PROBLEM OF BIAS IN MODELS TO APPROXIMATE OCEAN MORTALITY, MATURITY, AND ABUNDANCE SCHEDULES OF SALMON FROM KNOWN SMOLTS AND RETURNS

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ABSTRACT

The problem of methodological bias in estimating ocean mortality or survival, maturity, and abundance of multireturn species of Pacific salmon (*Oncorhynchus* spp.) is examined heuristically with a data base for which no unbiased estimators exist. The case of hatchery coho salmon (*O. kisutch*) is emphasized to treat the problem in its simplest form (two returns). Models previously reported by Ricker, Fredin, and Cleaver are considered in the context of their application in biomass computations and the particular problem of bias in approximating average and interval-specific mortality coefficients during ocean life. A new scheme is introduced as the limit-mean model, and the assumptions in all four models are contrasted. Numerical examples for a hypothetical cohort demonstrate a wide range of bias in estimates of different parameters from the same model and also in estimates of the same parameter from different models applied in different situations. For the hypothetical data, overall performance is best for the limit-mean model with the offshore catch known; this model also provides estimates of natural and fishing mortality rates offshore during the last year at sea. For coho and chinook salmon, (*O. tshawytscha*) caught off western North America, it is recommended that 1) maturity be directly sampled to help provide nominally unbiased estimates for certain of the parameters and 2) research be intensified on determining offshore catch by origin independently of marking smolts.

Three oceanic fisheries have motivated research on the geographic origins, distribution patterns, and changes in biomass during the marine life of salmon. One is the Japanese mothership fishery, since 1952 by drift gill nets west of long 175°W in the North Pacific Ocean—mainly for pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon (Fukuhara, 1953). Another is the offshore troll and sport fishery from California to Alaska for chinook (*O. tshawytscha*) and coho (*O. kitsutch*) salmon (Godfrey, 1965; Mason, 1965). Third is the drift net fishery for Atlantic salmon (*Salmo salar*), since 1964 off southeast Greenland and northern Norway (Horsted, 1971).

The results of biomass computations based on growth and natural mortality estimates must be combined with catches (real or assumed) by natal origin in order to assess the impact of offshore vis-a-vis inshore fishing (Taguchi,

1961a, 1961b; Doi, 1962; Ricker, 1962, 1964; Parker, 1963; Fredin, 1964; Hirschhorn, 1966; Cleaver, 1969; Henry, 1971, 1972). Investigators have recognized the scarcity of existing field data, the high cost of direct marking/recovery at sea, and the technical difficulties of obtaining unbiased data and constructing realistic models to approximate the time distribution of mortality (Ricker, 1962; Parker, 1960, 1962, 1963, 1968; Fredin, 1964; Lander et al., 1967; Cleaver, 1969).

Biased estimates can distort the interpretation of actual time changes in biomass of a cohort and impede the application of rational conservation measures. On the other hand, reasonably accurate approximations to interval-specific mortality can be useful not only in biomass computations: they may help also to predict returns from the sea and thereby to improve management of inshore salmon fisheries (e.g., Gilbert, 1963).

In this report I review three published models for approximating ocean mortality schedules

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as applied in biomass computations, examine the particular problem of bias in mortality estimates, and introduce another model to extend the indirect approach developed by Parker (1962), Ricker (1962), Fredin (1964), and Cleaver (1969). Bias in estimated maturity and abundance schedules is examined also.

METHODS AND LIMITATIONS

The indirect approach is applicable to species in which maturing adults from the seaward migrants in a given year (or smolt class) return to their natal area in 2 or more years: single-return pink salmon are excluded. The following minimum data are required for multireturn species: 1) origin-specific number of seaward migrants or smolts in a given year, 2) number of survivors returning from the ocean each year until the smolt class is extinct, and 3) intervals between times of seaward migration and of each return or spawning escapement. An offshore fishery may or may not exist; origin-specific catch data for the inshore fishery or an offshore fishery may or may not be available. No unique solution exists for the mortality, maturity, and abundance schedules from the foregoing data base: different combinations of mortality and maturity schedules can generate the same set of observed data.

I consider only the bias due to the absence of unique solutions in estimating models. Data on the numbers of smolts and returning adults may be biased additionally in practice; in fact, the very existence of basic data is unfortunately the exception in wild stocks (e.g., Gilbert, 1963). Data as observed in practice are assumed here to be accurate in order to emphasize the methodological problem.

The number of mortality, maturity, and abundance parameters increases formidably with the number of returns and with the possible regimes of offshore-inshore exploitation. The case of only two returns, typical of hatchery and most wild stocks of coho salmon south of British Columbia (Shapovalov and Taft, 1954; Godfrey, 1965; Drucker, 1972), is emphasized throughout.

Finally, the study is heuristic. Explicit equations for bias are available for only two of the four models as treated here. The equation for one of the two is tedious to write for just one parameter—say the monthly coefficient of total mortality between times of outmigration and of the last return—and descriptive equations for bias are very cumbersome when estimates for all mortality, maturity, and abundance parameters are considered. Relations among all parameters are evident from initial description of the actual situation, however, and are utilized for some numerical comparisons from a set of hypothetical data. These numerical comparisons of bias are selective also with respect to the two general cases considered: 1) catch data unknown and 2) catch data known from marking (or otherwise identifying) smolts and from sampling the catch for recoveries. I try to avoid unfair comparisons between models, to compare them where justified, and to demonstrate how small bias in one parameter estimate may translate to large bias in another estimate from the same model.

ACTUAL SITUATION

Pertinent events of the life history (Shapovalov and Taft, 1954; Godfrey, 1965; Johnson, 1970; Drucker, 1972), observational data, and parameters are related below for coho salmon in the southern part of their freshwater range in North America.

Spawning occurs during November-January and typically the surviving fry are free-swimming during the next February-April. The cohort stays in fresh water until downstream migration of survivors begins about a year later at time $t = t_0$; the actual time of entry to the ocean, some weeks later, depends on physiological condition, stream flow and temperature, and distance from spawning areas. Our mortality schedule starts at time $t = t_0$ and includes downstream mortality of smolts unless their number is known when they enter the sea.

The first return from the sea is in the year of outmigration (6-9 mo later) and occurs at time $t = t_1$, usually during October-December or about 2 years after eggs are spawned. This first return is all or nearly all males or "jacks."

Few jacks are recorded from offshore fisheries but some are taken in freshwater fisheries. Time $t = t_1$ ends our first mortality interval and starts the second.

The immature age-2 fish remaining at sea (males plus females) are reduced in numbers by natural mortality alone for about 6-8 more mo until their recruitment to offshore fishing at time $t = t_r$. For about 5 mo thereafter, offshore then inshore fishing operate along with natural mortality. About a year after the jacks return, age-3 adults appear in the final escapement at time $t = T$ to render the smolt class extinct for our purposes. Thus t_1 and t_r divide the effective life span, $T - t_0$, into three subintervals.

Basic notation follows:

N_0 = number of smolts at time $t = t_0$

E_1 = number of jacks in first return or spawning escapement at time $t = t_1$

N_1 = number of age-2 immatures at sea at time $t = t_1$

N_r = number of recruits to offshore fishing at time $t = t_r$

C = number of fish caught offshore

E_2 = number of adults in second (last) return or spawning escapement at time $t = T$

m = fraction of the cohort which matures as jacks near time $t = t_1$

s_1, s_2 = survival fractions during $t_1 - t_0$ and $t - t_1$, respectively

Z_1, Z_2 = monthly coefficients of natural plus fishing mortality during $t_1 - t_0$ and $T - t_1$, respectively

M_2 = monthly coefficient of natural mortality during $T - t_1$

F = monthly coefficient of fishing mortality in offshore waters during $T - t_r$

Z_T^* = monthly coefficient of total mortality during $T - t_0$

u = exploitation rate in offshore fisheries

e = base of natural logarithms.

The following relations summarize the actual situation:

$$E_1 = N_0 s_1 m = m N_0 e^{-Z_1(t_1 - t_0)}. \tag{1}$$

$$N_1 = N_0 s_1 (1 - m)$$
$$= (1 - m) N_0 e^{-Z_1(t_1 - t_0)}. \tag{2}$$

$$N_r = N_1 e^{-M_2(t_r - t_1)}. \tag{3}$$

$$C = u N_r = [F/(F + M_2)]$$
$$\times [1 - e^{-(F + M_2)(T - t_r)}] N_r. \tag{4}$$

$$E_2 = N_r e^{-(F + M_2)(T - t_r)}$$
$$= N_1 e^{-M_2(T - t_1) - F(T - t_r)}$$
$$= N_1 s_2 = N_1 e^{-Z_2(T - t_1)}$$
$$= N_0 s_1 s_2 (1 - m) = N_0 s_1 s_2 - E_1 s_2$$
$$= (1 - m) N_0 e^{-Z_T^*(T - t_0)}. \tag{5}$$

We have also the general definitions of the mortality coefficients:

$$Z_T^* = (-\ln s_1 s_2)/(t - t_0)$$
$$= [Z_1(t_1 - t_0) + Z_2(T - t_1)]/(T - t_0). \tag{6}$$

$$Z_2 = (-\ln s_2)/(T - t_1)$$
$$= [M_2(T - t_1) + F(t - t_r)]/(T - t_1). \tag{7}$$

$$Z_1 = (-\ln s_1)/(t_1 - t_0). \tag{8}$$

If the smolts are not marked (or otherwise identified) to estimate C and the inshore catch by origin, then the escapement data (E_i) come from hatchery counts or natural spawning areas. If only the inshore catch is identified by origin, a value of E_i is the sum of inshore catch plus "escapement" from inshore fishing to the spawning area in a given year (usually called the "return" or "run" by salmon biologists); it occurs somewhat earlier in time and of course exceeds the value of E_i without inshore catch data available. Thus with inshore catch data available, $Z_1 = M_1$ (the offshore catch of jacks being absent or negligible), Z_2 includes only offshore mortality, and $Z_2 = M_2$ if no offshore fishery exists ($F = C = 0$). The indirect approach was developed mainly from data without offshore fishing mortality but with inshore catches known. If an offshore fishery exists (as on the coho salmon emphasized

here), both C and the inshore catch may be identified by origin (e.g., Worlund, Wahle, and Zimmer, 1969; Johnson, 1970). The possibilities of 1) C known but inshore catch unknown with respect to origin or 2) offshore fishing present but inshore fishing absent are too remote for consideration here. Our two general cases—C known and unknown—are therefore defined and the inshore catch is implicit in E_i. Figure 1 contrasts the extinction of a smolt class with and without offshore fishing.

It is evident from Equations 1-5 that the s_i and m are confounded, and no unique solution exists. This fact and the existence of offshore salmon fisheries led to development of the indirect approach.

ESTIMATING MODELS

Three existing models are reviewed in terms of biomass computations, bias in estimated mortality schedules is considered, and a new estimating scheme is introduced.

Ricker's (1962) Model

This model is based on convincing if indirect evidence (not direct measurements) that most natural mortality during the ocean life of sockeye salmon occurs well before the fish are large enough to be recruited to an offshore fishery. In the context of Equations 6-8 with $F = C = 0$:

$$[M_1(t_1 - t_0) + M_2(t_r - t_1)]/(t_r - t_0)$$
$$= M_r^* > M_2. \qquad (9)$$

In Equation 9, M_r^* is the average monthly rate of natural mortality during $t_r - t_0$, t_0 being the date when (say) half the smolt class enters the sea in 1 year and t_r the date of potential recruitment offshore the next year (say). Parker (1968) demonstrated from direct marking/recovery of pink salmon that natural mortality is highest during the first few weeks of ocean life. To my knowledge, salmon biologists all agree that $M_1 > M_2$.

In the absence of direct measurements,

Ricker's model assumes $m = 0$ and $s_2 = 1.0$ on the E_1 jacks (Equations 1 and 5); it treats $E_1 + E_2 = \Sigma E_i$ as a single escapement at time $t = T$, with the following result from Equation 5:

$$\hat{Z}_T^* = \hat{Z}_i = \hat{M}_i = M_{rL}^* = M_{2U}$$
$$= -\ln(\Sigma E_i/N_0)/(T - t_0). \qquad (10)$$

In Equation 10 the caret symbol (^) denotes an estimate, and the subscripts L and U denote lower and upper limits, respectively.

Because $M_{2U} < \hat{G}$ (the estimated growth coefficient) after $t = t_r$ for most age and maturity groups of commercial size in offshore waters, Ricker (1962) concluded that offshore fishing is biologically wasteful. Those biomass computations assume 100% availability to an offshore fishery, however, and overestimate minimum losses. Ricker (1964) later mentions the availability in connection with the growth-mortality balance in pink and chum salmon and computes weight losses from offshore fishing as a fraction of maximum possible yield (inshore fishing only) for any fixed spawning escapement required for reproduction. Biomass calculations of Parker (1963) and Fredin (1964) also assume full availability. Although the evidence indicates offshore fishing reduces total yield (see also Cleaver, 1969; Henry, 1971, 1972), I emphasize that schedules of growth, mortality, and availability must be combined in order to assess the impact of existing or potential offshore fisheries: management restrictions, fleet size, and bad weather always prevent continuous, complete availability of a stock offshore.

Ricker's model (Equation 10) was applied only to situations where $F = C = 0$. The direction if not the magnitude of bias in the mortality schedule is known from evidence already cited, i.e., $\hat{M}_1 < M_1$ and $\hat{M}_2 > M_2$. When an offshore fishery exists ($F > 0$ in Equation 4) and $Z_1 = M_1$ as noted for coho salmon, Equation 10 may be used as the estimator, $\hat{Z}_T^* = \hat{Z}_1 = \hat{Z}_2$, and the bias defined in terms of known data and the unknown maturity parameter, m. Absolute bias (B) is defined as:

$$B = \text{estimate minus parameter value.} \qquad (11)$$

Applying Equations 10 and 11 and the actual values of Z_i from Equations 1 and 5 when C is unknown:

$$B_{(\hat{Z}_T^*)} = [T - t_0]^{-1} [-\ln(\Sigma E_i/N_0) + \ln(E_2/N_0) - \ln(1 - m)]. \quad (12)$$

$$B_{(\hat{Z}_1)} = [T - t_0]^{-1} [-\ln(\Sigma E_i/N_0)] + [t_1 - t_0]^{-1} [\ln(E_1/N_0 - \ln m]. \quad (13)$$

$$B_{(\hat{Z}_2)} = [T - t_0]^{-1} [-\ln(E_i/N_0)] + [T - t_1] [\ln(E_1/N_0) - \ln(E_2/N_0) - \ln m + \ln(1 - m)]. \quad (14)$$

Fredin's (1964) Model

Ricker's model accounts for the magnitude but not for the actual timing of preultimate returns (again, for the magnitude of E_1 in Equations 1-5 here). Fredin (1964) accounts both for magnitude and actual timing. His Model 1 is based on Equation 11 of Parker (1962), who separates relatively high natural mortality on small juveniles plus returning adults—both in inshore waters—from relatively low natural mortality in offshore waters. Parker's results actually derive, however, from his Equations 13 and 14 and utilize data from paired groups of marked smolts. I consider only the information available from a single group of smolts (marked or unmarked).

Thus Model 1 of Fredin (1964) assumes with Ricker (1962) that $Z_T^* = Z_1 = Z_2$; more strictly, the assumption is again that $M_T^* = M_1 = M_2$ because Fredin deals also with data not influenced by offshore fishing. Substituting the assumption in Equation 5 gives an estimator in the relation:

$$E_2/N_0 = e^{-\hat{Z}_T^*(T - t_0)} - (E_1/N_0)e^{-\hat{Z}_T^*(T - t_1)}. \quad (15)$$

Equation 15 is solved by trial and error unless one applies more advanced mathematical properties. Equation 15 differs from Equation 10, so values of $\hat{Z}_T^*$ from the same data obviously will differ. We anticipate less bias in $\hat{Z}_T^*$ from Equation 15 because it accounts for the actual timing of the E_1 jacks. With no explicit defini-

tion for $\hat{Z}_T^*$ in Equation 15, however, relations for bias (e.g., Equations 12-14) cannot be written and Equation 15 is later evaluated numerically.

Finally, Fredin's Models 2-4 employ various assumptions to accord with the reality, $Z_1 > Z_2$ (or $M_1 > M_2$). Although no "estimators" in the sense of Equation 15 are available from his Models 2-4 in the indirect approach, it is interesting that calculated maturity schedules were relatively insensitive to the different time distributions of mortality Fredin assumed between his Models 1-4.

Cleaver's (1969) Model

This model was developed specifically to utilize inshore and offshore catch data as known from a landmark study which evaluated the bioeconomic contribution of 1961-64 brood chinook salmon from Columbia River hatcheries (Worlund et al., 1969). Its basic assumption in the context of Equations 1-5 is that $M_2 = 0$ during $T - t_1$. The result is one-sided limits for certain parameters:

$$E_2/(C + E_2) = s_{2U} = e^{-Z_{2L}(t - t_1)}. \quad (16)$$

$$N_{1L} = E_2/s_{2U} = C + E_2. \quad (17)$$

$$m_U = E_1/(E_1 + N_{1L}). \quad (18)$$

As actually applied (Cleaver, 1969; Henry, 1971), the model used data on four escapements to the river (E_i) at ages 2-5 from a given smolt class and data on offshore catches (C_i) of immature plus currently maturing fish at ages 3-5 (unfortunately, marked recoveries in the offshore catch were not sampled for maturity—the catch being taken by small vessels and landed dressed with heads on). Values of E_i and C_i led to rejection of the hypothesis that Z_i was constant for ages 3-5 in offshore waters (certain resulting values of $m_i > 1.0$ implying more mature fish than were present in the total marked populations). Rejection of constant Z_i was deduced (by values of C_i and E_i) to be mainly from variation in F_i. Recalling the basic assumption ($M_i = 0$ during the last year or $M_2 = 0$ here), the authors then examined

the effects on M_i, F_i, and N_i of constant, non-trivial values of natural mortality, M_c, on all recruited age groups ($M_2 > 0$ during $T - t_r$ in our notation). The effect of offshore fishing on hatchery stocks in terms of age-specific escapements to the river was computed (with $F = 0$) for different values of M_c.

The model yields no point estimators and therefore no equations for bias, but is important here for several reasons. First, it utilizes known offshore catch data for the first time in the indirect approach. Second, it emphasizes the need for direct sampling of the offshore catch for maturity by origin (i.e., after marking smolts): the resulting $\hat{m}$ would give nominally unbiased estimates of all parameters but F and M_2 in Equations 1-8. Third, the calculated maturity schedules changed little with changes in M_c after recruitment to offshore fishing (Cleaver, 1969; Henry, 1971); this agreement with Fredin's (1964) result, based on varying the time distribution of natural mortality during all of ocean life for sockeye salmon, evidently is quite general for the 3-4 returns these three authors treated. Finally, reliance of the Cleaver model on one-sided limits (Equations 15-17) led directly to development of the last model.

Limit-Mean Model

Given the foregoing development of the indirect approach, it is natural to consider 1) devising two-sided limits on (say) Z_i or s_i initially and 2) taking for each parameter a value intermediate between these limits as a nontrivial estimator with unknown bias. The opposite and usual procedure in population problems is to derive nominally unbiased estimators and their variances (thus confidence limits) from statistical theory (e.g., the change-in-ratio estimators reported definitively by Paulik and Robson, 1969).

Offshore Catch Unknown

In this case C may be considered "unknown" because either 1) no offshore fishery exists ($Z_i = M_i$) on the target population and we deal actually with the M_i as Ricker (1962) and

Fredin (1964) did, or 2) an offshore fishery exists (Z_2 includes $F > 0$ as in our coho salmon) but techniques to evaluate $C > 0$ are not applied. The survival product, $s_1 s_2$, is the target parameter. Limits on the s_i are devised initially with the help of Assumption 1 ($s_{1U} = s_{2L} = s$) and Assumption 2 ($s_{2U} < 1.0$).

Assumption 1 is based on the evidence cited earlier which demonstrates almost incontrovertibly that $M_1 > M_2$. Now $t_1 - t_0$ (Equation 1) is shorter for coho salmon emphasized here—6-9 mo at the outside—than the $T - t_1 \simeq 12$ mo of ocean life remaining in the stocks south of British Columbia (Shapovalov and Taft, 1954; Godfrey, 1965; Drucker, 1972). It is most unlikely that $s_1 > s_2$, however, even when the intensive offshore fishery during $T - t_r \simeq 4$-5 mo is considered. Assumption 1 gives from Equation 5 the quadratic:

$$s^2 - (E_1/N_0)s - E_2/N_0 = 0 = s_{1U} s_{2L}$$
$$= (s_1 s_2)_L . \qquad (19)$$

Only one root is possible and the solution of Equation 19 is:

$$s = s_{1U} = s_{2L}$$
$$= 0.5 \left\{ E_1/N_0 + [(E_1/N_0)^2 + 4E_2/N_0]^{1/2} \right\}. \quad (20)$$

A reasonable value for Assumption 2 ($s_{2U} < 1.0$) depends on the stock and species. Murphy's (1952) often cited point estimates for coho salmon during their last year of ocean life serve as a guide for later numerical illustration. His estimates are 16-51% for 12 successive smolt classes (1938-49); only three estimates exceed 50%, of which two are 51%. Today's more intensive offshore fishery probably reduces s_2 below that in 1947 to which his estimated maximum, $\hat{s}_2 = 57\%$, applied. [In the next section I use $s_{2U} = 50\%$ but assign no value here. Other estimates and limits warrant mention: 68% by Parker (1962) as a point value grossly averaged for various smolt classes, stocks, and species; 51-80% as point estimates for sockeye salmon by Fredin (1965) and Mathews (1968); and 39-73% as upper limits by Cleaver (1969) for chinook salmon of ages 3-5 taken along with coho salmon

offshore.] Applying Assumption 2 in Equation 5:

$$(E_2 + E_1 s_{2U})/N_0 = s_{1L} s_{2U} = (s_1 s_2)_U. \quad (21)$$

The geometric mean of limits in Equations 19 and 21 is then taken arbitrarily to be the estimator:

$$[(s_1 s_2)_L (s_1 s_2)_U]^{1/2}$$

$$= [\{0.25 E_1/N_0 + [0.25(E_1/N_0)^2 + E_2/N_0]^{1/2}\}$$

$$\times (E_2 + E_1 s_{2U})/N_0]^{1/2}$$

$$= \widehat{s_1 s_2} = e^{-\hat{Z}_T^* (T - t_0)}. \quad (22)$$

From Equations 1-3, 5, and 22 we finally have:

$$\hat{s}_2 = (\widehat{s_1 s_2} - E_2/N_0)/(E_1/N_0)$$

$$= e^{-\hat{Z}_2 (T - t_1)}. \quad (23)$$

$$\hat{s}_1 = \widehat{s_1 s_2}/\hat{s}_2 = e^{-\hat{Z}_1 (t_1 - t_0)}. \quad (24)$$

$$\hat{N}_1 = E_2/\hat{s}_2. \quad (25)$$

$$\hat{m} = [1 - E_2/E_1 \hat{s}_2]^{-1} = E_1/(E_1 + \hat{N}_1). \quad (26)$$

$$\hat{N}_r = \hat{N}_1 e^{-\hat{Z}_2 (t_r - t_1)}. \quad (27)$$

The form of the middle member of Equation 26 (from the ratio of Equation 5 to Equation 1) is included for its practical import: if an offshore catch is identified by origin from any technique whatsoever, then subsampling it for maturity gives an independent estimate ($\hat{m}$) from which s_2 then can be estimated without data on the number of smolts. As noted in connection with Cleaver's model, an independent maturity estimate also gives nominally unbiased estimators for the system when N_0 is known (excluding, again, the subdivision of $\hat{Z}_2$ into $\hat{F}$ and $\hat{M}_2$ as evident from Equation 7 when $t_r \neq t_1$). Even though all estimates contain unknown bias, with no offshore fishery the values of $\hat{Z}_2$ ($= \hat{M}_{2U}$) from Equation 23 and of $\hat{N}_r$ from Equation 27 might prove useful in biomass computations.

Offshore Catch Known

It is not necessary to assume as in the Cleaver model that $M_2 = 0$ during all of $T - t_1$. Assumption 3 is: $M_2 = 0$ during $T - t_r$ when offshore fishing occurs. This gives:

$$N_{rL} = C + E_2. \quad (28)$$

Solving Equation 20 (as in the case of C known) and inserting the result in Equation 2:

$$N_{1U} = N_0 s_{1U} + E_1. \quad (29)$$

Assumption 4 is: $F = 0$ during $T - t_r$. By Assumptions 3 and 4 we would observe $C + E_2$ instead of just E_2 at time $t = T$ (similarly, Ricker's model utilizes $E_1 + E_2$ at time $t = T$). Because $C + E_2$ and N_{1U} are both too high, the coefficient, X, relating these artificial population sizes may be defined and used as below:

$$X = -\ln[(C + E_2)/N_{1U}]/(T - t_1). \quad (30)$$

$$N_{rU} = N_{1U} e^{-X(t_r - t_1)}. \quad (31)$$

The geometric mean of limits in Equations 28 and 31 is taken arbitrarily as the estimator:

$$(N_{rL} N_{rU})^{1/2} = \hat{N}_r. \quad (32)$$

We then have from Equations 4 and 5, 7, and 32:

$$C/\hat{N}_r = \hat{u}. \quad (33)$$

$$-\ln(E_2/\hat{N}_r)/(t - t_r) = \widehat{F + M_2}. \quad (34)$$

$$(\hat{u})(\widehat{F + M_2})/[1 - e^{-(\widehat{F + M_2})(T - t_r)}] = \hat{F}. \quad (35)$$

$$(\widehat{F + M_2}) - \hat{F} = \hat{M}_2. \quad (36)$$

$$[\hat{M}_2(T - t_1) + \hat{F}(T - t_r)]/(T - t_1) = \hat{Z}_2. \quad (37)$$

Given $\hat{Z}_2$ from Equation 37, remaining estimates for the case of C known may be calculated in

the following sequence from relations given previously:

Estimate	Relation
$\hat{s}_2$	Equation 7
$\hat{N}_1$	Equation 5
$\hat{m}$	Equation 26
$\hat{s}_1$	Equation 1
$\hat{Z}_1 (= \hat{M}_1)$	Equation 8
$(\widehat{s_1 s_2}), \hat{Z}_T^*$	Equation 6
$\hat{M}_l^*$	Equations 9 and 36

Bias

Equations for bias in $\hat{Z}_T^*$ and in other estimates can be written for the cases of C unknown and known. The equations are much longer than for the Ricker model (e.g., Equations 12-14), however, because estimators from the limit-mean model involve so many substitutions. The equations are therefore not written out but the next section gives numerical examples of bias.

NUMERICAL EXAMPLES OF BIAS

Cleaver's model gives no unique estimators as noted earlier, and it is evident that bias from the Ricker and Fredin models cannot be compared fairly with bias from the limit-mean model when offshore fishing is absent. Thus Equations 10 (Ricker model) and 15 (Fredin model) utilize the information that $M_1 \geq M_r > M_2$ (Ricker, 1962; Parker, 1968), hence $\hat{M}_l = M_{2U}$ as mentioned with Equation 10. For the limit-mean model without offshore fishing, however, it is interesting to see how relative bias differs among the estimates of mortality or survival, maturity, and abundance.

With offshore fishing present and $C > 0$ unknown, we expect $\hat{Z}_2 - Z_2$ or $\hat{Z}_T^* - Z_T^*$ to be less from the Ricker and Fredin models than $\hat{M}_2 - M_2$ or $\hat{M}_T - M_T$ without offshore fishing. For comparisons with bias from the limit-mean model, I use $\hat{Z}_T^* = \hat{Z}_2$ and the resulting $\hat{s}_2$ as the initial estimate for the Ricker model; $\hat{Z}_T^*$ and $\widehat{s_1 s_2}$, for the Fredin model. With $C > 0$ known I illustrate bias for the limit-mean model only—again to avoid possibly unfair comparisons with the Ricker and Fredin models.

Data published by Johnson (1970) guided selection of certain hypothetical values for input parameters: the resulting values of Ei/N_0 are intermediate between those he reported for small and large smolts (1964 brood), and in that respect may be typical of coho salmon reared at hatcheries on the lower Columbia River. The value of F assigned here is close to that calculated recently by K.A. Henry of the Northwest Fisheries Center, National Marine Fisheries Service, NOAA, and myself for the 1965-66 brood coho salmon reared at a group of Columbia River hatcheries. All time intervals are accurate to within 1.0 mo and probably to within 0.5 mo as actually
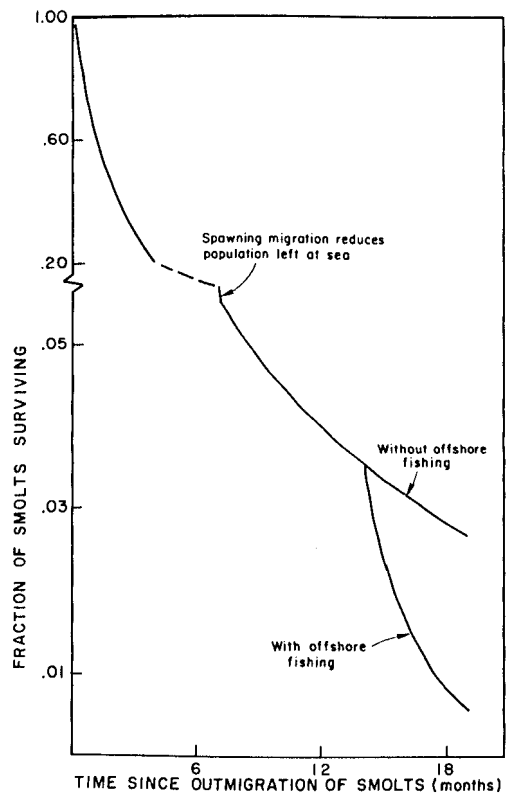

FIGURE 1.—Extinction of a hypothetical smolt class of coho salmon with and without offshore fishing during the last year at sea. Natural mortality is $M_1 = 0.40$/mo during the first $t_1 - t_0 = 7$ mo and 10% of the population matures as jacks; $M_2 = 0.06$/mo during the last $T - t_1 = 12$ mo with or without offshore fishing; and an offshore fishing rate of $F = 0.30$/mo during the last $T - t_r = 5$ mo gives a final population $(E_2/N_0$, including the inshore catch in both cases) about 22% of that with $F = 0$.

recorded for most coho salmon reared artificially in that watershed. I assume the intervals are known to within 1.0 mo even if $C > 0$ is unknown. Incidentally, all input values are the same as used for Figure 1 to illustrate the extinction of a smolt class with and without offshore fishing.

Table 1 summarizes the hypothetical input values, data, models, assumptions, and estimating schemes as applied to calculate the estimates and values of bias in Table 2. The latter incorporates a few measures to simplify presentation and facilitate comparisons within and between models. Parameter values are repeated from Table 1 and all values are rounded to four places after carrying six in

TABLE 1.—Parameter values, data, models, assumptions, and estimating equations as numbered in text and applied in Table 2 to a hypothetical smolt class of coho salmon.

Parameter value used as input and defined from Equations 1-9		Data	Models, assumptions, and equations
$M_1 = 0.40$/mo $M_2 = 0.06$/mo $F = 0, 0.30$/mo $Z_2 = 0.185000$/mo (for $F = 0.30$/mo) $M_r^* = 0.230000$/mo $M_T^* = 0.185263$/mo $Z_T^* = 0.264211$/mo (for $F = 0.30$/mo) $m = 0.10$ $t_1 - t_0 = 7$ mo $t_r - t_1 = 7$ mo $T - t_r = 5$ mo	$t_r - t_0 = 14$ mo $T - t_1 = 12$ mo $T - t_0 = 19$ mo $s_1 = 0.060810$ $s_2 = 0.486752$ (for $F = 0$) $s_2 = 0.108609$ (for $F = 0.30$) $s_1 s_2 = 0.029599$ (for $F = 0$) $s_1 s_2 = 0.006605$ (for $F = 0.30$) $u = 0$ (for $F = 0$) $u = 0.695584$ (for $F = 0.30$)	$E_1/N_0 = 0.006081$ $C/N_0 = 0$ (for $F = 0$) $C/N_0 = 0.025013$ (for $F = 0.30$) $E_2/N_0 = 0.022640$ (for $F = 0$) $E_2/N_0 = 0.005944$ (for $F = 0.30$) Time intervals as at left	1. With no offshore fishing ($F = C = 0$), apply limit-mean model by assuming $s_{1U} = s_{2L} = s$ (Equation 20) and $s_{2U} = 0.50$ (Equation 21). Solve Equations 22-27. 2. With offshore fishing but $C > 0$ unknown, assume $m = 0$ and $s_2 = 1.0$ on E_1/N_0, hence $\hat{Z}_i = \hat{Z}_T^*$ for Ricker model (Equation 10): use $\hat{Z}_T^* = \hat{Z}_2$, solve Equation 7 for $\hat{s}_2$, then Equation 5 for $s_1 \hat{s}_2 = E_2/N_0 + (E_1/N_0)\hat{s}_2$, and Equations 24-27. For Fredin model, assume $\hat{Z}_i = \hat{Z}_T^*$ and solve Equations 15 and 22-27. For limit-mean model, proceed as in Item 1 above, noting E_2/N_0 is now smaller. 3. With offshore fishing and $C > 0$ known, apply limit-mean model by assuming $s_{1U} = s_{2L} = s$ (Equation 20), $M_2 = 0$ during $T - t_r$ (Equation 28) and $F = 0$ during $T - t_r$. Solve Equations 20 and 28-37, then Equations 7, 5, 26, 1, and 6. 4. Although $\hat{M}_2$, $\hat{F}$ and $\hat{u}$ are solved only as in Item 3 above, solutions for various mortality coefficients are available from Equations 6-9 by applying survival estimates and $F \geq 0$ as appropriate in Items 1-2 (see section on Actual Situation in text).

							$N_1/N_0 = 0.054729$				
							$N_r/N_0 = 0.035960$				

TABLE 2.—Values of parameters, selected estimates, and relative bias in estimates (read each set down in that order), from models as summarized in Table 1. Values are rounded to four places after carrying six in calculations; a dash (—) indicates no estimate.

Offshore fishing	Offshore catch	Model	$s_1 s_2$	s_1	s_2	m	N_1/N_0	N_r/N_0	F	M_2	u
Absent	0	Limit-mean	0.0296	0.0608	0.4868	0.1000	0.0547	0.0360	0.0000	0.0600	0.0000
			0.0286	0.0910	0.3143	0.0668	0.0432	0.0432	—	—	—
			-0.0354	0.4962	-0.3544	-0.3317	0.6060	0.2000	—	—	—
Present	>0, unknown	Ricker	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0063	0.1031	0.0613	0.0590	0.0970	0.0195	—	—	—
			-0.0436	0.6947	-0.4356	-0.4100	0.7719	-0.4588	—	—	—
		Fredin	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0062	0.1536	0.0403	0.0396	0.0475	0.0232	—	—	—
			-0.0629	1.5261	-0.6290	-0.6041	-0.1315	-0.3553	—	—	—
		Limit-mean	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0076	0.0279	0.2726	0.2181	0.0218	0.0102	—	—	—
			0.1510	-0.5414	1.5099	1.1806	-0.6016	-0.7159	—	—	—
Present	>0, known	Limit-mean	0.0066	0.0608	0.1086	0.1000	0.0547	0.0360	0.3000	0.0600	0.6956
			0.0065	0.0758	0.0852	0.0802	0.0697	0.0383	0.2884	0.0850	0.6526
			-0.0215	0.2468	-0.2152	-0.1979	0.2742	0.0659	-0.0384	0.4165	-0.0617

calculations. Bias is expressed as the ratio, (estimate-parameter value)/parameter value. Values for F, M_2, and n are given for the limit-mean model with $C > 0$ known but values for mortality and bias are not given for the other examples. Values of E_j/N_0 include the inshore catch as if smolts are marked. It should be noted for the last two items that 1) bias in estimated mortality coefficients not shown in Table 1 can be calculated readily from the survival estimates, Equations 6-9, and parameter values in Table 1; and 2) whenever the E_j/N_0 are from spawning areas only, $C > 0$ and the inshore catch are unknown but the calculations proceed exactly as in Tables 1 and 2 with lower values of E_j/N_0 which include the effects of inshore fishing (see section on Actual Situation).

Table 2 shows striking contrasts in bias between estimates of different parameters from a given model. The limit-mean model with no offshore fishing, for instance, underestimates the target parameter, $s_1 s_2$, by only 4% but overestimates N_1/N_0 by 61% and N_j/N_0 by 20%. Also in that example, $\hat{s}_2 \simeq 49\%$ is close to the assumed upper limit, $\hat{s}_{2U} = 50\%$ (Table 1); s_2 is 35% too low and $\hat{M}_2 \simeq 0.0965$/mo (calculation from Equation 7 with $F = 0$ not shown) exceeds $M_2 = 0.0600$/mo. Thus $\hat{M}_2 = M_{2U}$ and $(\hat{N}_j/N_0) = (N_j/N_0)_U$ in the example.

With $C > 0$ and unknown, the Ricker model as used here gives smaller bias in estimates of $s_1 s_2$, s_1 and m; the Fredin model as used here, of N_1/N_0 and N_j/N_0; and the limit-mean model, of m. For these and all examples, bias in estimates of $s_1 s_2$, s_2 and m is in the same direction; of the s_j and of s_1 and m, in opposite directions: this result is completely general and is dictated by the fixed relations between these parameters and data (N_0 and E_j) in Equations 1 and 5. Again evident is the wide range of bias values for different parameter estimates within a model: -4% to 77% for the Ricker model, -6% to 153% for the Fredin model, and -72% to 151% for the limit-mean model.

With $C > 0$ known, N_j/N_0 (instead of $s_1 s_2$) is the target parameter (Table 1) and the estimate is 6% too large. In addition to providing the only point estimates shown for F, M_2 and n, the limit-mean model performs better in these

examples for the six other parameters than when offshore fishing is absent or when $C > 0$ is unknown. Bias in all six estimates is in the same direction as without offshore fishing and opposite in direction to bias from the limit-mean model with $C > 0$ unknown. Finally, the addition of offshore catch data given the smallest range of bias values for estimates of all six parameters: -22% to 27%.

SUMMARY AND CONCLUSIONS

1. The indirect approach for approximating interval-specific mortality parameters is applicable to multireturn species of salmon when data are available on at least a) the origin-specific number of smolts, b) the origin-specific numbers of adults returning from the sea each year until the smolt class is extinct, and c) the time intervals between seaward migration of smolts and each return. An offshore fishery may or may not exist and the origin-specific catches inshore or offshore may be known (as from marking/recovery experiments) or unknown.

2. Nominally unbiased estimators of mortality (or survival), maturity, and abundance do not exist in this situation because different combinations of mortality and maturity schedules can generate the same set of observable data. In connection with biomass computations, Parker (1962), Ricker (1962), Fredin (1964), and Cleaver (1969) developed models for approximating interval-specific mortality. The latter three models are reviewed in connection with the problem of bias and a new model is introduced. Observable data are assumed to be accurate in order to focus attention on bias from the models themselves. To sharpen the focus, the problem is reduced to the case of two returns and the pertinent portion of the life history of coho salmon south of British Columbia is emphasized.

3. Equations 1-9 and Figure 1 summarize the actual situation and include the situation with no offshore fishing ($F = C = 0$) to help relate the case of two returns to models developed mainly with data from more returns and, except for Cleaver's model, with natural but

not fishing mortality operating in offshore waters.

4. Mortality estimates from the Ricker (1962) and Fredin (1964) models (Equations 10 and 15, respectively) both utilize for biomass computations the independent evidence that natural mortality coefficients are highest in small, "prerecruit" stages of ocean life and lowest in later stages when fish are large enough to be exploited in offshore as distinct from inshore waters; both models give an average rate of natural mortality which is an upper limit for "prerecruits" and a lower limit for "post-recruits" (quotation marks above indicate these models were developed and applied to hypothetical as distinct from actual offshore fisheries). Ricker's model treats preultimate returns or spawning escapements as if none of those fish mature and all survive until the end of ocean life as observed with the last actual return. Equations 12-14 express absolute bias in mortality estimates from the Ricker model in terms of the unknown maturity parameter and observable data without offshore fishing or with an offshore catch unknown. Fredin's model accounts for actual timing of all returns and therefore approximates more closely than Ricker's model the actual mortality coefficients for any set of data taken when no fishery operates offshore. Fredin's model is solved by trial and error so explicit bias equations cannot be written. When offshore fishing occurs but the origin-specific offshore catch is unknown, it is reasonable to expect from both models less (unknown) bias in mortality coefficients than without offshore fishing; i.e., to use calculated values along with the fixed relations in Equations 1 and 5 as estimates of actual mortality rather than as limits for natural mortality.

5. Biomass computations of Ricker (1962), Parker (1963), and Fredin (1964) overestimate minimum losses in yield. Although the evidence indicates growth typically exceeds mortality in potential and actual postrecruits, the implicit assumption of full availability is in error: management restrictions, fleet size, and bad weather always prevent continuous, complete availability of a stock in offshore waters.

6. Cleaver's (1969) model is the first actually to utilize known offshore catches (but see Equation 7 of Ricker, 1964). Its basic assumption is that natural mortality is absent during the last year of ocean life; the assumption leads to certain one-sided limits, e.g., to the minimum population about a year before the last return (Equations 16-18). The model does not give unique estimators or bias equations but is the basis for the limit-mean model.

7. The limit-mean model with offshore fishing absent or offshore catch unknown assumes a) the survival between times of outmigration and of the first return does not exceed survival between times of the first and second returns (Equations 19-20) and b) the latter survival is less than 1.0 (Equation 21). The result is lower and upper limits on the product of these two survival fractions. The geometric mean of limits is taken arbitrarily as an estimator of the product (Equation 22), then the fixed relations among parameters and observable data (Equations 1-5) give estimates of the survival, maturity, and abundance schedules (Equations 23-27). With an offshore catch known by origin, the first assumption above (Equation 20) gives an upper limit for the number of immatures at sea near the time of the first return (Equations 2 and 29). The additional assumptions of no fishing or natural mortality after recruitment offshore gives lower and upper limits for the number recruited (Equations 28 and 31). The geometric mean is taken arbitrarily as an estimator (Equation 32) to give estimates of the exploitation rate, fishing, and natural mortality coefficients (Equations 33-37). Other estimates for survival, mortality, maturity, and abundance are then available. The limit-mean model involves many substitutions and the cumbersome bias equations are not given.

8. Numerical examples of relative bias for a hypothetical smolt class of coho salmon are explained and presented in Tables 1 and 2. Values are chosen for close agreement with data and estimates for coho salmon actually reared at Columbia River hatcheries. The four examples in Table 2 show a wide range of bias in estimates of different parameters from the same model, and also for the same parameter as estimated from different models in

different situations. Overall performance is best with these hypothetical values for the limit-mean model with offshore catch known, and this model also provides estimates of fishing and natural mortality rates offshore.

9. Direct sampling for maturity in offshore catches, when known by origin, would give nominally unbiased estimators for all parameters but those mentioned last in Item 8 above, and further would permit estimation of survival or mortality during about the last year at sea *without* data on the number of smolts. Although Atlantic salmon caught off Greenland are nearly all immature (Horsted, 1971), it may be recommended for coho and chinook salmon caught off western North America that a) maturity be monitored systematically by time and area and b) research be intensified on determining catch by origin independently of marking smolts (e.g., separating hatchery fish from wild fish by scale patterns).

ACKNOWLEDGMENTS

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