

ESTIMATING NATURAL AND FISHING MORTALITIES OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE OCEAN, BASED ON RECOVERIES OF MARKED FISH

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ABSTRACT

In this paper I demonstrate the method of calculating estimates of fishing mortality (F) and natural mortality (M) occurring in the ocean for 1961 and 1962 brood Columbia River hatchery fall chinook salmon, *Oncorhynchus tshawytscha*, based on assumed values of the proportion of fish that mature annually (m) and on recoveries of marked fish.

The advantages of this method over the method of assuming fixed natural mortality rates and back calculating estimates are discussed. It was possible to develop estimates of 1962 Spring Creek data up to the fourth year of life and to compare these estimates with values for the 1961 brood whereas no estimates had been possible with the back calculation method. Thus, estimates of M_1 are higher for the 1962 brood; estimates of M_2 are very similar for the two broods and the estimates of M_3 are slightly higher for the 1962 brood. A major difference between the two methods is that natural mortality was assumed to be constant for the back calculation method whereas estimates of natural mortality were obtained separately each year using assumed proportions maturing. Thus, for the 1962 brood general marked fish, an $M = 0.60$ was used in the back calculation method while estimates of $M_1 = 5.814$, $M_2 = 0.510$, $M_3 = 0.653$, and $M_4 = 0.727$ were obtained by assuming varying proportions maturing.

A series of graphs are developed that permit a quick analysis of any combination of proportions of fish maturing, fishing mortality, and natural mortality and which clearly depict the relationship between these various factors.

Cleaver (1969) developed a method for estimating fishing mortalities and percentages of maturing fish for each age group of fall chinook salmon, *Oncorhynchus tshawytscha*,² from the Columbia River using selected values of natural mortality. Cleaver's estimates were based on data obtained from a cooperative marking experiment by fishery agencies along the Pacific Coast. This experiment started in 1962 and was designed to measure the contribution of fall chinook salmon from Columbia River hatcheries to the various fisheries. Cleaver's analysis was specifically directed towards returns for the 1961 brood year. The procedure used catches and escapements, by age, along with selected natural mortality values to back calculate, from year 5 to year 2, annual estimates of fishing mortality and proportion of fish that mature annually.

Henry (1971) utilized Cleaver's method to obtain similar estimates for the 1962 brood releases of Columbia River hatchery fall chinook salmon.

Lander and Henry (1973), in analyzing returns from marking experiments for Columbia River coho salmon, *O. kisutch*, pointed out two methods for estimating the various pertinent parameters mentioned above from salmon mark/recovery data: 1) assume selected values for M (natural mortality) and 2) assume selected values for m (proportion maturing).

Although both methods gave identical estimates of the parameters, their concepts differ. In selecting a value for natural mortality, as was done by Cleaver (1969) and Henry (1971), one has to start at the end of the life cycle and work backwards since the calculated parameters are sequentially dependent in that manner (Cleaver and Henry also assumed a constant M for all ages to simplify computations); by selecting values for the proportion of fish that mature annually, one begins at the younger age-groups and calculates the various parameters sequentially towards the end of the life cycle. This method more closely parallels the actual life history of the salmon. Furthermore, today's salmon management schemes are directed at preserving existing runs and their fisheries, i.e., changing diets, releasing fish at different times and at different sizes, transporting fish to avoid

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²Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall depending on the time of year that the adults enter the river to spawn.

excessive mortalities (related to passage at dams and unfavorable environmental conditions caused by dams and reservoirs), or transporting fish to make a more direct input to a certain fishery. All of these efforts may affect the maturity, growth, fishing mortality, and the natural mortality for a particular stock of fish. In this paper, I describe a method by which such changes can be accounted for in the estimating procedure as soon as they are determined. Thus, the present method reduces the need for assumptions regarding constancy of natural mortality in salmon stocks, and the results may be more realistic, particularly if the maturity values selected are reasonable.

In discussing their method of selecting values for the proportion of fish that mature annually and then calculating the remaining parameters for coho salmon, Lander and Henry (1973) pointed out that the procedure also could be applied to chinook salmon, although they also noted that "... this gets to be very complicated to display graphically ...", since coho salmon have a much simpler life history than fall chinook salmon— m (proportion of fish that mature annually), M (natural mortality), and F (fishing mortality) need to be estimated for 1 yr only for each brood of coho salmon, but these parameters need to be estimated for three separate years for each brood of chinook salmon. Furthermore, the estimated values from this method are quite complicated to apply to chinook salmon. In fact for each m_1 (the subscript represents the different years of life covered by the calculations) value selected, there is a series of possible m_2 values, and for each of the possible m_2 values there is again a series of possible m_3 values. Thus, if n separate calculations are made for each m_i , and there are three of them, as for the chinook

salmon, the total calculations potentially needed for a brood year would be $n_1 + n_2^2 + n_3^3$.

METHOD OF ESTIMATING PARAMETERS

In this paper I demonstrate the method of calculating estimates of fishing mortality (F) and natural mortality (M) based on assumed values of the proportion of fish that mature annually (m) for the 1961 and 1962 brood Columbia River fall chinook salmon. In particular, I compare data for the 1961 and 1962 broods of Spring Creek fish.

To aid in understanding the various parameters I estimate, in Figure 1 I have portrayed graphically certain features of the fall chinook salmon's life history, particularly the various parameters for the period from the release of the fish as smolts until final return to the Columbia River as adults—approximately 54 mo.

Figure 1 shows that as a result of this series of events, I end up with eight items of observed data: 1) number of smolts released (N_0); 2) number maturing as 2-yr-olds (E_1); 3) number caught by the ocean troll and sport fisheries as 3-yr-olds (C_1); 4) number maturing and returning to the river as 3-yr-olds (E_2); 5) number caught by the ocean troll and sport fisheries as 4-yr-olds (C_2); 6) number maturing and returning to the river as 4-yr-olds (E_3); 7) number caught by the ocean troll and sport fisheries as 5-yr-olds (C_3); and 8) number maturing and returning to the river as 5-yr-old fish (E_4). From these eight known values I want to estimate: 1) monthly fishing mortality rate on 3-, 4-, and 5-yr-old fish (F_1, F_2 , and F_3 , respectively) over the last 6-mo period of each year; 2) monthly natural

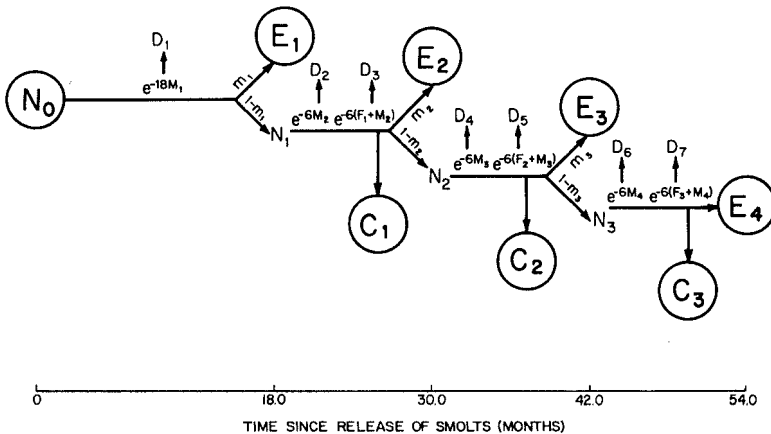


FIGURE 1.—Diagram depicting the life history of Columbia River fall chinook salmon for the period from release as smolts until their return to the Columbia River as adults—approximately 54 mo. Circled items indicate observed data. See text for identification of lettered symbols.

TABLE 1.—Estimated total recoveries of marked Columbia River hatchery fall chinook salmon of the 1961-62 broods.

	1962 Brood			1961 Brood		
	General mark	Spring Creek	Kalama	General mark	Spring Creek	Kalama
E_1	94	18	7	272	68	0
C_1	3,565	376	293	10,774	2,511	696
E_2	1,597	321	29	4,451	934	51
C_2	1,416	150	190	3,373	367	761
E_3	936	120	84	4,849	833	575
C_3	126	14	31	442	5	115
E_4	45	0	15	280	20	160
N_0	5,249,079	866,892	437,669	5,446,439	1,133,019	475,964

mortality rate for the 18-mo period from release as smolts until the mature 2-yr-old fish return to the river (M_1); 3) monthly natural mortality rates for each year as 3-, 4-, and 5-yr-old fish (M_2 , M_3 , and M_4 , respectively); and 4) proportion maturing as 2-, 3-, and 4-yr-old fish (m_1 , m_2 , and m_3 , respectively). A few of these fish are caught as 2-yr olds; however, to avoid further complicating the analyses I have included these in the estimate of M_1 for the first 18 mo at sea. The number of chinooks remaining at sea at the start of each year (N_1 , N_2 , and N_3) also can be calculated, but since this had already been done for certain parameters by Henry (1971), the calculations will not be repeated here. The D_i 's shown represent the number of fish dying naturally. Thus, the entire initial

group of smolts (N_0) is either caught (C), escapes into the river (E), or dies naturally (D), by the time $i = 7$. The fishing season runs generally from mid-April to mid-October.

Mark recovery data used in this paper are listed in Table 1. Catches of marked fish are estimates based on sampling (see Worlund et al. 1969). Each escapement is the total number of fish returning to the river and includes the river catch and returns to the hatchery for a given mark.

To expand the analysis used by Lander and Henry (1973) from coho salmon to chinook salmon, the events in Figure 1 can be depicted by a multinomial model with N_0 smolts falling into the following seven observed categories with certain probabilities O_i ($i = 1-8$) as follows:

Probabilities of

$$E_1 = \theta_1 = m_1 e^{-18M_1}. \quad (1)$$

$$C_1 = \theta_1 = (1-m_1)e^{-18M_1}e^{-6M_2} \frac{F_1}{F_1+M_2} (1-e^{-6(F_1+M_2)}). \quad (2)$$

$$E_2 = \theta_3 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-(F_1+M_2)}m_2. \quad (3)$$

$$C_2 = \theta_4 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3} \frac{F_2}{F_2+M_3} (1-e^{-6(F_2+M_3)}). \quad (4)$$

$$E_3 = \theta_5 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}m_3. \quad (5)$$

$$C_3 = \theta_6 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4} \frac{F_3}{F_3+M_4} (1-e^{-6(F_3+M_4)}). \quad (6)$$

$$E_4 = \theta_7 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}e^{-6(F_3+M_4)}. \quad (7)$$

$$D = \theta_8 = 1 - \theta_1 - \theta_2 - \theta_3 - \theta_4 - \theta_5 - \theta_6 - \theta_7$$

where $D = D_1 + D_2 + D_3 + D_4 + D_5 + D_6 + D_7 =$ Total fish dying naturally. (8)

The maximum likelihood estimators of the θ_i are:

$$\hat{\theta}_1 = E_1/N_0 \tag{9}$$

$$\hat{\theta}_2 = C_1/N_0 \tag{10}$$

$$\hat{\theta}_3 = E_2/N_0 \tag{11}$$

$$\hat{\theta}_4 = C_2/N_0 \tag{12}$$

$$\hat{\theta}_5 = E_3/N_0 \tag{13}$$

$$\hat{\theta}_6 = C_3/N_0 \tag{14}$$

$$\hat{\theta}_7 = E_4/N_0 \tag{15}$$

$$\hat{\theta}_8 = 1 - \theta_1 - \theta_2 - \theta_3 - \theta_4 - \theta_5 - \theta_6 - \theta_7. \tag{16}$$

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, θ_i (Graybill 1961). Beyond that, however, there exists no unique transformation, or function, to obtain maximum likelihood estimates of $m_1, m_2, m_3, F_1, F_2, F_3, M_1, M_2, M_3,$ and M_4 . Any given set of observed data can generate a variety of combinations of parameter estimates.

Since no unique solution exists, the only practical solution is to assume values for one of the unknown parameters and solve the equations for the remaining parameters. Thus Cleaver (1969) and Henry (1971) assumed values for M_i (natural mortality) for hatchery chinook salmon and calculated values for the remaining parameters. However, they assumed M to be constant (M_1) throughout the life of the salmon to simplify computations. Lander and Henry (1973), on the other hand, assumed values for m (proportion of fish that mature annually) for coho salmon and then calculated the remaining parameters.

Assuming fixed values for the proportion of fish that mature annually (m_i) permits a unique solution to Equations (1)-(8), combined with Equations (9)-(16), so that with:

$$m_1 = m_1 \text{ (fixed)} (\hat{\theta}_1 < m_1 < 1). \tag{17}$$

$$m_2 = m_2 \text{ (fixed)} (\hat{\theta}_3 < m_2 < 1). \tag{18}$$

$$m_3 = m_3 \text{ (fixed)} (\hat{\theta}_5 < m_3 < 1). \tag{19}$$

$$M_1 = -\frac{1}{18} \ln \frac{\hat{\theta}_1}{m_1}. \tag{20}$$

$$\frac{\ln k_2 + 12M_2}{\ln k_2 + 6M_2} (1 - e^{\ln k_2 + 6M_2}) e^{-6M_2} = k_1 \tag{21}$$

$$\text{where } k_1 = \frac{\hat{\theta}_2}{1 - m_1} e^{18M_1}$$

$$k_2 = \frac{\hat{\theta}_3}{(1 - m_1)m_2} e^{18M_1}$$

$$F_1 = -\frac{\ln k_2 + 12M_2}{6}. \tag{22}$$

$$k_2 e^{-6M_3} \frac{\ln k_4 - \ln k_2 + 12M_3}{\ln k_4 - \ln k_2 + 6M_3}$$

$$(1 - e^{\ln k_4 - \ln k_2 + 6M_3}) = k_3 \tag{23}$$

$$\text{where } k_3 = \frac{\hat{\theta}_4}{(1 - m_1)(1 - m_2)} e^{18M_1}$$

$$k_4 = \frac{\hat{\theta}_5}{(1 - m_1)(1 - m_2)m_3} e^{18M_1}.$$

$$F_2 = -\frac{\ln k_4 - \ln k_2 + 12M_3}{6}. \tag{24}$$

$$k_4 e^{-6M_4} \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 6M_4}$$

$$(1 - e^{\ln k_6 - \ln k_4 + 6M_4}) = k_5 \tag{25}$$

$$\text{where } k_5 = \frac{\hat{\theta}_6}{(1 - m_1)(1 - m_2)(1 - m_3)} e^{18M_1}$$

$$k_6 = \frac{\hat{\theta}_7}{(1 - m_1)(1 - m_2)(1 - m_3)} e^{18M_1}.$$

$$F_3 = -\frac{\ln k_6 - \ln k_4 + 12M_4}{6}. \tag{26}$$

The derivations of Equations (17)-(26) are verified in the Appendix. For a particular value of m_1 (Equation (17)), one solves Equation (20) explicitly for M_1 . Then using these values of m_1 and M_1 plus a selected value for m_2 in Equation (18), M_2 in Equation (21) is found by iteration. Then F_1 is computed from Equation (22). Next, for a particular value of m_3 in Equation (19) plus the other values already determined, M_3 in Equation

(23) is found by iteration, and F_2 is calculated from Equation (24). Finally, M_4 in Equation (25) is found by iteration and F_3 is calculated from Equation (26).

In developing the computer program to do the above computations, I assigned a beginning value of 0.001 to m_1 and then computed the smallest m_2 possible that would give me nonnegative values for all the M 's and F 's. For these particular values of m_1 and m_2 , I then incremented m_3 over a range of values as long as $m_3 < 1$ or the M_3, M_4, F_2 , and F_3 values were nonnegative. The program would then go back and increment m_2 and compute another series of m_3 values and dependent parameters. When m_2 was incremented to a level where $m_2 = 1$ or that would no longer give positive values for either M_3, M_4, F_2 , or F_3 , the program would increment m_1 and the process would begin again. A sample of the printout for selected values is shown in Table 2.

COMPARISON OF TWO METHODS

To assist in comparing the results from: 1) assuming a given value for M_i (natural mortality) or 2) assuming given values for each m_i (proportion of fish that mature each year), I have listed in Table 3 the results for the 1962 brood data for the general marked fish based on assuming a given m . (The R_i shown in the table are equivalent to the N_i discussed in this paper.) One difficulty in making these comparisons is that the results from the two methods appear in quite different form. In Table 3, there are six lines of estimated values for six different levels of M . On the other hand, by assuming fixed values of m_i for the same data for the fish in the general mark category, the complete printout of results has a total of 48 groups of data, similar to the selected 10 groups shown in Table 2. Of course, the number of groups of data by the latter method is dependent on just how the m_i 's are incremented.

One obvious difference in the two sets of results is that Table 3 (assuming fixed M) was computed using a single constant value for the M_i , whereas Table 2 (assuming fixed m_i) had separate estimates for each M_i . Although an exact comparison of the results is not possible since I did not use exactly the same m_i as shown in Table 3, many of my results are close enough to make useful comparisons. For example, for $M = 0.60$ in Table 3, I calculated $F_3 = 1.275, F_2 = 0.698, F_1 = 0.410, m_3 = 0.761, m_2 = 0.262$ and $m_1 = 0.006$. From Table 2 we can select values of m_i that are fairly compar-

able, i.e., $m_1 = 0.006, m_2 = 0.256, m_3 = 0.756$, which gives $F_1 = 0.405, F_2 = 0.669 (0.11143 \times 6), F_3 = 1.177 (0.19614 \times 6)$ (F 's are summed over 6 mo).

The major difference between the two sets of results is the natural mortality estimates with $M_1 = 5.814, M_2 = 0.510, M_3 = 0.653$, and $M_4 = 0.727$ (M_1 is summed over 18 mo, M_{2-4} summed over 12 mo) from my calculations using estimates for the proportion of fish that mature annually compared with the $M = 0.60$ in Table 3. The comparatively large natural mortality in the first 18 mo of existence is not too surprising; however, the increasing values for M from M_2 to M_4 do not seem reasonable. Since the natural mortality values listed include the loss of "shakers" (fish released by fishermen because they are too small or out of season), one would expect the M_2 value to be largest because this is the time these fish would be most vulnerable to shaker losses. Estimates of shaker mortality have ranged from 15 to 45% (Wright³).

What these increasing estimates of M_i indicate is that the m_i 's selected in this comparison are not realistic— m_i values for which the M_i 's are at least equal, or even decreasing with increased age might be better. Although the relation shown between these values will vary depending on the value of m_2 (the M_3 value computed for a given m_3 value decreases as m_2 increases), at a certain value of m_3 or above, $M_4 \leq M_3$.

The relationship between the various parameters computed are shown more clearly in Figures 2-5 for the 1961 brood Spring Creek data. Thus, in Figure 2 is shown the relation between m_1 and M_1 . As m_1 increases, M_1 also increases but at a diminishing rate. In Figure 3 is depicted the relation between F_1 and F_2 and m_1, m_2 , and m_3 . F_1 is affected by both the m_1 and m_2 values selected, whereas F_2 reacts to both the m_2 and m_3 values chosen. Both F_1 and F_2 increase as m_2 increases for a particular value of m_1 or m_3 . Also, for a given value of m_2 , both F_1 and F_2 increase with increasing m_1 and m_3 values, respectively. In Figure 4 is shown the relation between M_2 and M_3 for selected values of m_1, m_2 , and m_3 . With increasing m_2, M_2 increases but M_3 decreases. For a given m_2, M_3 increases with increasing m_3 , and M_2 decreases with increasing m_1 . Finally, in Figure 5 is shown

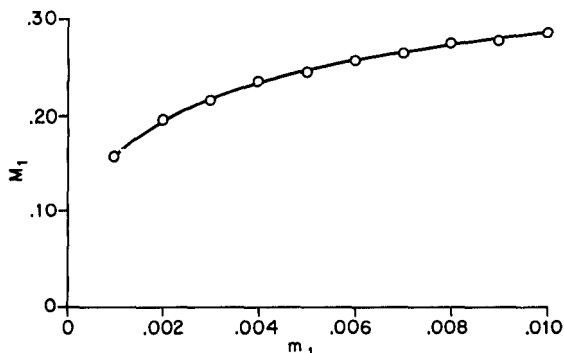
³Wright, S. 1970. A review of the subject of hooking mortalities in Pacific salmon. Wash. Dep. Fish., Manage. Res. Div., 38 p. (Report, prepared for the Salmon Research Staff of the Pacific Marine Fisheries Commission.)

TABLE 2.—Partial computer output for program designed to calculate fishing mortalities (F) and natural mortalities (M) for selected values of proportions of fish maturing (m)—1962 brood general marked Columbia River hatchery fall chinook salmon.

m_3	M_3	F_2	M_4	F_3	m_3	M_3	F_2	M_4	F_3
$m_1 = 0.001000 M_1 = 0.22347 m_2 = 0.20999 M_2 = 0.01389 F_1 = 0.00735$					$m_1 = 0.003000 M_1 = 0.28450 m_2 = 0.106000 M_2 = 0.04519 F_1 = 0.03113$				
0.016000	0.01819	0.00378	0.57439	0.04353	0.121000	0.03339	0.02562	0.37489	0.08652
0.066000	0.13289	0.01056	0.43839	0.07066	0.171000	0.05879	0.03247	0.33569	0.09751
0.116000	0.17739	0.01555	0.37949	0.08530	0.221000	0.07709	0.03862	0.30449	0.10680
0.166000	0.20509	0.01988	0.33919	0.09646	0.271000	0.09119	0.04441	0.27779	0.11515
0.216000	0.22509	0.02376	0.30739	0.10586	0.321000	0.10269	0.04963	0.25389	0.12288
0.266000	0.24079	0.02706	0.28029	0.11439	0.371000	0.11229	0.05456	0.23169	0.13041
0.316000	0.25349	0.03037	0.25619	0.12212	0.421000	0.12059	0.05903	0.21059	0.13773
0.366000	0.26429	0.03325	0.23389	0.12959	0.471000	0.12769	0.06353	0.18999	0.14518
0.416000	0.27349	0.03620	0.21269	0.13696	0.521000	0.13409	0.06755	0.16959	0.15261
0.466000	0.28169	0.03871	0.19209	0.14432	0.571000	0.13969	0.07162	0.14879	0.16057
0.516000	0.28889	0.04130	0.17159	0.15195	0.621000	0.14479	0.07541	0.12729	0.16892
0.566000	0.29539	0.04371	0.15089	0.15976	0.671000	0.14939	0.07912	0.10449	0.17804
0.616000	0.30129	0.04602	0.12949	0.16805	0.721000	0.15369	0.08250	0.07969	0.18818
0.666000	0.30659	0.04843	0.10689	0.17700	0.771000	0.15759	0.08587	0.05179	0.19989
0.716000	0.31159	0.05050	0.08229	0.18710	0.821000	0.16119	0.08915	0.01889	0.21416
0.766000	0.31619	0.05255	0.05479	0.19858	0.871000	0.16449	0.09240	0.00000	0.21416
0.816000	0.32039	0.05468	0.02249	0.21257					
0.866000	0.32439	0.05660	0.00000	0.21257					
$m_1 = 0.001000 M_1 = 0.22347 m_2 = 0.071000 M_2 = 0.11029 F_1 = 0.01758$					$m_1 = 0.006000 M_1 = 0.32301 m_2 = 0.256000 M_2 = 0.04249 F_1 = 0.06746$				
0.096000	0.05379	0.01944	0.39969	0.08017	0.306000	0.00329	0.06289	0.26079	0.12070
0.146000	0.08549	0.02592	0.35389	0.09241	0.356000	0.01259	0.06951	0.23819	0.12822
0.196000	0.10709	0.03180	0.31939	0.10227	0.406000	0.02039	0.07582	0.21679	0.13564
0.246000	0.12339	0.03707	0.29069	0.11110	0.456000	0.02719	0.08157	0.19619	0.14263
0.296000	0.13649	0.04171	0.26559	0.11902	0.506000	0.03309	0.08711	0.17569	0.15042
0.346000	0.14719	0.04632	0.24259	0.12673	0.556000	0.03829	0.09242	0.15509	0.15813
0.396000	0.15639	0.05042	0.22099	0.13418	0.606000	0.04289	0.09757	0.13389	0.16627
0.446000	0.16429	0.05444	0.20029	0.14136	0.656000	0.04709	0.10236	0.11149	0.17523
0.496000	0.17129	0.05815	0.17979	0.14889	0.706000	0.05099	0.10683	0.08739	0.18501
0.546000	0.17749	0.06175	0.15919	0.15667	0.756000	0.05439	0.11143	0.06059	0.19614
0.596000	0.18309	0.06516	0.13819	0.16462	0.806000	0.05759	0.11570	0.02939	0.20965
0.646000	0.18809	0.06858	0.11609	0.17337	0.856000	0.06059	0.11974	0.00000	0.20965
0.696000	0.19269	0.07181	0.09239	0.18297					
0.746000	0.19699	0.07477	0.06619	0.19386					
0.796000	0.20089	0.07778	0.03609	0.20671					
0.846000	0.20459	0.08054	0.00000	0.20671					
$m_1 = 0.001000 M_1 = 0.22347 m_2 = 0.371000 M_2 = 0.23059 F_1 = 0.05256$					$m_1 = 0.009000 M_1 = 0.34554 m_2 = 0.361000 M_2 = 0.02449 F_1 = 0.09267$				
0.751000	0.00159	0.12610	0.06339	0.19503	0.686000	0.00159	0.11820	0.09729	0.18097
0.801000	0.00449	0.13105	0.03279	0.20813	0.736000	0.00489	0.12332	0.07169	0.19154
0.851000	0.00719	0.13574	0.00000	0.20813	0.786000	0.00789	0.12828	0.04259	0.20379
					0.836000	0.01069	0.13296	0.00759	0.21916
					0.886000	0.01329	0.13744	0.00000	0.21916
$m_1 = 0.002000 M_1 = 0.26198 m_2 = 0.086000 M_2 = 0.06509 F_1 = 0.02423$					$m_1 = 0.010000 M_1 = 0.35139 m_2 = 0.326000 M_2 = 0.00889 F_1 = 0.08914$				
0.106000	0.04349	0.02190	0.38919	0.08280	0.541000	0.00449	0.09871	0.16129	0.15583
0.156000	0.07229	0.02870	0.34639	0.09440	0.591000	0.00909	0.10424	0.14029	0.16387
0.206000	0.09249	0.03464	0.31329	0.10409	0.641000	0.01329	0.10937	0.11839	0.17240
0.256000	0.10779	0.04026	0.28549	0.11263	0.691000	0.01699	0.11449	0.09489	0.18189
0.306000	0.12019	0.04519	0.26079	0.12070	0.741000	0.02039	0.11934	0.06899	0.19263
0.356000	0.13049	0.04982	0.23819	0.12822	0.791000	0.02339	0.12422	0.03939	0.20519
0.406000	0.13919	0.05432	0.21679	0.13564	0.841000	0.02629	0.12863	0.00359	0.22101
0.456000	0.14679	0.05848	0.19619	0.14283	0.891000	0.02889	0.13306	0.00000	0.22101
0.506000	0.15349	0.06242	0.17569	0.15042					
0.556000	0.15949	0.06612	0.15509	0.15813					
0.606000	0.16479	0.06987	0.13389	0.16627					
0.656000	0.16969	0.07329	0.11149	0.17523					
0.706000	0.17419	0.07653	0.08739	0.18501					
0.756000	0.17829	0.07973	0.06059	0.19614					
0.806000	0.18209	0.08281	0.02939	0.20965					
0.856000	0.18559	0.08584	0.00000	0.20965					
$m_1 = 0.002000 M_1 = 0.26198 m_2 = 0.336000 M_2 = 0.16069 F_1 = 0.06016$					$m_1 = 0.010000 M_1 = 0.35139 m_2 = 0.376000 M_2 = 0.01659 F_1 = 0.09752$				
0.551000	0.00119	0.10083	0.15719	0.15730	0.761000	0.00010	0.12775	0.05769	0.19739
0.601000	0.00569	0.10631	0.13599	0.16555	0.811000	0.00299	0.13255	0.02599	0.21107
0.651000	0.00969	0.11163	0.11379	0.17431	0.861000	0.00559	0.13732	0.00000	0.21107
0.701000	0.01329	0.11676	0.08989	0.18401					
0.751000	0.01659	0.12164	0.06339	0.19503					
0.801000	0.01959	0.12639	0.03279	0.20813					
0.851000	0.02239	0.13088	0.00000	0.20813					

TABLE 3.— F , m , and R values for general marked fall chinook salmon of the 1962 brood; M is survival for 12 mo and F for 6 mo (adapted from Henry 1971).

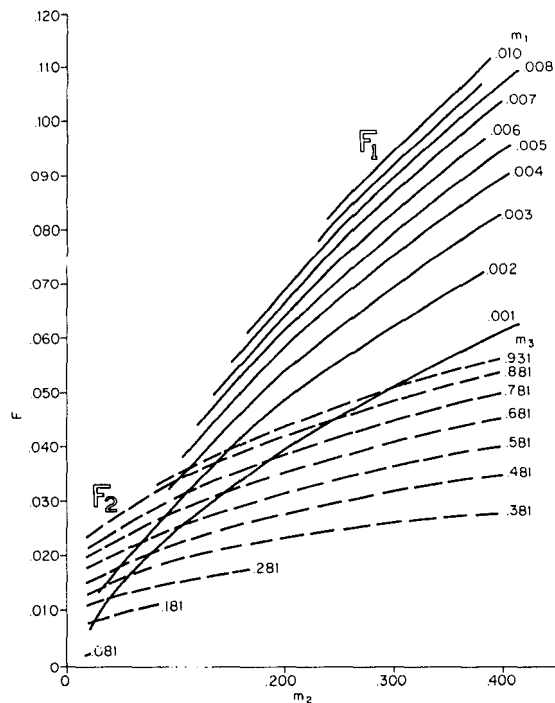
Natural mortality M	Fishing intensity			Proportion maturing			Recruitment		
	F_3	F_2	F_1	m_3	m_2	m_1	R_5	R_4	R_3
0.24	1.346	0.781	0.535	0.810	0.332	0.009	220	3,216	10,441
.45	1.304	.733	.460	.783	.290	.007	260	3,912	13,681
.48	1.298	.727	.449	.779	.284	.007	266	4,028	14,238
.60	1.275	.698	.410	.761	.262	.006	293	4,516	16,736
.72	1.251	.671	.372	.743	.240	.005	323	5,076	19,831
.96	1.206	.616	.301	.705	.199	.003	393	6,438	28,320

FIGURE 2.—Relation between computed monthly natural mortality (M_1) during the first 18 mo after release as smolts and selected values of proportions of salmon maturing after 18 mo (m_1)—1961 brood of fall chinook salmon from Spring Creek hatchery.

the relation between M_4 , F_3 , and m_3 . As the m_3 value increases, F_3 also increases and M_4 decreases. It should be noted that for M_4 values < 1.0 (summed over 12 mo), m_3 must be well over 0.800.

Although it is not possible to obtain unique estimates of the various parameters (only a range of estimated values) by selecting either the M_i or the m_i , the detailed relationships between the parameters—based on selecting m_i values—give a very good insight into the effect of each of these values on the other and the interrelationships between them. Furthermore, the graphic presentation of these relationships as shown in this paper permit any assumptions about the various parameters to be quickly examined. For example, to obtain estimates of the various parameters based on Cleaver's (1969) assumption that the M_i ($i = 2-4$) are equal for the 1961 Spring Creek data, we could go to Figure 5 and observe the m_3 and F_3 values for selected values of M_4 .

Next, from Figure 4 for $M_4 = M_3 = M_2$ and the appropriate m_3 values, we could calculate the proper m_2 and m_1 values. Then from Figure 3 for these m_1 , m_2 , and m_3 values we could determine the proper F_1 and F_2 values and finally from Fig-

FIGURE 3.—Relations between certain computed monthly ocean fishing mortalities (F_1 , F_2) and selected values of proportions of salmon maturing annually (m_1 , m_2 , m_3)—1961 brood of fall chinook salmon from Spring Creek hatchery.

ure 2, the correct estimate of M_1 . Of course, any other assumed relationships between the parameters also can be examined readily from these graphs.

COMPARISON OF 1961 AND 1962 BROOD SPRING CREEK DATA

I have selected the Spring Creek data to discuss in this paper because in my earlier paper (Henry 1971) I stated, "It is unfortunate that no analysis could be made for Spring Creek marks of the 1962 brood." This was due to the fact that there were no fifth year recoveries recorded for the river ($E_4 = 0$),

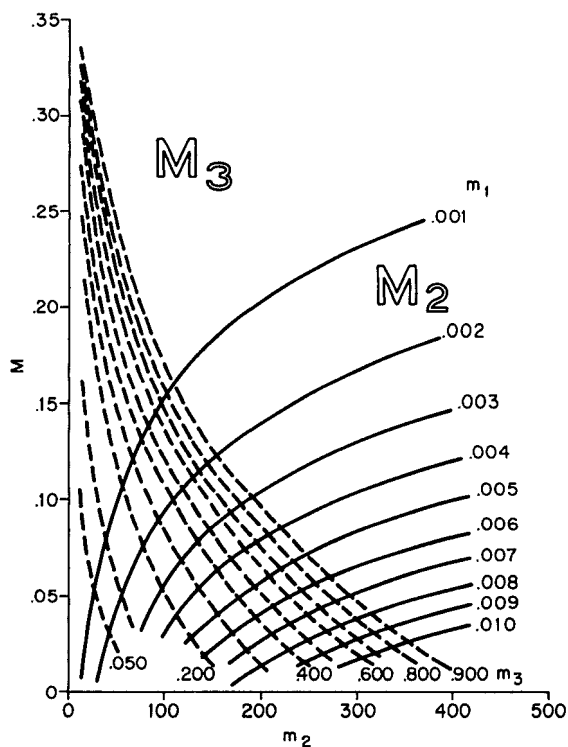


FIGURE 4.—Relations between certain computed monthly natural mortalities (M_2 , M_3) and selected values of annual proportions of salmon maturing (m_1 , m_2 , and m_3)—1961 brood of fall chinook salmon from Spring Creek hatchery.

so back calculations were not possible with the method of assuming a fixed value for M_1 . However, by assuming fixed values of m_i and working from the early life history of the salmon onward, it is possible to calculate estimates of the various parameters up to the fifth year.

Although, as previously explained, it is not possible to compute M_4 and F_3 values (for the fifth year) for the 1962 Spring Creek data, estimates of the other parameters are possible. Therefore, the relations between m_1 , m_2 , m_3 and M_2 , M_3 , for the 1962 brood, are shown in Figure 6; between m_1 , m_2 , m_3 and F_1 , F_2 in Figure 7; and finally, the relations between m_1 and M_1 are shown in Figure 8 for both the 1961 and 1962 broods.

Since it is now possible to calculate estimates of some of the parameters for the 1962 brood Spring Creek fish, it is interesting to compare some general conclusions I made (Henry 1971) with these estimates. I stated that "... the data suggest that the 1962 Spring Creek fish survived and entered the ocean fishery in about the same proportions as

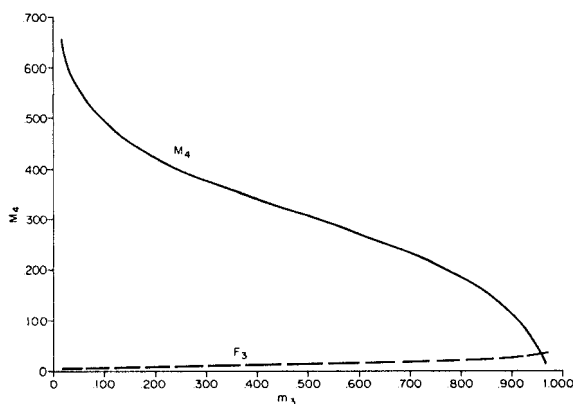


FIGURE 5.—Relations between computed last year of life monthly natural mortality (M_4) and last year of life ocean fishing mortality (F_3) for selected values of proportions of salmon maturing the previous year (m_3)—1961 brood of fall chinook salmon from Spring Creek hatchery.

Kalama fish (Kalama 0.003, General 0.003) but in much smaller proportions than the 1961 Kalama brood (Kalama 0.011, Spring Creek 0.007)." In other words, I indicated that the first 18 mo of natural mortality after release as smolts for the Spring Creek fish was higher for the 1962 brood than for the 1961 brood. This tentative conclusion is now supported by the data shown in Figure 8 where the M_1 values for the 1961 and 1962 broods of Spring Creek fish are shown. It is apparent that for any given value of m_1 , the estimate of M_1 is higher for the 1962 brood and it would require a considerably higher value of m_1 for the 1961 brood, compared with 1962, to have comparable estimates of M_1 for the two broods.

Another tentative conclusion made in my earlier paper, "... that the ocean fishery was less intense on the 1962 brood Spring Creek fish ..." also can be examined in greater detail with these new calculations. Thus, we see that when the data for the two brood years are compared, for fixed values of m_1 , m_2 , and m_3 (Table 4), the estimated fishing mortality for the 3-yr-old fish (F_1) from the 1962 brood was about half that for the 1961 brood. However, for the 4-yr-old fish (F_2) the estimated fishing mortality for the 1962 brood was about twice as large as that estimated for the 1961 brood. Since most of the catch was made as 3-yr-old fish (F_1) for both brood years, the overall catch (mortality) was less for the 1962 brood. These relations between the F_1 and F_2 values for the two broods can be more clearly seen by comparing Figure 3 (the 1961 brood) with Figure 7 (the 1962 brood).

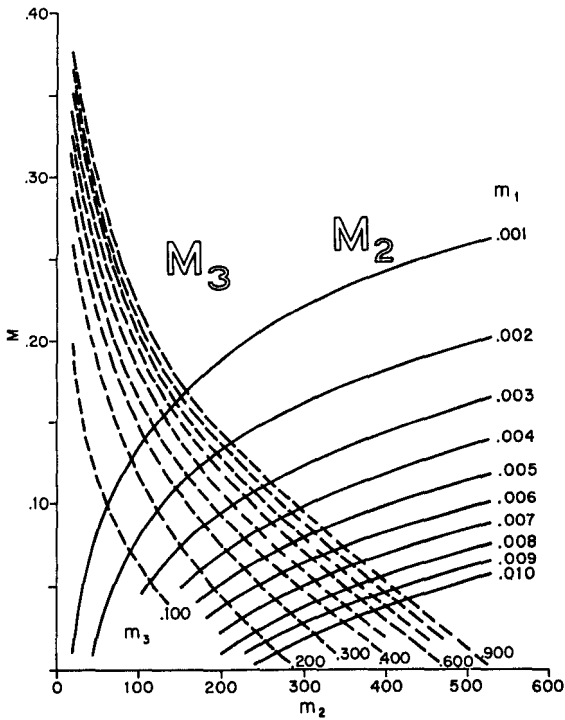


FIGURE 6.—Relations between certain computed monthly natural mortalities (M_2 , M_3) and selected values of annual proportions of salmon maturing (m_1 , m_2 , and m_3)—1962 brood of fall chinook salmon from Spring Creek hatchery.

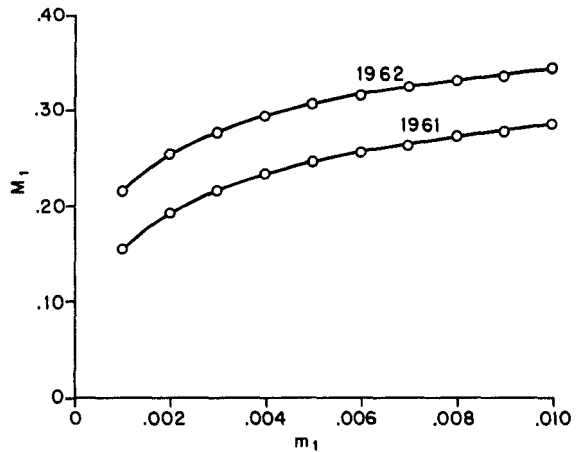


FIGURE 8.—Relations between computed monthly natural mortality (M_1) during the first 18 mo after release as smolts and selected values of proportions of salmon maturing after 18 mo (m_1)—1961 and 1962 broods of fall chinook salmon from Spring Creek hatchery.

TABLE 4.—Comparison of estimates of fishing mortality (F) for the 1961 and 1962 broods of marked fall chinook salmon from Spring Creek hatchery for fixed values of proportion of salmon maturing annually (m).

	1961 brood	1962 brood		1961 brood	1962 brood
m_1	0.001	0.001	m_3	0.600	0.600
m_2	.300	.300	F_2	.037	.078
F_1	.051	.026			

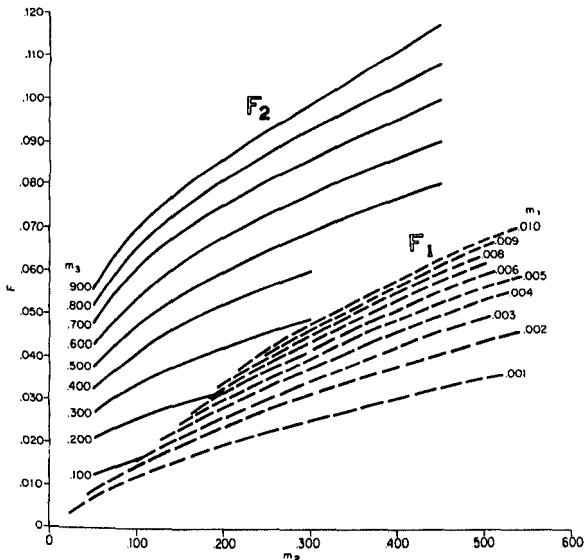


FIGURE 7.—Relations between certain computed monthly ocean fishing mortalities (F_1 , F_2) and selected values of proportions of salmon maturing annually (m_1 , m_2 , and m_3)—1962 brood of fall chinook salmon from Spring Creek hatchery.

Thus, for a given value of m_2 , the generally higher F_1 values compared with F_2 for the 1961 brood is quite different from the generally higher F_2 values compared with F_1 for the 1962 brood data shown in Figure 7.

A general comparison between the calculated M_2 and M_3 values can be obtained by comparing Figure 4 with Figure 6. There is considerable similarity between the pattern of mortality estimates for these two broods. In both cases, as m_2 increases, M_2 increases and M_3 decreases. However, for a given m_2 and m_3 , the estimates of M_3 are slightly higher for the 1962 brood, whereas for a given m_2 and m_1 , the estimates of M_2 are very similar for the two broods.

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APPENDIX

Derivation of Text Equations

As pointed out in the text, the probabilities of

$$E_1: \theta_1 = m_1 e^{-18M_1}. \quad (1)$$

$$C_1: \theta_2 = (1-m_1)e^{-18M_1}e^{-6M_2} \frac{F_1}{F_1+M_2} (1-e^{-6(F_1+M_2)}). \quad (2)$$

$$E_2: \theta_3 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}m_2. \quad (3)$$

$$C_2: \theta_4 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3} \frac{F_2}{F_2+M_3} (1-e^{-6(F_2+M_3)}). \quad (4)$$

$$E_3: \theta_5 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}m_3. \quad (5)$$

$$C_3: \theta_6 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4} \frac{F_3}{F_3+M_4} (1-e^{-6(F_3+M_4)}). \quad (6)$$

$$E_4: \theta_7 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}e^{-6(F_3+M_4)}. \quad (7)$$

and maximum likelihood estimates of the θ_i are:

$$\hat{\theta}_1 = \frac{E_1}{N_0} \text{ or } \hat{\theta}_1 = m_1 e^{-18M_1} \text{ from Equation (1)}. \quad (8)$$

$$\hat{\theta}_2 = \frac{C_1}{N_0} \text{ or } \hat{\theta}_2 = (1-m_1)e^{-18M_1}e^{-6M_2} \frac{F_1}{F_1+M_2} (1-e^{-6(F_1+M_2)}) \text{ from Equation (2)}. \quad (9)$$

$$\hat{\theta}_3 = \frac{E_2}{N_0} \text{ or } \hat{\theta}_3 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}m_2 \text{ from Equation (3)}. \quad (10)$$

$$\hat{\theta}_4 = \frac{C_2}{N_0} \text{ or } \hat{\theta}_4 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3} \frac{F_2}{F_2+M_3}$$

$$(1-e^{-6(F_2+M_3)}) \text{ from Equation (4)}. \quad (11)$$

$$\hat{\theta}_5 = \frac{E_3}{N_0} \text{ or } \hat{\theta}_5 = (1-m_1)e^{-1.8M_1}e^{-6M_2}e^{-6(F_1+M_2)} (1-m_2)e^{-6M_3} e^{-6(F_2+M_3)} m_3 \text{ from Equation (5)}. \quad (12)$$

$$\hat{\theta}_6 = \frac{C_3}{N_0} \text{ or } \hat{\theta}_6 = (1-m_1)e^{-1.8M_1}e^{-6M_2}e^{-6(F_1+M_2)} (1-m_2)e^{-6M_3} e^{-6(F_2+M_3)} (1-m_3)e^{-6M_4}$$

$$\frac{F_3}{F_3+M_4} (1-e^{-6(F_3+M_4)}) \text{ from Equation (6)}. \quad (13)$$

$$\hat{\theta}_7 = \frac{E_4}{N_0} \text{ or } \hat{\theta}_7 = (1-m_1)e^{-1.8M_1}e^{-6M_2}e^{-6(F_1+M_2)} (1-m_2)e^{-6M_3}$$

$$e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}e^{-6(F_3+M_4)} \text{ from Equation (7)}. \quad (14)$$

Then for $m_i = m$ (fixed) ($\theta_1 < m_1 < 1$) ($\theta_3 < m_2 < 1$) ($\theta_5 < m_3 < 1$), text Equations (17) to (19), by rearranging Equation (8) and taking natural logarithms we obtain

$$-1/18 \ln \left(\frac{\hat{\theta}_1}{m_1} \right) = M_1 \text{ (text Equation (20))}.$$

Then Equation (10) can be rewritten as

$$\frac{\hat{\theta}_3}{(1-m_1)m_2} e^{1.8M_1} = e^{-6M_2} e^{-6(F_1+M_2)} = e^{-6M_2-6F_1-6M_2} = e^{-(6F_1+12M_2)} = k_2.$$

The natural logarithm of k_2

$$\ln k_2 = -(6F_1+12M_2) \quad (15)$$

which can be solved for F_1 as follows:

$$-6F_1 = \ln k_2 + 12M_2$$

$$F_1 = -\frac{\ln k_2 + 12M_2}{6} \text{ (text Equation (22))}. \quad (16)$$

Equation (9) can be written

$$\frac{\theta_2}{(1-m_1)} e^{1.8M_1} = e^{-6M_2} \frac{F_1}{F_1+M_2} (1-e^{-6(F_1+M_2)}) = k_1 \quad (17)$$

and since $e^{-6(F_1+M_2)} = e^{-6F_1-12M_2+6M_2} = e^{-(6F_1+12M_2)+6M_2} = e^{\ln k_2+6M_2}$ (from Equation (15))

and (from Equation (16))

$$\frac{F_1}{F_1+M_2} = \frac{\frac{\ln k_2 + 12M_2}{6}}{\frac{\ln k_2 + 12M_2}{6} + M_2} = \frac{-(\ln k_2 + 12M_2)}{-(\ln k_2 + 12M_2) + 6M_2} = \frac{\ln k_2 + 12M_2}{\ln k_2 + 12M_2 - 6M_2} = \frac{\ln k_2 + 12M_2}{\ln k_2 + 6M_2}$$

then Equation (17) becomes

$$\frac{\hat{\theta}_2}{(1-m_1)} e^{18M_1} = e^{-6M_2} \frac{\ln k_2 + 12M_2}{\ln k_2 + 6M_2} (1 - e^{\ln k_2 + 6M_2}) = k_1 \text{ (text Equation (21)).}$$

Solve for M_2 by iteration.

Next, Equation (12) can be written as

$$\begin{aligned} \frac{\hat{\theta}_5}{(1-m_1)(1-m_2)m_3} e^{18M_1} &= e^{-6M_2} e^{-6(F_1+M_2)} e^{-6M_3} e^{-6(F_2+M_3)} = e^{-(6F_1+12M_2)} e^{-(6F_2+12M_3)} \\ &= k_2 e^{-(6F_2+12M_3)} = k_4. \end{aligned}$$

The natural logarithm of k_4

$$\ln k_4 = -(6F_2 + 12M_3) + \ln k_2 \quad (18)$$

which can be solved for F_2 as follows:

$$\begin{aligned} -6F_2 &= \ln k_4 + 12M_3 - \ln k_2 \\ F_2 &= -\frac{(\ln k_4 - \ln k_2 + 12M_3)}{6} \text{ (text Equation (24)).} \end{aligned} \quad (19)$$

$$\text{Since } e^{-6M_2} e^{-6(F_1+M_2)} = e^{-(6F_1+12M_2)} = k_2,$$

Equation (11) can be written

$$\frac{\hat{\theta}_4}{(1-m_1)(1-m_2)} e^{18M_1} = k_2 e^{-6M_3} \frac{F_2}{F_2+M_3} (1 - e^{-6(F_2+M_3)}) = k_3 \quad (20)$$

$$\text{and since } e^{-6(F_2+M_3)} = e^{-6F_2-12M_3+6M_3} = e^{-6(F_2+12M_3)+6M_3} = e^{\ln k_4 - \ln k_2 + 6M_3} \text{ (from Equation (18))}$$

and (from Equation (19))

$$\begin{aligned} \frac{F_2}{F_2+M_3} &= \frac{-\left[\frac{\ln k_4 - \ln k_2 + 12M_3}{6}\right]}{-\left[\frac{\ln k_4 - \ln k_2 + 12M_3}{6}\right] + M_3} = \frac{-(\ln k_4 - \ln k_2 + 12M_3)}{-(\ln k_4 - \ln k_2 + 12M_3) + 6M_3} \\ &= \frac{\ln k_4 - \ln k_2 + 12M_3}{\ln k_4 - \ln k_2 + 12M_3 - 6M_3} = \frac{\ln k_4 - \ln k_2 + 12M_3}{\ln k_4 - \ln k_2 + 6M_3} \end{aligned}$$

then Equation (20) becomes

$$\frac{\hat{\theta}_4}{(1-m_1)(1-m_2)} e^{18M_1} = k_2 e^{-6M_3} \frac{\ln k_4 - \ln k_2 + 12M_3}{\ln k_4 - \ln k_2 + 6M_3} (1 - e^{\ln k_4 - \ln k_2 + 6M_3}) = k_3 \text{ (text Equation (23)).}$$

$$\text{Since } e^{-(6F_1+12M_2)} = k_2 \text{ and } e^{-(6F_2+12M_3)} = \frac{k_4}{k_2}$$

then, Equation (14) can be written as

$$\begin{aligned} \frac{\hat{\theta}_7}{(1-m_1)(1-m_2)(1-m_3)} e^{18M_1} &= e^{-6M_2} e^{-6(F_1+M_2)} e^{-6M_3} e^{-6(F_2+M_3)} e^{-6M_4} e^{-6(F_3+M_4)} \\ &= k_2 \frac{k_4}{k_2} e^{-6M_4} e^{-6F_3-6M_4} \\ &= k_4 e^{-(6F_3+12M_4)} = k_6. \end{aligned}$$

The natural logarithm of k_6

$$\ln k_6 = \ln k_4 - (6F_3 + 12M_4) \quad (21)$$

which can be solved for F_3 as follows:

$$\begin{aligned} -6F_3 &= \ln k_6 - \ln k_4 + 12M_4 \\ F_3 &= \frac{-(\ln k_6 - \ln k_4 + 12M_4)}{6} \quad (\text{text Equation (26)}). \end{aligned} \quad (22)$$

Equation (13) can be written

$$\frac{\hat{\theta}_6}{(1-m_1)(1-m_2)(1-m_3)} e^{18M_1} = k_2 \frac{k_4}{k_2} e^{-6M_4} \frac{F_3}{F_3+M_4} (1-e^{-6(F_3+M_4)}) = k_5 \quad (23)$$

and since $e^{-6(F_3+M_4)} = e^{-6F_3-12M_4+6M_4} = e^{-(6F_3+12M_4)+6M_4} = e^{\ln k_6 - \ln k_4 + 6M_4}$ (from Equation (21))

and (from Equation (22))

$$\begin{aligned} \frac{F_3}{F_3+M_4} &= \frac{\frac{\ln k_6 - \ln k_4 + 12M_4}{6}}{\frac{\ln k_6 - \ln k_4 + 12M_4}{6} + M_4} = \frac{-(\ln k_6 - \ln k_4 + 12M_4)}{-(\ln k_6 - \ln k_4 + 12M_4) + 6M_4} \\ &= \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 12M_4 - 6M_4} = \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 6M_4} \end{aligned}$$

then Equation (23) becomes

$$\frac{\hat{\theta}_6}{(1-m_1)(1-m_2)(1-m_3)} e^{18M_1} = k_4 e^{-6M_4} \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 6M_4} (1-e^{\ln k_6 - \ln k_4 + 6M_4}) = k_5 \quad (\text{text Equation (25)}).$$