

Analysis of Mark—Recapture Data from Hatchery-Raised Salmon Using Log-Linear Models

Philip E. J. Green

Department of Mathematics, Statistics and Computing Science, Dalhousie University, Halifax, N.S. B3H 3J5

and P. D. M. Macdonald

Department of Mathematics and Statistics, McMaster University, 1280 Main Street West, Hamilton, Ont. L8S 4K1

Green, P. E. J., and P. D. M. Macdonald. 1987. Analysis of mark—recapture data from hatchery-raised salmon using log-linear models. *Can. J. Fish. Aquat. Sci.* 44: 316–326.

Large numbers of hatchery-raised juvenile Pacific salmon are routinely marked with coded-wire tags before release from the hatchery. Log-linear models are an appropriate statistical technique to analyze the numbers of recaptures in different fisheries, and the numbers of tagged fish returning to the hatchery, in terms of such factors as brood year, treatment at the hatchery, timing of release, and size at release. Log-linear analysis of catches and hatchery returns of chinook salmon (*Oncorhynchus tshawytscha*) from Robertson Creek, British Columbia, indicates that all of these factors are important, but variation between brood years overrides all other factors. Within a brood year, the conditions that maximize the number of returns to the hatchery do not necessarily maximize the number of recaptures in the fishery. Log-linear analysis of hatchery returns from a designed experiment on a single brood year of coho salmon (*O. kisutch*) from Rosewall Creek, British Columbia, quantifies the effects of the various factors but will be of limited value until the causes of variations between brood years are better known.

Des étiquettes métalliques codées sont systématiquement fixées avant le lâcher à de grands nombres de saumons du Pacifique juvéniles d'élevage. Des modèles linéaires—logarithmiques constituent une technique statistique appropriée pour analyser le nombre de poissons recapturés au cours de différentes pêches et le nombre de poissons étiquetés qui reviennent à la pisciculture, du point de vue de facteurs comme l'année de génération, les traitements en pisciculture, le moment du lâcher et la taille au lâcher. L'analyse linéaire—logarithmique sur les prises et les retours aux piscicultures de saumon quinnat (*Oncorhynchus tshawytscha*) du ruisseau Robertson (Colombie-Britannique) révèle que tous ces facteurs sont importants, mais la variation entre les années de génération l'emporte sur tous les autres facteurs. Dans une année de génération, les conditions qui maximisent le nombre de saumons revenant à la pisciculture ne maximisent pas forcément le nombre de recaptures au cours de la pêche. Une analyse linéaire—logarithmique des retours aux piscicultures obtenue dans le cadre d'une expérience portant sur une seule année de génération du saumon coho (*O. kisutch*) fréquentant le ruisseau Rosewall (Colombie-Britannique) quantifie les incidences des divers facteurs; toutefois, cette analyse n'aura qu'une valeur limitée tant que les causes de la variation entre les années de génération ne seront pas mieux comprises.

Received July 30, 1985
Accepted October 8, 1986
(J8348)

Reçu le 30 juillet 1985
Accepté le 8 octobre 1986

Many salmon hatcheries on the Pacific coast of Canada and the United States routinely carry out extensive coded-wire tagging operations before the young are released. Commercial fisheries, sports fisheries, and returning spawners are sampled for tags. The objectives of the coded-wire tagging program are to determine the survival rates, migration patterns, and contributions to different fisheries of the different stocks. This paper examines data from two hatcheries on Vancouver Island, the Robertson Creek hatchery and the Rosewall Creek hatchery.

In this paper, we address three management problems. First, we examine whether hatchery procedures can affect the ratio of Alaskan to Canadian catches. Second, we look at whether hatchery procedures can affect the number of fish returning to

the hatchery. Finally, we compare the year-to-year variability to the hatchery-induced variability. To answer these questions we apply a class of log-linear models. We introduce log-linear models and discuss the statistical problems associated with them. For this type of mark—recovery data, they are seen as preferable to analysis in terms of the catch equation and also to conventional analysis of variance on untransformed counts. Log-linear models are then used to analyze data on chinook salmon (*Oncorhynchus tshawytscha*) released from the Robertson Creek hatchery in 1972–77 and coho salmon (*O. kisutch*) released from the Rosewall Creek hatchery in 1975. The Rosewall Creek experiment was designed by Bilton (1980) and originally analyzed by a response surface analysis (Bilton et al. 1982).

In a companion paper (Green 1987), chinook migration patterns were studied by graphical analyses of the Robertson Creek chinook data.

Methods

Fish are marked with coded-wire tags before they are released from the hatchery. They are sampled for tags at the end of their lives, either through recapture in the fishery or on their return to the hatchery to spawn. Their life cycle begins in the hatchery, where fertilized eggs from returning salmon are incubated for several months until hatching and the fry are reared in large ponds until ready for release. Some of the maturing fry are marked with a 1-mm coded-wire tag (CWT) implanted into the nose cartilage. The adipose fins of the tagged fish are clipped to permit their identification later.

The rearing fry are kept in different ponds. Some ponds are designated as "production", while others may be given special treatments such as experimental diets. All fish treated similarly have the same tag code. When a group of fish is released, the average weight and the release date are noted. The number of tagged fish released is known from counters on the tagging machines, while the number of untagged fish is estimated from egg inventory data.

After release, the fish migrate to the Pacific Ocean. Each fish will eventually suffer one of the following possible fates: it may return to the hatchery to spawn; it may spawn elsewhere; it may be caught by troll, net, or sports fishermen; or it may die of "natural" mortality. The main factors in "natural" mortality are disease and predation. The life span of these fish is at most 6 yr after fertilization. In this paper, the age of the fish is the number of calendar years after the year in which the eggs were fertilized (the brood year).

Every fish returning to the hatchery is examined for a clipped adipose fin. The commercial catches are also sampled for fish with clipped adipose fins. Tagged fish are measured and their heads sent to a dissection laboratory. The tags are excised from the nose cartilage and the code is read under a microscope.

The catches in the commercial fisheries are too large to permit examination of every fish. A proportion of the boats is sampled and the number of marks in a geographical region is inflated with an "expansion factor" which is the reciprocal of the sampling proportion (proportion of catch sampled) for that geographical region. The expanded number is calculated for biweekly or monthly time intervals. The statistical effects of expansion are considered later in this paper. The data for the sport fishery depend on fishermen voluntarily bringing in the heads of salmon with missing adipose fins to head depots. Since the proportion doing so is unknown, the sport catches cannot be expanded. It is estimated that sport fishing accounts for approximately 21% of the total chinook catch (Pearse 1982).

These coded-wire mark-recapture programs are different from other mark-recapture experiments in several respects. The most important difference is that the population size is known from the outset of the experiment, whereas in most mark-recapture experiments that is the parameter to be estimated. Sampling for coded-wire tags is destructive so there is no possibility of multiple recaptures. The marking is done only at age zero, which causes some problems when estimating survival rates (Brownie et al. 1978). Finally, virtually all of the marked and unmarked fish that escape both the fishery and natural mortality return, at the end of their lives, to their orig-

inal point of release. In principle, all of the returning fish may be sampled; however, some of them spawn in the river below the hatchery; the proportion doing so is not known, and these fish escape sampling.

In this analysis we are studying the effects of auxiliary variables on recapture probabilities, in a fashion similar to Pollock et al. (1984). This is different from mark-recapture experiments in which the purpose is to estimate biologically meaningful parameters such as population size or survival rates, without considering auxiliary variables. In this modelling exercise, parameters are still estimated; however, these are estimates of the effects of the auxiliary variables.

Log-Linear Models

Models of the general class used in this paper are called log-linear models. They have the form

$$(1) \quad \vec{\pi} = e^{\vec{X}\vec{\beta}}$$

where $\vec{\pi}$ is an $n \times 1$ vector of probabilities, \vec{X} is an $n \times p$ design matrix of full rank, and $\vec{\beta}$ is a $p \times 1$ vector of parameters. Exponentiation of a vector is defined as exponentiation element by element. The model is called "linear" because the term $\vec{X}\vec{\beta}$ is a linear function of the parameters. If, for example, one column of \vec{X} is used for a covariable and another is used for its square, the model will allow for a quadratic response to that covariable, but it would still be called a linear model.

In this paper, the probabilities are probabilities of recapture for different categories of fish. The different categories correspond to different combinations of the factors of interest. The model can also be written $\vec{\mu} = E(\vec{Y}) = e^{\log(\vec{N}) + \vec{X}\vec{\beta}}$, where \vec{Y} is an $n \times 1$ vector of random variables whose elements Y_i are the numbers of recaptures, $E(\vec{Y}) = \vec{\mu}$ is the vector of expected numbers of recaptures in the different categories, and \vec{N} is an $n \times 1$ vector of the numbers of fish released from the hatchery. In the vector \vec{N} , each number of fish released may appear several times, once for each combination of factors under which that group was recaptured. The logarithm of a vector is defined by taking logarithms element by element. There is a column in the design matrix for each parameter in the model. The parameters in the vector $\vec{\beta}$, with the exception of the grand mean parameter, are called "effects." They measure the effects, on the baseline recapture probability, of different values of continuous auxiliary variables (covariables) such as weight at release, and different levels of categorical auxiliary variables (factors) such as treatment. The grand mean parameter is the logarithm of the baseline recapture probability. Interactions between categorical variables, and between categorical and continuous variables, may also be estimated. For more on this topic the reader is referred to Searle (1971) or McCullagh and Nelder (1983).

This class of models was chosen because the effects are combined multiplicatively. Multiplicative models, unlike additive models, cannot lead to negative expected counts. Bilton et al. (1982) fitted an additive model to untransformed counts and noted that the possibility of negative expected counts could be a problem.

The most suitable error distribution is Poisson; hence, the models can be treated as log-linear models. We can assume this here because the estimated probabilities of recapture are all less than 5%, so the extra complications of the hypergeometric distribution (Seber 1982) can be avoided. Log-linear models are easy to use with the computer package GLIM (Baker and

Nelder 1978). GLIM allows estimation of the parameters and fitting of the models by maximum likelihood. GLIM will handle data from unbalanced as well as balanced experimental designs and will determine if any parameters are aliased. By using GLIM we do not need to develop special computer programs for maximum-likelihood estimation of mark-recovery data, such as Conroy and Williams (1984) did. Conroy and Williams (1984) were primarily concerned with the estimation of survival rates, not the effects of auxiliary variables. Cormack (1981) has shown how GLIM can be used to estimate biological parameters from multiple mark-recapture data, again by the use of log-linear models. We also justified the use of log-linear models, at least for the continuous auxiliary variables, by plots which showed linear relationships between the logarithms of the recapture probabilities and the covariates weight and Julian day of release.

The model-fitting procedure is similar to that of stepwise regression. Parameters are entered into the model, by adding appropriate columns to the design matrix, and estimated by maximum likelihood. The goodness-of-fit of the model is then examined. The parameters are entered one at a time and in different sequences, since, in general, they are nonorthogonal. The parameters that cause large improvements in the goodness-of-fit are then included in the model and more are added subsequently. Only main effects are entered at first, followed by selected interactions. In this way, the most important auxiliary variables, those that most improve the fit of the model, are found. The data from Robertson Creek are inherently very messy (in the sense of, for example, Urquhart and Weeks 1978), since they do not come from a designed experiment. In the cross-classifications of the variables under study, there are many empty cells. Fitting high-order interactions leads to much aliasing and hence difficulty in interpreting the results. Fitting only main effects and low-order interactions leads to a more parsimonious model. The emphasis during model fitting is not so much to find a "best" model but rather to determine which sources contributed most to an improvement in the fit. This is done by examining reductions in "deviance", as explained below. Little emphasis is put on significance testing, since this is largely irrelevant when we are primarily interested in relative reductions in deviance. Furthermore, there are distributional uncertainties due to the expansion factors and overdispersion, also considered below, which would make suspect any calculation of a *p*-value. Salsburg (1985) criticized the use of significance testing as the sole tool of statistics, and we agree with his comments.

For a detailed discussion on how the goodness-of-fit of the models is examined, the reader is again referred to McCullagh and Nelder (1983, chap. 2). A brief description is given here to introduce the concept of "deviance."

Let y_i be the i th element in a vector \vec{y} of independent observations. A density function of the form

$$f_Y(y_i; \theta, \phi) = \exp\{((y_i\theta - b(\theta))/a(\phi)) + c(y_i, \phi)\}$$

is said to be a member of an exponential family of distributions for a known value of ϕ , given functions a , b , and c and some θ . The parameter ϕ is called the dispersion parameter. For the Poisson distribution, for example,

$$f_Y(y_i; \mu_i) = e^{-\mu_i} \mu_i^{y_i} / y_i!$$

where, in our case, $\mu_i = E(Y_i) = N_i \exp \sum_{j=1}^p \beta_j x_{ij}$, p being the number of parameters in the model and Y_i the random variable corresponding to the observed value y_i . The density function f_Y

can be reexpressed in the exponential family form

$$f_Y(y_i; \theta_i, \phi) = \exp((y_i\theta_i - e^{\theta_i}) - \ln(y_i!))$$

where $\theta_i = \ln \mu_i$, $a(\phi) = 1$, $b(\theta_i) = e^{\theta_i}$, $c(y_i, \phi) = -\ln(y_i!)$ and $\phi = 1$. The general form of the log likelihood, considered to be a function of $\vec{\theta} = (\theta_1, \dots, \theta_n)$ with the data vector $\vec{y} = (y_1, \dots, y_n)$ being given, is written

$$(2) \quad l(\vec{\theta}; \vec{y}) = \sum_i ((y_i\theta_i - b(\theta_i))/a(\phi) + c(y_i, \phi)).$$

The deviance, expressed in terms of the mean value parameter $\vec{\mu}$ (McCullagh and Nelder 1983, p. 25), is defined as

$$(3) \quad \text{deviance} = -2(l(\vec{\mu}; \vec{y}) - l(\vec{y}; \vec{y}))$$

where $l(\vec{y}; \vec{y})$ is the maximum log likelihood achievable for an exact fit in which fitted values equal the data (the "saturated" model). The deviance is a measure of the discrepancy of a fit. If we calculate the maximum-likelihood estimate of $\vec{\mu}$ for the current model and denote it $(\hat{\mu}_1, \dots, \hat{\mu}_n)$, then for the Poisson distribution the deviance is

$$\text{deviance} = 2 \sum (y_i \ln(y_i/\hat{\mu}_i) - (y_i - \hat{\mu}_i))$$

with summation over all categories. This is the statistic labelled G^2 by Bishop et al. (1975) with $a(\phi) = 1$. It is also equivalent to the likelihood ratio statistic and is distributed asymptotically as a chi-square random variable (Bishop et al. 1975, chap. 14). The deviance is equivalent to $2 \sum y_i \ln(y_i/\hat{\mu}_i)$, since $\sum (y_i - \hat{\mu}_i) = 0$. Deviance is a general term describing the discrepancy of a fit. For the normal distribution the deviance is the familiar residual sum of squares.

There are three special considerations for the present application. The first is the effect of the expansion factors. The number of recaptures found in the sampled boats is multiplied by an expansion factor to give an estimate of the total number of recaptures in the catch. This use of an expansion factor means that the choice of the function $a(\phi) = 1$ in the exponential model will cause the variance to be underestimated. To see this, let Y_s be the number of sampled recaptures, Y the total number of recaptures, both sampled and unsampled, and f the sampling fraction. Then Y_s/f is the estimate of Y . If we assume that Y_s is distributed as a Poisson random variable with mean μ_s and that Y is Poisson with mean μ , then $\mu_s = f\mu$ and

$$E(Y_s) = \mu_s, \text{Var}(Y_s) = \mu_s$$

$$E(Y) = \mu, \text{Var}(Y) = \mu.$$

If we expand the sampled recaptures by the sampling fraction (the inverse of the expansion factor), then $E(Y_s/f) = \mu_s/f = \mu$ but

$$(4) \quad \text{Var}(Y_s/f) = \mu_s/f^2 = \mu/f.$$

However, the assumption of Poisson errors implies that

$$E(Y_s/f) = \text{Var}(Y_s/f) = \mu.$$

Comparing this with (4) shows that the Poisson assumption will underestimate the variance of the expanded recaptures. To correct this, we can set

$$(5) \quad a(\phi) = \phi/f$$

by use of a weighting vector during model fitting with GLIM. During fitting it is sufficient to set $\phi = 1$; then ϕ can be estimated by

$$\hat{\phi} = G^2/(n-p)$$

when a satisfactory fit is found (McCullagh and Nelder 1983, p. 133). Using (5) with $\phi = 1$, we have

$$\text{Var}(Y/f) = \mu a(\phi) = \mu/f$$

which agrees with (4). The deviance will be decreased by the use of (5) as we can see by examining (2) and (3).

The second consideration is the problem of overdispersion relative to the model of Poisson variation, i.e. $\text{Var}(Y/f) > \mu/f$. This indicates that $\phi > 1$. This can occur if the observations are not independent, which would happen, for example, if the marked fish were in any way clumped together. Since ϕ can be estimated from the data, we can estimate the amount of overdispersion. If there is overdispersion, we cannot assume a Poisson distribution but will assume that the data are distributed as a scaled Poisson.

The estimate of the dispersion parameter can be used for testing. If there are two models whose deviances we denote G_1^2 and G_2^2 , then an approximate chi-square statistic for testing whether the second model offers a significant improvement over the first can be calculated from

$$\{(G_1^2 - G_2^2)/(p_2 - p_1)\} (\hat{\phi}_2)^{-1}$$

where p_i is the number of parameters fitted in model i ($i = 1, 2$), $p_2 > p_1$, all the parameters of the first model are included in the second, and $\hat{\phi}_2 = G_2^2/(n - p_2)$. This is analogous to an F -test using error sums of squares for two models to test whether the second significantly improves the fit. The estimate of dispersion is given in the analysis of deviance tables because it is a good measure of the goodness-of-fit. The smaller the dispersion, the better the fit, or the less unexplained deviance.

The third consideration is the method by which the initial population size vector \vec{N} is treated during model fitting. Taking logarithms of the log-linear model gives

$$\log(E(\vec{Y})) = \log(\vec{N}) + \vec{X}\vec{\beta}.$$

We do not wish to estimate $\log(\vec{N})$, since it is a known vector of constants whose regression coefficient is known to be 1. By specifying that it is an "offset" in GLIM terminology, it is subtracted from the log-transformed data and the result regressed on the remaining covariates (Baker and Nelder 1978).

The log-linear models presented in this paper are proposed as an alternative to models for commercial mark-recapture data based on the "catch equation", that is

$$N_t = N_0 e^{-(F+M)t}$$

where N_t is the number of individuals remaining after t time intervals from the initial population size N_0 and F and M are the instantaneous coefficients of fishing and natural mortality, respectively. Using the catch equation, it can be shown that

$$\pi_i = \frac{F_i}{F_i + M_i} \left\{ \exp\left(-\sum_{j=1}^{i-1} (F_j + M_j)\right) \right\} \times \left\{ 1 - \exp(-(F_i + M_i)) \right\}$$

where π_i is the probability of recapture in time period i and the subscripts on F and M denote the fact that they vary with time. This approach has been used by Nicholson and Pope (1977) and Gulland (1955), for example, and is described in Seber (1982). In this paper we are not relating the recapture probabilities to F and M , but to a set of auxiliary variables. In any case, F and M are not separately estimable. In the data set under study there is no information on natural mortality. The total natural mor-

tality can be estimated but it is not possible to estimate the M_i , as the times of death are not known. There is no way to estimate F_i unless values for the M_i are assumed. The context in which they are being assumed, with or without fishing mortality, must be made clear. As Lawless (1982, p. 491) pointed out, estimating the hazard function that would result if other causes of death were removed requires strong assumptions. Furthermore, fishing mortality is clearly age and time dependent because of the type of gear used in the troll fishery. There may also be mortalities due to fishing that are not observed as fishing mortality and would hence be incorrectly classified as natural mortalities. Examples are damage to fish that escape or predation by seals or sea lions while on the hook (Ricker 1976). Thus "natural mortality" could be different at different fishing mortalities.

On the other hand, by excluding F and M from the models in our analysis, our conclusions cannot be extrapolated to different fishing strategies or to changes in management techniques or to conditions under which a component of natural mortality not modelled by any of the auxiliary variables may change.

Chinook Salmon from the Robertson Creek Hatchery

The data set consists of 20 tag-code groups from brood years 1972-77 (Table 1). In their raw form, the recapture data are given by month for 12 regions along the Pacific coast, ranging from Oregon State to the top of the Alaskan Panhandle (Fig. 1), for all years in which the salmon were caught by the three types of fishing gear. The hatchery-return data include only the total number of returns of each CWT group per year. No information on fishing effort was available to us. The average weight refers to the average weight of a sample of fish taken from the CWT group at the time of release.

The treatments EWOS and OMP in Table 1 refer to two different food types; however, some sources say that groups 2 and 3 were production groups, that is, grown under the usual, nonexperimental conditions. As such, two classifications of treatments were established for model fitting. The first, denoted T_1 , places groups 2 and 3 with the production groups and thus has five levels; the second, denoted T , considers them to be separate treatments, and thus has seven levels. Groups 13-18 were designated as "early", "mid", or "late" release time. This factor is similar to the Julian day of release, but not quite the same. For example, the "mid" treatment group in 1976 (No. 17 in Table 1) was released on the same Julian day as the "early" treatment group in 1975 (No. 15). A measure of incubation and pond rearing time would be more useful than the day of release, since the "ideal" day of release probably depends on many factors, such as degree-days accumulated, which vary from year to year. Unfortunately, the hatchery managers could not provide us with this information.

Groups 5 and 12 were not included in many of the analyses because they were found to be too unusual due to their very high and low release weights, respectively.

Analysis of Fishery Recaptures

This was an attempt to model the response (number of recaptures) in Alaska and British Columbia as a function of various effects and covariables. The model was of the log-linear form (1). The factors or effects modelled were age at recapture (A),

TABLE 1. Description of the coded wire tag groups (Robertson Creek).

Group No.	Tag code	Treatment	Release weight	Tagged release	Total release	Release day	Brood year
1	02/05/01	Production	5.7	26 881	510 739	129	1972
2	02/08/01	EWOS	5.5	2 627	2 627	171	1972
3	02/11/01	OMP	5.4	39 013	222 819	171	1972
4	02/02/03	Production	5.9	23 480	603 717	191	1973
5	02/08/06	Supersmolt	41.3	20 777	73 094	448	1973
6	02/06/02	Production	5.0	16 137	29 352	172	1973
7	02/05/06	Production	6.3	27 726	520 930	196	1973
8	02/04/06	Production	6.3	27 444	438 094	191	1973
9	02/06/06	Production	5.2	46 194	1 003 877	162	1974
10	02/09/06	Production	5.3	27 383	453 766	162	1974
11	02/12/06	Production	4.5	11 674	11 674	158	1974
12	02/14/06	Production	2.7	28 283	228 940	162	1974
13	02/04/09	Late	5.2	47 724	462 985	162	1975
14	02/04/08	Mid	5.2	50 731	487 145	155	1975
15	02/13/05	Early	5.4	10 702	10 829	146	1975
16	02/16/29	Early	5.3	59 227	63 054	130	1976
17	02/16/30	Mid	5.4	64 550	3 188 072	146	1976
18	02/16/31	Late	5.3	69 203	442 487	159	1976
19	02/22/17	Production	4.4	70 816	4 178 531	156	1977
20	02/22/18	Production	5.3	66 725	3 553 187	154	1977
Total				737 297	16 485 919		

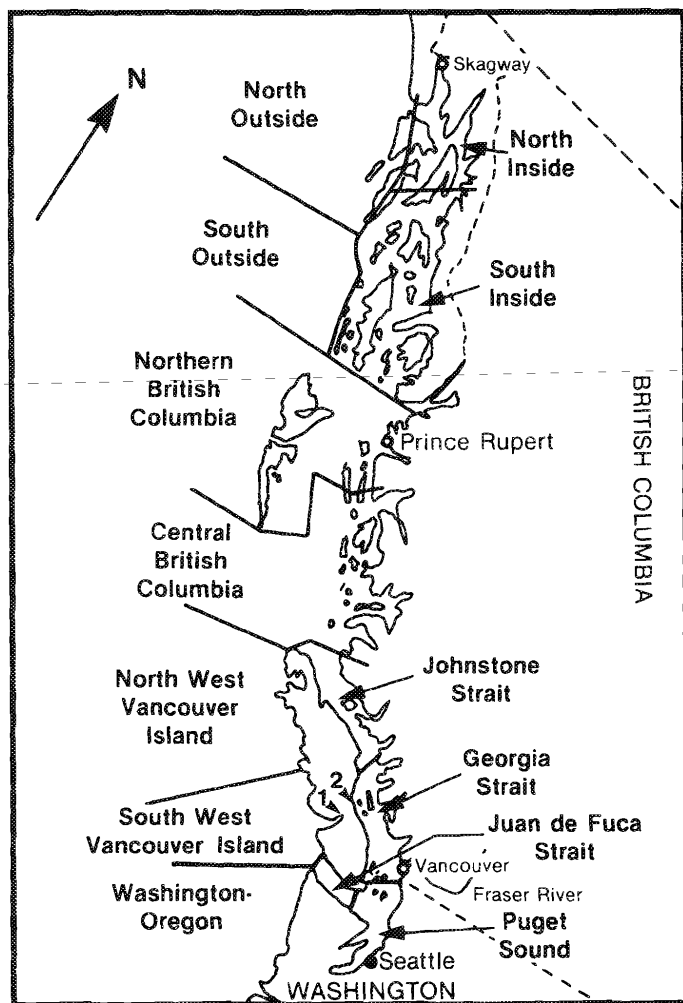


FIG. 1. Commercial catch regions for the Pacific coast. 1 = Robertson Creek Hatchery, 2 = Rosewall Creek Hatchery.

prerelease treatment (T or T_1), brood year (B), and place of recapture (R). Place of recapture was characterized as 12 different locations (Fig. 1), without taking into account the geographical relationships between the statistical areas. The covariables were weight at release (W) and Julian day of release (J).

A model that includes all the main effects could be written out in full as

$$(6) \quad E(Y_{hijkl}) = N_{hjk} \exp(\omega + \alpha_i + \tau_j + \xi_k + \gamma_l + \theta_1 W_{hjk} + \theta_2 J_{hjk})$$

where ω is the grand mean, α_i is the effect due to age at recapture i , τ_j is the effect due to treatment j , ξ_k is the effect due to brood year k , γ_l is the effect due to the place of recapture l , and θ_1 and θ_2 are the slopes of the log observations versus the two covariables. The index h indicates the release group. The number of recaptures, Y_{hijkl} , is assumed to be distributed as a scaled Poisson with expected value $E(Y_{hijkl})$. In terms of the general log-linear model notation (1), parameters ω , the α 's, the τ 's, the ξ 's, the γ 's and θ_1 and θ_2 are successive elements in the vector β . The nonzero N_{hjk} 's are successive elements in the vector N .

Before fitting was begun we did some preliminary plots and calculations which showed that the ratio of recaptures in Alaska to those in British Columbia varied considerably over the lifetimes of the fish (Table 2). No age 2 fish were recaptured in Alaska and very few in British Columbia. Generally, more age 3 fish were caught in British Columbia than in Alaska, but for ages 4 and 5 this ratio was reversed. Hardly any age 6 fish were caught in either place. The age 2 fish are small, have a low commercial value, and are not caught in large quantities. The age 6 fish have a higher commercial value but are not numerous in the fishery or elsewhere. For these reasons, only ages 3–5 were included in the model.

A weighting vector for GLIM was defined by taking the reciprocal of the sampling fraction for each recapture group. The sampling fractions for yearly totals were known for most

TABLE 2. Alaska/British Columbia recapture ratios by age (troll fishery) (BC = fish caught only in British Columbia; AL = fish caught only in Alaska).

Group	Age 2	Age 3	Age 4	Age 5	Age 6
1		0.31	BC	5.14	
2		BC	1.55	2.23	AL
3		0.35	0.67	3.33	AL
4		0.05	0.83	1.67	
5		BC	0.93	0.67	
6		0.12	2.00	AL	
7		0.11	3.38	1.77	
8		BC	0.44	0.60	0.67
9	BC	0.49	1.23	2.95	
10		0.53	1.13	3.92	
11		0.39	0.84	AL	
12	BC	1.25	1.67	2.00	
13	BC	0.28	1.14	1.15	
14	BC	0.19	1.27	2.18	
15		0.24	3.00	2.00	
16	BC	0.35	0.99	3.86	
17	BC	0.26	1.04	1.23	
18	BC	1.15	1.79	1.79	
19		0.09	1.80	2.86	
20		0.63	1.79	5.33	

of the CWT groups at the three ages and two locations. Where they were not known, the mean sampling fraction was used.

The importance of an auxiliary variable or interaction is indicated by its relative reduction in deviance (Table 3). Model 2 is the simplest and includes only main effects. The reduction in deviance achieved by adding brood year shows that there are very large differences in the recapture rates for different brood years. These differences are greater than those due to the different treatments. The reduction in deviance obtained with the second classification of the treatments is much larger than that obtained using T_1 , so the food pellets that CWT groups 2 and 3 were given had some effect on the recapture rates. CWT group 2 showed a greater recapture rate than group 3, which was less than, but quite close to, that of the production groups. Treatment 6 ("mid" release time) produced the most recaptures.

Model 6 shows that there is an important interaction between age at recapture and place of recapture (Table 3). This confirms the tendency, noted above, for the British Columbia fishery to exploit the younger fish (age 3), while the Alaskan fishery exploits ages 4 and 5.

Models 7 and 8 show that Julian day of release has a stronger effect than weight at release on the recapture rates. Model 9 fits individual slopes for recapture rates against weight at release and Julian day of release, for each age at recapture and each place of recapture. All the slopes for Julian day are negative when it is entered first, except for age 5 in British Columbia for which it is positive. This suggests that as Julian day of release is increased, recaptures in British Columbia increase, while recaptures in Alaska decrease. When the release weights are added to the model, this difference in slopes disappears; however, a similar relationship appears for the release weights, indicating that as release weights rise, recaptures increase slightly faster in British Columbia than in Alaska. Note, however, that this applies over the range of release weights and Julian days observed in this data set, and the relations will not necessarily hold true when extrapolated.

Models 11–15 examine some of the interactions. It appears from these models that the interaction of brood year with age

at recapture is important and the other interactions much less so, since $\hat{\phi}$ is smallest for those models which include that interactions.

The most important result from this analysis is the large reduction in deviance achieved by adding the brood year effect. This could mean that there are large yearly changes in fishing effort, in the genetics of the broods, in conditions at the hatchery such as water quality, in water level in the rivers leading to the ocean, in mortality after marking, and possibly other factors as well.

The differences in recapture rates in Alaska and British Columbia due to release weight and Julian day are in fact slight and it is doubtful whether it is worth trying to manipulate these in an attempt to increase recaptures in British Columbia. It is difficult to interpret the increasing recaptures due to increasing Julian day in the light of the fact that "mid" release time (treatment 6) was found to increase recaptures more than "early" or "late" release (treatments 5 and 7).

The large deviances in the anODEV table can be misleading. Deviance is a measure of discrepancy between the fitted and observed values. Any model is an idealization and, except for the case of a saturated model where the number of fitted parameters equals the number of observations, there will always be a discrepancy between the fitted model and the observed data. With large sample sizes this discrepancy is almost certain to be detected by a statistical test, even though it may be small for practical purposes. Considerations of parsimony suggest that it is not desirable to add many more parameters solely for the purpose of reducing the goodness-of-fit to a statistically insignificant level, as the resulting model would be too complicated to interpret and, typically, the standard errors of the fitted parameters would be too large for the fitted model to be useful. What is needed is a measure of whether the discrepancy between observed and expected values is small enough that the fitted model can safely be used for prediction. This is not so much a statistical problem as a management one. How much of a discrepancy, or error, between predicted and observed values is acceptable from a management point of view?

The models presented here, or other related models, could be used to predict the catch of stocks of salmon in different locations. A model could be adapted to fit the requirements of fishery managers; for example, they may wish to have predicted catches broken down into smaller geographical regions. Confidence intervals could be constructed for the predictions, as is done in the next section. Since it is not possible to know what the brood year effect is until after the entire brood is dead; or until we learn the causes of the brood year effect, the manager could be asked to select between optimistic and pessimistic scenarios, and brood year effects would be chosen based on experience with previous estimates in former year-classes. This model would be more credible for predicting catches than would a simulation model that is not based on parameters estimated from data. Of course, the dangers of extrapolation remain.

Analysis of Hatchery Returns

In order for the hatchery to increase the number of salmon at sea and available for the fisheries, the hatchery managers must know the factors that affect the probabilities of capture. Are these the same factors that influence the number of salmon returning to the hatchery? By analyzing the hatchery-return data we can attempt to answer this question.

When the migrating salmon return to the hatchery at ma-

TABLE 3. Analysis of deviance for Robertson Creek recapture model. The symbols for the factors are as follows (combinations indicate interactions): M = grand mean, A = age at recapture, R = place of recapture, B = brood year, T₁ = treatments (first classification), T = treatments (second classification), J = Julian day of release (counted from January 1 and taking leap years into account), W = mean weight at release.

Model	Main effects	First-order interactions	Second-order interactions	Deviance	df	$\hat{\phi}$
1	M			3223	107	30.1
2	M,A,R			2147	104	20.6
3	M,A,R,B			1096	99	11.1
4	M,A,R,B,T ₁			1055	97	10.9
5	M,A,R,B,T			767	95	8.1
6	M,A,R,B,T	AR		462	93	5.0
7	M,A,R,B,T,J	AR,AJ,RJ	ARJ	365	87	4.2
8	M,A,R,B,T,W	AR,AW,RW	ARW	378	87	4.4
9	M,A,R,B,T	AR,AW,RW,AJ				
	J,W	RJ	ARW,ARJ	314	81	3.9
10	M,A,R,B,T	AR,BA,AW,RW				
	J,W	AJ,RJ	ARW,ARJ	182	71	2.6
11	M,A,R,B,T	AR,BA,TA				
	J,W	AW,RW,AJ,RJ	ARW,ARJ	172	63	2.7
12	M,A,R,B,T	AR,BA,TA				
	J,W	AW,RW,AJ,RJ,BR	ARW,ARJ,BAR	111	48	2.3
13	M,A,R,B,T	AR,BR				
	J,W	AW,RW,AJ,RJ	ARW,ARJ	286	76	3.8
14	M,A,R,B,T	AR,TA				
	J,W	AW,RW,AJ,RJ	ARW,ARJ	239	71	3.4
15	M,A,R,B,T	AR,BA,AW				
		RW,AJ,RJ,BR	ARW,ARJ,BAR	119	56	2.1

turity, all of them are sampled. There are no expansion factors, no variable fishing effort, and so the statistical problems encountered in the previous section are avoided. The major problem encountered in analyzing these data is that not all of the fish that return to spawn return to the hatchery; many spawn in the river below the hatchery, and nothing is known about the proportion doing so. Factors affecting the number spawning below the hatchery could include water conditions and crowding at the hatchery entrance.

The factors that we may wish to include in a model for these data are the ages of the returning fish, their brood year, the year in which they returned, and the prerelease treatment. The effect of the average release weight and Julian day of release should also be included. Obviously, age at return and brood year will be aliased with the return year, since return year is the sum of age at return plus brood year. This means that there is no way of estimating, separately from age at return and brood year effects, the effects due to water conditions and other factors in the year that the fish return.

The data set consists of four returning age groups for the same 20 CWT groups described earlier. The two anomalous CWT groups were omitted from this analysis, leaving a total of 72 observed cases. The number of observations is quickly exceeded by the number of parameters when the interactions are fitted (well before the saturated model is reached) and there is much aliasing, especially between brood year and treatments. In particular, treatment 4 is aliased with the other treatments and treatment 7 is aliased with the 1976 brood year. When the brood year by treatment interaction is fitted, for example (model 20 of Table 4), there are an additional 30 parameters entered into the design matrix of model 4 to get model 20, but 28 of these are aliased. Thus, the degrees of freedom decline by only 2, from 59 to 57. This forces us to look

for a very parsimonious model. With four return ages, six brood years, and seven treatments, there are a total of 168 possible categories. Less than 72 of these have data in them, since some have replicate observations. With such messy data, we should not be surprised if we cannot find a model which adequately explains the underlying mechanisms. The emphasis should be on trying to find effects that contribute a relatively large amount to the reduction in deviance, as in the previous section.

We are modelling in the log-linear form the probability of a fish returning to the hatchery. The treatments are those of the second classification of treatments, T, used in the recapture model. Model 4 includes main effects only, all of which significantly reduce the deviance (Table 4). Models 5 and 6 show that Julian day of release is, by a small margin, more important than weight at release as a covariable, if the slope is assumed to be the same in each response category.

Models 7–12 examine reductions in deviance obtained by fitting different slopes for the two covariables at each of the three main effects. None of these models are clear “winners.” In all cases, Julian day of release causes a greater reduction in deviance than does weight at release, especially in interaction with age at return.

Models 13–15, 16–19, and 20–22 fit first-order interactions between different pairs of main effects and a different slope for either Julian day of release or release weight at each level of these interactions. It is not possible to fit any more interactions than this due to the structure of the data. While in some cases there may appear to be enough degrees of freedom remaining to fit another interaction, the interaction will usually be aliased with parameters already in the model. Hence, model 21 turns out to be identical to model 9, so nothing was gained by fitting the additional interactions. Similarly, model 22 is

TABLE 4. Analysis of deviance for Robertson Creek hatchery return model. The symbols for the factors are as follows (combinations indicate interactions): M = grand mean, A = age at return, B = brood year, T = treatments (second classification), J = Julian day of release, W = mean weight at release. Interactions shown in lowercase are completely aliased with other terms and may be omitted from the model without affecting the fit.

Model	Main effects	First-order interactions	Second-order interactions	Deviance	df	No. of parameters aliased	$\hat{\phi}$
1	M			5115	71	—	72.0
2	M,A			3309	68	—	48.7
3	M,A,B			1349	63	—	21.4
4	M,A,B,T			1113	59	2	18.9
5	M,A,B,T,W			1081	58	2	18.6
6	M,A,B,T,J			994	58	2	17.1
7	M,A,B,T,W	AW		929	55	2	16.9
8	M,A,B,T,J	AJ		851	55	2	15.5
9	M,A,B,T,W	BW		1007	54	3	18.7
10	M,A,B,T,J	BJ		1002	55	4	18.2
11	M,A,B,T,W	TW		1024	56	6	18.3
12	M,A,B,T,J	TJ		980	56	6	17.5
13	M,A,B,T	BA		601	44	2	13.7
14	M,A,B,T,W	BA,BW,AW	BAW	417	22	3	17.3
15	M,A,B,T,J	BA,BJ,AJ	BAJ	239	21	3	11.4
16	M,A,B,T	TA		868	44	5	19.7
17	M,A,B,T,W	TA,AW,TW	TAW	515	29	18	17.8
18	M,A,B,T,J	TA,AJ,TJ	TAJ	533	29	18	18.4
19	M,A,B,T	TA,TW,tj					
	J,W	AW,AJ	TAW,taj	398	25	42	15.9
20	M,A,B,T	BT		1050	57	30	18.4
21	M,A,B,T,W	bt,BW,tw	btw	1007	54	69	18.7
22	M,A,B,T,J	BT,BJ,TJ	btj	979	54	69	18.1

nearly identical to model 12. The model with the lowest dispersion and deviance and the most unaliased parameters is model 15. Model 14 is also quite good.

These two models show that including either release weight or Julian day of release with the interaction between brood year and return age improves the fit over that of a model which fits a common slope. Inclusion of Julian day of release causes the greatest improvement. The hatchery managers are well aware that weight and time of release are very important in determining the number that return. These analyses show that weight and time of release have different effects depending on the brood year and on the age of the fish that return. Even though these effects may appear to be slight, accounting for all of these differences does improve the overall ability of the model to predict returns.

Again the modelling effort shows that differences between brood years are very significant and emphasizes the need for further research on the causes of these differences. Bilton et al. (1982) analyzed the influence of time and size at release of juvenile coho salmon on returns at maturity to Rosewall Creek by using a response surface analysis. However, the entire experiment was carried out for only one brood. While a certain combination of size and time at release may produce high returns within a given brood, the differences in returns between broods might completely overshadow any gains obtained by manipulating hatchery conditions. The fact that brood year has such a strong effect in both hatchery-return data and fishery-recapture data shows that if it is fishing effort that causes the brood year effect, then fishing must kill a high enough proportion of the fish that there are significantly fewer fish available for spawning in the hatchery. If variations of effort in the

troll fishery cause the observed brood year effect in the recapture models, then the terminal fishery (which operates in Alberni Inlet just before the salmon migrate up the Somass River to Robertson Creek) could contribute to the brood year effect in the hatchery-return models (Schnute and Sibert 1983). Terminal fishery catches could be built into this model. There are also sport and Indian fisheries but no data are available for these. It seems to us that a matter of utmost importance is to have reliable data on the effort in each fishery. Without these data it is impossible to determine whether there are factors other than fishing that influence both recaptures and returns, and, given the strength of the brood year effect, this is a serious gap in our understanding of the resource.

The sign of the slopes of the returns with respect to the two covariables at different brood years was examined (Table 5). It is striking that in brood year 1972 the estimates of the slopes are all greater than or equal to zero, whereas in brood year 1975 they are all less than or equal to zero. If two researchers had done separate mark-recapture experiments in these years, they would have reached opposite conclusions! This indicates that the value of the experiment of Bilton et al. (1982) will not be realized until it is repeated in other years.

Model 15 is used to demonstrate the use of this type of model for predicting returns (Fig. 2). This model (or a similar one) could be used to determine if there was a differential mortality between marked and unmarked fish. The model estimates the percentage of returning marked fish. It could similarly be used to predict the percentage of returning unmarked fish. By making these predictions for several years' releases, the total number of fish returning to the hatchery each year could be estimated. If these predicted numbers were consistently lower than

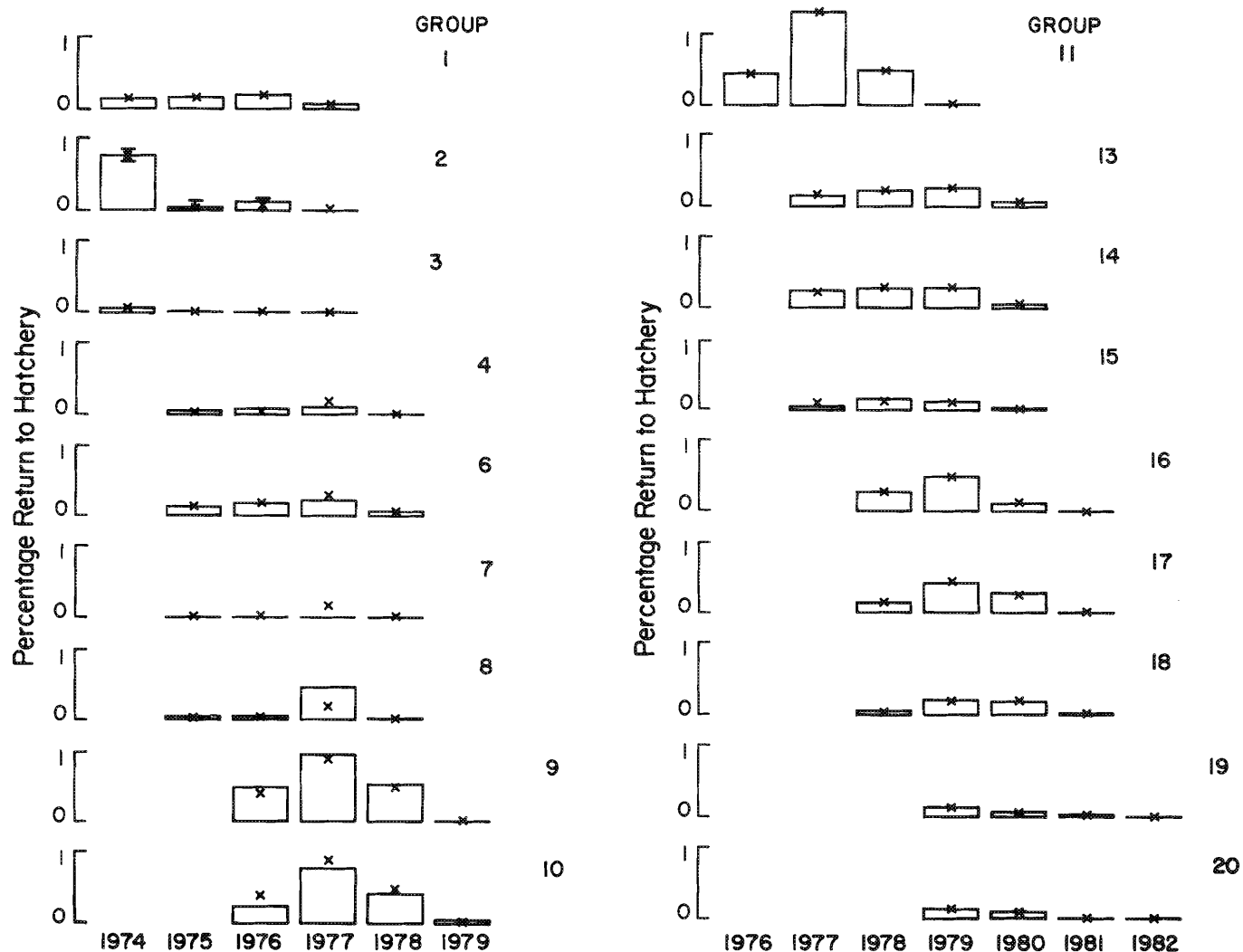


FIG. 2. Observed and estimated percentage returns from the Robertson Creek hatchery return model (model 15, Table 4). The bars represent the observed percentage returns for a given group of fish. The crosses show the returns estimated by the log-linear model. In most cases the range of the 95% confidence intervals on the model estimates was narrower than the width of the crosses; when the confidence intervals were large enough, they were plotted as horizontal lines above and below the crosses. The five bars are for ages 2–5. They are offset to show the effects of calendar years. The scale of the plots is shown in percentage points along the left. This figure shows that the model is quite accurate at estimating the observed values, even though the confidence intervals on some occasions do not overlap with the observed percentage returns. The difference between estimated and observed returns in these cases is only a fraction of a percentage point.

TABLE 5. Slopes of responses to covariables weight (W) and Julian day (J) for hatchery-return model (+ = positive slope, – = negative slope, 0 = not significantly different from zero, A = aliased, cannot be estimated).

Broodyear	Age 2		Age 3		Age 4		Age 5	
	W	J	W	J	W	J	W	J
1972	A	+	+	0	+	0	+	A
1973	–	–	0	–	0	0	0	–
1974	0	0	0	–	0	0	0	0
1975	–	0	–	0	–	0	–	0
1976	0	0	0	0	+	0	0	0
1977	0	0	0	0	0	0	A	0

the observed numbers, this would be an indication of greater mortality for marked fish.

The plot of estimated and observed values for model 15 (Fig. 2) is useful for demonstrating the close fit of the model

to the data. The confidence limits of the estimated returns do not always include the observed number of returning fish. The difference is generally only a small fraction of a percentage point, which for practical purposes, and given the messiness of the data, is quite tolerable. If data were available on the sex of the returning fish, the fit could be improved, since males and females do not return to the hatchery at the same ages in the same proportions. There are virtually no 2- or 3-yr-old females returning to the hatchery, and no 5-yr-old males.

Coho Salmon from the Rosewall Creek Hatchery

We used log-linear models to reanalyze a set of data previously analyzed by Bilton et al. (1982). They used a response surface analysis to analyze the influence of time and size at release of coho salmon on their returns at maturity to Rosewall Creek. The data set consisted of six pond populations, three size groups (small, medium and large), and four release dates, giving a $6 \times 4 \times 3$ factorial design. The release dates were

TABLE 6. Analysis of deviance for Rosewall Creek hatchery returns. The symbols for the factors are as follows (combinations indicate interactions): M = grand mean, A = age at return, P = rearing pond, J = Julian day of release, W = mean weight at release.

Model	Main effects	First-order interactions	Second-order interactions	Deviance	df	$\hat{\phi}$
1	M			3703	111	33.4
2	M,A			3286	110	29.9
3	M,J			2076	108	19.2
4	M,P			3639	106	34.3
5	M,A,J			1659	107	15.5
6	M,A,P			3223	105	30.7
7	M,J,P			2026	103	19.7
8	M,A,J,P			1610	102	15.8
9	M,A,J,P,W			1412	101	14.0
10	M,A,J,P,W	AJ		1246	98	12.7
11	M,A,J,P,W	JP		1348	91	14.8
12	M,A,J,P,W	AW		941	100	9.4
13	M,A,J,P,W	JW		1354	98	13.8
14	M,A,J,P,W	PW		1408	96	14.7
15	M,A,J,W	AJ,AW,JW	AJW	333	96	3.5
16	M,A,J,P,W	AJ,AW,JW	AJW	311	91	3.4

Julian days 104, 132, 161, and 189, all in the year 1975. On Julian day 189 there was only one pond population released. If the size groups were considered levels of a factor, the design would be nested, as all three size groups increased with the day of release. Since the average weight at release of each tag group was known, we treated weight as a covariable. Bilton et al. (1982) modelled both weight and Julian day as covariables, but we have treated Julian day as a factor. This gives a 6×4 design with five empty cells and three replicates in all other cells. Bilton (1980) gave a complete description of the data set.

Bilton et al. (1982) analyzed the sum of the hatchery returns and the commercial and sport catches of adult coho salmon, but only hatchery-return data for jacks (males that mature early at age 2). They assumed that the effects of time and size at release were additive and that errors were normally distributed and additive. Their model was nonlinear and consisted of eight unknown parameters which had no simple biological interpretation. One problem with their model was the assumption of normally distributed errors. As the authors stated, with this assumption the predicted responses could take physically impossible negative values. The effects were also entered additively, even though this is not recommended for count data (Bishop et al. 1975, p. 23–24). There were four release dates. They treated Julian day of release as a continuous covariable but it is treated here as a four-level factor, since the data were already grouped. This has advantages in estimating interactions.

Only the hatchery returns were modelled, as there were no data available on the expansion factors for sampling of the fishery. Adding the hatchery returns to the commercial and sport catches could have implications for the variance structure of the data. As discussed earlier, the variance and probability distribution of the commercial catches are affected by the expansion factors used, whereas the hatchery returns are not. How should the data be weighted when part of the count is expanded and part is not? There is a more fundamental reason for not adding the two counts: do the catches and returns really respond in the same way or should separate modelling attempts be made, as in this paper?

The factors included in our models were rearing pond (P),

Julian day of release (J), and age at return (A). The age factor was used to differentiate between jacks and adults. The only covariable was release weight (W).

Analysis of Hatchery Returns

Two of the main effects, age at return and Julian day of release, were significant, irrespective of their order of entry into the model (Table 6). For practical purposes it is not worth including the pond effect; the six different pond populations contribute relatively little to reducing the deviance, although in a strictly statistical sense the reduction is significant, assuming the reduction in deviance to be distributed as a chi-square random variable.

Amongst the first-order interactions not involving the covariable weight at release, the interaction between age at return and Julian day of release is the strongest. Amongst those involving release weight, the interaction between age at return and release weight is the strongest. However, adding the second-order interaction between return age, Julian day, and release weight drastically reduces the deviance. Models 15 and 16 are proposed as suitable fits. The return age by Julian day terms are intercepts, and the return age by Julian day by release weight terms are slopes, for the logarithms of the returns as a function of release weight at each combination of return age and Julian day of release. Plots of the log returns against release weight showed that a linear relationship existed for all the return age by Julian day combinations. This relationship was strongest for the jacks. Correlations of log jack returns versus release weight for each Julian day were as high as 0.89. These plots and the estimates of the parameters from the models showed that the return of jacks is an increasing function of weight at release whereas the return of adults is a decreasing function. Moreover, there is some tendency for the slopes to approach zero at the later Julian days.

This implies that greater returns of jacks may be obtained by early release of larger juveniles, exactly as Bilton et al. (1982) found. In the case of adults, the maximum predicted returns are obtained by late release of small juveniles. This is contrary to the predictions of Bilton et al. (1982), probably due to the inclusion of commercial and sport catches in their analysis.

This may also explain why they found quadratic rather than linear relationships. The proportion of adult coho caught in the fisheries is about 5–10 times greater than the proportion returning to the hatchery. Thus, the factors maximizing hatchery returns are masked by those maximizing catches, and the same conditions will not maximize both.

Discussion

The analysis of the Robertson Creek chinook data was an attempt to use statistical models to extract as much information as possible about the effects of hatchery manipulations, from what was, in a statistical sense, an unplanned experiment. Because production from the hatchery could not be jeopardized, only minor variants from established procedures and a limited number of different combinations of variants could be tried. As a result, aliasing limited the complexity of models that could be fitted. Also, our findings cannot be extrapolated to conditions vastly different from normal production. Nonetheless, something was learned from the analysis.

The analyses of the Robertson Creek recaptures and returns show that the hatchery-induced variability is small compared with the variability between brood years. This implies that, within reasonable limits, there is little a hatchery manager can do to affect the recaptures and returns of fish until the factors causing the brood year variability are understood better. The analyses also established that the conditions which maximize returns to the hatchery will not necessarily be the same conditions which maximize catches in the fishery.

The experiment at Rosewall Creek was well designed using classical experimental design concepts. However, it was carried out only for one brood year. The Robertson Creek analyses showed that yearly variations are very large and there may be interactions between brood years and the other factors. This means that extrapolation of the results of the model developed here, or the model of Bilton et al. (1982), to predict the returns and/or catches of coho salmon in later years may give poor predictions. Manipulation of hatchery conditions based on these models could even decrease rather than increase the returns and catches for some brood years. Bilton et al. (1982) did some comparisons of their results with those from other hatcheries in Washington State and British Columbia and found a poor correspondence. They concluded that other as yet unrecognized factors may be influencing the results. We agree, and again emphasize the need for further research to determine what these factors are.

Acknowledgements

We are grateful to Stephen Smith and Jon Schnute for helpful

comments on earlier versions of the paper, and also to Ken Pitre, Paul Starr, Howard Smith, and the staff of the Robertson Creek Hatchery.

References

- BAKER, R. J., AND J. A. NELDER. 1978. The GLIM system, Release 3, Generalized linear interactive modelling. Numerical Algorithms Group, Oxford, U.K.
- BILTON, H. T. 1980. Returns of adult coho salmon in relation to mean size and time at release of juveniles to the catch and the escapement. Can. Tech. Rep. Fish. Aquat. Sci. 941: 41 p.
- BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426–447.
- BISHOP, Y. M. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, MA. 557 p.
- BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1978. Statistical inference from band-recovery data: a handbook. U.S. Fish Wildl. Serv. Resour. Publ. No. 131: 212 p.
- CONROY, M. J., AND B. K. WILLIAMS. 1984. A general methodology for maximum likelihood inference from band-recovery data. Biometrics 40: 739–748.
- CORMACK, R. M. 1981. Loglinear models for capture–recapture experiments on open populations, p. 197–215. In R. W. Hiorns and D. Cooke [ed.] The mathematical theory of the dynamics of biological populations II. Academic Press, London.
- GREEN, P. E. J. 1987. New graphical techniques for analyzing salmon migration in mark–recapture experiments. Can. J. Fish. Aquat. Sci. 44: 327–336.
- GULLAND, J. A. 1955. On the estimation of population parameters from marked numbers. Biometrika 42: 269–270.
- LAWLESS, J. F. 1982. Statistical models and methods for lifetime data. Wiley, New York, NY. 580 p.
- MCCULLAGH, P., AND J. A. NELDER. 1983. Generalized linear models. Chapman and Hall, London. 261 p.
- NICHOLSON, M. D., AND J. A. POPE. 1977. The estimation of mortality from capture–recapture experiments, p. 77–85. In J. H. Steele [ed.] Fisheries mathematics. Academic Press, London.
- PEARSE, P. H. 1982. Turning the tide. A new policy for Canada's Pacific fisheries. The Commission on Pacific Fisheries Policy, Final Report. Department of Supply and Services, Ottawa, Ont.
- POLLOCK, K. H., J. E. HINES, AND J. D. NICHOLS. 1984. The use of auxiliary variables in capture–recapture and removal experiments. Biometrics 40: 329–340.
- RICKER, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Board Can. 33: 1483–1524.
- SALSBERG, D. S. 1985. The religion of statistics as practiced in medical journals. Am. Stat. 39: 220–223.
- SCHNUTE, J., AND J. SIBERT. 1983. The salmon terminal fishery: a practical, comprehensive timing model. Can. J. Fish. Aquat. Sci. 40: 835–853.
- SEARLE, S. R. 1971. Linear models. John Wiley, New York, NY. 532 p.
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Macmillan, New York, NY. 654 p.
- URQUHART, N. S., AND D. L. WEEKS. 1978. Linear models in messy data: some problems and alternatives. Biometrics 34: 696–705.