Estimating the influence of temperature on the survival of chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento – San Joaquin River Delta of California

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Abstract: Data from the U.S. Fish and Wildlife Service are used to investigate the relationship between water temperature and survival of hatchery-raised fall-run chinook salmon (*Oncorhynchus tshawytscha*) smolts migrating through the Sacramento – San Joaquin Delta of California. A formal statistical model is presented for the release of smolts marked with coded-wire tags (CWTs) in the lower Sacramento River and the subsequent recovery of marked smolts in midwater trawls in the Delta. This model treats survival as a logistic function of water temperature, and the release and recovery of different CWT groups as independent mark–recapture experiments. Iteratively reweighted least squares is used to fit the model to the data, and simulation is used to establish confidence intervals for the fitted parameters. A 95% confidence interval for the upper incipient lethal temperature, inferred from the trawl data by this method, is 23.01 ± 1.08°C This is in good agreement with published experimental results obtained under controlled conditions (24.3 ± 0.1 and 25.1 ± 0.1°C for chinook salmon acclimatized to 10 and 20°C, respectively): this agreement has implications for the applicability of laboratory findings to natural systems.

Résumé : Des données du U.S. Fish and Wildlife Service sont utilisées pour l'étude du lien entre la température de l'eau et la survie de saumoneaux quinnat (*Oncorhynchus tshawytscha*) de remonte automnale élevées en pisciculture, migrant par le delta des rivières Sacramento et San Joaquim, en Californie. Un modèle statistique conforme est présenté pour la libération des saumoneaux munis d'une micromarque magnétisée codée (MMC) dans le cours inférieur de la Sacramento et la récupération subséquente dans le delta, au moyen de chaluts pélagiques. Ce modèle considère la survie comme une fonction logistique de la température de l'eau et de la libération et la récupération subséquente de différents groupes de MMC comme des expériences distinctes de marquage et de recapture. La méthode des moindres carrés respondérés itérativement est utilisée pour ajuster le modèle aux données et on utilise la simulation pour établir des intervalles de confiance pour les paramètres ajustés. La température létale supérieure initiale déduite des données recueillies au moyen du relevé au chalut, grâce à cette méthode, se situe à 23,01 ± 1,08°C, avec un niveau de confiance de 95%. Cette valeur correspond aux résultats publiés d'expériences, obtenus dans des conditions contrôlées, donnant respectivement 24,3 ± 0,1 et 25,1 ± 0,1°C, pour le quinnat acclimaté à 10 et 20°C. Cette correspondance ouvre des possibilités quant à l'applicabilité aux systèmes naturels des résultats obtenus en laboratoire. [Traduit par la Rédaction]

Introduction

For many years, the U.S. Fish and Wildlife Service (USFWS), in cooperation with the California Department of Fish and Game (CDFG) through the Inter-Agency Ecological Study Program, has conducted trawls for chinook salmon (*Oncorhynchus tshawytscha*) smolts near Chipps Island in the Sacramento – San Joaquin Delta of California during the main periods of smolt outmigration (USFWS

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1983–1992). The data arising from the Chipps Island trawls are used by USFWS and others to address a variety of questions about California's chinook salmon, such as smolt abundance, timing of outmigration, migration rates, and survival (Stevens et al. 1984; USFWS 1987; Kjelson et al. 1989).

An important part of these data consists of the recoveries of hatchery-reared fall-run smolts bearing coded-wire tags (CWTs) from a series of releases by USFWS and CDFG since 1978. These releases are made at a number of locations in the lower Sacramento River and northern delta specifically to provide information about smolt survival in the delta.

The usual treatment of these data has been as follows: an estimate is made of the survivorship associated with each individual release, the estimates are plotted against proposed explanatory variables (water temperature, smolt size, etc.), and a hypothesized survival curve is fitted through these points. Disagreements over the interpretation of the data have turned on the method used to estimate the individual survivorships and the functional form of the curve to be fitted (Kjelson et al. 1989; Baker et al. 1992).

This approach is reasonable and straightforward. It also has some limitations: it does not provide objective ways of assessing the extent to which a proposed survival function is consistent with the data, and it does not produce confidence bounds on fitted parameters that might be used to make informed policy decisions. Questions about goodness of fit and statistical uncertainty can only be formulated properly in the context of statistical models.

In this paper, we restrict our attention to the problem of estimating smolt survival as a function of water temperature, from trawl recoveries of CWT-marked smolts released at a single location. We show that a biologically reasonable model fits the data well enough to permit quantitative assessments of the uncertainty in the fitted parameters. The fitted values are shown to agree well with the results of laboratory studies.

Data

In this paper, r denotes the number of smolt release groups. For the ith release, $1 \le i \le r$, n_i is the number of smolts released, m_i is the number of smolts recovered, p_i is the trawl effort, and T_i is the water temperature at Ryde at the time of release, in degrees Celsius.

The data used in the models are those from the 15 releases in the lower Sacramento River at Ryde from 1983 through 1990 that are listed in Table 1. These data were assembled from USFWS (1983–1992) and Johnson and Longwill (1991). The smolts were all fall-run chinook salmon, reared at the Feather River Hatchery and released at Ryde in May or June. The average weight of these smolts ranged in different years from 5.15 to 9.40 g. Peak trawl recoveries at Chipps Island ranged from 2 to 5 d after release at Ryde.

Ryde is about 48 km upstream of Chipps Island, just below the last major distributary branching of the Sacramento River as it enters the delta. From each of the other release locations, there are alternate routes to Chipps Island and a variety of conditions to be found along the different routes. Smolts released at Ryde have only one direct route to Chipps Island (a second route, around Sherman Island via Three Mile Slough, is probably of minor importance), and survival along this route is likely to be less affected by factors other than water temperature than is survival through most other parts of the Delta. For this reason, the Ryde releases are commonly recognized as the most natural ones to consider when temperature is the primary variable of interest (Kjelson et al. 1989). Figure 1 shows the region of the delta under discussion.

What we are calling trawl effort is defined in USFWS reports as the ratio of the time spent in actual trawling to the total time interval covered by the surveys, multiplied by the ratio of the net width to the channel width. Although the USFWS reports do not always report the trawl effort, it is possible to recover it from the information that is reported. We will use the trawl effort as an estimate of the probability of capture; this assumption will be examined briefly later in this paper. The USFWS itself scrupulously refers to this quantity as simply an expansion factor, and to values calculated from it as survival indices.

The base model

All of our models begin with the assumption that the different CWT releases can be treated as independent mark–recapture experiments. For our first model, we treat each individual release as a binomial experiment, whose parameter is broken down into two components: the probability of survival from Ryde to Chipps Island, which we will take to be a logistic function $\phi(T_i)$ of water temperature T_i, and the probability of capture at Chipps Island, the known constant p_i. The parameters to be fitted are the location and scale parameters b_1, b_2 of the logistic function ϕ.

This corresponds to the likelihood function

$$L = \prod_{1}^{r} \pi_i$$

where

$$[1] \quad \begin{aligned} \pi_i &= \pi(m_i \mid n_i, \phi_i, p_i) = \binom{n_i}{m_i}(p_i\phi_i)^{m_i}(1 - p_i\phi_i)^{n_i - m_i} \\ \phi_i &= \phi(T_i) = \frac{1}{1 + e^{-b_1 - b_2 T_i}} \end{aligned}$$

This is a generalized linear model with canonical link function, in the terminology of McCullagh and Nelder (1989). A model of this kind is completely specified by its mean and the dependence of the variance on the mean. In this case:

$$[2] \quad \begin{aligned} E[m_i] &= p_i \phi_i n_i \\ V[m_i] &= E[m_i] - \frac{1}{n_i} E[m_i]^2 \end{aligned}$$

The maximum likelihood estimate for (b_1, b_2) is easily found from Eq. 2 by the algorithm of iteratively reweighted least squares.

Table 1. Data for the release and recovery of selected coded-wire-tag groups of chinook salmon smolts released in the Sacramento River at Ryde, Calif. (From USFWS 1983–1992.)

i	Coded-wire-tag No(s).	Date of release	Average weight (g)	Temperature (°C), T_i	No. released, n_i	No. recovered, m_i	Trawl effort, p_i
1	06–62–23	5/20/83	5.89	16.1	92 693	95	0.000 833 24
2	06–42–09						
	06–62–29	6/13/84	5.15	18.9	59 998	37	0.000 880 98
3	06–62–35	5/11/85	5.82	18.9	107 161	88	0.001 066 49
4	06–62–48	5/30/86	5.34	23.3	101 320	74	0.001 123 63
5	06–62–55	4/29/87	5.79	19.4	51 103	46	0.001 058 99
6	06–62–58	5/2/87	6.21	17.8	51 008	47	0.001 071 42
7	06–31–01	5/3/88	8.40	17.2	52 741	106	0.002 138 11
8	06–31–02	5/6/88	8.56	16.1	53 238	146	0.002 142 50
9	06–62–63	6/22/88	8.25	23.9	53 961	46	0.002 131 17
10	06–31–03	6/25/88	8.72	23.3	53 942	39	0.002 126 47
11	06–31–12	5/3/89	7.00	16.7	51 046	65	0.001 070 05
12	06–31–07	6/2/89	9.40	19.4	50 601	26	0.001 070 47
13	06–01–14–01–02	6/16/89	7.83	22.8	51 134	8	0.000 977 82
14	06–31–20	5/9/90	5.04	20.6	51 878	87	0.001 036 47
15	06–31–22	5/31/90	6.87	18.3	50 837	67	0.001 057 73

A biologically natural alternative to the parameterization (b_1, b_2) of the survival curve is (LT50, α), where LT50 is the temperature at which the predicted survival is 0.50, and α is the slope of the survival function at T = LT50. We will report results in both forms.

For the data in Table 1, maximum likelihood estimation gives $b_1 = 15.89$, $b_2 = -0.6873$. Equivalently, LT50 = 23.12, $\alpha = -0.1718$.

The Pearson χ^2 for the fit is 104.5 with 13 degrees of freedom. The log-likelihood ratio statistic D, which is also approximately distributed as a χ^2 statistic with 13 degrees of freedom, is 103.4. Both of these values are very highly significant, indicating that the base model does not fit very well.

Table 2 shows the expected and observed numbers of trawl captures, with Pearson and deviance residuals. The residuals are plotted against water temperature in Fig. 2. Because there is no clear trend in the residuals, we do not attribute the lack of fit to a fundamental defect in the model structure, such as an inadequate choice of the functional form for ϕ. That is, the model's handling of temperature is acceptable, but the model is not flexible enough to account for all of the noise in the data from factors not included.

Overdispersion

The overdispersion of the data with respect to the base model is not necessarily a fatal defect; in fact, overdispersion is so common in models such as this that its absence would be more remarkable than its presence (cf. McCullagh and Nelder 1989, section 4.5.1).

A conventional way to deal with overdispersion in a situation like this is to simply inflate the variance by some constant σ^2. In this case, one would replace Eq. 2 by

$$[3] \qquad \begin{aligned} E[m_i] &= p_i\phi_i n_i \\ V[m_i] &= \sigma^2\left(E[m_i] - \frac{1}{n_i}E[m_i]^2\right) \end{aligned}$$

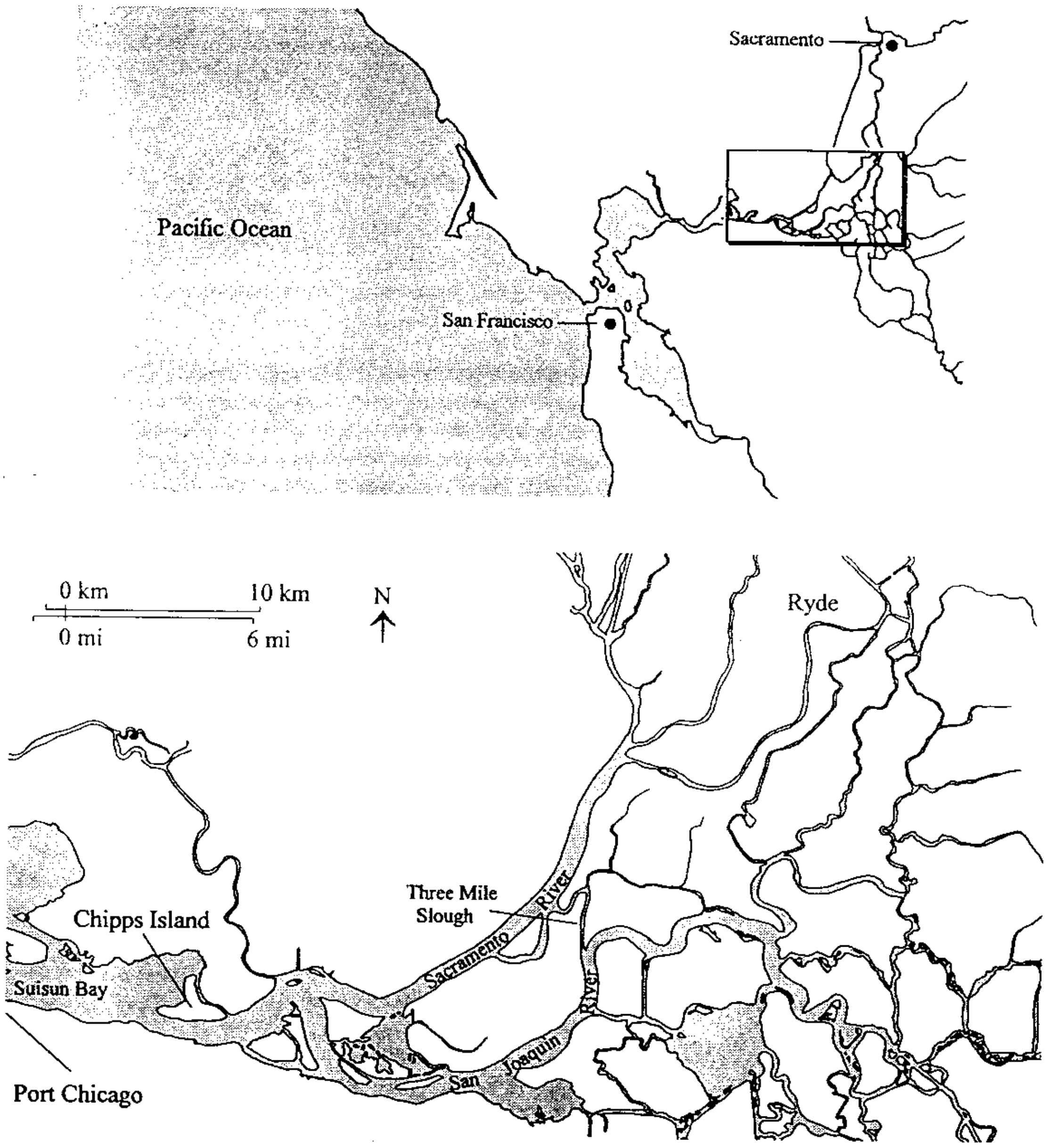
The maximum-likelihood estimate for (b_1, b_2) is not affected at all by the introduction of the dispersion parameter σ^2, so we are free to give σ^2 whatever value we want. In particular, we could force the model to have an acceptable chi-square fit simply by setting $\sigma^2 = \chi^2$df, where χ^2 is the fit of the original model.

The main criticism one can make of this procedure is that it seems rather arbitrary. If a model does not fit the data, the model assumptions are inadequate in some way, and should at least be reexamined. After all, the fitted values of the model parameters will not be meaningful if the model itself has no relation to reality, regardless of how we assign confidence levels.

In fact, there is an extensive literature on the subject, which basically justifies using the unadorned model to estimate parameters like b_1 and b_2, and dealing with overdispersion as indicated above (see references in McCullagh and Nelder 1989; Burnham et al. 1987). Nevertheless, we prefer to tailor our approach to the specifics of our situation.

There are many possible sources of overdispersion in these experiments: the probability of survival surely depends on factors other than water temperature; fish from different release groups have different histories; and fish from the same release group recovered in different trawls have different histories. However, we believe that the most important uncertainty is in the capture probabilities p_i. It is clear from the nature of the experiment that these numbers could be in error by very large amounts. It is easy to imagine that smolts could have a preference for regions of the

Fig. 1. Study area in the north-central region of the Sacramento – San Joaquin Delta, California.



channel cross section that are especially likely or unlikely to be sampled in a particular trawl, or that they travel past Chipps Island in clumps that might or might not coincide with a trawl pass.

Furthermore, the data from some of the individual releases clearly point to errors in the capture probability estimates. In the first of the two 1990 releases, 51 878 smolts were released, of which 87 were recovered; even if the survival were 100%, the probability of recovering as many as 87 smolts, assuming that the probability of capture was really 0.001036, would be on the order of 10^{-5}.

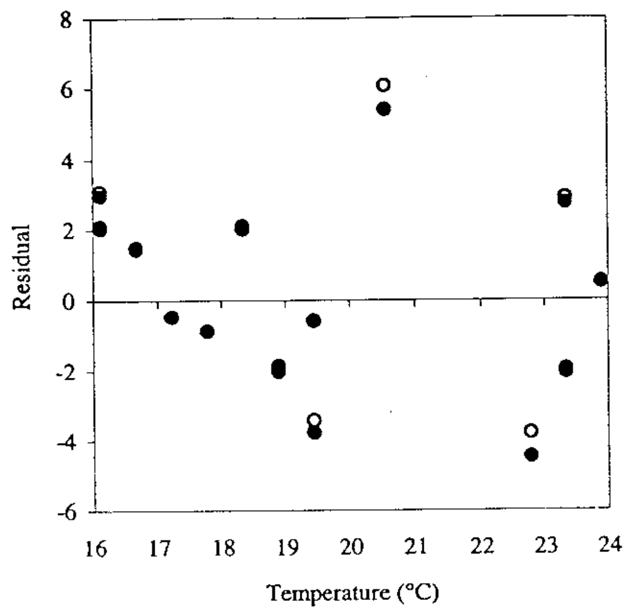
On the other hand, there is evidence that the recovery probability estimates are not systematically too high or too low. Fish from the CWT groups released at Ryde are also recovered in the ocean fishery as adults; information about these recoveries is available through the Pacific States Marine Fisheries Commission. These recoveries can be used to generate estimates of delta smolt survival.

The CWT groups are recovered as 2-, 3-, 4-, and 5-year-olds (the nominal ages of fall-run chinook salmon are based on the calendar years in which spawning took place). By comparing the ocean recovery rates of 2 year olds from the Ryde groups with the ocean recovery rates for 2 year olds from groups of similar smolts released near Chipps Island at about the same time, it is easy to obtain estimates of survival (S) from Ryde to Chipps Island from individual releases. In fact, the closest release site to Chipps Island is Port Chicago, about 8 km downstream, so that what is being estimated is survival from Ryde to Port Chicago:

Table 2. Comparison of the trawl recoveries predicted by the fitted base model for the Ryde release groups with the corresponding actual trawl recoveries.

i	Expected recoveries	Actual recoveries	Pearson residuals	Deviance residuals
1	77	95	2.10	2.02
2	50	37	−1.86	−1.95
3	108	88	−1.96	−2.03
4	53	74	2.91	2.74
5	50	46	−0.58	−0.59
6	53	47	−0.86	−0.88
7	111	106	−0.46	−0.46
8	113	146	3.09	2.96
9	43	46	0.50	0.50
10	53	39	−1.95	−2.05
11	54	65	1.50	1.45
12	50	26	−3.41	−3.76
13	28	8	−3.78	−4.46
14	46	87	6.07	5.39
15	52	67	2.11	2.01

Fig. 2. Pearson (open circles) and deviance (solid circles) residuals for the fitted base model, plotted against water temperature.



$$S_{\text{ocean}} = \frac{m_{\text{Ryde}} / n_{\text{Ryde}}}{m_{\text{PC}} / n_{\text{PC}}}$$

where n_{Ryde} is the number released at Ryde, n_{PC} is the number released at the Port Chicago, and m_{Ryde} and m_{PC} are the corresponding numbers recovered as 2 year olds in the ocean. These can be compared with simple estimates of survival from Ryde to Chipps Island for the same releases: $S_{\text{trawl}} = m_i/n_ip_i$ where n_i, m_i, and p_i are as defined earlier (cf. USFWS 1987).

Survival from Chipps Island to Port Chicago should be high, because the distance between them is fairly small, so that S_{ocean}, S_{trawl} are essentially estimates of the same quantity. As there is no reason to expect both estimates to be biased in the same direction and to the same extent, each serves as a check on the other. Formal analysis confirms the impression of Fig. 3, that the hypothesis $S_{\text{ocean}} = S_{\text{trawl}}$ cannot be rejected at the 95% confidence level. We interpret this as evidence that the p_i can be used as estimates of the expected values of the true recovery probabilities (although the co-occurrences of ocean-based estimates greater than 1 with trawl-based estimates greater than 1 remains puzzling).

More information on the relationship between the trawl-recovery and ocean-recovery estimates can be obtained from the authors.

The relaxed model, the quasilikelihood estimator, and simulation

We modify the base model (Eq. 1) to allow for uncertainty in the capture probabilities by assuming that the capture probability P in the ith release is itself a random variable with mean p_i and variance $\rho^2 p_i^2$. Here ρ^2 is taken to be the same for all release groups. (Because the capture probabilities are necessarily non-negative, and we expect the errors in the p_i to be large, a multiplicative error structure seems called for; this leads to the assumption that the coefficient of variation, rather than the variance itself, is constant from release to release.) This gives

$$[4] \quad \begin{aligned} &\pi(m_i|n_i, \phi_i p_i) = \int_0^1 \binom{n_i}{m_i} (P\phi_i)^{m_i} (1 - P\phi_i)^{n_i - m_i} f_i(P)\, dP \\ &\phi_i = \phi(T_i) = \frac{1}{1 + e^{-b_1 - b_2 T_i}} \end{aligned}$$

where f_i is the density for P. We will call this the relaxed model.

Because we have not specified the distribution f_i, this is not yet a well-defined likelihood. No matter what distribution we use, however, we will always have

$$[5] \quad \begin{aligned} &E[m_i] = p_i \phi_i n_i \\ &V[m_i] = E[m_i] + \left(\frac{n_i - 1}{n_i} \rho^2 - \frac{1}{n_i} \right) E[m_i]^2 \end{aligned}$$

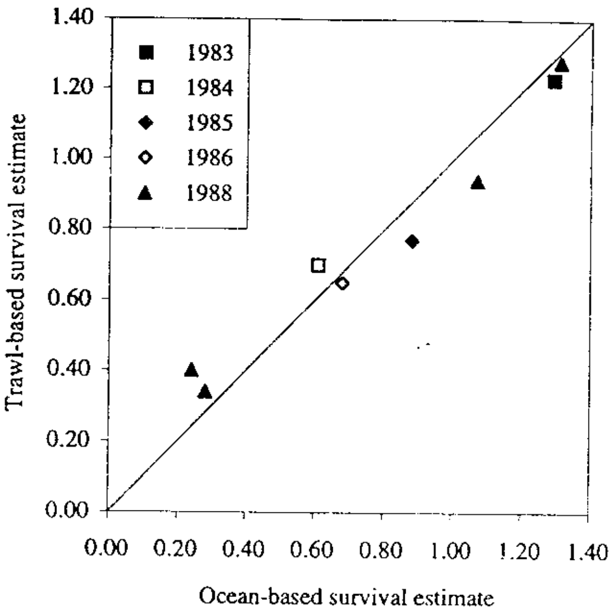
equivalently,

$$E[m_i] = E[m_i | P = p_i],$$

$$\frac{V[m_i]}{E[m_i]^2} = \frac{V[m_i | P = p_i]}{E[m_i | P = p_i]^2} + \frac{n_i - 1}{n_i} \rho^2.$$

If the π_i were in a suitable exponential family, this would be all the information necessary to find the maximum-likelihood estimate for (b_1, b_2) by iteratively reweighted least squares. This algorithm is in any case a perfectly legitimate estimator, that one would expect to inherit some of the properties of a genuine maximum-likelihood

Fig. 3. Two methods of estimating smolt survival from Ryde to Chipps Island. The diagonal line (trawl-based survival = ocean-based survival) is provided for reference.



estimator. We will refer to this as the quasilikelihood estimator, for reasons to be discussed in the next section.

We are interested not only in the parameter estimates themselves, but in statistical properties of the estimator such as bias and variance. The conventional way to assign confidence intervals to the parameter estimates is by the δ-method. In the case of generalized linear models fitted by iteratively reweighted least squares, the covariance matrix emerges naturally from the algorithm; when a model that is not necessarily of this form is fitted by the iteratively reweighted least-squares algorithm, the algorithm gives the covariance matrix asymptotically. In either case, the estimators are approximately unbiased and asymptotically normal (McCullagh and Nelder 1989).

However, maximum-likelihood estimators can be very far from either unbiased or normal when the number of samples is not large. In any case, these compromises are entirely unnecessary. For any particular choice of f_i, the properties of the quasilikelihood estimator can be determined to any desired accuracy by simulation.

We will consider two simple examples, the uniform distribution:

$$f_i(P) = \begin{cases} \dfrac{1}{2w}, & \text{if } |P - p_i| < w \\ 0, & \text{otherwise} \end{cases}$$

where

$$w = p_i\sqrt{3\rho^2}$$

and the triangular distribution

$$f_i(P) = \begin{cases} \dfrac{1}{w}\left(1 - \dfrac{1}{w}|P - p_i|\right), & \text{if } |P - p_i| < w \\ 0, & \text{otherwise} \end{cases}$$

where

$$w = p_i\sqrt{6\rho^2}$$

The largest value of ρ^2 consistent with the uniform distribution is one-third, and the largest value consistent with the triangular distribution is one-sixth. Notice that the uniform distribution has the largest variance of any unimodal distribution symmetric about p_i, and so sets an upper limit on the amount of extra variation that can be reasonably attributed to uncertainty in p_i. Confidence estimates based on this distribution should therefore be conservative.

We have defined a model (or at least a family of models) and a fitting procedure. It still remains to choose a value for ρ^2. We have no good basis for selecting a value a priori. Not only do we lack a suitable understanding of the trawl capture process, but the parameter is absorbing extra variation associated with ϕ and with the approximation of the trawl recovery as a simple binomial process. There are methods for fitting ρ^2 formally as a model parameter (McCullagh and Nelder 1989), but for a data set of this size we find it more appropriate to simply pick a value that results in a reasonable model fit. We have followed the usual practice of forcing the Pearson χ^2-statistic of the fit to equal the degrees of freedom (Williams 1982).

For the data in Table 1, the fitting procedure described above produced the estimate $\rho^2 = 0.1503$. This value for ρ^2 seems plausible to us. It is close to the ρ^2 for the maximally broad triangular distribution, and comfortably within the range of ρ^2-values that are consistent with the derivation of the model.

For this value of ρ^2, the fitted parameters are $b_1 = 15.56$, $b_2 = -0.6765$, so that LT50 = 23.01 and $\alpha = -0.1691$.

Confidence intervals and bias for b_1, b_2, LT50, and α were estimated by simulation: the model (4) was used with both the uniform and triangular distributions for f_i to generate 5000 data sets each, assuming the values for ρ^2, b_1, and b_2 given above. Each simulated data set was fitted to the model (holding ρ^2 constant), yielding 10 000 pairs (b_{1k}, b_{2k}).

The mean, standard deviation, and bias of these data, and some order statistics, are shown in Table 3. Standard formulas show that the mean and standard deviation are determined by the simulation to within 2% at the 95% confidence level. The quasilikelihood estimator for LT50 is seen to be essentially unbiased, confirming the naturalness of this quantity as a model parameter. The shortest 95% confidence intervals were 21.96°C < LT50 < 24.10°C for the uniform distribution and 22.59°C < LT50 < 23.41°C for the triangular distribution. The corresponding symmetric 95% intervals were 21.93°C < LT50 < 24.08°C and 22.60°C < LT50 < 23.42°C, respectively.

The results of the simulation are shown more vividly in Fig. 4. For each model, one point has been plotted at a randomly chosen temperature on each of the 5000 fitted survival curves, to give some feeling for the shapes of the confidence surfaces.

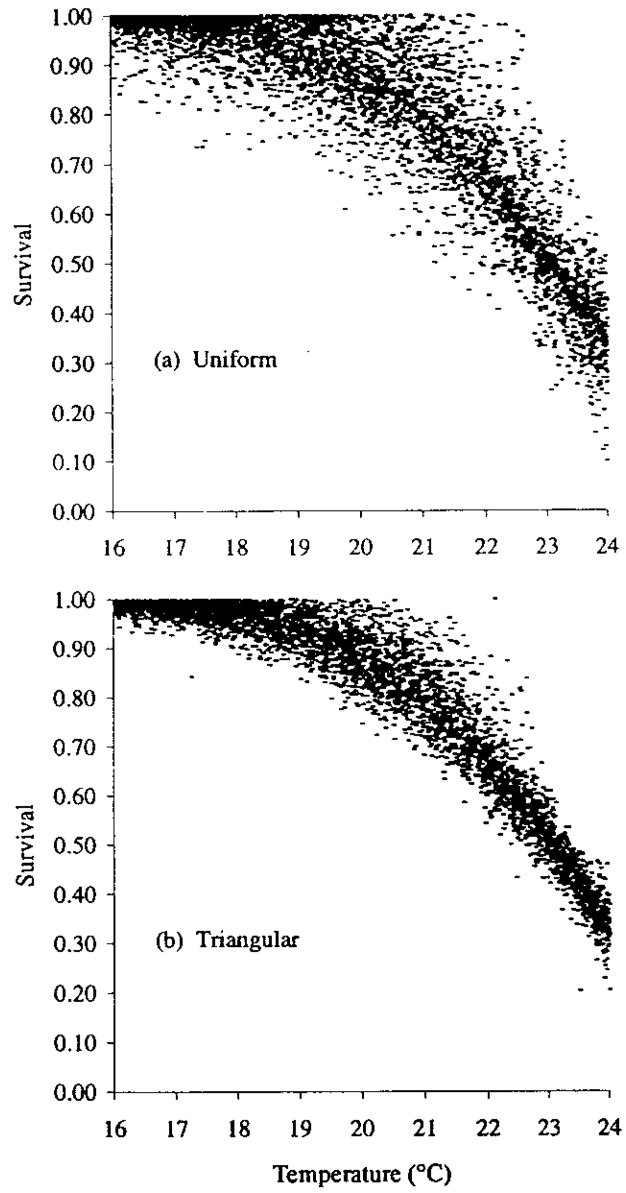
The quasilikelihood-generating model

Our goal in this section is to clarify just what the quasilikelihood estimator of the preceding section is maximizing.

Table 3. Statistical properties of the quasilikelihood estimators, determined by simulation with respect to two models of capture probability.

	Canonical parameters		Natural parameters	
	b_1	b_2	LT50	α
Fitted	15.56	−0.6765	23.01	−0.1691
Uniform				
Mean	18.65	−0.8080	23.06	−0.2020
SD	10.18	0.4356	0.57	0.1089
Bias	3.08	−0.1315	0.05	−0.0329
P1	5.72	−2.6166	21.64	−0.6542
P2.5	7.40	−2.0770	21.95	−0.5193
Q1	13.09	−0.8957	22.85	−0.2239
Median	15.80	−0.6880	23.03	−0.1720
Q3	20.70	−0.5722	23.26	−0.1430
P97.5	47.97	−0.3168	24.10	−0.0792
P99	60.60	−0.2352	24.63	−0.0588
Triangular				
Mean	16.80	−0.7291	23.01	−0.1823
SD	5.06	0.2163	0.21	0.0541
Bias	1.23	−0.0526	0.01	−0.0132
P1	10.09	−1.5716	22.47	−0.3929
P2.5	10.75	−1.3101	22.57	−0.3275
Q1	13.62	−0.8028	22.88	−0.2007
Median	15.62	−0.6810	23.02	−0.1703
Q3	18.54	−0.5941	23.16	−0.1485
P97.5	30.32	−0.4690	23.40	−0.1172
P99	36.23	−0.4414	23.48	−0.1103

Fig. 4. Distributions of quasilikelihood estimates of smolt survival from Ryde to Chipps Island, for the fitted model, assuming that the probability of capture is drawn from (*a*) the uniform distribution and (*b*) the triangular distribution.



From a practical point of view, the question is moot, in that the simulations described there establish completely rigorous confidence regions for the estimated parameters. This section can be skipped by readers who are primarily interested in the biological results.

Quasilikelihood theory was developed to deal with situations in which one has some (usually empirical) information about the relationship between the expected value and variance of a quantity, over a series of similar experiments, but not about the statistical mechanisms that give rise to this relation and, therefore, no way to construct a likelihood function. In such a situation, one can construct a function called a quasilikelihood, which turns out to have many of the properties of a true likelihood function arising from a generalized linear model. In particular, the method of iteratively reweighted least squares can be used to maximize the quasilikelihood, and much of the asymptotic theory of maximum likelihood estimation carries over to maximum quasilikelihood (McCullagh and Nelder 1989).

Our case is rather different, in that we have the definite model (4) in mind, which is only incomplete in that we are trying to avoid committing ourselves to a particular form for the functions f_i.

If there were a suitable exponential family distribution having the same mean and variance as Eq. 4, the quasilikelihood estimate would be exactly the maximum likelihood estimate for this distribution. Unfortunately, it is not hard to show that no such distribution exists. The obstacle here turns out to be the requirement that the distribution is supported on the integers from 0 to n. If this condition is relaxed to require only that the distribution be supported on non-negative integers, there is a (unique) exponential family distribution with the desired properties:

$$[6] \quad \pi(m_i|n_i,\phi_i,p_i) = \begin{cases} \binom{n_i/\gamma_i}{m_i}(\gamma_i p_i\phi_i)^{m_i}(1-\gamma_i p_i\phi_i)^{n_i/\gamma_i - m_i}, & \text{for } 0<\gamma_i<1 \\ \dfrac{(p_i\phi_i n_i)^{m_i}}{m_i!}e^{-p_i\phi_i n_i}, & \text{for } \gamma_i = 0 \end{cases}$$

$$\binom{-n_i/\gamma_i + m_i - 1}{m_i}(-\gamma_i p_i \phi_i)^{m_i}(1-\gamma_i p_i \phi_i)^{n_i/\gamma_i - m_i}, \quad \text{for } \gamma_i < 0$$

where $\gamma_i = 1 - (n_i - 1)\rho^2$.

Except for a constant factor, this turns out to be identical to the quasilikelihood function constructed from Eq. 5, so that it reasonable to call Eq. 6 the quasilikelihood generating model.

Because the number of smolts in each release ($\approx 10^4$, 10^5) is very much larger than the typical number recovered ($\approx 10^1$, 10^2), it would have been quite reasonable to model the underlying survival–capture process as a Poisson process. After all, the binomial model is also only an approximation (for example, smolts from one release are actually recovered over several trawls), and it would be difficult to argue convincingly that it is a better one than the Poisson in this case. If we imitate the development of the previous section, beginning from the Poisson model, things work out pretty much as before. The mean and variance functions of the relaxed model become

$$[7] \quad \begin{aligned} E[m_i] &= p_i \phi_i n_i \\ V[m_i] &= E[m_i] + \rho^2 E[m_i]^2 \end{aligned}$$

and the quasilikelihood-generating distribution takes the form:

$$= \frac{(p_i \phi_i n_i)^{m_i}}{m_i!} e^{-p_i \phi_i n_i}, \quad \text{for } \gamma_i = 0$$

$$[8] \quad \pi(m_i | n_i, \phi_i, p_i)$$

$$= \binom{-n_i/\gamma_i + m_i - 1}{m_i}(-\gamma_i p_i \phi_i)^{m_i}(1-\gamma_i p_i \phi_i)^{n_i/\gamma_i - m_i}, \quad \text{for } \gamma_i < 0$$

where $\gamma_i = -n_i \rho^2$ (so the first case of Eq. 6 never arises). These equations are identical to Eqs. 5 and 6 except for obviously negligible terms of order $1/n_i$.

The second (negative binomial) distribution of Eq. 8, however, can also be exhibited as the model that results from the Poisson base model when the parameter p_i is replaced by a gamma variate with mean p_i and variance $\rho^2 p_i^2$. That is, the quasilikelihood estimate is indeed a maximum-likelihood estimate for a perfectly natural model. Our only reason for preferring the language of quasilikelihood is that the maximum-likelihood interpretation depends very delicately on making the right approximations.

Discussion

We have shown that a simple and natural model of smolt survival can be fit to the data. This model predicts mean smolt survival at a given temperature to about 10% at the 95% confidence level (cf. Fig. 4).

Taking the most conservative error bounds, we have estimated that chinook salmon released at Ryde and migrating to Chipps Island experience 50% mortality at 23.01 ± 1.08°C. It is interesting to compare this estimate of survival under natural conditions with the results of laboratory studies.

Laboratory studies of the direct effects of high temperatures on animal survival have been conducted in two different ways: the method of abrupt transfer and the method of slow heating (Kilgour and McCauley 1986). These result in somewhat different measures of lethality. For our purposes we will regard the upper incipient lethal temperature (UILT) found in abrupt transfer experiments as comparable with the LT50 of the fitted model. We will regard the temperatures at which given fractions of the sample are lost in slow heating experiments as comparable with the temperatures at which these same losses are predicted by the model. In both kinds of experiments, the results depend on the temperature to which the animals were acclimatized.

The classic abrupt transfer experiments involving chinook salmon are those of Brett (1952):

	Brett (1952)				Fitted
Acclimation (°C)	10	15	20	24	—
UILT	24.3±0.1	25.0±0.1	25.1±0.1	25.1±0.1	23.01±1.08

We regard this as a reasonable agreement.

The temperatures predicted by the fitted model to result in 10, 50, and 90% mortality are also consistent with the results of several slow-heating experiments reproduced in the survey of Houston (1982):

	Houston (1982)						Fitted
Acclimation (°C)	10	10	11	13	18	20	—
10% loss	22.9	20.5	23.0	19.5	20.0	23.8	19.76
50% loss	—	—	23.5	—	—	24.7	23.01
90% loss	24.5	23.5	23.8	23.0	23.5	24.8	26.26

The laboratory studies cited above examine the effects of temperature alone. In the natural environment, however, it may be difficult or impossible to separate the direct effects of temperature from indirect effects on the ability of salmon to survive other threats, such as predation and disease. It is reasonable to inquire about the magnitude of these indirect effects.

The UILTs found by Brett for salmon acclimatized to 15°C and above are about 2°C higher than the LT50 found here. In addition, the range of temperatures at which significant temperature-related mortality occurs is greater in the fitted model than in any of the laboratory studies referred to above. Both of these observations would be consistent with the presence of significant indirect effects of temperature on survival in the delta. If the possibility of differences in temperature tolerance between Central Valley salmon stocks and the more northerly stocks used in the laboratory studies is considered, there may be even more room for indirect temperature effects. On the other hand, the model makes no provision for possible sources of mortality independent of temperature. If mortality from such sources could be accounted for separately, the LT50 associated with the remaining mortality would probably be higher.

Our analysis shows that direct effects of high temperature are sufficient to explain a large part of the smolt mortality actually observed in the delta. In particular, the observed LT50 of 23.01 ± 1.08°C is remarkably consistent with the results of controlled experiments. This reaffirms the relevance of laboratory findings to natural systems.

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