant production has been almost identical for pinks and chums in each recorded year (Tables III, IX). In this stream the two species utilize approximately the same areas and the spawning periods do not differ greatly in time. Ecologically they approach the status of a single population. However, the mere fact that both species have continued to maintain themselves in abundance in the same geographical areas, with no physical barriers against the effects of competition, indicates that in general pink and chum salmon occupy somewhat different ecological niches. In fact, one or other usually predominates in a given stream or portion of a river system and the situation at Hooknose Creek may represent an intermediate or overlapping condition between two such niches or habitats.

Very frequently chum salmon utilize streams which are quite unstable in respect to water flow and permanency of gravel beds, or in which large stones

replace finer deposits. A rather extreme example is provided by Nile Creek. Factors which must give this species an advantage over pink salmon in offsetting these rigorous physical conditions are: (1) the greater egg-production, enabling the chum to withstand greater losses, on a percentage basis, (2) the larger size of the fish, enabling it to move larger stones and also to deposit its eggs at a deeper level, (3) the less rigid life span, which prevents the effects of a "bad year's" reproduction from being entirely localized in a single recurrent cycle.

These advantages, which could account for the greater success of chums under adverse physical conditions, do not explain the failure of the species to oust pink salmon from the more favourable physical habitats of the latter. In this connection it may also be supposed that the balance of mortality due to superimposition would favour the later-spawning chum. The following suggestions, however, can be offered. (1) As already pointed out, chum salmon do not distribute themselves as advantageously in relation to the potential spawning grounds and probably cannot seed utilized ground as thoroughly. (2) The later and more prolonged spawning season of the chum produces a later and less concentrated fry migration. This probably results in heavier losses to predators (see p. 51) which can be expected to be especially numerous in the relatively stable streams which are preferred by pink salmon.

In general support of these views on the different adaptations of the two species, certain population changes which appear to have taken place in some Vancouver Island streams may be cited. Following deforestation, which is presumed to have caused more extreme variation in stream flow, pink salmon populations declined to a very low level in such streams as Amor de Cosmos Creek, Oyster River and Nile Creek. At the same time chum salmon were able to maintain their numbers sufficiently well to become the dominant species in these waters.

It is concluded that, on average, production of fry-migrants by chum salmon is somewhat less, on a percentage basis, than that of pink salmon and that it also tends to be more variable.

MORTALITY AND SURVIVAL IN THE OCEAN

Because of the longer life span of chum salmon, data have not yet been accumulated which would furnish a guide to the percentage of outgoing fry from a given stream which eventually return to fresh water. However, if we accept 5% as being a reasonable figure for the natural ocean survival of pink salmon, a simple calculation will suggest rather narrow limits within which the average chum survival should lie. On the basis of egg-production, total survival from egg to spawning adult (in stable populations) should be $17/27$ times pink salmon survival. If the higher mortality of the chum takes place entirely in fresh water, the natural ocean survival should be the same in both species. If the difference lies wholly in the salt water phase, the survival during this period should be $5 \times 17/27 = 3.15\%$. The possibility that chum salmon survival is much lower in one phase and somewhat higher in the other is difficult to entertain. We have already expressed the view that average fresh-water survival is lower than for pink salmon. Marine survival would not be expected to be higher than for pinks, in view of the longer period for which the chum is exposed to ocean hazards. During a considerable part of their first summer, when the greatest marine mortality is presumed to occur, the two species have been observed feeding in company and losses may be presumed to be of similar magnitude.

It is therefore suggested that average natural ocean survival for chum salmon in British Columbia is not less than 4%.

Chum salmon fishing is prosecuted by the same methods as pink salmon fishing. The division between catches and escapements in the Central region, based on information of the kind discussed on page 15, is shown in Table X.

Table X. Reported catch and escapement of chum salmon in the central region of British Columbia

<u>Year</u>	<u>Catch</u>	<u>Escapement</u>	<u>Total run</u>	<u>% caught</u>
1934	589,560	558,375	1,147,935	51
1935	1,029,640	957,200	1,986,840	52
1936	668,040	1,515,850	2,183,890	31
1937	899,450	828,725	1,728,175	52
1938	993,850	962,950	1,956,800	51
1939	598,990	414,775	1,013,765	59
1940	568,090	640,875	1,208,965	47
1941	836,700	962,975	1,799,675	47
1942	591,370	544,800	1,136,170	52
1943	833,600	654,250	1,487,850	56
1944	587,010	464,650	1,051,660	56
1945	1,035,460	1,092,225	2,127,685	49
1946	1,801,410	874,450	2,675,860	67
1947	2,243,010	1,178,200	3,421,210	66
1948	1,809,160	385,250	2,194,410	82
1949	1,098,590	705,080	1,803,670	56

According to these figures the average catch constitutes a somewhat smaller proportion of the run than is the case with pink salmon, -- about 60% for the last 8 years shown, as against 70% for the latter species. A somewhat similar difference was obtained in the tagging experiments involving the two species (p. 17). Total chum tag returns from the commercial fishery were only 16% as compared with about 30% for pinks. The conclusion seems quite justified that the total chum populations are generally somewhat less heavily fished than the pink salmon stocks. This conclusion is in general agreement with results obtained from fish tagged in Johnstone Strait in 1945, although quite probably both species are somewhat more heavily exploited in these southern areas than in the Central region (cf. DeLacy & Neave 1947; Foerster & Chatwin 1951). Average exploitation in the Central region, by reasoning along lines indicated on page 17, should approximate 40 - 50%.

A lower rate of exploitation of chums would be expected since fishing is usually closed before the later chum runs have passed through the fishing areas, whereas the more compact pink salmon migration is well covered by the fishing season (although temporary closures of the fishery are applied in accordance with estimated conservational requirements).

CHANGES IN ABUNDANCE OF ADULT CHUM SALMON

Examples of annual changes in chum salmon runs, catches or escape-ments are presented in Figs. 7 to 9.

The fluctuations shown by these graphs are of considerable amplitude and irregular frequency. There is no tendency for cyclical recurrence of large or small runs; nor is there evidence of sudden change to persistent new levels of higher or lower abundance. These features are no doubt associated with the varying life span, which to some extent distributes over two or more years the effects of mortality changes taking place in a single season. Nevertheless, pronounced peaks and depressions occur. These do not synchronize with the

Fig.7. Reported catch and escapement of chum salmon in the central region of British Columbia. (1) Total run (2) Catch.

Fig.8. Reported catch of chum salmon in Skeena River area.

Fig.9. Reported escapement of chum salmon in Vancouver Island district.

length of the life cycle, whether this be taken as four years (which is usually true for a large majority of the individual fish) or whether some allowance be made for a percentage of fish of other ages. Evidently abundance is commonly determined by factors other than the size of the escapement.

THE MECHANISM CONTROLLING POPULATION LEVELS

As is the case with pink salmon, the mortality attending the life cycle of the chum may be compensatory, depensatory or extrapensatory in its effects.

Compensatory mortality is again attested by the fact that the species is still commercially plentiful after many years of fishing which, even if somewhat less severe than that which has been applied to pink salmon, can yet be described as intensive.

It must again be supposed that this type of mortality is characteristic of the period between the entrance of the adults into fresh water and the emergence of the fry, that is, the period in which density is at a maximum due to environmental limitations. Owing, however, to the variable physical conditions in the chum salmon streams hitherto examined, a good inverse relationship between population size and reproductive efficiency cannot be demonstrated by a short sequence of annual records. It would presumably become apparent as a long-term average but in any given year compensatory effects are likely to be outweighed by extrapensatory factors. In view of the character of the streams commonly utilized by chums, this is likely to be generally true for the species.

The effects of predation on migrating fry have been investigated at Nile Creek and Hooknose Creek by the liberation of marked fry at a distance above the counting fence at intervals during the period of fry migration. At Nile Creek experiments were conducted by the writer in 1946 and 1947 and in subsequent years by Mr. W. P. Wickett. A similar experiment was performed in

Fig.10. Survival of marked chum fry-migrants in Hooknose Creek, in relation to number of fish migrating and progress of time.

○—○ average daily number of surviving fry-migrants

●—● % survival of marked fry

○---○ estimated average daily number of emerged fry (before predation)

* estimated from samples comprising more than half the total surviving fry-migrants.

1951 at Hooknose Creek by Mr. J. G. Hunter, at the writer's request.

The general features of predation during this phase of the life history of the chum salmon are in conformity with the data obtained by Cameron (1941) for pink salmon at McClinton Creek. Conclusions may be summarized as follows:

1. Percentage mortality increases with the distance over which the fry travel.
2. Percentage mortality decreases with increasing number of migrants.
3. Percentage mortality increases during the progress of the run.

Points (2) and (3), which are of chief interest for our present study, are illustrated by Fig. 10 which presents Hunter's data for Hooknose Creek. While unfortunately a predation test was not feasible during the peak week of the migration, a general relationship between number of migrants and percentage survival is indicated, as is also the fact that predation becomes more intensive during the later weeks of the run. The end result therefore appears to depend on (a) the size of the fry population, (b) the timing of the migration, and (c) the compactness of the migration. (a) involves a depensatory relationship. Variations in (b) and (c) will be extrapensatory in effect and may therefore either reinforce or reduce the effects due to (a). For example, the advantage possessed by a large population would presumably be reduced if its exodus were spread over a long period so that the numbers migrating at any one time were relatively small. A late migration would also be at a disadvantage unless a similar lag occurred in the presence or activity of predators.

In comparing the fry runs of different years, the following estimates have been made for chum salmon at Nile Creek.

<u>Year</u>	<u>Recorded fry migration</u>	<u>Estimated emergence</u>	<u>Survival %</u>
1946	138,388	223,000	62
1947	8,319	18,500	45
1948	4,808	8,600	56
1949	23,188	66,800	35
1950	782	2,170	36

The size of the runs at Nile Creek during these years has been so small that little range is presented for exhibiting ~~decompensatory~~ compensatory effects at varying levels of abundance. However, the one "large" run which produced 138,000 survivors was accompanied by an estimated loss of 38% whereas the four runs which yielded survivals of from 800 to 23,000 individuals showed an average mortality rate of about 57%. Actually the discrepancy was probably greater, since the 1946 tests were made over a longer distance of travel which presumably involved increased mortality.

It is concluded that the very considerable effects of fry losses work generally to the detriment of populations which have become small through other causes.

Whereas compensatory mortality tends to maintain a uniform abundance from year to year and depensatory mortality tends to increase and perpetuate such deviations as can still arise, the considerable and irregular fluctuations which in fact occur point to the variability of mortality which cannot be referred to either of these categories. It has already been suggested (p.45) that the freshwater habitats of chum salmon are particularly susceptible to variation in physical conditions and these are regarded as providing a major source of the fluctuations observed. Other extrapensatory variations are no doubt imposed in the ocean.

The same general processes determine population levels in both pink and chum salmon. The features which distinguish the pattern of variation of the latter species are associated with the relatively greater part played by extrapensatory mortality and the greater flexibility of the life span.

RELATIVE EFFECTS OF FRESHWATER, NATURAL OCEAN AND FISHING MORTALITY IN DETERMINING POPULATION LEVELS

As already indicated, average marine mortality is considered to be at most only slightly different from that of pink salmon and there seems to be no reason for supposing that it is more variable. The situation is

otherwise, however, with regard to freshwater losses. The combined results of Nile Creek and Hooknose Creek show an efficiency of fry-migrant production ranging from 15% to 0.08%, or a ratio of 187:1. Such extreme variation of course cannot be expected to apply to the populations of large areas containing numerous spawning streams but, taken in conjunction with the opinion expressed previously that marine mortality is largely non-compensatory, it gives good grounds for supposing that freshwater conditions play the major part in determining changes in the abundance of adult populations. This conclusion is supported by the correlation established by Wickett (Neave and Wickett 1949) between seasonal stream flow and the abundance of adult chums 4 years later, in the Vancouver Island district. The effect on the spawning stock of varying rates of freshwater survival and fishing intensity are shown in Fig. 11. In these graphs a figure of 4% has been assumed to represent average natural ocean survival (p. 47). Average egg-production per pair of fish is taken as 2700.

On the basis of these assumptions the average freshwater survival in the absence of any fishery should be less than 2%. To maintain a constant level with a 50% fishing mortality, which has been suggested as an approximate average (p. 49), freshwater survival should be 3.7%. It can be seen from Table IX that in the combined Nile Creek and Hooknose Creek records this level has been definitely exceeded in four instances, definitely not attained in four other instances and approximately equalled in the remaining instance.

CONSERVATION PROBLEMS

Trends in the chum salmon stocks of large areas are difficult to assess because (a) the collection of accurate statistics has been impeded by the varied manner in which this species is commercially processed and sold (Hoar 1951) (b) the large and irregular fluctuations prevent the drawing of sound conclusions from data which do not extend over a long period of years.

Fig.11. Relation between freshwater survival of chum salmon and size of spawning stock at various levels of fishing intensity. An average natural ocean survival of 4% is assumed. F.M. = fishing mortality.

The data available for the Central region (Fig. 7) do not show a pronounced upward or downward trend. However a decline, at least in the size of escapements, is certainly suggested by the graph for the Vancouver Island region (Fig. 9). A decline in escapement, caused by increasing fishing intensity, might of course be made good by increased reproductive efficiency. The downward trend in this instance, however, seems to have continued over a long period and there must come a point at which compensation cannot close the gap. This is an area of relatively intensive fishing but if Nile Creek results are indicative, some of the streams are in fact yielding a very low percentage output in many years, instead of responding to the reduced density of the spawning populations. As far as this stream is concerned, the fry output in three out of five observed seasons would, by any reasonable calculation, produce a smaller returning population even if no fishery were operating. While Nile Creek probably represents an extreme case, concern may well be felt regarding the productivity of other streams in this region at the present time. A chronic condition of low reproductive efficiency caused by the physical condition of the spawning streams cannot be cured by regulation of the fishery.

The fact that relatively small spawning escapements may produce large returning populations, and vice-versa, may suggest that the size of adult runs, within existing limits, is independent of the size of escapements and that a more intensive fishery could be prosecuted without harming the stocks. It may be strongly urged, however, that the observed fluctuations are in large measure caused by mortality which is non-compensatory. Observed instances of large spawning populations producing small returns do not permit the establishment of a generalization regarding the inefficiency of large escapements. The probability must be envisaged that a smaller population would have produced an even smaller return in the particular cycles concerned. Runs could, of course, be utilized more economically if it were possible to foresee the particular climatic conditions to which their eggs and alevins

will be exposed. The minimum size of escapement required to produce a given output of sea-going fry would vary greatly from year to year. The existence of an underlying compensatory process cannot be doubted but the extrapensatory variations which are imposed upon it are so large that "slumps" and "booms" frequently occur. The difference between pink and chum salmon in this respect is of course in degree only and is considered to be largely a reflection of an average difference in freshwater habitat. Under similar conditions, as shown by the results at Hooknose Creek, populations of the two species react in a similar manner.

Speaking broadly, pronounced instability of physical conditions in spawning streams is viewed as tending to eliminate pink salmon, by reason of the low egg-production and rigid life span. With chum salmon it induces great variation in population size. Maintenance of favourable conditions during incubation and alevinage would tend both to increase the average output and to reduce fluctuations. If this were achieved by controlling the flow of spawning streams (or portions of them), it could be expected that compensatory effects would become apparent, -- that is, a stricter relationship between the size of the escapement and the efficiency of individual reproduction would be observed. The intriguing possibility that increased stability might tend to enable pink salmon to displace chums is also presented.

The general effects of predation have ^{been} shown to be similar with respect to the fry-migrants of both species, in that small populations will tend to suffer relatively heavier losses than large populations. Elimination of, or protection from, predators should therefore be a major consideration in establishing new runs or in building up stocks which have reached a low level of abundance.

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