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A PRELIMINARY ANALYSIS OF NORTHERN CALIFORNIA SALMON AND STEELHEAD RUNS[1]

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INTRODUCTION

Considerable effort is spent each year in finding out how many salmon and steelhead there are in various populations along the Pacific Coast. These data are generally derived from two sources: counts over fishways

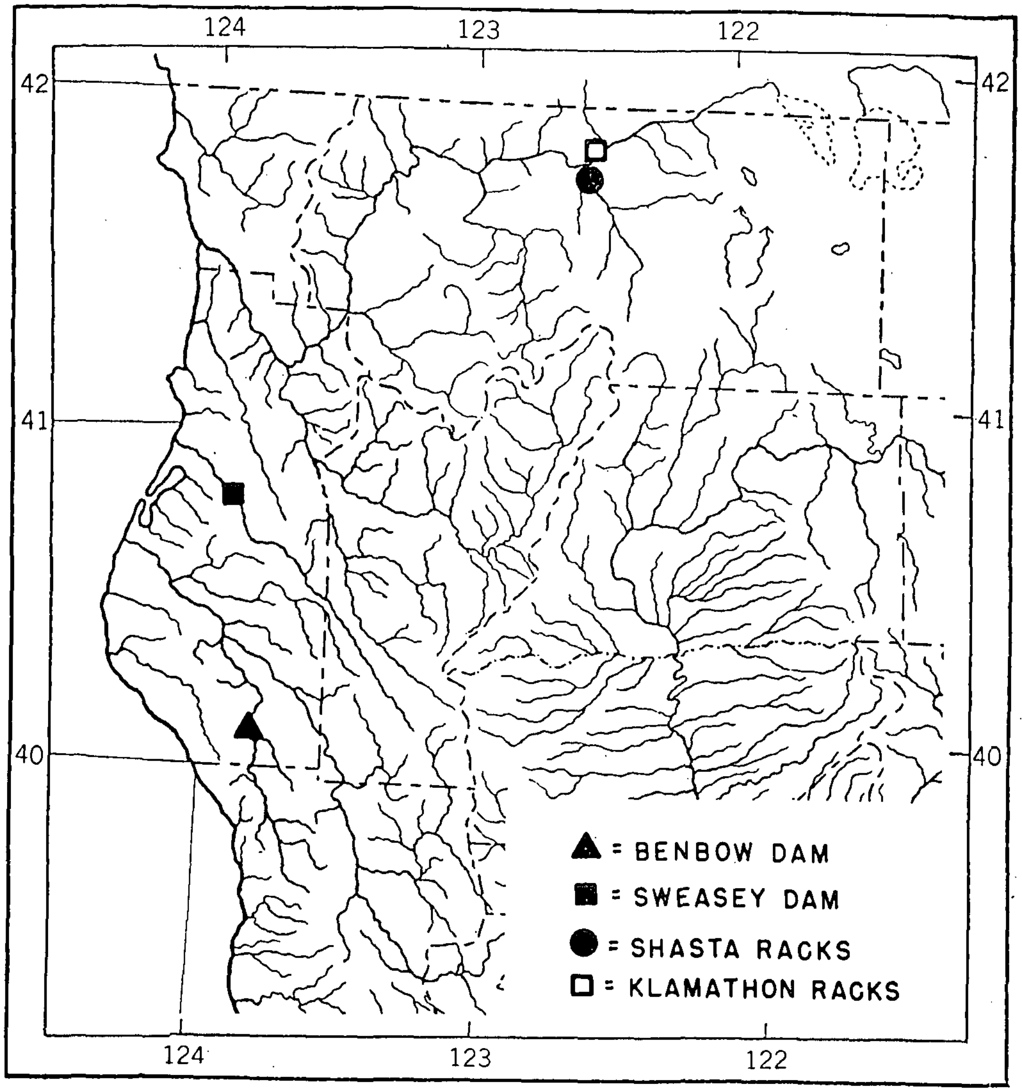

FIGURE 182. Map of northwestern California, showing locations of the four counting stations

[1] Submitted for publication May, 1950.
[2] Now with the U. S. Fish and Wildlife Service, P. O. F. I., Honolulu, T. H.

and measurements of the catch. Both furnish measures of the abundance of these valuable sport and commercial fishes. Counts over fishways are exact measures of abundance. The commercial catch generally also affords a reasonably good measure of abundance, as the demand for salmon is usually heavy, inducing fishermen to take all they can (Fry, 1949).

This report has two purposes. The first is to present the data gathered at four counting stations: Benbow Dam on the South Fork of the Eel River; Sweasey Dam on the Mad River; Klamathon Racks on the Klamath River; Shasta Racks on the Shasta River. These stations are shown in Figure 182. The second is to relate these counts to catch statistics from the commercial fishery on the Pacific Coast, particularly that of California. A discussion of certain phases of the biology of the salmons and steelhead is included.

NORTHERN CALIFORNIA FISH COUNTS

As a result of the growing realization of the need for exact data on the sizes of the runs of anadromous fishes, counts were initiated on the South Fork of the Eel and Mad rivers in 1938. These counts, as well as those from the Klamath and Shasta rivers, are given in Table 1. Weekly totals for the South Fork of the Eel and Mad rivers for the 1948-1949 season are shown in Table 2, as an example of the pattern of the runs in one year. The first run at the counting stations on these streams invariably follows the first heavy rains, since summer flows are too low to permit the fish to ascend the riffles to reach them.

TABLE 1

Northern California Fish Counts

Year	South Fork of the Eel River (Benbow Dam)			Mad River (Sweasey Dam)			Klamath River (Klamathon Racks)	Shasta River (Shasta Racks)
	King salmon	Silver salmon	Steel-head	King salmon	Silver salmon	Steel-head	King salmon	King salmon
1925[1]	-----	-----	-----	-----	-----	-----	10,420	-----
1926	-----	-----	-----	-----	-----	-----	9,387	-----
1927	-----	-----	-----	-----	-----	-----	-----	-----
1928	-----	-----	-----	-----	-----	-----	-----	-----
1929	-----	-----	-----	-----	-----	-----	4,031	-----
1930	-----	-----	-----	-----	-----	-----	2,392	19,338
1931	-----	-----	-----	-----	-----	-----	12,611	81,844
1932	-----	-----	-----	-----	-----	-----	13,740	34,689
1933	-----	-----	-----	-----	-----	-----	-----	11,570
1934	-----	-----	-----	-----	-----	-----	10,340	48,668
1935	-----	-----	-----	-----	-----	-----	14,051	74,537
1936	-----	-----	-----	-----	-----	-----	10,398	46,115
1937	-----	-----	-----	-----	-----	-----	33,144	33,255
1938	6,051	7,370	12,995	1,273	498	3,110	16,340	9,090[3]
1939	3,424	8,629	14,476	1,257	725	3,118	-----	28,169
1940	14,691	11,073	18,308	1,293	73	5,706	14,965	55,155
1941	21,011	13,694	17,356	3,139	308	4,583	11,204	13,252
1942	10,612	15,037	25,032	1,676	378	6,650	13,038	11,425
1943	7,264	13,030	23,445	1,236	259	4,921	-----	10,022
1944	13,966	18,309	20,172	-----	-----	-----	-----	11,498
1945	12,488	16,731	13,626	-----	-----	-----	-----	18,191
1946	16,024	14,109	19,005	1,181	415	5,106	-----	7,590
1947	13,160	25,289	18,225	717[2]	510	3,582	-----	341
1948	16,312	12,872	13,963	672	515	3,139	5,821	37
1949	3,803	7,495	13,715	484	512	4,074	11,504	139

[1] 1925 refers to counting year 1925-26, etc.

[2] Does not include an estimated 250 fish that passed the dam before counting started.

[3] Counting station moved seven miles upstream from the original location. This may account for some of the decrease in the counts.

TABLE 2

Weekly Counts, South Fork of the Eel River and Mad River, 1948-1949

Week beginning	South Fork of the Eel River (Benbow Dam)			Mad River (Sweasey Dam)		
	King salmon	Silver salmon	Steelhead	King salmon	Silver salmon	Steelhead
October 3	291	0	0	0	0	0
October 10	194	0	0	0	0	0
October 17	0	0	0	0	0	0
October 24	0	0	0	0	0	0
October 31	5,150	0	0	171	12	3
November 7	237	0	0	36	9	3
November 14	2,337	1,419	27	313	42	19
November 21	58	376	92	103	56	11
November 28	189	403	103	31	68	2
December 5	1,942	3,945	1,233	4	159	6
December 12	3,525	4,003	1,571	0	15	3
December 19	372	246	345	6	67	125
December 26	1,814	1,214	1,684	6	39	29
January 2	157	430	698	0	9	2
January 9	0	0	5,753	0	0	0
January 16	12	10	10	0	9	0
January 23	0	0	0	0	5	1
January 30	0	19	35	0	8	1
February 6	2	742	1,758	2	17	297
February 13	20	65	3,752	0	0	61
February 20	12	0	1,518	0	0	423
February 27	0	0	361	0	0	307
March 6	0	0	294	0	0	211
March 13	0	0	190	0	0	597
March 20	0	0	170	0	0	114
March 27	0	0	110	0	0	406
April 3	0	0	12	0	0	404
April 10	0	0	0	0	0	86
April 17	0	0	0	0	0	25
April 24	0	0	0	0	0	3

The data presented in Table 1 evoke three interesting questions: (1) Do they indicate any general upward or downward trends in these salmon and steelhead populations? (2) Do they indicate any relationship between the size of any particular year's run and the number of progeny from that run? (3) Are there any significant relationships between the sizes of the runs in these four streams; and do the sizes of these runs bear any relationship to the commercial catch?

The first question can be readily answered by simple inspection of the data. There have been definite upward and downward fluctuations at all stations, but, with two possible exceptions, no long-range trends are apparent. The first of the exceptions concerns the king salmon run in the Mad River. The counts in recent years in the Mad River are low enough to warrant careful inquiry, but may well be within the range of normal variation. The lowest count on record (1949) bears about the same relation to the highest count as does the lowest count for the South Fork of the Eel River to the highest. On the other hand, the recent king salmon counts for the Shasta River appear to be disastrously small. Referring again to the Mad River counts, some observers, viewing the low counts for the period 1947-49, are prone to blame the fishway for the poor runs. (Sweasey Dam was constructed in 1938.) This is in part refuted by the counters stationed at the dam. They report that fish have trouble entering the fishway at certain water stages, but that the block is far from complete and that the unfavorable water stages are of short duration. Further refutation of this claim is contained in the counts themselves. If the fishway is to blame for the low counts, why the lag of five successive cycles after the first return cycle of 1941-42 before the decline?

The question, does a big run in one year produce a big run in another, is best approached by the use of the correlation coefficient. This is a measure of the degree of relationship between any two sets of numerical data. A coefficient of 0 indicates no relationship, while coefficients of +1 and —1 indicate perfect positive and negative correlations, respectively. The significance of other coefficients depends upon the number of pairs of values and is determined from published tables. (See Snedecor, 1948, page 149.)

With this brief introduction to the correlation coefficient, we may return to the data in Table 1. Adopting a four-year cycle for king salmon and steelhead and a three-year cycle for silver salmon, it is apparent from visual examination that the relationship between size of a parental run and size of the offspring run is not very close. A big run does not necessarily produce a big run. The three "parent-offspring" correlations listed in Table 3 give some suggestion of a positive relationship for king and silver salmon, but none of the three is statistically significant.

It is easy to suggest reasons for this lack of correlation. Conditions for survival in the streams and ocean vary independently of the number of adults in a spawning run. A small run of adults may meet good

TABLE 3

Correlation Between Sets of Salmon and Steelhead Data

Species	Data		Period included	Number of years	Coefficient of correlation	Probability of significance
KS	Sacramento River[1]	Eureka[1]	20–49	30	.493	<.01
KS	Columbia River[1]	Eureka[1]	35–49	15	.239	>.05
KS	Eureka[1]	San Francisco[1]	20–49	30	.162	>.05
KS	Sacramento River[1]	San Francisco[1]	20–49	30	.555	<.01
KS	Columbia River[1]	San Francisco[1]	35–49	15	—.265	>.05
KS	Columbia River[1]	Sacramento River[1]	35–49	15	.054	>.05
KS	Columbia River[1]	South Fork Eel River	38–49	12	.766	<.01
KS	South Fork Eel River	Eureka[1]	38–49	12	.498	>.05
KS	South Fork Eel River	Mad River	38–49	10	.493	>.05
SH	South Fork Eel River	Mad River	38–49	10	.820	<.01
SS	South Fork Eel River	Mad River	38–49	10	—.084	>.05
KS	South Fork Eel River 4-year cycle	Parent-offspring	38–49	8	.295	>.05
SH	South Fork Eel River 4-year cycle	Parent-offspring	38–49	8	—.248	>.05
SS	South Fork Eel River 3-year cycle	Parent-offspring	38–49	9	.419	>.05
KS	Klamath River	Eureka[1]	25–49	16	.297	>.05
KS	Shasta River	Eureka[1]	30–49	20	—.005	>.05
KS	South Fork Eel River	Shasta River	38–49	12	.044	>.05
KS	Shasta River	Klamath River	30–49	13	.160	>.05
KS	Mad River	Shasta River	38–49	10	.238	>.05

KS—King salmon (Oncorhynchus tshawytscha).
SS—Silver salmon (Oncorhynchus kisutch).
SH—Steelhead trout (Salmo gairdnerii).
[1] Commercial catch. Data taken from publications of the California Division of Fish and Game and the Washington Fish Commission.

spawning conditions, good survival of young in the stream, and good survival in the ocean and so produce a good run of fish four years later. On the other hand, an exceptionally large run may find unfavorable conditions throughout and produce a small return run. A further complicating factor is that not all individuals in a spawning run are of the same age, and the percentage returning at each age may vary from year to year.

The third question evoked by the data, i.e., is a large run in one stream accompanied by large runs in other streams, can also be approached through a study of correlation.

Referring again to the data in Table 3, a significant correlation between the runs in any two rivers would indicate that the two populations had been subjected to common factors affecting their survival. A significant relationship between the commercial catch in a given area of the ocean and the run in some particular stream would indicate that the ocean catch was made up, at least in part, of fish from that particular river, or that the runs in all rivers are closely correlated.

The only significant correlations shown in Table 3 are:

1. *King Salmon:* Sacramento River commercial landings, San Francisco commercial landings.
2. *King Salmon:* Sacramento River commercial landings, Eureka commercial landings.
3. *King Salmon:* Columbia River commercial landings, South Fork Eel River counts.
4. *Steelhead:* South Fork Eel River counts, Mad River counts.

The significant correlations between the commercial catch of the Sacramento River and the San Francisco and Eureka troll fisheries indicate that a high percentage of the salmon caught in the troll fisheries are Sacramento River fish.

The high correlation between the South Fork of the Eel River king salmon counts and the Columbia River catch either indicates unexplained common factors, or is a "nonsense correlation," a meaningless correlation that is frequently found in time series (Snedecor, 1948, p. 164). The latter appears to be the more likely explanation, in the light of the low correlations between the various rivers and the lack of any evidence of common factors.

The significant correlation between the steelhead counts for the South Fork of the Eel River and the Mad River is not surprising. Both streams lie in the same climatic zone. Good stream survival conditions in one river are probably accompanied by good conditions in the other; both are subject to about the same intensity of sport fishing.

It is easy to offer plausible explanations for some of the poor correlations, but for others it is more difficult. The lack of correlation between the South Fork of the Eel River and Mad River runs of king salmon and silver salmon must be due to some factor or factors greatly affecting the survival in one but not the other. The lack of correlation between the other stream counts is superficially surprising, considering that the Klamath River (at Klamathon) and Shasta River fish are in the same area and presumably conditions for survival would vary together; however, the two streams are quite different in character. The lack of correlation between the Sacramento River runs and the Columbia River runs is not surprising, since the two streams lie in very different climatic zones. Whatever the reasons, it is evident that there is little or no correlation between the sizes of the runs of anadromous fishes in the various streams for which data are available. This may explain lack of correlation between the size of the commercial catch of king salmon in the two areas of the California coast. The troll fishery appears to prey on fish from the various rivers indiscriminately.

In the absence of more complete information, the following appears to be the most reasonable explanation of the data at hand. The Sacramento-San Joaquin system, being at the southern end of the spawning range of the king salmon, and in addition presently supporting runs of the same magnitude as the Columbia River, probably supplies most or a large part of the salmon in the San Francisco troll catch. This is consistent with the good correlation between the San Francisco ocean catch and the Sacramento River gill net catch. The Eureka troll fishery, lying geographically between the Columbia River and the Sacramento River, and ''astride'' several lesser salmon streams, probably draws more heavily on the latter. This explanation is consistent with the correlations given in Table 3. None of these streams, with the exception of the South Fork of the Eel and Columbia rivers, is correlated with another. A fishery drawing from all of them in addition to the Sacramento River would tend not to be correlated with the San Francisco troll fishery (which probably draws mainly on the fish from one stream). And, such a fishery would tend to be more stable, as is the Eureka fishery, than one such as the San Francisco troll fishery, that is probably largely dependent upon the fish from a single stream system (the Sacramento).

THE FACTORS GOVERNING THE SIZES OF THE RUNS

Mortality of salmon and steelhead may be divided sharply into two segments: ocean and stream. In this connection, the question arises: to what extent do the fresh-water and the ocean habitats, respectively, impose the upper limit on salmon populations within their present range of abundance? This is a problem of particular importance to management. It may be roughly paraphrased as follows. Is stream mortality density dependent or independent, and is ocean mortality density dependent or independent? (Density-dependent mortality is caused by factors that operate more severely as the population level rises and density-independent mortality is caused by factors that cause a constant death rate, regardless of the population level.)

It may be that stream mortality is largely density dependent. Such factors as overcrowding of spawning areas, disease, and predation frequently may operate in a density-dependent manner, particularly when the salmon and steelhead form the dominant element or one of the dominant elements of the fauna.

We do not have available much critical information on the ecology of salmon and steelhead, particularly of the younger fish, in the ocean. However, some observations on king salmon in the lower Eel River, Humboldt County, made in 1950 are of interest. The young king salmon appeared to move downstream in fairly compact schools. These schools remained compact in the upper sections of tidewater, but observations at the mouth of the river indicated that the schools were breaking up, since the fingerlings seen there were not in compact groups. Bait fishermen seining in Humboldt Bay frequently catch one or two or three king salmon of the year along with herring and other fishes. This capture of scattered individuals is a further indication that the schools of fingerlings do break up. It is well known that the larger king salmon range widely in the ocean and appear to be concentrated in either schools or feeding aggregations.

It is possible to set up certain criteria which will help to decide if it is the density-dependent or independent factors which are of primary importance in the ocean, and if these factors operate in a coastwise manner or localized.

If the ocean is presently imposing the upper limit on the salmon and steelhead populations, it follows that there must be strong density-dependent mortality factors operating in it. If the factors operate in a coastwise manner and if they are strong enough to place an upper limit on the salmon and steelhead populations (at present levels), they should also cause a strong correlation between the sizes of the various runs. The hypothetical situation presented in Table 4 illustrates this point. The relative numbers of downstream migrants for each of the two hypothetical streams for each of the years were selected at random, from one to four. Since they were taken at random, no correlation is to be expected (correlation coefficient = 0.00). Now, if the chief factors limiting the

TABLE 4

Hypothetical Situation Illustrating the Effect of Varying Random Factors on the Correlation Coefficient of a Random Set of Paired Items[1]

Downstream migrants		Ocean factors	Returning adults	
A	B		A_1	B_1
2	2	2	4	4
1	1	1	1	1
3	3	2	6	6
4	1	1	4	1
3	2	3	9	6
1	3	1	1	3
4	3	3	12	9
2	4	1	2	4
3	2	4	12	8
2	3	4	8	12

Correlation coefficient A — B = 0.00.
Correlation coefficient A_1 — B_1 = 0.784.

[1] The Pearsonian coefficient of correlation is customarily used only when the association is linear and the distribution around this line is homoskedastic (the spread, or dispersion, around this line is the same at all points). The model gives a linear regression but the dispersion around the regression line is heteroskedastic. This does not invalidate the table as an example of the action of a common factor on two unrelated populations.

number of salmon are density-dependent factors in the ocean, then the carrying capacity of the ocean must fluctuate widely, since the numbers of returning adults fluctuate widely (Table 1). This changing mortality is represented in Table 4 by the column labeled ocean factors. These factors were also taken at random, but restricted to the range of one to four, so that the maximum possible variation between the resultant runs (16 X) would approximate the observed variation (see Table 1). The numbers of adults returning to the streams after going through the varying ocean mortality is represented in the last two columns. The correlation coefficient for these is 0.784 (highly significant). This is in direct opposition to the lack of correlation noted in the actual data (Tables 1 and 3) on the sizes of the salmon runs in the various streams, with the minor exceptions already noted. In other words, the lack of correlation revealed in Table 3 between the sizes of various individual salmon runs suggests the absence of any general, widespread density-dependent factors operating upon these fish in the ocean along the Pacific Coast at the present levels of population abundance. It may also be inferred that variation in density-*independent* coastwise factors in the ocean is slight from year to year (for variation in density-independent factors in the ocean sufficient to produce the observed wide fluctuations in the numbers of adults returning to streams would also produce significant positive correlations, as illustrated in Table 4).

It might be hypothesized that density-dependent factors are operating in localized areas along the coast in such a manner that they affect the salmonids from the various streams independently. However, it seems unlikely that any such localized factors would operate on the larger king salmon (over 20 inches in length), for example, since these fish are known to range freely along the coast. Fishing mortality might operate in a localized manner if the migrants for one stream were schooled together and were caught in exceptionally large numbers. This does not appear to be the usual pattern.

Small salmon and steelhead in their first season of ocean life remain as possible victims of strong density-dependent mortality factors. The most important of these is probably predation.

Predation probably operates at almost all population levels in a density-dependent manner. If the species under consideration is the major element of the population of that class of fish (forage fish in the case of young salmon), predation will be strongly population dependent. If the species under consideration forms a minor element in the total population of that class of fish, predation will be only weakly population dependent (with respect to that species), the increase in predation rate increasing only slightly with increase of the species, and in effect resembling density-independent mortality.

One of the writers (G. I. M.) on studying the largemouth black bass population of Clear Lake, California, was able to point out a portion of the life history of the bass during which they were frequently simultaneously the chief forage fish and the chief predator (Murphy, 1949, 1950). It is obvious that in such a situation both competition for food and predation are density dependent.

Observations on the estuary of the Eel River in 1950 indicated that young salmon were a relatively minor element in the total population of small forage fish. In the ocean young salmon obviously constitute a small segment of the total forage fish population. Until special situations such as were found in the case of young bass in Clear Lake are determined to exist, we must conclude that ocean and estuarine mortality of small salmon is nearly density independent. A density-dependent situation might, however, exist in the estuaries of small coastal streams not frequented by large numbers of other small marine fishes. (On the other hand, the estuary might be regarded as an extension of the fresh-water environment.)

The considerations in the preceding paragraph do not preclude the existence of wide variations in density-independent mortality on a localized basis. (However, coastwise factors appear precluded by the lack of correlation between the runs.) In this connection it is of interest to note the differences between the amounts of fluctuation for the three species counted in the South Fork of the Eel River (Table 1). Fluctuations in the king salmon are on the order of seven times; in the silver salmon of three times; and in the steelhead of two times. Perhaps these differences may be laid to the size at which the various species go to sea: king salmon in their first year; silver salmon as yearlings; and steelhead as yearlings and older fish.

Silver salmon runs in several streams along the Oregon coast exhibit a high degree of correlation, judging from commercial catch statistics (McKernan, Johnson, and Hodges, 1950). However, these writers were able to correlate variation in some of the streams with environmental factors affecting the stream phase of the life of the silver salmon. They were unable to relate the fluctuations in the runs to any known changes in the ocean. Without ruling out this latter possibility, the writers concluded that the correlation between the runs (they did not evaluate this correlation numerically) was due to common factors affecting these streams. The presence of common factors would not be surprising, since the streams under consideration all lie in the same geographic belt.

Another line of evidence tending to dispute the contention that mortality in the ocean is density dependent lies in the consideration of the present abundance of salmon in relation to past abundance. It is reasonably well established that salmon are less abundant now than in the early days of exploitation, at a time when streams were relatively unspoiled. Many examples of once-existent runs that today are either gone or severely reduced can be cited. Runs that are healthy today are not producing at their former levels. Even if we assume that the factors affecting ocean mortality are density dependent, and that the former high level of abundance represented the maximum possible density, it follows that the populations of today are below the maximum and could be increased by increasing the number of seaward migrants.

DISCUSSION

The data and arguments presented above indicate, insofar as our present knowledge of the species under discussion extends, that most fluctuations in abundance may be laid to factors operating in the fresh-water phase of their life cycles or to density-dependent factors in the ocean operating on a local basis. Assuming that this is true, we could increase the populations by increasing the numbers of seaward migrants.

Briefly, this might be accomplished by the following means:

1. Regulation and vigilant law enforcement, to insure that enough adults reach the spawning beds to fully utilize them.
2. Stream improvement, to enlarge the available spawning and nursery areas. This is obvious; since larger stream systems support larger runs of fish, it follows that enlargement of existing stream systems will be followed by larger runs of fish.
3. Maintaining natural conditions in existing stream systems.
4. Screening diversions, rescuing stranded young fish, and other similar measures.

These four are sound measures already well based in fact. Further management of anadromous fish runs awaits developments along two lines.

The first of these, artificial propagation, was at one time the only management tool available, and it was expected that hatcheries would maintain the runs. We know today that there are major flaws in this belief. Operation of hatcheries was originally based on the assumption that natural spawning was inefficient and that the eggs of a few females sheltered in a hatchery would produce as many fry as the eggs of many females spawning naturally. Today we know that the percentage of hatch under normal stream conditions is about as high as it is in the hatchery. Since in the case of the anadromous salmonids we have to take eggs that would have hatched naturally in order to stock our hatchery, it follows that the expense involved in operating the hatchery is wasted, insofar as production and planting of fry are concerned.

As indicated in this paper, there are a number of factors that cause mortality in the stream phase of the life of the salmons and steelhead. The thought has been advanced that better results than from natural propagation could be obtained by taking eggs from natural runs, hatching the fry, and, instead of planting them soon after, rearing the offspring until their normal downstream migration period. Theoretically, at least, this procedure should circumvent a considerable amount of stream mortality and result in an increase in the number of returning adults over the number that would have been produced if all fish had been allowed to spawn naturally. This, of course, assumes that survival of hatchery fish from egg to adult is considerably greater than that of wild fish. Before such a program can be put on a production basis, we must know if the cost of running the hatchery will be fully repaid by the increase in the runs. In other words, we must get at least a dollar's worth of fish back for each dollar expended. Possible exceptions to this yardstick might be in the case of the rehabilitation of a badly depleted run of fish, in the event a dam precludes any natural spawning, or in the case of new environment opened up by stream clearance. An experimental program designed to test the economic feasibility of a hatchery program as outlined above is being initiated on the Mad River in Northern California.

The second line of endeavor looking towards expansion of our anadromous fish resources must start with an answer to the question, "Why do streams produce small runs one year and large runs another?" Obviously, if we could maintain production at peak levels in all streams each year, we would greatly increase these resources. There is little hope of accomplishing this until we know why the runs fluctuate. This is a difficult thing to determine, as evidenced by the uncertain results obtained by Silliman (1950) and McKernan, Johnson, and Hodges (1950), but in view of its importance, it justifies the expenditure of considerable effort.

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