SURVIVAL, MATURITY, ABUNDANCE, AND MARINE DISTRIBUTION OF 1965-66 BROOD COHO SALMON, *ONCORHYNCHUS KISUTCH*, FROM COLUMBIA RIVER HATCHERIES

ROBERT H. LANDER AND KENNETH A. HENRY[1]

ABSTRACT

Data are presented estimating the survival, maturity, and abundance of marked coho salmon, *Oncorhynchus kisutch*, of the 1965-66 broods from 18 to 20 Columbia River hatcheries. Also presented are data depicting the distribution of these fish as caught in the northeastern Pacific Ocean. Compared to fish from hatcheries on the upper reaches of the river, coho salmon from hatcheries near the estuary had a better survival until recruitment to the ocean fishery, a greater proportion maturing as jacks (2-yr olds), and an apparent differential migration pattern in the ocean. For hatcheries from all river sections combined, the parameter estimates differed little between broods. Estimates for both broods are as follows: 9-10% surviving during the 6.0 mo between release of smolts and the return of young males or jacks to the Columbia River; 3-4% of survivors maturing as jacks; 10-12% surviving during the last 12.0 mo of ocean life; 5-6% of the original number of smolts surviving until the time of recruitment to ocean fishing 13.5 mo after release; and exploitation rates of 68-70% in the ocean fishery during the last 4.5 mo of life at sea.

A cooperative program was undertaken among the various Pacific coast fishery agencies in the United States and Canada to estimate the contribution to various fisheries of coho salmon, *Oncorhynchus kisutch*, produced by 20 Columbia River hatcheries. The hatcheries were placed into four groups according to their locations on the river (Figure 1). About 10% of the fish released from each of the hatcheries on each of the four river sections were identified with section-specific marks (certain fins or bones excised) for the 1965-66 brood years:

Group	*Location boundaries*	*Fins or bones excised*
Lower River	Mouth of Columbia River to mouth of Cowlitz River	Adipose-right maxillary (Ad-RM)
Middle River	Mouth of Cowlitz River to Bonneville Dam	Adipose (Ad)
Upper River	Bonneville Dam to The Dalles Dam	Adipose-left maxillary (Ad-LM)
Uppermost River	Above The Dalles Dam	Dorsal-adipose (D-Ad) Dorsal-adipose-left maxillary (D-Ad-LM) Dorsal-adipose-right maxillary (D-Ad-RM)

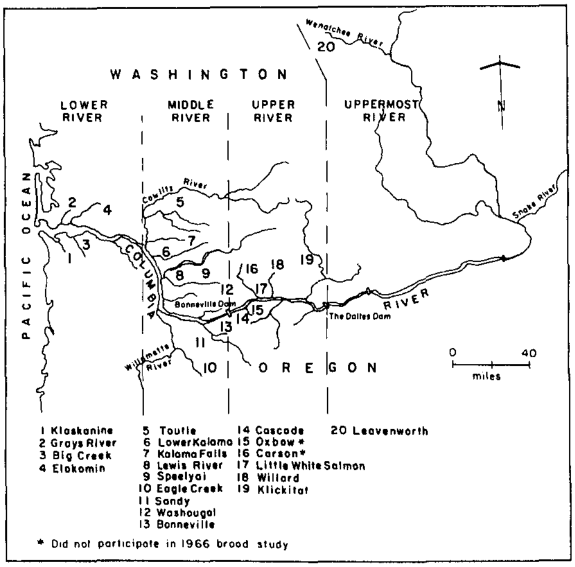

FIGURE 1.—Grouping of Columbia River hatcheries by release area and marks applied to evaluate the contribution of 1965-66 brood coho salmon.

Such studies are needed to determine the economic justification for the large scale hatchery program that has been developed for the

---

[1] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

Manuscript accepted January 1973.
FISHERY BULLETIN: VOL. 71, NO. 3, 1973.

Columbia River to supplement natural spawning and to compensate for loss of and damage to natural spawning areas by construction of dams.

A brief resume of the life history of these coho salmon may be helpful. Most of the salmon used in these studies were released as small fish during April and May, approximately 1 yr after hatching in the hatcheries. About 10% of them were marked just before release. The young salmon then migrated to the ocean. After a few months in the ocean a relatively small portion of the fish—mainly 2-yr-old males called jacks—matured and returned to their hatcheries in the Columbia River. At that time, a few were captured in the Columbia River sport and commercial fisheries. Most of the fish, however, remained in the ocean over the winter. During the following summer, many were captured in the ocean commercial troll and sport fisheries. During late August through October, all the remaining fish (3-yr olds) from each brood then began to mature and reenter the Columbia River, where some were captured in the commercial gill net and sport fisheries. Those escaping these fisheries returned in the late fall to their hatchery streams, where their eggs were taken artificially for rearing in the hatchery. Coho salmon, like all Pacific salmon, die after spawning and the cycle is then complete.

In a report by Wahle, Vreeland, and Lander,[2] the economic contributions of all hatcheries combined have been analyzed for these two broods of fish. These benefit/cost calculations rely mainly on release and recovery data. Such biological parameters as fishing and natural mortality, age at maturity, abundance, and time/area distribution were not considered. These are important in developing a proper management plan for these fish, so we have developed estimates of them for these two brood years. These will be timely supplements to the benefit/cost analysis of Wahle et al. (See footnote 2.)

The estimates of survival, maturity, and abundance in the present report mainly are average values for all hatcheries combined. Limitations in the basic data reduce the reliability of separate evaluations for hatcheries on each of the four sections of the Columbia River, particularly for the 1966-brood data. The distribution of hatchery fish in marine fisheries is compared between the four river sections for each brood.

PROBLEMS OF ESTIMATING PARAMETERS

To aid in understanding the various parameters we wish to estimate, in Figure 2 we have portrayed graphically certain features of the coho salmon's life history, particularly as they pertain to the various parameters for the period from release as smolts until their return to the Columbia River as adults—approximately 18 mo. The time sequence shown in Figure 2 is accurate to approximately 0.5 mo. It readily can be seen from Figure 2 that there are four known values: 1) number of smolts released (N_0), 2) number maturing as jacks (E_1), 3) number caught by the ocean troll and sport fisheries (C), and 4) number returning as adults (E_2). From these four known values we wish to estimate: 1) fishing mortality rate over the last 4.5-mo period (F), 2) proportion maturing as jacks (m), 3) natural mortality rate for the 6.0-mo period from release of smolts until the jacks mature (M_1), 4) natural mortality rate for the 12.0-mo period from the time jacks mature until the adults return to the Columbia River (M_2), 5) number of coho remaining at sea when the jacks have returned (N_1), and 6) number of coho

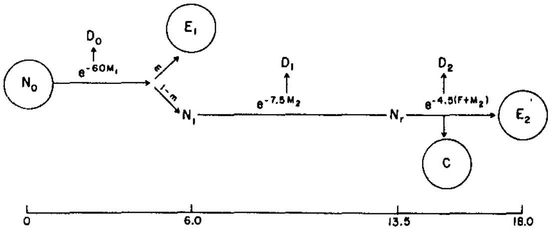

FIGURE 2.—Diagram depicting the life history of the coho salmon for the period from release of smolts until their return to the Columbia River as adults—approximately 18 mo (circled items indicate observed data).

---

[2] Wahle, R. J., R. R. Vreeland, and R. H. Lander. Bioeconomic contribution of 1965-66 brood coho salmon from Columbia River hatcheries. Columbia Fish. Program Off., Natl. Mar. Fish. Serv., NOAA, Portland, Oreg., and Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash. [Unpubl. manuscr.]

available at the start of the commercial troll fishery (N_r). The D_i represent the number of fish dying naturally.

The known data for the two brood years are listed in Tables 1 and 2. The catch data shown are estimated numbers based on sampling (see footnote 2). Each escapement value is the sum of the river catch and returns to the hatchery for a given mark. In making our computations we have made some additional assumptions: 1) the data in Tables 1 and 2 are accurate, 2) adipose only marks (Ad) were not regenerated, 3) all recoveries of fish with appropriate marks were hatchery fish, and 4) all pertinent hatchery marks in catch samples and hatchery returns were detected and reported.

The events in Figure 2 can be depicted by a multinominal model with the N_0 smolts falling

TABLE 1.—Estimated total recapture of 1965 brood marked Columbia River hatchery coho salmon, grouped by river section.

Year of life	Ocean catch (C)	River catch	Number spawning	River total (E)	Grand total
Lower River (Ad-RM) 508,294 released; 2.92% recovered					
2	—	155	1,568	1,723	1,723
3	10,435	841	1,864	2,705	13,140
Total	10,435	996	3,432	4,428	14,863
Middle River (Ad) 845,674 released; 9.83% recovered					
2	—	346	4,391	4,737	4,737
3	63,829	5,197	9,399	14,596	78,425
Total	63,829	5,543	13,790	19,333	83,162
Upper River (Ad-LM) 837,829 released; 1.41% recovered					
2	—	—	1,125	1,125	1,125
3	7,933	846	1,882	2,728	10,661
Total	7,933	846	3,007	3,853	11,786
Leavenworth Uppermost River (D-Ad) 101,734 released; 2.82% recovered					
2	—	7	38	45	45
3	2,448	238	138	376	2,824
Total	2,448	245	176	421	2,869

TABLE 2.—Estimated total recapture of 1966 brood marked Columbia River hatchery coho salmon, grouped by river section.

Year of life	Ocean catch (C)	River catch	Number spawning	River total (E)	Grand total
Lower River (Ad-RM) 385,630 released; 3.98% recovered					
2	—	88	2,067	2,155	2,155
3	9,802	1,639	1,771	3,410	13,212
Total	9,802	1,727	3,838	5,565	15,367
Middle River (Ad) 764,262 released; 9.30% recovered					
2	—	666	2,191	2,857	2,857
3	53,967	8,501	5,769	14,270	68,237
	53,967	9,167	7,960	17,127	71,094
Upper River (Ad-LM) 493,110 released; 2.43% recovered					
2	—	103	624	727	727
3	7,691	2,505	1,075	3,580	11,271
Total	7,691	2,608	1,699	4,307	11,998
Leavenworth (D-Ad) 174,735 released[1]; 1.07% recovered					
2	—	6	8	14	14
3	1,570	283	—	283	1,853
Total	1,570	289	8	297	1,867

[1] Includes 92,250 D-Ad-LM and 73,011 D-Ad-RM, and 9,474 D-Ad.

into the observed categories with certain probabilities θ_i ($i = 1 \cdot\cdot 4$) as follows:[3]

$$\text{Probability of } E_1 = \theta_1 = me^{-6M_1}. \qquad (1)$$

$$\text{Probability of } C = \theta_2 = (1-m)e^{-6M_1}e^{-7.5M_2}\left[\frac{F}{F+M_2}\right]\left[1-e^{-4.5(F+M_2)}\right]. \qquad (2)$$

$$\text{Probability of } E_2 = \theta_3 = (1-m)e^{-6M_1}e^{-7.5M_2}e^{-4.5(F+M_2)}. \qquad (3)$$

$$\text{Probability of } D = \theta_4 = 1 - \theta_1 - \theta_2 - \theta_3,$$

$$\text{where } D = D_0 + D_1 + D_2. \qquad (4)$$

The maximum likelihood estimators of the θ_1 are:

$$\hat{\theta}_1 = E_1/N_0. \qquad (5)$$

$$\hat{\theta}_2 = C/N_0. \qquad (6)$$

$$\hat{\theta}_3 = E_2/N_0. \qquad (7)$$

$$\hat{\theta}_4 = 1 - \hat{\theta}_1 - \hat{\theta}_2 - \hat{\theta}_3. \qquad (8)$$

A maximum likelihood estimator of a function of the parameters θ_i is obtained by replacing the parameter values by the corresponding maximum likelihood estimates, $\hat{\theta}_i$. Beyond that, however, there exists no unique transformation or function to obtain maximum likelihood estimates of M_1, m, M_2, and F: any given set of observed data can generate a variety of combinations of parameter estimates.

METHODS OF ESTIMATING PARAMETERS

Estimations Based on Selection of m or M_2

Since no unique solution exists, the only practical solution is to assume some values for one of the unknown parameters and solve the equations for the remaining parameters. This in effect is what Cleaver (1969) and Henry (1971) did for hatchery chinook salmon, *O. tshawytscha*, (with 3-4 spawning escapements from a given release group). In their calculations, however, they assumed various values for M_2 (natural mortality during the last year of life) and then calculated values for the remaining parameters. In applying this method to the 1965-66 brood coho salmon data, the appropriate equations, based on the time periods and notations shown in Figure 2, would be:

$$C/E_2 = \frac{F}{F+M_2}\left(e^{4.5F+4.5M_2}-1\right) \quad \text{solve for } F \qquad (9)$$

$$N_r = E_2\, e^{4.5M_2+4.5F} \quad \text{solve for } N_r \qquad (10)$$

$$\frac{E_2}{E_1} = \frac{e^{-12M_2-4.5F}(1-m)}{m} \quad \text{solve for } m. \qquad (11)$$

The resulting values for these computations at six different levels of natural mortality for all hatcheries combined for each brood year are listed in Table 3. It is apparent from these data that the changes in natural mortality have a relatively greater effect on the proportion maturing as 2-yr-old fish (m), and on the number of recruits to the third year of life (N_1) and to the fishery (N_r), than on the fishing mortality (F).

As mentioned previously, it is difficult to analyze the data separately from the four sections of the river. For the 1966 brood two additional groups of marked fish were released —approximately 92,000 D-Ad-LM in the Middle River areas and about 73,000 D-Ad-RM in the Uppermost River area (see footnote 2). Obviously, any fin regeneration or fins missed in sampling from this group would confound data from the other marked groups, making a comparison of individual markings for the 1966 brood much more questionable. Nevertheless, in Table 4 are listed the parameter values for

---

[3] We are indebted to Jerome Pella who, as editorial referee, suggested that the relationships affecting the coho salmon be depicted in this manner and pointed out a relation between the proportion maturing as jacks (m) and the rates of natural mortality that we had not considered earlier. Pella's suggestions greatly improve the understanding and description of the actual situation.

TABLE 3.—Values of F, m, N_1, N_r, and N_r/N_0 at various levels of natural mortality for 1965-66 broods of marked Columbia River coho salmon (F is summed for 4.5 mo, data from all hatcheries combined).

$12M_2$	F	m	N_1	N_r	N_r/N_0
1965 brood:					
0.24	1.594	0.056	127,585	109,861	0.0479
.45	1.554	.048	151,378	114,247	.0498
.48	1.549	.047	155,055	114,917	.0501
.60	1.526	.043	171,020	117,532	.0512
.72	1.504	.039	188,629	120,261	.0524
.96	1.406	.032	229,472	125,966	.0549
1966 brood:					
.24	1.437	.048	115,244	99,175	.0546
.45	1.400	.040	137,010	103,413	.0569
.48	1.395	.039	140,478	104,020	.0572
.60	1.374	.036	155,097	106,579	.0586
.72	1.353	.033	171,237	109,151	.0600
.96	1.312	.027	208,941	114,639	.0631

TABLE 4.—Values of F, P, N_1, N_r, and N_r/N_0 for 1965-66 broods of marked coho salmon from various Columbia River locations (F is summed for 4.5 mo; M_2 = 0.06).

Area	F	m	N_1	N_r	N_r/N_0
1965 brood:					
Mouth to Cowlitz River (Lower)	1.449	0.068	23,667	15,091	0.0297
Cowlitz River to Bonneville (Middle)	1.545	.033	140,576	89,620	.1060
Bonneville to The Dalles (Upper)	1.243	.055	19,425	12,385	.0148
Above The Dalles (Uppermost)	1.865	.009	4,987	3,179	.0312
Combined	1.504	.039	188,629	120,261	.0524
1966 brood:					
Mouth to Cowlitz River (Lower)	1.235	.082	24,088	15,356	.0398
Cowlitz River to Bonneville (Middle)	1.434	.023	122,997	78,401	.1026
Bonneville to The Dalles (Upper)	1.040	.034	20,809	13,273	.0269
Above The Dalles (Uppermost)	1.733	.004	3,289	2,098	.0120
Combined	1.353	.033	171,237	109,151	.0600

hatcheries from these four sections as well as for the combined data for $12M_2$ = 0.72 for the 1965-66 brood years, respectively. The quite different results for the Middle River releases are believed due primarily to the maxillary and dorsal fins either regenerating or being overlooked in the sampling (see footnote 2). Ignoring the Middle River releases for the moment and assuming that the effect of fin regeneration or sampling equally affects the other marks, certain trends in the data are of interest. Thus, the estimated proportion maturing (m) at age 2 consistently decreases from the Lower River to the Uppermost River hatcheries for both brood years. In other words, these data suggest that at the end of their second year, a greater portion of the Lower River coho salmon matured as jacks, and the proportion maturing as jacks consistently decreased for coho salmon released farther and farther upriver.

Another statistic of interest in Table 4 is the estimated proportion of released fish that survived to enter the fishery (N_r/N_0). The results were not consistent for the two brood years in that the Uppermost releases showed the highest estimated recruitment to the fishery for the 1965 brood and lowest recruitment to the fishery for the 1966 brood. However, in comparing only the two groups of similarly marked fish (Ad-RM, Lower River; Ad-LM, Upper River) the Upper River marked fish had a lower estimated recruitment to the fishery for both brood years. Also, recruitment was higher for the 1966 brood from both these river sections. Few hatchery returns of the 1966 brood, Leavenworth (Uppermost) marked coho salmon, were obtained because of passage difficulties at John Day Dam due to construction of fish ladders and mortalities caused by trapping at Priest Rapids Dam. This factor undoubtedly contributed to the relatively low estimated recruitment for the 1966 brood from this area.

Instead of assuming a certain value for M_2 as we have done using the Cleaver model, as pointed out by Jerome Pella (see footnote 3), assuming a fixed value for the proportion maturing (m) permits unique solutions to Equations 1-4, combined with Equations 5-8, so that with:

$$m = m \text{ (fixed) } (\hat{\theta}_1 < m < 1). \tag{12}$$

$$M_1 = -\frac{1}{6} \ln\left(\frac{\hat{\theta}_1}{m}\right) \tag{13}$$

$$\left[\frac{\ln k_2 + 12M_2}{\ln k_2 + 7.5M_2}\right]\left[1 - e^{-(\ln k_2 + 7.5M_2)}\right] e^{-7.5M_2} = k_1 \tag{14}$$

$$\text{where } k_1 = \left(\frac{\hat{\theta}_2}{1 - m}\right) e^{6M_1}$$

$$k_2 = \left(\frac{\hat{\theta}_3}{1 - m}\right) e^{6M_1}$$

$$F = -\left[\frac{\ln k_2 + 12M_2}{4.5}\right] \tag{15}$$

The derivations of Equations 12-15 are verified in the Appendix. For a particular value of m (Equation 12), one solves Equation 13 explicitly for M_1. Then using these values of m and M_1, M_2 in Equation 14 is found by iteration. Finally, one obtains the proper F from Equation 15.

Using Equations 12-15, we again calculated values for the various parameters for the 1965-66 broods, based on selected values of the proportion maturing (m). These values are listed in Table 5 and graphed in Figure 3. Only values of m that gave non-negative values of M_1, M_2, and F were used. Values of the average monthly rate during all 18.0 mo, Z_T, were calculated from the relation, $Z_T = (6.0M_1 + 12.0M_2 + 4.5F)/18.0$. Other rates of monthly mortality that can be calculated from these data are:

Average total mortality during last 12.0 mo of ocean life:

$$Z_2 = (12.0M_2 + 4.5F)/12.0.$$

Average natural mortality from time of smolt release until beginning of commercial troll fishing:

$$M_r = (6.0M_1 + 7.5M_2)/13.5.$$

Total mortality during last 4.5 mo of ocean life:

$$F + M_2.$$

Comparison of Two Methods

Before examining Figure 3 in detail, we would like to compare briefly these two possible approaches: 1) assuming selected values for M_2 (natural mortality during second year) and 2) assuming selected values for m (proportion maturing as jacks). First of all, it should be recognized that the values obtained by either method as used here (Cleaver applied an approximation formula noted before his Equation 20) are identical because Equation 9, used in the calculation for a given value of M_2, is simply $\frac{\text{Equation 2}}{\text{Equation 3}}$ used in calculations based on a fixed value of m. Furthermore, whenever a fixed value for either M_2 or m is selected, all the other unknown parameters are uniquely determined.

Although either of these approaches give identical results, their conceptual basis differs. In selecting a fixed value for M_2, one starts at the end of the life cycle and work backwards; by selecting m values, one more closely parallels the actual life history of the coho salmon. Furthermore, a wide range of selected values for

TABLE 5.—Calculated values of m (proportion maturing as jacks), M_1 (natural mortality rate during first 6 mo after release of smolts), M_2 (natural mortality rate during last 12 mo of ocean life), F (fishing mortality during last 4.5 mo of ocean life) and Z_T (average total mortality for 18 mo after release of smolts) for 1965-66 brood Columbia River hatchery coho salmon.

m	M_1	M_2	F	Z_T
1965 brood:				
0.0033	0.0	0.3101	0.2218	0.2622
.0050	.0679	.2697	.2384	.2620
.0100	.1834	.2003	.2685	.2618
.0106	.1939	.1939	.2713	.2617
.0200	.2990	.1295	.3008	.2612
.0300	.3665	.0874	.3209	.2606
.0400	.4145	.0570	.3357	.2601
.0500	.4517	.0331	.3475	.2595
.0600	.4821	.0133	.3574	.2589
.0677	.5022	.0	.3641	.2584
1966 brood:				
.0032	.0	.2935	.2023	.2462
.0050	.0762	.2487	.2197	.2461
.0096	.1844	.1844	.2459	.2459
.0100	.1917	.1800	.2477	.2458
.0200	.3073	.1100	.2780	.2453
.0300	.3748	.0684	.2968	.2447
.0400	.4228	.0383	.3106	.2441
.0500	.4600	.0147	.3218	.2435
.0573	.4828	.0	.3287	.2431

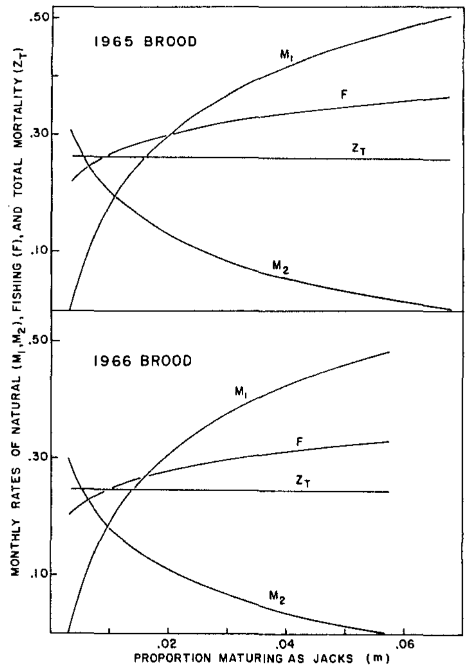

FIGURE 3.—Relations of monthly natural mortality (M_1, M_2), fishing mortality (F), and total mortality (Z_T) rates to the fraction maturing as jacks (m), for 1965-66 brood coho salmon from Columbia River hatcheries. For any particular value of m, the corresponding rates operated as follows: M_1-first 6.0 mo after release of smolts, M_2-last 12.0 mo of ocean life, F-last 4.5 mo of ocean life, and Z_T-all 18.0 mo from release of smolts to end of ocean life.

M_2 have a relatively lesser effect on the estimated values of m than the effect on M_2 by a corresponding range of selected values of m (Figure 3). For example, if the selected value of M_2 is increased four times, the estimated value of m is reduced by about one-half. On the other hand, if the selected values of m are increased four times the estimated value of M_2 is decreased to about one-fourth. Finally, the use of selected values of m (Equations 12-15) is based on a logical, probablistic, portrayal of the life history of the coho salmon whereas the use of selected values of M_2 is a more deterministic approach.

ANALYSIS OF 1965-66 BROOD DATA BASED ON SELECTION OF m

Let us return briefly to the estimates in Table 4. It might be argued that since m and M_2 are inversely related (this will be discussed in greater detail later), the declining estimates for m as one moves upriver are merely the result of using a fixed value for M_2 when in fact M_2 is different for the various sections of the river. To examine this possibility in greater detail, we assumed the proportion maturing as jacks (m) was the same for all river sections and again calculated the pertinent estimates of the parameters relating to these data. The results are listed in Table 6. In making these calculations we discovered that m had to be less than 0.008 before it was applicable to the data from all four river sections. Furthermore, again ignoring the Middle River data for reasons previously discussed, the estimates of M_2 (natural mortality in the last 12 mo) decreased from the Lower River to the Uppermost River.

We find these results based on an assumption of a constant m for all river sections difficult to accept for a number of reasons. The decreasing M_2 (natural mortality) as one moves upriver is suspect in view of the unobserved natural mortality that probably occurs during the upriver migration, as it does for chinook salmon (Merrell, Collins, and Greenough, 1969). Also,

TABLE 6.—Calculated monthly values of F, M_1, and M_2 for 1965-66 broods of marked coho salmon from Columbia River hatcheries — river sections combined (m = 0.0006).

Area	F	M_1	M_2
1965 brood:			
Mouth to Cowlitz River (Lower)	0.2130	0.0952	0.3084
Cowlitz River to Bonneville (Middle)	.2613	.0115	.2341
Bonneville to The Dalles (Upper)	.1878	.2495	.2816
Above The Dalles (Uppermost)	.3912	.4346	.1022
1966 brood:			
Mouth to Cowlitz River (Lower)	.1719	.0118	.3231
Cowlitz River to Bonneville (Middle)	.2570	.0789	.1954
Bonneville to The Dalles (Upper)	.1704	.2339	.2291
Above The Dalles (Uppermost)	.4047	.7193	.0235

the relatively low value of m (<0.008) needed to be comparable with all the data is considerably lower than we feel it should be because the calculated values of M_2 greatly exceed those for M_1 for the lower river areas as they also do for all coho salmon combined in Figure 3. This is contrary to all previously published data as discussed in the next section. On the basis of these analyses, we believe that the proportion maturing as jacks for these two brood years consistently decreased for coho salmon released farther and farther upriver.

Returning to Table 5 and Figure 3, these data show the same pattern for both broods as m increases. Thus M_1 and F both increase (M_1 much more rapidly), M_2 decreases sharply, and (the linear function) Z_t decreases so slightly as to be nearly independent of m. Figure 3 also shows that the lower limit of m (when $M_1 = 0$) is about 0.003 for both broods: $\hat{\theta}_1 = E_1/N_0 = 0.00333$ (1965 brood) and 0.00316 (1966 brood). The upper limit of m (when $M_2 = 0$) is about 0.068 for the 1965 brood but only about 0.057 for the 1966 brood. These latter values again agree with data in Table 1. Of course, when $M_2 = 0$, $m = E_1/(E_1 + C + E_2)$. This is the highest possible value of m.

Figure 3 emphasizes that a unique set of nominally unbiased estimates would be available if m were estimated independently. It is now evident from Cleaver's (1969) model and Equations 12-15 here that the same applies to hatchery chinook salmon, or indeed to any salmon stock or species with two or more returns when the offshore catch from a group of smolts is known by origin. Thus, for I returns one would use assigned values of m_i ($i = 1, 2 \cdot\cdot I-1$) and solve the extended counterparts of Equations 12-15 to estimate the various parameters (however, this gets to be very complicated to display graphically). Unfortunately, independent estimation of m_1 (m for coho salmon) is not feasible on a practical scale under present management of most ocean fisheries for coho and chinook salmon on the Pacific coast because minimum size limits are imposed.

Before turning to summary estimates with unknown bias, we emphasize that unique estimates could be obtained also if the present data included estimates of the sex ratio of the N_0 smolts and E_2 adults (Example 5 of Paulik and Robson, 1969). Change-in-ratio estimates for hatchery coho salmon are to be recommended highly: not only is the field work relatively inexpensive and straightforward, but these nominally unbiased estimates would provide definitive tests of other methods.

ANALYSES BASED ON CONSIDERATION OF INDEPENDENT ESTIMATES OF LIMITS FOR M_2

It is useful at this stage to note some published values (or derivatives thereof) which may help to 1) delimit from the possibilities shown for M_1 and M_2 in Figure 3 the actual time distribution of natural mortality in 1965-66 brood coho salmon, and 2) justify assumptions leading to unique estimates (other than in Tables 4 and 6) with unknown bias. The following include corrections for marking mortality; data in Table 1 (see footnote 2) and all our estimates are for marked fish.

Source	*Species*	*Value and explanation*
Parker (1962)	All *Oncorhynchus* except *O. masu*	$M_2 \simeq 0.026$/mo, a rough average for all species during offshore life only.
Ricker (1962)	*O. nerka*	M_1(lower) $>$ M_2(upper) $= 0.038$/mo during last 2 yr at sea.

Fredin (1964)	*O. nerka*	M_1(lower) > M_2(upper) = 0.042/mo after the first few months or first year at sea. Value is from Model 1 (constant natural mortality during all of ocean life), averaged for smolts migrating in their third third and fourth years.
Parker (1968)	*O. gorbuscha*	$M_1 \simeq$ 0.781/mo during first 40 days in coastal waters and M_2(upper) = 0.169/mo during last 410 days of ocean life (hence $M_1/M_2 \simeq 4.0$). Reported daily rates are averaged here for the 1961-63 broods and multiplied by 30.

In contrast to the situation for 1965-66 brood coho salmon, offshore fishing had a negligible effect on data from which the foregoing values were derived. Thus Ricker (1962) and Fredin (1964) demonstrated sharp decreases in the total and monthly average rates of natural mortality during all of ocean life as the size of smolts increased; they correctly emphasized that the actual risk of death is much greater during the first part of ocean life when fish are smallest. Their values for M_2(upper)—0.038/mo and 0.042/mo—are compatible with Parker's (1962) value of $M_2 \simeq$ 0.026/mo which excludes mortality on small, juvenile fish before they leave coastal waters. Although Lander (1973) contrasted the assumptions of Ricker's (1962) mortality computation and Model 1 of Fredin (1964), the distinction is mainly academic: natural mortality is the overwhelming agent of removal for salmon smolts and values calculated from a given set of real data differ little between the two models.

Parker's (1968) results appear to be the only ones which determine with reasonable success the real time distribution of natural mortality in salmon from direct marking/recovery at sea. Thus Parker's value of $M_1 \simeq$ 0.781/mo greatly exceeds the highest possible values in Figure 3: M_1(upper) is about 0.50/mo for the 1965 brood and 0.48/mo for the 1966 brood. This is not surprising since relatively higher natural mortality is associated with smaller sockeye salmon smolts as just noted (Ricker, 1962; Fredin, 1964). The pink salmon in Parker's analysis were tiny when marked during their first 40 days at sea—roughly 0.3-8.0 g judging from LeBrasseur and Parker (1964)—compared with average release weights of about 14.6-33.1 g (at different hatcheries) for 1965-66 brood coho salmon. Beyond this initial size difference, Parker's value of $M_1 \simeq$ 0.781/mo is for only the first 40 days at sea, but values of M_1(upper) for the coho data of about 0.50 (1965 brood) and 0.48 (1966 brood) are for the first 6.0 mo after release. With respect to M_2(upper) = 0.169/mo, Parker (1968) emphasized that his reported escapement was considerably low.

The foregoing evidence, although indirect so far as 1965-66 brood coho salmon are concerned, does suggest that $M_1 > M_2$, and further that M_2 is closer to the lower limit ($M_2 = 0$) than to $M_2 = M_1$ (Figure 3). Assuming $M_2 < M_1$, one can choose any value of M_2 in this range to get a reasonable idea of the relative magnitudes of survival during the first 6.0 mo (s_1) and last 12.0 mo (s_2) after smolts were released. Based on the observation that M_2(upper) = 0.038/mo (Ricker, 1962) or 0.042/mo (Fredin, 1964), we chose M_2 = 0.03/mo to illustrate relative magnitudes of s_1 and s_2. Values for M_1 and F were approximated from Figure 3, and values for s_1 and s_2 were calculated from the relations given below.

Relation	*1965 brood*	*1966 brood*
$s_1 = e^{-6.0M_1}$	0.06	0.08
$s_2 = e^{-12.0M_2 - 4.5F}$	.14	.17

To present unique point estimates with unknown bias for all parameters, we applied the limit-mean model; its basic assumption is that s_1 (upper) = s_2 (lower) = s (Lander, 1973). Its possible effect on estimates is discussed in the Appendix, where the scheme for calculating is summarized also.

The resulting estimates for all parameters are in Table 7. The exploitation rate (μ) in offshore fisheries evidently was slightly higher for the 1965 brood (70%) than the 1966 brood (68%). The proportion of smolts recruited to oceanic fishing was slightly lower for the 1965 brood (5%) than the 1966 brood (6%), as noted earlier. The estimates indicate also that slightly more of the surviving smolts matured as jacks in the

TABLE 7.—Estimates of mortality (monthly), maturity, survival, and abundance parameters for 1965-66 brood coho salmon from Columbia River hatcheries—river sections combined.

Parameter	Estimated value	
	1965 brood	1966 brood
m	0.0373	0.0321
M_1	.4029	.3862
M_2	.0644	.0613
F	.3320	.3000
μ	.6969	.6670
N_1/N_0	.0858	.0954
N_r/N_0	.0530	.0602
s_1	.0891	.0985
s_2	.1037	.1243

1965 brood (4% compared with 3%). In general, estimates of all parameters are very similar for both broods. It should be remembered that despite the similarity between broods for all river sections combined, there was considerable variation between sections (Tables 4, 5).

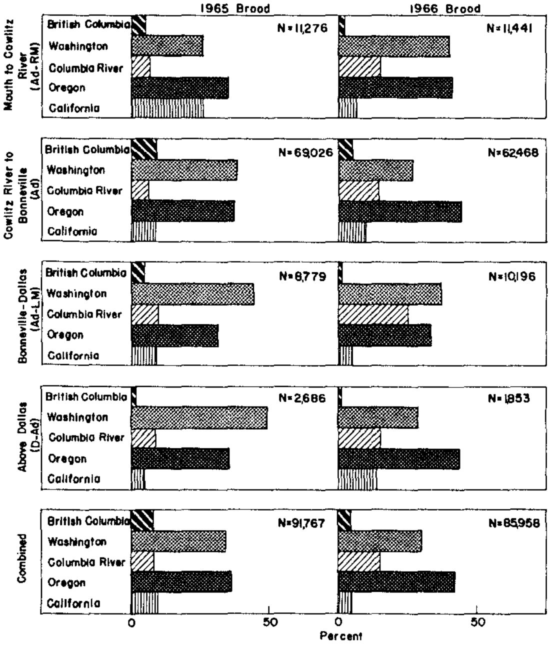

FIGURE 4.—Calculated recoveries (in percent) in various fishing areas of marked 3-yr-old coho salmon from Columbia River hatcheries.

DISTRIBUTION

Distribution by Area

Figure 4 depicts the calculated recoveries of the different groups of marked coho salmon in the different fisheries for both the 1965-66 broods. Because any fish which had a regenerated maxillary mark, or for which the maxillary mark was not observed, would be listed with the adipose only marked fish, in all probability this Ad-only group of recoveries actually includes many fish from the other groups of marks. This also is suggested by the large number of recoveries of Ad-only marks compared with the other groups (see footnote 2).

Despite these difficulties, however, it is possible to compare directly the Ad-LM (Upper River) and Ad-RM (Lower River) recoveries. There appears to be a tendency for a greater percentage of the Lower River marks (Ad-RM) to be recovered in the California troll fishery, indicating a greater tendency to migrate south from the Columbia River; this was particularly evident for the 1965 brood fish. Also, there appears to be a tendency for a greater percentage of the Lower River fish to be caught in the Oregon ocean fisheries compared with the Washington ocean fisheries, whereas the reverse was true for the Upper River (Ad-LM) marks. Again this would be consistent with the possibility that a greater portion of the Lower River fish (Ad-RM) tend to migrate south from the Columbia River compared with the Upper River fish (Ad-LM). As might be expected from the greater exposure to river fishing, a greater percentage of Upper River fish were recovered in the Columbia River fisheries.

The marks from above The Dalles (D-Ad) were not consistent in this respect, although they did show a greater percentage recovery in California fisheries than in British Columbia fisheries. This possibly indicates a greater portion of these fish also migrated south from the Columbia River.

Finally, when the recoveries from all hatcheries are combined, the data indicate that the percentage of these fish caught in the British Columbia and California ocean fisheries is about equal (less than 10%), whereas the percentage recovered in the Oregon ocean fisheries is somewhat greater (from less than 1 to over 12%) than that recovered in the Washington fisheries.

TABLE 8.—Tests of the hypothesis that recoveries of 1965-66 brood coho salmon in ocean troll and sport fisheries are independent of hatcheries of origin. Chi-square was tested at the 95% level.

Fishery	1965 brood			1966 brood		
	LR[1]	UR[2]	Total	LR	UR	Total
Washington:						
Sport	1,206	1,809	3,015	526	482	1,008
Commercial	1,716	2,051	3,767	356	432	788
Total	2,922	3,860	6,782	882	914	1,796
χ^2	—	—	21.06	—	—	9.93
Test result	—	—	Reject	—	—	Reject
Oregon:						
Sport	420	265	685	107	86	193
Commercial	3,564	2,530	6,094	911	622	1,533
Total	3,984	2,795	6,779	1,018	708	1,726
χ^2	—	—	2.04	—	—	1.12
Test result	—	—	Accept	—	—	Accept
California:						
Sport	331	30	361	22	14	36
Commercial	2,617	789	3,406	158	102	260
Total	2,948	819	3,767	180	116	296
χ^2	—	—	42.33	—	—	0.002
Test result	—	—	Reject	—	—	Accept

[1] LR = number of Lower River mark (Ad-RM) recoveries.
[2] UR = number of Upper River mark (Ad-LM) recoveries.

Distribution by Ocean Commercial and Sport Fisheries

It also is possible to compare the recovery of marks from the Lower River (Ad-RM) and the Upper River (Ad-LM) hatcheries in the ocean commercial and sport fisheries for the different states. This is done in Table 8 for both the 1965-66 broods by means of Chi-square tests. The commercial fishery usually operates farther from shore than the sport fishery, so the analysis also may test differences in offshore distribution between these two marks. In Table 8 we see the hypothesis of independence is rejected for the Washington fisheries for both brood years. In other words, the recovery of marks in the Washington commercial and sport fisheries was different for these two groups of marked coho salmon for both brood years. For Oregon, on the other hand, the differences were not significant for either brood year. For California recoveries, the difference in the recoveries between the two marks and two fisheries was significant for the 1965 brood but not for the 1966 brood. As was pointed out earlier, it was these 1965 brood recoveries of Ad-RM marks in California which showed the high percentage recovery in Figure 4. To summarize these analyses, the two marks (Ad-RM; Ad-LM) showed no significant difference in recoveries in the Oregon ocean sport and commercial fisheries, were significantly different for the Washington fisheries, and were significantly different for the 1965 brood for the California fisheries. This suggests a definite differential distribution pattern north of the Columbia for both broods and also a differential distribution pattern south of the Columbia River, at least for the 1965 brood fish.

Distribution by Time

The Upper River (Ad-LM) and Lower River (Ad-RM) mark recoveries also can be examined to see if the data indicate any difference in time of recovery in certain fisheries. In Table 9 are listed the calculated seasonal recoveries (in percent) for selected ports along the Pacific coast. In general, data for most of the ports not listed either showed a similar pattern or had insufficient sampling data for this analysis.

The data listed in Table 9 clearly indicate that there was a definite difference in timing between these two groups of fish for both the British Columbia and Washington recoveries for both brood years, the Upper River fish (Ad-LM) disappearing first from the ocean fisheries. This difference in time of capture also persisted for

TABLE 9.—Calculated recoveries (in percent), by time, of Upper River (UR) and Lower River (LR) marked, 1965-66 brood coho salmon in the various ocean fisheries.

	California				Br. Columbia		Washington				Oregon			
	Fishing period	Ft. Bragg		Fishing period	Area 40		Neah Bay		Westport		Tillamook		Newport	
Brood		UR[1]	LR[2]		UR	LR	UR	LR	UR	LR	UR	LR	UR	LR
1965	Month ending			Two weeks ending										
	30 May	9.8	16.0	15 June	0.3	—	—	—	0.2	—	0.6	0.3	2.1	1.4
	30 June	43.8	29.1	29 June	5.3	1.1	13.0	2.4	12.3	5.8	10.7	4.5	22.5	14.4
	31 July	46.4	42.3	13 July	22.2	3.3	2.9	0.0	5.3	13.1	11.3	7.7	21.1	14.1
	31 Aug.	—	12.0	27 July	5.0	3.3	15.9	4.7	11.9	8.5	56.8	48.7	36.8	23.0
	30 Sept.	—	0.7	10 Aug.	14.9	10.0	11.6	4.7	16.2	6.6	15.8	31.0	17.5	37.4
				24 Aug.	21.5	10.5	14.5	11.8	25.6	9.0	4.8	5.2	—	7.8
				7 Sept.	26.5	44.5	42.0	68.2	23.1	28.2	—	0.6	—	2.0
				21 Sept.	4.3	20.9	—	8.2	5.7	19.7	—	—	—	—
				5 Oct.	—	6.5	—	—	—	9.2	—	—	—	—
Number of fish[3]		153	719		302	449	69	85	438	412	336	310	280	348
1966														
	30 June	19.3	18.9	28 June	13.0	16.2	34.3	10.0	3.6	—	6.1	11.9	27.1	20.1
	31 July	75.4	76.2	12 July	10.4	12.6	11.4	17.5	4.1	9.8	26.3	11.9	30.3	37.7
	31 Aug.	5.3	4.9	26 July	9.1	7.9	0.0	0.0	8.0	3.2	9.5	7.7	13.8	14.2
				9 Aug.	26.0	28.5	0.0	0.0	12.6	13.5	31.3	34.5	16.0	14.7
				23 Aug.	41.6	12.6	17.1	7.5	28.8	29.7	24.6	34.0	8.3	8.3
				6 Sept.	—	14.2	37.1	65.0	28.6	21.6	2.2	—	4.4	5.1
				20 Sept.	—	7.9	—	—	11.3	15.0	—	—	—	—
				4 Oct.	—	—	—	—	3.0	7.3	—	—	—	—
Number of fish[3]		285	391		77	253	35	40	364	468	179	194	587	1,042

---

[1] UR = Upper River mark (Ad-LM) recoveries.
[2] LR = Lower River mark (Ad-RM) recoveries.
[3] Calculated number of marked fish recovered during the fishing season.

recoveries in the Oregon and California ocean fisheries for the 1965 brood but was not evident for the 1966 brood data. We also can look at recoveries in the Zone 1 (lowest) fishery in the Columbia River (Table 10). For both brood years the Upper River marks (Ad-LM) peaked earlier and disappeared first from the catches when compared with the Lower River marks (Ad-RM). Of course, in view of the longer migration up the Columbia River for the Upper River fish, this phenomenon might be expected.

Table 10.—Calculated recoveries (in percent) by time of marked Upper River and Lower River coho salmon in the Columbia River Zone 1[1] fishery.

Brood	Fishing record	Upper River	Lower River
	Week ending		
1965	8/24	13.8	2.1
	8/30	—	—
	9/7	68.6	27.7
	9/14	6.3	4.0
	9/21	11.4	38.5
	9/28	0.0	0.0
	10/5	0.0	27.7
	10/12	—	—
Calculated number of fish		414	325
1966	8/23	—	—
	8/29	0.0	0.7
	9/6	—	—
	9/13	—	—
	9/20	74.5	58.1
	9/27	25.5	30.7
	10/4	0.0	10.5
	10/11	0.0	0.0
Calculated number of fish		545	602

[1] Zone 1 extends from the mouth of the Columbia River to the Elokomin River (see Figure 1).

LITERATURE CITED

Cleaver, F. C.
1969. Effects of ocean fishing on 1961-brood fall chinook salmon from Columbia River hatcheries. Fish Comm. Oreg., Res. Rep. 1(1), 76 p.

Fredin, R. A.
1964. Ocean mortality and maturity schedules of Karluk River sockeye salmon and some comparisons of marine growth and mortality rates. U.S. Fish. Wildl. Serv., Fish. Bull. 63:551-574.

Henry, K. A.
1971. Estimates of maturation and ocean mortality for Columbia River hatchery fall chinook salmon and the effect of no ocean fishing on yield. Fish. Comm. Oreg., Res. Rep. 3:13-27.

Lander, R. H.
1973. Problem of bias in models to approximate ocean mortality, maturity, and abundance schedules of salmon from known smolts and returns. Fish. Bull., U.S. 71:513-525.

Merrell, T. R., Jr., M. D. Collins, and J. W. Greenough.
1971. An estimate of mortality of chinook salmon in the Columbia River near Bonneville Dam during the summer run of 1955. U.S. Fish Wildl. Serv., Fish. Bull. 68:461-492.

Parker, R. R.
1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. 19:561-589.
1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757-794.

Paulik, G. J., and D. S. Robson.
1969. Statistical calculations for change-in-ratio estimators of population parameters. J. Wildl. Manage. 33:1-27.

Ricker, W. E.
1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. J. Fish. Res. Board Can. 19:531-560.

APPENDIX

Derivations of Text Equations 12-15

As pointed out in the text,

The probability of E_1: $\theta_1 = m\,e^{-6M_1}$. (1)

The probability of C: $\theta_2 =$

$$(1 - m)e^{-6M_1}e^{-7.5M_2}\left(\frac{F}{F + M_2}\right)e^{-4.5(F + M_2)}. \quad (2)$$

The probability of E_2: $\theta_3 =$

$$(1 - M)e^{-6M_1}e^{-7.5M_2}\,e^{-4.5\,(F + M_2)} \quad (3)$$

and maximum likelihood estimators of the θ_i are:

$$\hat{\theta}_1 = \frac{E_1}{N_0} \text{ or } \hat{\theta}_1 = m\,e^{-6M_1} \text{ from (1).} \quad (4)$$

$$\hat{\theta}_2 = C/N_0 \text{ or } \hat{\theta}_2 = (1 - m)\,e^{-6M_1}e^{-7.5M_2}\left(\frac{F}{F + M_2}\right)e^{-4.5\,(F + M_2)} \text{ from (2).} \quad (5)$$

$$\hat{\theta}_3 = E_2/N_0 \text{ or } \hat{\theta}_3 = (1 - m)e^{-6M_1}e^{-7.5M_2}e^{-4.5\,(F + M_2)} \text{ from (3).} \quad (6)$$

Then for $m = m$ (fixed) ($\hat{\theta}_1 < m < 1$), text Equation 12, by rearranging Equation 4 and taking natural logarithms we obtain

$$-\frac{1}{6}\ln\left(\frac{\hat{\theta}_1}{m}\right) = M_1 \quad \text{(text Equation 13).}$$

Then, Equation 6 can be rewritten as

$$\frac{\hat{\theta}_3}{(1 - m)}\,e^{6M_1} = e^{-7.5M_2}e^{-4.5\,(F + M_2)}$$

$$= e^{-7.5M_2 - 4.5F - 4.5F - 4.5M_2}$$

$$= e^{-(4.5F + 12M_2)}$$

$$= k_2.$$

The natural logarithm of k_2

$$\ln k_2 = -(4.5F + 12M_2) \quad (7)$$

which can be solved for F as follows:

$$-4.5F = \ln k_2 + 12M_2$$

$$F = -\left[\frac{\ln k_2 + 12M_2}{4.5}\right] \text{(text Equation 15).} \quad (8)$$

Equation 5 can be written

$$\frac{\hat{\theta}_2}{(1 - M)}\,e^{6M_1} = e^{-7.5M_2}\left(\frac{F}{F + M_2}\right)\left(1 - e^{-4.5\,(F + M_2)}\right) = k_1 \quad (9)$$

and since

$$e^{-4.5\,(F + M_2)}$$

$$= e^{-4.5F - 12M_2 + 7.5M_2}$$

$$= e^{-(4.5F + 12M_2) + 7.5M_2}$$

$$= e^{\ln k_2 + 7.5M_2} \quad \text{(from Equation 7)}$$

and

$$\left(\frac{F}{F + M_2}\right) = \frac{-\left(\frac{\ln k_2 + 12M_2}{4.5}\right)}{-\left(\frac{\ln k_2 + 12M_2}{4.5}\right) + M_2} \quad \text{(from Equation 8)}$$

$$= \frac{-(\ln k_2 + 12M_2)}{-(\ln k_2 + 12M_2) + 4.5M_2}$$

$$= \frac{\ln k_2 + 12M_2}{\ln k_2 + 12M_2 - 4.5M_2}$$

$$= \frac{\ln k_2 + 12M_2}{\ln k_2 + 7.5M_2}$$

then Equation 9 becomes

$$\frac{\theta_2}{(1 - m)} e^{6M_1} = \left[\frac{\ln k_2 + 12M_2}{\ln k_2 + 7.5M_2}\right] e^{-7.5M_2}$$

$$1 - e^{(\ln k_2 + 7.5M_2)} = k_1$$

(text Equation 14).

Failure of the Basic Assumption in the Limit-Mean Model

The basic assumption of the limit-mean model is that survivial (s_1) from the time N_0 smolts start seaward until E_1 jacks return from the ocean does not exceed survival (s_2) thereafter until E_2 adults return. For sockeye and pink salmon not fished in offshore waters, the text discusses certain evidence (Ricker, 1962; Fredin, 1964; Parker, 1962, 1968) indicating almost incontrovertibly that $M_1 > M_2$, i.e., the monthly natural mortality rate during the "early" part of ocean life exceeds the rate thereafter. The same probably applies to coho salmon and to all other anadromous salmonids. Coho salmon smolts are about the same size as most sockeye salmon smolts when they enter the sea; on general grounds we would expect relatively little difference, on the basis of smolt size alone, in the values of M_1 and M_2 between these two species for a common time base. (By contrast, text Figure 3 shows for coho salmon that monthly M_1, as averaged for the first 6.0 mo after release, is much less than monthly $M_1 \simeq 0.781$/mo for tiny pink salmon during only the first 40 days at sea.) Fredin (1964, Table 2) reported about 13-15 mo as the time between the outmigration of sockeye salmon smolts and the first return. For our data, coho salmon first returned as jacks after only 6 mo; furthermore, those that stayed at sea were fished quite heavily in offshore waters but the sockeye salmon in Fredin's analysis suffered natural mortality alone until they entered the coastal fishery. Even if $M_1 > M_2$ in hatchery coho salmon, the shorter time for s_1 and the effect of oceanic fishing on s_2 might conceivably result in $s_1 > s_2$—instead of $s_1 \leq s_2$ as assumed in the limit-mean model.

Bias in estimates from the limit-mean model (text Table 7), or in any model giving a single set of estimates where in fact only various possible sets can be determined (as in text Figure 3), must be evaluated with hypothetical data. To get a fairly realistic notion of how the assumption, $s_1 \leq s_2$, might have affected the estimates in text Table 7, we 1) used the same time intervals as in the text, 2) chose hypothetical values of m, s_2, and M_2 (hence F) which were quite close to the estimates, then 3) varied s_1 so that $s_1 = 0.5\ s_2$, $1.0\ s_2$, and $1.5\ s_2$. Values for the data as observed in practice (E_1/N_0, C/N_0, and E_2/N_0) were calculated from relations given in the text.

Estimates of all parameters in Appendix Table 1 contain less relative bias in Example 2, where $s_1 = s_2$ ($= 0.10$), than in Example 1 ($s_1 = 0.5\ s_2$) or Example 3 ($s_1 = 1.5\ s_2$). In Example 3, estimates of m and s_2 are too large and the estimate of s_1 is too small. The converse happens in Example 1. The direction of bias in these three estimates is the same in Examples 1 and 2. It is interesting to note in all examples the decrease in relative bias (estimate minus parameter value/parameter value) as one proceeds (in the life of a cohort) from $\hat{N}_1/N_0$ to $\hat{N}_r/N_0$:

	Relative bias (%) in abundance estimate	
Example	$\hat{N}_1/N_0$	$\hat{N}_r/N_0$
1	+29	+6
2	- 4	-2
3	-18	-4

Applicable values in Appendix Table 1 were rounded to three places before calculating the above percentages.

This result is perhaps not surprising because 1) N_r/N_0 is actually the target parameter in estimation by the limit-mean model when the offshore catch is known and 2) the lower and upper limits for N_r/N_0 were found during calculation to bracket the true values quite closely in all three examples despite the fact

APPENDIX TABLE 1.—Comparison of "actual" values, as calculated from assigned input parameters, with estimates from the limit-mean model. For m, s_2, and M_2 (hence F) fixed near the estimates for 1965-66 brood coho in Table 7 of the text, the three hypothetical examples show how the basic assumption of $s_1 \leqq s_2$, which Example 3 violates, might have biased the estimates.

Input parameters with fixed values in all examples	Items with values that vary between examples		Example 1		Example 2		Example 3	
	Data	Parameter	Actual	Estimated	Actual	Estimated	Actual	Estimated
m = 0.0350000	—	—	—	0.027	—	0.036	—	0.042
s_2 = .1000000	—	—	—	.077	—	.104	—	.122
M_2 = .0600000	—	—	—	.086	—	.056	—	.040
F = .3516856	—	—	—	.339	—	.354	—	.362
—	E_1/N_0	—	0.001750	—	0.003500	—	0.005250	—
—	C/N_0	—	.022176	—	.044352	—	.066528	—
—	E_2/N_0	—	.004825	—	.009650	—	.014475	—
—	—	s_1	.0500000	.064	.1000000	.096	.1500000	.124
—	—	M_1	.4992887	.458	.3837642	.390	.3161867	.348
—	—	N_1/N_0	.0482500	.062	.0965000	.093	.1447500	.119
—	—	N_r/N_0	.0307656	.033	.0615312	.061	.0922967	.088

$s_1 \neq s_2$ in Examples 1 and 3. The latter comparison and estimates are summarized below:

Example	*Lower limit*	N_r/N_0	*Upper limit*	N_r/N_0
1	0.0270	0.0308	0.0394	0.033
2	.0540	.0615	.0689	.061
3	.0810	.0923	.0962	.088

Noting finally that absolute bias (estimate minus parameter value) is not excessive for any estimate or example in Appendix Table 1, the foregoing analysis leads us to believe that estimates in text Table 7 of the text are quite close to reality for 1965-66 brood coho salmon from Columbia River hatcheries (data from all river sections combined).

Procedure for Calculating Estimates

The estimating scheme is described elsewhere (Lander, 1973). That account may not be available to the reader; furthermore, it discusses also the situations where offshore catch is not known and an offshore fishery does not occur, and therefore is not a compact summary. Appendix Table 2 briefly reviews the assumptions and calculating methods for the case where offshore catch is known by origin.

APPENDIX TABLE 2.—Assumptions and calculating procedure for the limit-mean model when the offshore catch is known by origin.

Known values			Assumptions and a calculating sequence
N_0	=	number of smolts	Noting $E_2 = N_0 s_1\ (1 - m)s_2 = N_0 s_1 s_2 - E_1 s_2$, *assume* s_1(upper) = s_2(lower) = s. Solve $s^2 - (E_1/N_0)s - (E_2/N_0) = 0$ and find $s + (E_1/N_0) = N_1$(upper). Evaluate X in $(C + E_2)/N_1$ (upper) = $e^{-(t_2 + t_3)X}$, then note and find (N_r/N_0)(upper) = (N_1/N_0)(upper)$e^{-t_2 X}$. *Assume* $M_2 = 0$ during t_3 and find (N_r/N_0)(lower) = $(C + E_2)/N_0$. Find $(\hat{N}_r/N_0)$ = [(N_r/N_0)(upper) X (N_r/N_0)(lower)]$^{1/2}$ as the geometric mean of limits used here or take another abitrary and intermediate value as the estimate. Find $\hat{\mu} = C/\hat{N}_r$ and evaluate $(\widehat{F + M_2})$ in $E_2/\hat{N}_r = e^{-t_3\,(\widehat{F + M_2})}$. Rearranging the general definition of μ, find $\hat{F} = \hat{\mu}(\widehat{F + M_2})/[1 - e^{-t_3\,(\widehat{F + M_2})}]$, then $\hat{M}_2 = (\widehat{F + M_2}) - \hat{F}$. Find $\hat{Z}_2 = \hat{M}_2 + [t_2/(t_2 + t_3)]\hat{F}$ and $\hat{N}_1/N_0 = (E_2/N_0)/e^{-t_2 + t_3)\hat{Z}_2} = (\hat{N}_r/N_0)/e^{-t_2\hat{M}_2}$. Find $\hat{s}_2 = E_2/\hat{N}_1$, $\hat{m} = 1/(1 + E_2/E_1\hat{s}_2)$, and $\hat{s}_1 = (E_1/N_0)/\hat{m}$. Evaluate $\hat{M}_1$ in $\hat{s}_1 = e^{-t_1\hat{M}_1}$. If desired, $\hat{M}_r$, $\hat{M}_T$, and $\hat{Z}_T$ can be found from relations noted near Table 7 of the text.
C	=	number in offshore catch	
E_i	=	number of jacks (i = 1) and adults (i = 2) in inshore and river fishery plus escapement to spawning site.	
t_1	=	months between outmigration of smolts and return of jacks.	
t_2	=	months between return of jacks and start of offshore fishing.	
t_3	=	months between start of offshore fishing and return of adults.	