Analysis of Coded Wire Tag Returns from Commercial Catches

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Three alternative but equivalent approaches to the analysis of coded wire tag (CWT) data using log-linear models are presented. All three use iteratively weighted least squares to estimate treatment effects in hatchery releases under the assumption that the variance of a count is proportional to its expected value. The commonly made assumption of normal distributions with constant variance for recovery rates is inefficient. Analysis of tag recovery at the most disaggregated level (i.e. the level at which the sample fraction f is measured) is found necessary for valid inferences. Failure to include zero counts in analyses of recovery data is also shown to induce or mask interactions among CWT recoveries. Recoveries of CWT from coho salmon (*Oncorhynchus kisutch*) are used to illustrate the method of analysis. Coordinated CWT releases to facilitate mixing of stocks is recommended in the design of hatchery studies.

Nous présentons trois méthodes différentes mais équivalentes pour l'analyse des données sur les micromarques magnétisées codées à l'aide de modèles log-linéaires. Les trois méthodes font appel de façon itérative aux moindres carrés généralisés pour estimer les effets du traitement dans les lâchers de poissons d'élevage en prenant pour hypothèse que la variance d'un effectif est proportionnelle à sa valeur prévue. L'hypothèse couramment utilisée selon laquelle on obtiendrait des distributions normales avec une variance constante pour les taux de reprises n'est pas efficace. L'analyse des reprises d'étiquettes au degré le plus élevé de désagrégation (c.-à-d. niveau où on mesure la fraction f de l'échantillon) est nécessaire si l'on veut faire des inférences valides. Le fait de ne pas inclure les dénombrements zéro dans les analyses des données sur les reprises peut induire ou masquer des interactions parmi les reprises de poissons portant des micromarques. Nous nous servons pour illustrer la méthode d'analyse des reprises de micromarques implantées dans des saumons cohos (*Oncorhynchus kisutch*). Nous recommandons dans la conception des études sur les poissons d'élevage de coordonner les lâchers de poissons marqués pour faciliter le mélange des stocks.

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Much potential information about the contribution of hatchery and wild salmonids to Pacific coast fisheries is generated, at great expense, by intense programs of coded wire tagging (CWT). Millions of young fish have a CWT implanted in the nose cartilage before release. The tag identifies the fish to a specific treatment or release group from a specific hatchery or wild stock, with removal of the adipose fin as an external indicator of a tagged fish. Catches throughout the area are sampled, with widely varying levels of intensity, all fish in the samples being inspected for fin removal, with subsequent tag identification where possible. Thousands of tags are recovered annually, with numbers recovered identified as to location, time, gear type, etc., of capture. Data bases also include information on the sampling fraction f (or its reciprocal, the expansion factor e) of the stratum which was subjected to tag inspection. Despite all this effort and expense, there appears to be no consensus on the statistical methodology appropriate for extracting valid, useful information from such data. The monograph by Burnham et al. (1987) concentrates on studies with multiple recaptures. The extensive set of multinomial models developed by Brownie et al. (1985) for band-recovery studies concentrates on the separation of annual survival rates from recovery data within a program of multiple releases into a single population over several years. Their extension by Schwarz et al. (1988) to incorporate postrelease stratification, often at time of recovery, brings them closer to the special requirements of data from commercial fisheries, but still with a different emphasis and no formulation of the problem of subsampling the catch. Green and Macdonald (1987) advocated the use of log-linear models fitted using the computer package GLIM (Baker and Nelder 1978), analysing the observed counts as independent Poisson variables and summarising the biological structure in models for the expectation of these variables. The aim of this paper is to give strong support to the approach of Green and Macdonald (1987) and to discuss some aspects of such analyses, in particular the effects of aggregating or compositing different recovery units. Computer packages other than GLIM have programs for log-linear models but with less immediacy in their interactive nature.

The fundamental unit of recapture is a collection of fish caught in a specific type of fishery within a geographic region and over a specified duration of time that was inspected for tagged fish. Although the collection may extend over a long period of time and a wide spatial area, it is this fundamental sampling unit that provides a datum for tag analysis. Denote by n_{ij} the number of fish with code i, from an initial release of R_i fish with that code, that are observed in the inspected sample from catch unit j. Then the expected value of n_{ij} is

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TABLE 1. Notation used in the analysis of CWT data.

Type	Symbol	Definition
Indices	i	Label for different tag release groups
	j	Label for different catch units
	$+$	Replaces a label when it is summed over
Fixed Number	R_i	Number released bearing tag code i
	f_j	Proportion of catch j inspected for tags
	$e_j = 1/f_j$	Expansion factor for catch j
Observations	n_{ij}	Number of fish with tag code i found in the inspected sample from catch j
	$E_{ij} = n_{ij}\, e_j$	Expanded number of tags code i in catch j
	$y_{ij} = n_{ij}\, e_j/R_i$	Recovery rates of tag code i in catch j
Parameters	θ_{ij}	Probability that a fish with tag code i is caught in catch j
	$\mu_{ij} = R_i f_j \theta_{ij}$	$E(n_{ij})$: number of fish with tag code i expected to be found in the sample inspected from catch j
	σ_{ij}^2	Var (n_{ij}): variance of n_{ij}
	$\phi = \sigma_{ij}^2/\mu_{ij}$	Variance-to-mean ratio for n_{ij}, when this is assumed constant

$$E(n_{ij}) = R_i \theta_{ij} f_j$$

where θ_{ij} is the probability that a fish with code i contributes to catch j and f_j is the fraction of catch j that is sampled. From the data (n_{ij}, R_i, f_j), a statistical model for the n_{ij} is selected in order to find a parsimonious description of the θ_{ij} in terms of a structure on the release suffix i (different hatcheries, experimental treatments, etc.) and the recovery suffix j (type, location, and timing of fishery, etc.) and to give point estimates and confidence intervals for the θ_{ij} and appropriate combinations of them. Although combinations of the θ_{ij} may be of particular interest, we recommend modelling and analysing the data (n_{ij}) at the fundamental, most disaggregated level at which the sampling fractions f_j are defined. The consequences of trying to analyse aggregated data are considered later. For convenience, all notation is summarised in Table 1.

Statistical Model

Variance Structure

Since R_i is typically very large and θ_{ij} small, a natural first choice of model would be to assume independent Poisson distributions for the n_{ij}. This model explicitly assumes that different sampling strata do not interact and implicitly assumes that individual fish behave independently with respect to the overall process from release to capture and sampling. Overall validity of the Poisson assumption can be tested, and possible interactions between specific fisheries (e.g. between a rivermouth and an upstream fishery) can be examined in terms of the correlation between the residuals from the model. Shoaling behavior of fish and the fact that fishermen respond to it are just two of many reasons to suggest that some clustered distribution would be expected to provide a better fit than a Poisson model. The mechanisms of sampling and subsampling of the catch are also likely sources of additional variability. The overall result, commonly experienced, is that the variance of true replicate counts tends to be greater than their mean.

For a Poisson distribution, the variance equals the mean. The variance to mean ratio, $s^2/\bar{x}$, among k replicate counts is $1/(k - 1)$ times the index of dispersion, widely used in ecology as a test of nonrandomness (i.e. $s^2(k-1)/\bar{x} \sim \chi^2_{k-1}$; Ripley 1981, p. 104). How should data be analysed when there is an a priori expectation of overdispersion and evidence from the data that this expectation has been fulfilled? Three approaches can be distinguished: (1) ignore the variance structure, (2) develop a detailed model of the overdispersion, and (3) make inferences about the parameters θ_{ij} using a robust method which allows for overdispersion without modelling it in detail. We will discuss each of these approaches below.

The first approach comes in three forms. In the first of these (Table 2, Model 1), the recovery rates $y_{ij} = n_{ij}\, e_j\, /R_i$ are regarded as normally distributed variables with constant variance. This neglects both the likely relationship between variance and mean and the necessary dependence of the variance on both the number released and the expansion factors. It also ignores the fact that a normal distribution with constant variance is virtually impossible for any nonnegative variable which can be very small. A variant of this (Table 2, Model 2) assumes log (y_{ij}) to be normally distributed with constant variance. This overcorrects the dependence of Var (n_{ij}) on number released and on the expansion factors, and in implying that the variance of y_{ij} is roughly proportional to the square of its mean is likely to give too little weight to large observations. Model 2 also has the difficulty of requiring an arbitrary modification when the return rate is zero. The third form ignores the likely presence of overdispersion, assuming a Poisson distribution with variance equal to mean. Although in our opinion much superior to the normality assumptions above, this assumption leads, in the presence of any overdispersion, to understatement of the variance of estimated effects and the overstatement of the significance of possible explanatory factors.

If the primary interest lies in the causes of the variability in the number of tags recaptured within a stratum, then the second approach is necessary. This would require special experimentation and be very difficult. Assuming that the observations follow, say, a negative binomial distribution — often used as a description because it can be derived from a number of ecological processes, although not if more than one is operating — is not developing a detailed model. Making an inference which depends specifically on the distributional form of the negative binomial is dangerous because the data seldom provide adequate evidence for or against the negative binomial rather than any other clustered distribution. The property which is important and about which the data set does provide some evidence is that its variance $\sigma^2 = \mu + \mu^2/k$ when its mean is μ.

Following Green and Macdonald (1987), we recommend the third approach. We make no assumption about the probability distribution of the observations n_{ij}, but do assume that their variances σ_{ij}^2 are related in a specified way to their means μ_{ij}. This relation can include an unknown parameter to be estimated from the data. The negative binomial form $(\mu_{ij} + \mu_{ij}^2/k)$ would be one possibility, but there are theoretical and computational advantages in including the extra parameter as a scale factor, taking $\sigma_{ij}^2 = \phi\mu_{ij}$ where $\phi > 1$ represents overdispersion. This forms Model 3A (Table 2) called a scaled Poisson by Green and Macdonald (1987) although, taken literally, a Poisson variable multiplied by a scale factor in general takes values that are not integers. Although we prefer to consider this as a model for n_{ij}, the number of tags actually observed, the same form of model applies to the recovery rate y_{ij} (Model 3C) or, as used

TABLE 2. Possible statistical models used in the analysis of CWT data.

Model	Dependent variable	Mean	Variance	Error distribution	Fitting constants: Weight	Fitting constants: Offset
1	y_{ij}	θ_{ij}	Constant	Normal	1	None
2	$\log(y_{ij})$	$\alpha_i + \beta_j + \gamma_{ij}$	Constant	Normal	1	None
3A	n_{ij}	$\mu_{ij} = R_i\,\theta_{ij} f_j$	$\phi\mu_{ij}$	Scaled Poisson	1	$\log(R_i f_j)$
3B	E_{ij}	$R_i\theta_{ij}$	$\phi\theta_{ij}\,e_j$	Scaled Poisson	f_j	$\log(R_i)$
3C	y_{ij}	θ_{ij}	$\phi\theta_{ij}\,e_j/R_i$	Scaled Poisson	$R_i f_j$	None

by Green and Macdonald (1987), to the expanded catch E_{ij} (Model 3B), since these are known multiplies of n_{ij}. The multipliers have to be incorporated as weights in any analysis.

The choice between the two forms of variance function, negative binomial and scaled Poisson, is not as important as maybe first thought. Over the range of means encountered at the disaggregated level, they may not be readily distinguishable. Furthermore, there exists evidence that "even relatively substantial errors in the assumed functional form of Var(Y) generally have only a small effect on the conclusions" (McCullagh and Nelder 1989, p. 199). It should be noted also that the structure $\sigma_{ij}^2 = \phi\mu_{ij}$ does not greatly restrict the probability distribution of the counts: any family of discrete distributions indexed by two or more parameters includes members which take this structure.

Formulated in this way, the variance of n_{ij} incorporates the variability in survival of young fish between release and capture in the fishery, in sampling the catch, and in extraction and recording of the tag. These variances will be greater than those presented by Clark and Bernard (1987) which incorporated only the subsampling of the catch. Their variances are appropriate to estimation of past catch in a given time period. If the complete catch were counted, then the size of that catch and its component parts would be known exactly. However, one would not know exactly the relative contributions to be expected from different hatcheries in another year, nor would one quote with zero variance the differential effects of two treatments (e.g. time of release) on the fishery return.

Method of Fitting

For data at the fundamental level of disaggregation, the time–area fishery stratum over which f_j was originally measured, the observed number n_{ij} of tag recaptures has expected value (Table 2, Model 3A)

$$E(n_{ij}) = \mu_{ij} = R_i\theta_{ij}f_j\,.$$

This is a log-linear model

$$\log(\mu_{ij}) = \log(R_i f_j) + \log(\theta_{ij})$$

with associated variance Var $(n_{ij}) = \phi\mu_{ij}$ where ϕ is an unknown constant of proportionality. The $\log(\theta_{ij})$ can be further partitioned by an additive factorial model representing the structure of the study, for example, release treatments or regions and times of recapture.

Most statistical packages contain options for fitting log-linear models to counts n_k, assumed Poisson, with means μ_k given by

$$\log(\mu_k) = \sum_l \beta_l x_{kl}\,.$$

In our case, one of the x-variables is $\log(R_i f_j)$ whose regression coefficient is forced to be 1. Such a variable is said to be offset. A referee has pointed out that if $\log(R_i f_j)$ is written as $\log(R_i) + \log(f_j)$ and only $\log(f_j)$ is offset, the regression coefficient of $\log(R_i)$ would reflect density-dependent mortality of the release groups (Peterman 1982). The other factors are indicator variables, zero or one, for the different categories of release and recapture, but covariables such as effort can be included provided they can be modelled within the log-linear form. Analysis of E_{ij} or y_{ij} requires different offsets, given in Table 2, and also the use of weights to adjust the variances, as discussed by Green and Macdonald (1987). The algorithm in GLIM converges more slowly for Model 3C. Maximum likelihood estimates $\hat{\beta}_l$ are obtained, together with their asymptotic standard errors. The overall fit of any model is assessed by comparison of observations n_k with their fitted values $\hat{\mu}_k$ by means of the deviance

$$2\sum_k n_k \log\left(\frac{n_k}{\hat{\mu}_k}\right) - 2\sum_k (n_k - \hat{\mu}_k).$$

If the model includes a constant term, the second term in this expression is zero. See, for example, Green and Macdonald (1987) or McCullagh and Nelder (1989, Section 2.3).

Different nested models for $\log(\theta_{ij})$ can be compared, in a way exactly parallel to the analysis of variance of a factorial experiment, by examination of differences between the deviances from different models. Estimates and asymptotic variances and covariances of $\log(\theta_{ij})$ under the selected model yield normal confidence intervals on this scale. To obtain confidence intervals for a function of a linear combination of $\log(\theta_{ij})$, for example, the relative contribution of two treatments θ_{1j}/θ_{2j} to a fishery, limits for the function on the log scale are converted by exponentiation to limits for the required function. Confidence limits for sums or differences of θ_{ij} can be approximated by the assumption of a normal distribution for $\hat{\theta}_{ij}$, with variance obtained by the usual Taylor series expansion of the appropriate function of the estimators of $\log\theta_{ij}$ (Seber 1982, p. 7–9).

With the Poisson distribution, the above log-linear model belongs to the class of generalized linear models (GLMs) introduced by Nelder and Wedderburn (1972). They showed that the maximum likelihood estimates could be obtained by a weighted least squares procedure, where the weights are determined iteratively by the variance of each observation, a procedure which makes no use of the specific probability distribution.

When the Poisson distribution is not assumed, and the additional unknown parameter ϕ is introduced as the constant variance-to-mean ratio, the same method of analysis can still be used. The theoretical difference is that the justification is now in terms of weighted least squares and quasi-likelihood (McCullagh and Nelder 1989, Chapter 9). The only practical differences are that: (1) since ϕ is no longer known to be 1, it has to be estimated by $\hat{\phi}$, the Pearson goodness-of-fit χ^2 from the most complicated model considered, divided by its degrees of freedom ($\hat{\phi} = \chi^2/\text{df}$): if this is less than unity, however, we

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take $\hat{\phi} = 1$, since underdispersion is a priori unlikely, (2) standard errors of estimates must be multiplied by $\hat{\phi}^{1/2}$, and (3) in model selection, differences between deviances should be divided by $\hat{\phi}$ before comparison with the appropriate χ^2 distribution (Breslow 1990). These recommendations for practical data analysis are discussed further in the final section of the paper.

Potential difficulty in the analysis of CWT data can occur if the number n_{ij} is zero. Zero observations are real data and should be included in the analysis, particularly when comparisons are being made between treatment groups, some of which make a nonzero, some a zero, contribution to a particular recovery stratum. Even if zeroes are not recorded in a data base, they may be implied by other records and should not be ignored. For example, a data base may record one fish from hatchery H_3 recovered in area A_2 during period W_3. The absence of any mention of a fish from hatchery H_2 being recovered in A_2 during period W_3 implies a zero record for that combination. However, before drawing the corresponding conclusion from the absence of any record from H_3 in A_1 during W_3, we must be sure that samples were taken in A_1 during W_3.

The situation in which no tagged fish at all are recorded in a particular stratum requires further consideration. If the structure of the model assumed for θ_{ij} contains a separate parameter for that stratum, then the fitted values for all observations in that stratum will also be zero. This stratum thus makes zero contibution to the χ^2 goodness-of-fit and would reduce the estimate of ϕ if the df were not correspondingly reduced, giving a false precision to inferences about other strata. The stratum as a whole should be removed from the analysis. If the model for θ_{ij} results in small nonzero fitted values, a satisfactory resolution is less straightforward. We suggest that the data be reanalysed with such sets of zeroes omitted and any major difference in the outcomes of the two analyses regarded as a need for cautious interpretation.

Aggregation

Methodology of previous sections concentrates on inferences about the contribution of a particular treatment release to a particular recovery stratum. Notation was kept simple by allocating a single index j to all recovery strata. However, information is often wanted on aggregations of these fundamental units, aggregations over any combination of time, area, gear type, or complete fishery. Notation has to be extended to allow at least the minimum structure on strata. To make it specific, we denote by n_{ijk} the number of tags from release i recaptured in area j during week k while noting this, or a more general notation, can be applied to any known structure on the recoveries or the releases. Interest lies in area totals. The observed numbers n_{ijk} and the expanded numbers $E_{ijk} = n_{ijk}e_{jk}$ are added up to obtain area totals: $n_{ij+} = \sum_k n_{ijk}$ and $E_{ij+} = \sum_k E_{ijk}$. Indeed, these totals are sometimes all that are reported in derived analyses. The individual sampling fractions have been discarded and what is reported is an aggregated expansion factor $e_{ij} = E_{ij+}/n_{ij+}$ which is itself now a random variable. What analyses are possible using only the aggregated values n_{ij+}, E_{ij+}, and hence, e_{ij}?

Corresponding to Model 3A, n_{ij+}, aggregated over some fisheries for a single release, is distributed with mean $\mu_{ij+} = R_i \sum_k (\theta_{ijk}/e_{jk})$, a function which depends on the discarded individual expansion factors e_{jk} and consequently does not yield information about θ_{ijk} or $\theta_{ij+} = \sum_k \theta_{ijk}$. On the other hand, E_{ij+} has expectation $R_i\theta_{ij+}$, and $y_{ij+} = E_{ij+}/R_i$ has expectation θ_{ij+}, which is the probability of a fish from code i contributing to the fishery in area j. Thus, with aggregated data, Models 3B and 3C describe variables whose expected values are of interest whereas Model 3A does not. However, an analysis which is fully valid requires knowledge of how the variance of each variable is related to its mean under the model. Now

$$\text{(1)} \quad \begin{aligned} \mathrm{Var}\,(y_{ij+}) &= \frac{\phi \sum_k \theta_{ijk}e_{jk}}{R_i} \\ \mathrm{Var}\,(E_{ij+}) &= \phi \sum_k R_i\theta_{ijk}e_{jk} \end{aligned}$$

so that in both cases, the variance depends on the θ_{ijk}, which cannot be estimated from the aggregated data, and on the e_{jk}, which have been discarded. Thus, no analysis can be based on an exact model for the mean and variance of aggregated data.

Can an approximation to the variance be found in terms of the known e_{ij} and the parameter of interest θ_{ij+}? Formula (1) can be rewritten as follows:

$$\begin{aligned} \mathrm{Var}\,(y_{ij+}) &= \left(\frac{\phi}{R_i}\right) \sum_k \theta_{ijk}\,[e_{ij} + (e_{jk} - e_{ij})] \\ &= \frac{\phi e_{ij}\theta_{ij+}}{R_i} + \left(\frac{\phi}{R_i}\right) \sum_k \theta_{ijk}\,(e_{jk} - e_{ij}) \end{aligned}$$

with a corresponding form for Var (E_{ij+}). If the second term is negligible, these are Models 3C and 3B of Table 2, at the aggregated level.

If all the expansion factors within an area are the same for different weeks, the second term vanishes and analysis of Model 3 at the aggregated level is valid. Otherwise, since e_{ij} is a weighted average of the e_{jk}, the second term depends on the covariance or correlation between θ_{ijk} and e_{jk}. Observations on these have been discarded. Since θ_{ijk} is a parameter of the process linking release to capture in a fishery, and e_{jk} is a parameter of the sampling process after capture, this correlation would be expected to be small on average. However, for a particular treatment group i, it can be substantial, of either sign. Consider, for example, the effect of severe undersampling in one week in one area, thus generating a high e_{jk} $(= 1/f_{jk})$. Then a treatment group that is expected to make a higher than average contribution to that stratum will have a variance higher than that indicated by the model, and conversely for a group making a low contribution to that stratum. No information on this situation is available from the aggregated data alone, and this phenomenon may add greatly to the noise already distorting empirical attempts to model variance–mean relationships of aggregated data. The effects will be demonstrated in the next section.

By contrast, aggregation over treatment groups creates no problems for analysis. Interest lies in $\theta_{Ij} = \sum_{i \in I} R_i\theta_{ij} \Big/ \sum_{i \in I} R_i$, the average contribution of fish in release I to the jth recovery stratum weighted by the number of fish of each type in the aggregated release I. Under the model, the total of the observed numbers $n_{ij} = \sum_{i \in I} n_{Ij}$ has expected value

TABLE 3. CWT releases of coho reported in Clark and Bernard (1987) and recoveries (n_{ij}) by area and week.

Area	Week	Expansion factors	Treatment:	1		2		3	
			No. released:	10 020	10 454	10 349	10 159	10 774	10 630
1	1	65.08		0	2	3	1	1	2
	2	5.98		2	3	7	4	3	1
	3	5.82		7	7	15	7	7	6
	4	4.37		39	27	38	45	9	15
	5	4.64		6	13	20	8	4	3
2	1	5.13		0	0	1	0	2	0
	2	3.76		4	3	1	3	5	1
	3	3.72		3	8	3	3	0	1
	4	3.99		4	4	5	6	2	3
	5	4.64		6	6	9	11	4	4
3	1	6.35		1	0	0	0	1	0
	2	2.84		0	1	1	1	0	0
	3	3.63		0	1	0	0	0	1
	4	4.22		1	1	5	5	1	1
	5	6.30		0	0	0	1	0	0
4	1	2.76		1	1	0	0	0	0
	2	3.38		0	1	0	2	1	1
	3	2.15		2	0	1	5	1	4
	4	2.73		5	4	5	16	3	7
	5	5.72		4	3	9	7	4	3

$$\mu_{Ij} = f_j \sum_{i \in I} R_i \theta_{ij} = f_j R_I \theta_{Ij}$$

and variance $\phi\mu_j$ where $R_I = \sum_{i \in I} R_i$. This is identical in form to Model 3A. Similarly, E_{Ij} and y_{Ij} have the correct structures for Models 3B and 3C.

The problem arises from the aggregation of unequal sampling fractions. Although aggregation of samples might be regarded as just another level of clustering of fish, the sampling of the catch introduces a different and difficult element into the analysis. We can gain some understanding of the variance structure only at the disaggregated level.

Example

Clark and Bernard (1987) quoted data on recaptures from five releases, two of chinook salmon (*Oncorhynchus tshawytscha*) and three of coho salmon (*O. kisutch*), from Whitman Lake Hatchery. Ten tag codes were used, two tag codes within each release group, because of insufficient supplies of tags of any one code. Recoveries from the southeast Alaska fisheries in one year are listed at a highly disaggregated level, the strata being defined by type of fishery (troll, seine, gill net, or fish-trap), by region, and by period of recovery. Since there are no recovery regions in common between the troll and other fisheries, and a high degree of further nonorthogonality in regions and periods between the other fisheries, it would be difficult to interpret a single all-embracing analysis. To demonstrate the methodology and its differences from other approaches, we analyse here data on the recoveries from the troll fishery of coho for which recoveries are recorded in four regions ($A = 1, \ldots, 4$) and five weekly sampling periods ($W = 1, \ldots, 5$), regarding the three separate releases as three hatchery treatments ($T = 1, \ldots, 3$), each having two tag codes. The first of these treatments differed from the others in being fish of a different stock released in a different place. The difference between second and third treatments is not defined by the authors. Each recovery stratum is indexed by region and week.

The coho data are given in Table 3 in a form that differs in certain respects from the originals in Clark and Bernard (1987, appendix E, tables 4, 6, and 8). The expansion factor for each recovery stratum has been deduced from the estimated contributions of each release to each fishery quoted by Clark and Bernard (1987). When no fish from either tag code of a treatment are observed in a stratum, such double zeroes are not listed explicitly in Clark and Bernard (1987). In Table 3, such zeroes are included with expansion factors inferred from the nonzero observations in that stratum from some other release. If other strata were fished and sampled but no tags were observed from any release, no information on such strata is available from Clark and Bernard (1987). The range of expansion factors, from 2 to 65 in the coho study, is not atypical. The roughly equal numbers of fish released in each group is atypical but not crucial for the analysis.

Recommended Analysis

Five different models for θ_{TAW}, the probability that a tagged fish from treatment group T is caught in region A during week W, are listed in decreasing order of complexity in Table 4. Measures of lack-of-fit of these models to the data are also listed: deviances and standard Pearson χ^2. Score tests, easily implemented in GLIM (Pregibon 1982), are an alternative to the tests based on deviance differences: they give very similar results. Model 1, the most general, allows a different value of θ for each treatment–region–week combination by allowing all interactions among the three factors (indicated by notation T*A*W). The fact that χ^2 is a little less than the residual df indicates that a Poisson distribution may be acceptable, i.e. with proportionality factor $\phi = 1$. This confirms that the observed variance is the result of process variability (random survival, catch, and sampling) alone. Fish seem to behave

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TABLE 4. Goodness-of-fit of models and tests of model differences for the six CWT releases of coho reported in Clark and Bernard (1987). Factors T, A, and W denote treatments, regions, and weeks, respectively; model $T + A$ includes main effects only, while $T*A$ also includes their interaction.

	Goodness-of-fit			Differences		
Model	Deviance χ^2	Pearson χ^2	df	Deviance	Pearson	df
Full: $T*A*W$	62.84	54.74	60			
θ_{TAW} all different				30.76	34.61	24
All 2-factor interactions						
$T*A + T*W + A*W$	93.60	89.35	84			
$\theta_{TAW} = \delta_{TA}\beta_{AW}\gamma_{TW}$				9.15	15.75	8
$T*A + A*W$	102.75	105.1	92			
$\theta_{TAW} = \delta_{TA}\beta_{AW}$				9.72	10.20	6
$T + A*W$	112.47	115.3	98			
$\theta_{TAW} = \delta_T\,\beta_{AW}$				94.62	124.70	12
$T + A + W$	207.09	240.0	110			
$\theta_{TAW} = \delta_T\,\beta_A\gamma_W$						

homogeneously and independently as they move through the process from their hatchery towards the fishery. Further models now explore differences and interactions between treatments, regions, and weeks of fishing. Model 2 sets the three-factor interaction to zero, and other interactions are removed in successive lines of Table 4 until the no-interaction Model 5 (i.e. $\theta_{TAW} = \delta_T\,\beta_A\gamma_W$) is reached.

At each stage from Model 2 onwards, other models were considered and the route chosen which minimised the increase in mean deviance (deviance/df). Thus, for example, Model 2 includes three two-factor interactions — treatment by region ($T*A$), treatment by week ($T*W$), region by week ($R*W$) — each of which was removed from the model in turn. Model 3 was chosen next because the interaction between T and W was least significant. The procedure is akin to backward selection of variables in multiple regression, although with three factors, all 19 hierarchical models can easily be fitted.

Model 5 is clearly unacceptable, since the difference in deviance between it and Model 4, a value of 94.6, is unacceptable as a value from a χ^2 distribution with 12 df ($P(\chi_{12}{}^2 > 94.6) \ll 0.001$) as is the residual χ^2 of 240.0 from a χ^2 distribution with 110 df ($P(\chi_{110}{}^2 > 240.0) \ll 0.001$). For all other models, both the overall χ^2 and the differences between deviances from successive models take values which are acceptable when assessed against the χ^2 distributions. We select as the most parsimonious acceptable Model 4: $\theta_{TAW} = \delta_T\beta_{AW}$ (where δ_T is the "effect" of release T and β_{AW} the "effect" of the fishery in region A, week W). For Model 4, the value of the Pearson χ^2 is acceptable ($P(\chi_{98}{}^2 > 115.3) = 0.11$) as is the cumulative difference in deviance between Model 1 and selected Model 4 ($P(\chi_{38}{}^2 > 49.6) = 0.10$).

Selection of an acceptable model on the basis of the asymptotic distribution of the deviance D or χ^2 may be questioned because of the small expected counts in several cells. Despite considerable work on the problems of sparse data, "general rules are difficult to prescribe for unsymmetrical null hypotheses" (Koehler and Larntz 1980). "It is good statistical practice not to rely on either D or χ^2 as an absolute measure of goodness-of-fit in these circumstances. it is much better to look for specific deviations from the model of a type that is easily understood scientifically" (McCullagh and Nelder 1989, p. 122).

Although Model 4 is acceptable with $\phi = 1$, its estimate is $\hat{\phi} = 115.3/98$ or 1.177. Since we argue that scientifically some clustering of fish is to be expected, we advocate using $\hat{\phi}$ in constructing confidence intervals. Failure to reject a null hypothesis is not proof of its truth. Model 5 is still overwhelmingly rejected compared with Model 4.

A desirable supplement to any analysis is to examine the residuals of observations from their fitted values under the model. Since our observations do not have constant variance and are not symmetrically distributed, a transformation is needed to give readily interpretable residuals. Pearson residuals:

$$r = \frac{(n - \hat{\mu})}{\hat{\mu}^{\frac{1}{2}}}$$

or Anscombe (1953) residuals:

$$r = 1.5\,\frac{[n^{\frac{2}{3}} - \hat{\mu}^{\frac{2}{3}}]}{\hat{\mu}^{\frac{1}{6}}},$$

the latter specifically designed for Poisson distributions, are very similar unless $\hat{\mu}$ is very small. The normal plot of r (Fig. 1a) shows no disturbing features.

A further safeguard would be to check the fit of the selected model by Monte Carlo simulation of Poisson observations with cell means given by the fitted values from the real observations and subsequent fitting of the same model to the simulated data sets. If fewer than 5% of the simulations result in a goodness-of-fit value greater than that calculated from the real data, the model would be rejected at the 5% level. In 200 simulations of Model 4, 25 or 12.5% had a deviance larger than the observed 112.5. Although not significant, this again suggests that some extra-Poisson variation may exist or that some other interaction term may be important. The mean and variance of the simulated deviances were 97.1 and 168 compared with the values of 98 and 196 for the assumed χ^2 distribution with 98 df.

Even if $\phi > 1$, the selected model indicates that, although the relative contributions of the different regions to the overall fishery change from week to week, the contributions of δ_T of each treatment code to every catch remain in the same ratio. In

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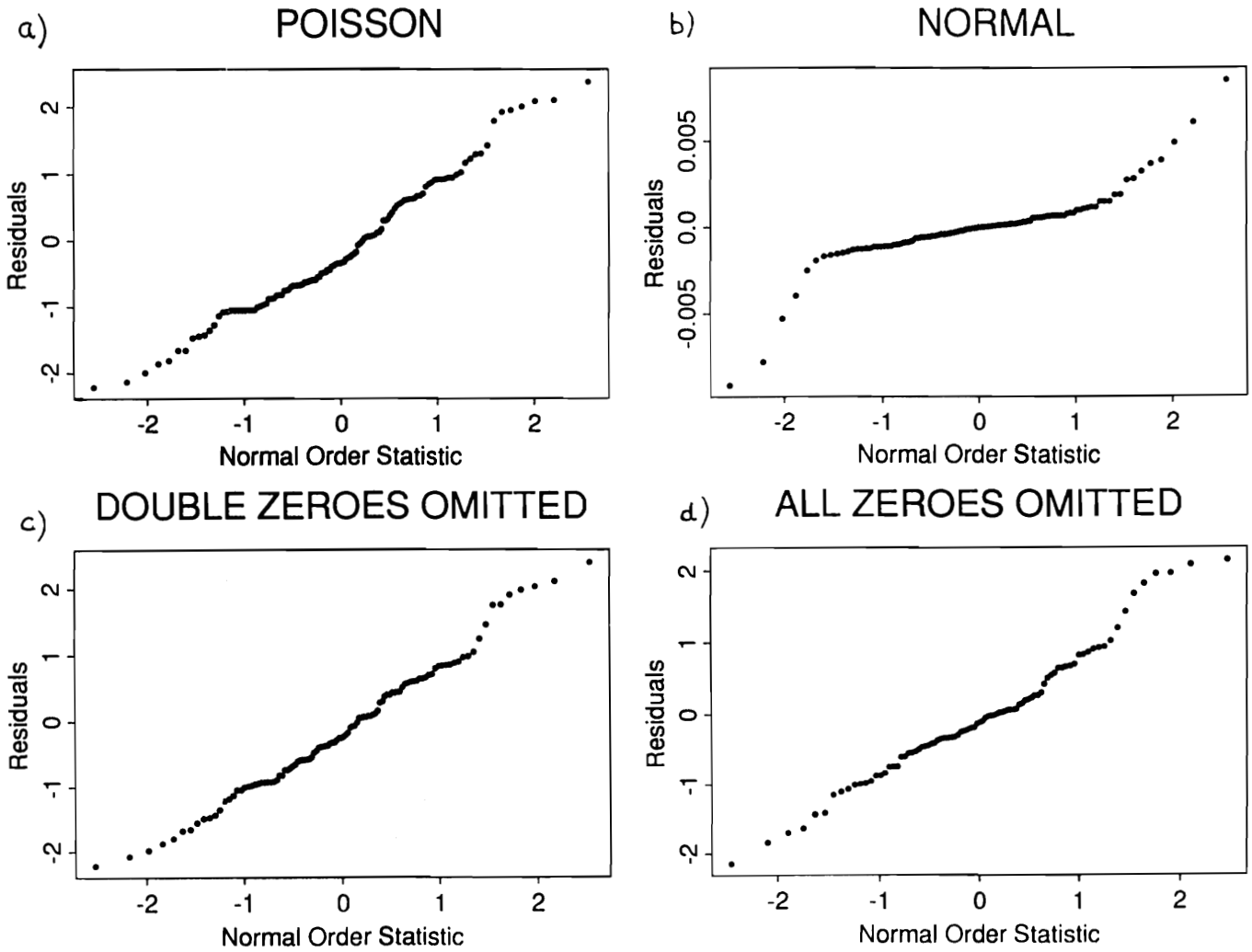

FIG. 1. Plots on normal probability paper of Anscombe-transformed residuals from the model $\theta_{TAW} = \delta_T \beta_{AW}$ to Clark and Bernard (1987) coho data. If the assumptions of the analysis are satisfied, the plot should be a straight line. (a) Residuals from the complete data fitted by the recommended model with observed recoveries assumed Poisson distributed; (b) residuals from the complete data fitted assuming observed recovery rates normally distributed with constant variance; (c) as in Fig. 1a but all categories omitted with no recoveries from any tag code; (d) as in Fig. 1a but all categories with no recoveries omitted.

other words, there seems to be reasonably uniform mixing of the various treatment groups over both space and time. The estimates of $(\log \delta_2 - \log \delta_1)$ and of $(\log \delta_3 - \log \delta_1)$ with their standard errors, incorporating $\hat{\phi}^{1/2}$, are respectively 0.376 $\pm$ 0.100 and -0.565 ± 0.126. Thus, on exponentiating, estimates are that for every 100 fish contributed to any recovery class from fish released in the first treatment, the same number of fish released by the second treatment will contribute 146 fish to that recovery class (95% confidence limits 118 to 180), while the same number of fish released by the third treatment will contribute 57 fish to that class (95% confidence limits 44 to 74).

Since the selected model ($\theta_{TAW} = \delta_T \beta_{AW}$) represents complete mixing of treatment groups of fisheries, an alternative simple comparison between treatment effects can be based on the observed counts, ignoring expansion factors. Merely dividing observed recoveries by numbers released on each treatment group gives estimated recovery rates respectively of 0.0083, 0.0121, and 0.0047 with $\log(\delta_2/\delta_1)$ estimated as 0.376 and $\log(\delta_3/\delta_1)$ as -0.565. These are identical to the values in Table 4 obtained by the log-linear analysis of the disaggregated data with variance proportional to mean and different from any analysis involving aggregation of expansion factors. The theoretical binomial standard errors of these comparisons are 0.099 and 0.125, respectively, the first being slightly less than the standard error from the log-linear analysis. Sample standard errors based on the difference between recovery rates from the duplicate codes are less than half the theoretical values, but being based on 1 df are highly unreliable and give wide confidence limits.

It should be noted that overdispersion and lack-of-fit cannot be distinguished from any overall measure. Perhaps Model 5 is acceptable with a large value of ϕ. The evidence against this lies in the pattern of residuals from Model 5 (Table 5). For example, Area 1 is high in Weeks 1, 2, and 3 and low in Week 5; Area 4 is low in Week 1 and high in Week 5.

Alternative Analyses

Other analyses which have been suggested in the literature were discussed earlier. What results do they give for this example?

Omitting zero catches

If the analysis is repeated omitting the region–week classes with no recoveries from any code, the results are very similar.

TABLE 5. Anscombe residuals of n_{ij} from Model 5: $T + A + W$ for the Clark and Bernard (1987) coho data.

		Treatment 1		Treatment 2		Treatment 3	
Area	Week	Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2
1	1	−0.8	2.1	2.6	0.8	1.4	2.6
	2	−1.0	−0.5	0.5	−0.7	0.4	−1.0
	3	0.2	0.1	1.5	−0.9	1.4	1.0
	4	2.7	0.3	0.2	1.4	−1.7	0.1
	5	−2.4	−0.4	−0.1	−3.1	−1.7	−2.1
2	1	−1.5	−1.5	−0.4	−1.8	1.5	−1.1
	2	1.5	0.9	−1.1	0.3	2.9	0.0
	3	0.1	2.5	−0.6	−0.6	−2.0	−0.6
	4	−1.3	−1.4	−2.0	−1.6	−1.3	−0.7
	5	1.1	1.0	1.3	2.1	1.0	1.1
3	1	1.4	−0.6	−0.8	−0.8	1.7	−0.5
	2	−1.1	0.6	0.3	0.3	−0.8	−0.8
	3	−1.2	0.4	−1.5	−1.5	−0.9	0.8
	4	0.5	−0.5	1.5	1.5	0.0	0.1
	5	−1.2	−1.2	−1.5	0.1	−0.9	−0.9
4	1	−0.2	−0.2	−2.0	−2.0	−1.3	−1.3
	2	−1.6	−0.2	−2.0	0.2	0.3	0.3
	3	−0.7	−2.7	−2.1	0.2	−0.7	1.3
	4	−0.8	−1.3	−1.9	1.7	−0.6	1.3
	5	1.3	0.6	2.8	2.0	2.0	1.4

TABLE 6. Test statistics for model $\theta_{TAW} = \delta_T \beta_{AW}$ for the Clark and Bernard (1987) coho data.

	Test of interaction			Test of residual		
Data form	df	Change in deviance	Change in χ^2	df	Deviance	χ^2
Diaggregated	38	49.6	60.6	60	62.8	54.7
Disaggregated (all zero counts ignored)	30	29.2	34.3	39	39.3	37.8
Aggregated over weeks	6	5.1	5.2	12	16.5	16.6
Aggregated over regions	8	18.2	15.0	15	24.9	31.2
Aggregated over both		None possible		3	6.6	6.7

The residual χ^2 from the full model $T*A*W$ remans approximately equal to its df (Table 6, right-hand section), while the evidence suggesting interactions of treatment with recovery stratum (Table 6, left-hand section) is now less strong. This pattern continues if all zero counts are omitted from the analysis. Residual plots (Fig. 1c and 1d) show slightly more evidence of heavy tails, suggesting that the assumptions of the analysis are less well satisfied.

Estimates, with standard errors, of log (δ_2/δ_1) and log (δ_3/δ_1) are given in Table 7, together with 95% confidence limits for the returns from Treatments 2 and 3 relative to 100 returns from Treatment 1. Again, omission of zero counts has little effect on the estimates. In this example, comparisons between treatments are not changed by omitting zero observations: comparisons between areas and between weeks are, however, seriously altered. With other models for the n_{ij}, elimination of zeroes could also distort estimates of treatment effects.

Negative binomial error

Table 7 shows that replacing the assumption $\sigma^2 = \phi\mu$ for the variance with $\sigma^2 = \mu + \mu^2/k$ makes little difference to the analysis. The difficulty of distinguishing the two variance structures can be seen from the plot of the variances between duplicate catches (Fig. 2).

Normal theory

Analysis of the recovery rate y, when correctly weighted as in Model 3C, gives identical results to the recommended analysis. Analysing y as a normal random variable with constant variance suggests a strong interaction between treatment and region ($F_{6,60} = 32.5$, $P < 0.01$), but both a graph of variance against mean, like Fig. 2, and the residual plot in Fig. 1b show that the assumptions of the analysis are untenable.

To analyse log (y), we must first add a constant to y to avoid taking the logarithm of zero. The arbitrary choice of this constant renders the procedure of doubtful value. The observed values of y are of the order of 10^{-4} to 10^{-3} so that log $(1 + y)$, a common choice, is little different form $(-y)$.

Aggregating data over regions or weeks

Finally, consider the effect of aggregating the data for analysis, which could here be done in either or both of two ways, over weeks and over regions of tag recoveries. The effects on the model selection process and on estimates of treatment comparisons are shown in the lower parts of Tables 6 and 7. Information is lost on possible interaction between treatments and any factors whose levels have been composited. Even in this example, when such interactions were not found to be impor-

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TABLE 7. Estimated comparisons between hatchery treatments based on assumptions of scaled Poisson ($\sigma^2 = \phi\mu$) and negative binomial ($\sigma^2 = \mu + \mu^2/k$) variances.

Data	Variance structure	$\log(\delta_2/\delta_1) \pm$ SE	95% CI δ_2/δ_1	$\log(\delta_3/\delta_1) \pm$ SE	95% CI δ_3/δ_1
Disaggregated	$\phi\mu$	0.376 ± 0.114	(116, 182)	−0.566 ± 0.144	(43, 75)
	$\mu(1 + \mu/k)$	0.396 ± 0.123	(117, 189)	−0.495 ± 0.144	(46, 81)
Disaggregated (zeroes ignored)	$\phi\mu$	0.360 ± 0.101	(118, 174)	−0.572 ± 0.126	(44, 72)
	$\mu(1 + \mu/k)$	0.364 ± 0.105	(117, 177)	−0.558 ± 0.130	(44, 74)
Aggregated over weeks	$\phi\mu$	0.450 ± 0.109	(127, 194)	−0.339 ± 0.138	(54, 93)
	$\mu(1 + \mu/k)$	0.453 ± 0.110	(127, 195)	−0.338 ± 0.134	(55, 93)
Aggregated over regions	$\phi\mu$	0.438 ± 0.143	(117, 205)	−0.534 ± 0.179	(41, 83)
	$\mu(1 + \mu/k)$	0.473 ± 0.169	(115, 223)	−0.419 ± 0.184	(46, 94)
Aggregated over both	$\phi\mu$	0.436 ± 0.148	(116, 207)	−0.359 ± 0.187	(48, 101)
	$\mu(1 + \mu/k)$	0.437 ± 0.152	(115, 208)	−0.364 ± 0.170	(50, 97)

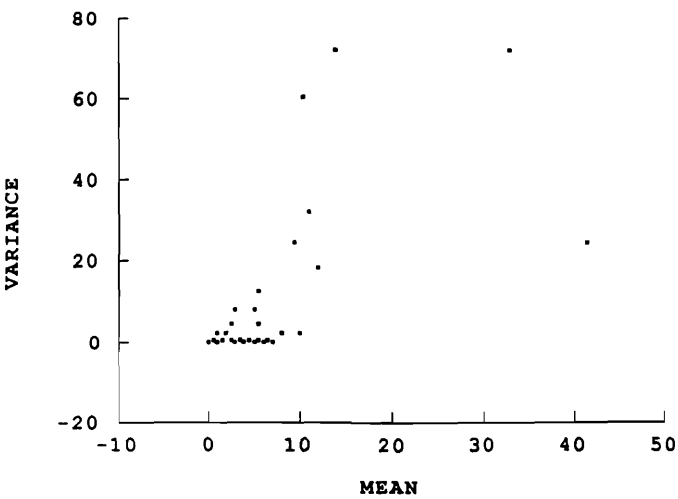

FIG. 2. Plot of variance against mean for the duplicate counts in Clark and Bernard (1987) coho data.

tant, major distortions are introduced into the results. Aggregation over weeks has little effect on model selection with no evidence in Table 6 of either interaction (between treatment and area) or lack-of-fit. By contrast, aggregation over regions leads to a residual χ^2 which is twice its df and to a comparable increase in the interaction deviance (between treatment and weeks). Substantial overdispersion has been introduced. This is shown by the increased standard errors and wider confidence intervals for treatment comparisons given in Table 7. Although our models allow for overdispersion, the particular estimates in Table 7 that would be quoted would depend on the particular form of variance function chosen, with little evidence for selecting one rather than the other. There seems no pattern in the estimates of hatchery differences between disaggregated and aggregated data analyses. Estimates for log (δ_2/δ_1) are roughly the same for all aggregated analyses, higher than for disaggregated, while estimates for log (δ_3/δ_1) are markedly increased by aggregation over weeks but not by aggregation over regions.

Aggregating over codes

If only a single tag code per hatchery had been used, no information would have been available on the adequacy of the most general model: the 60 residual df from the full model disappear. There is no information on whether an observed difference between hatcheries or fisheries represents a real difference in mean level or a lack of independence among fish from the same hatchery. The deviances from any simpler model using data aggregated over codes are identical to the deviance differences between the simpler and the full model (i.e. the tests of interaction in Table 6) using the unpooled data. No new analysis is needed. However, the χ^2 values are changed. In the example, the χ^2 value for Model 4 is 47.4 from the pooled data, less than the interaction value of 60.6 for unpooled data that gave some concern earlier about the selection of that model.

Discussion

The analysis of overdispersed counts is an area of much recent statistical research (Nelder and Pregibon 1987; Morton 1988; Tsutakawa 1988; McCullagh and Nelder 1989; Breslow 1990). The procedure recommended here is possibly the simplest to implement and understand because of its close correspondence to analysis of variance. Analysis of a negative binomial form with variance $\sigma^2 = \mu + \mu^2/k$ can readily be implemented by the iterative GLIM macros of Breslow (1984) or Bennett (1988). In this, as in the proportional Poisson form $\phi\mu$, the overdispersion parameter k is consistently estimated by the moment estimator obtained by dividing the Pearson χ^2 by its df. The question of how best to estimate ϕ or k is still open, since the estimator obtained by dividing the residual deviance D by its df, though inconsistent, has smaller mean square error than the $\hat{\phi}$ used in this paper.

The method of quasi-likelihood (QL) was introduced by Wedderburn (1974) as an extension of the method of least squares to the case where the variance is not constant but constant times a known function $\sigma^2(\mu)$ of the mean μ. A brief introduction to QL, and a clear statement of its large-sample distributional properties, is given in McCullagh (1986) with a more detailed discussion in Chapter 9 of McCullagh and Nelder (1989). Many of the commonly used variance functions $\sigma^2(\mu)$ are properties of standard probability distributions (e.g. $\sigma^2(\mu) = \mu$ for Poisson). In these cases, QL estimates are identical to the maximum likelihood estimates which would be obtained from that probability distribution, and deviance differences are −2 times log likelihood ratios. However, the QL estimators and tests have desirable asymptotic properties without any assumption about the probability distribution of the observations.

An extended study by Breslow (1990) compares the various possible tests for model selection when the true form of the observed overdispersion is both known and unknown. In the latter case, he finds that the procedure recommended in this

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paper is too liberal, rejecting the null hypothesis when true more often than the presumed α-level. In Breslow's examples of testing for significant differences between medical treatments, a liberal test does seem undesirable. The same considerations may apply when the main aim of the tag–recovery experiment is to compare hatchery treatments: we may not wish to assert the existence of treatment differences when they do not exist. But, for comparing different regions or time periods for the recovery process, it seems more reasonable to think that real differences do exist and that a simpler model is being sought for ease of interpretation and reduction of variances, and we may wish to be more sure than the test indicates that the simpler model is acceptable before using it. If overdispersion is observed, Breslow recommends the use of an empirical score test which approximates the correct α-level but which suffers from severe loss of power, particularly in experiments with few replicates and large α. Thus, this test also leads to retention of the simpler model when a more complex pattern of recovery rates is actually occurring.

Information about overdispersion comes from examination of the residuals from the full model. Without the use of more than one tag code per treatment, no such information is available. When treatments within a hatchery are to be compared, careful consideration needs to be given to the experimental design, including to which groups of fish different codes should be applied. Nonindependence or heterogeneity, both of which may be manifest in overdispersion, can invalidate the results of any experiment. In practice, neither the form of the variance function nor the existence or magnitude of interactions between the factors in the experiment is known. Uncertainty in both mean structure and variance structure makes selection of a valid model from data extremely difficult. Aggregation can induce or mask the appearance of interactions, as demonstrated in the example.

All the arguments, from statistical theory and fisheries methodology, support the principle of keeping overdispersion as low as possible by analysing the data at the most disaggregated level possible.

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References

ANSCOMBE, F. J. 1953. Contribution to the discussion of H. Hotelling's paper. J. R. Stat. Soc. B 15: 229–230.

BAKER, R. J., AND J. A. NELDER. 1978. The GLIM system, release 3. Numerical Algorithms Group, Oxford, U.K.

BENNETT, S. 1988. A general approach to overdispersion. GLIM Newslett. 17: 12–18.

BRESLOW, N. E. 1984. Extra-Poisson variation in log-linear models. Appl. Stat. 33: 38–44.

1990. Tests of hypotheses in overdispersed Poisson regression and other quasi-likelihood models. J. Am. Stat. Assoc. 85: 565–571.

BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1985. Statistical inference from band-recovery data — a handbook. 2nd ed. U.S. Fish Wildl. Serv. Resour. Publ. No. 131.

BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, MD.

CLARK, J. E., AND D. R. BERNARD. 1987. A compound multivariate binomial–hypergeometric distribution describing coded microwire tag recovery from commercial salmon catches in Southeastern Alaska. Alaska Dept. Fish Game Inf. Leafl. No. 261.

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.

KOEHLER, K. J., AND K. LARNTZ. 1980. An empirical investigation of goodness-of-fit statistics for sparse multinomials. J. Am. Stat. Assoc. 75: 336–344.

MCCULLAGH, P. 1986. Quasi-likelihood functions, p. 464–467. *In* S. Kotz, N. L. Johnson, and C. B. Read [ed.] Encyclopedia of statistical science. Vol. 7. Wiley-Interscience, New York, NY.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. 2nd ed Chapman and Hall, London.

MORTON, R. 1988. Analysis of generalized linear models with nested strata of variation. Aust. J. Stat. 30A: 215–224.

NELDER, J. A., AND D. PREGIBON. 1987. An extended quasi-likelihood function. Biometrika 74: 221–232.

NELDER, J. A., AND. R. W. M. WEDDERBURN. 1972. Generalized linear models. J. R. Stat. Soc. A 135: 370–384.

PETERMAN, R. A. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. 39: 904–913.

PREGIBON, D. 1982. Score tests in GLIM with applications, p. 87–97. *In* R. Gilchrist [ed.] GLIM82: Proceedings of the International Conference on Generalised Linear Models. Springer-Verlag, Berlin.

RIPLEY, B. D. 1981. Spatial statistics. Wiley, New York, NY.

SCHWARZ, C. J., K. P. BURNHAM, AND A. N. ARNASON. 1988. Post-release stratification in band recovery models. Biometrics 44: 765–785.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Griffin, London.

TSUTAKAWA, R. K. 1988. Mixed model for analyzing geographic variability in mortality rates. J. Am. Stat. Assoc. 83: 37–42.

WEDDERBURN, R. W. M. 1974. Quasi-likelihood functions, generalized linear models, and the Gauss–Newton method. Biometrika 61: 439–447.