Presentation of the San Joaquin Tributary Agencies
to the
State Water Resources Control Board
October 19, 1994
on
San Joaquin River Salmon & Striped Bass Issues

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B. Tuolumne River - (Modesto Irrigation District & Turlock Irrigation District)

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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 collected and reported by 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 mid-water 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. The upper incipient lethal temperature inferred from the trawl data by this method is 23.01 ± 1.08°C at the 95% confidence level. This is in good agreement with experimental results of Brett (1952) (24.3 ± 0.1°C and 25.1 ± 0.1°C for chinook salmon acclimatized to 10°C and 20°C, respectively), particularly when it is observed that Brett's results were obtained under controlled conditions, whereas the present work deals with survival in the natural environment. This agreement has implications for the applicability of laboratory findings to natural systems.

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 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, $1 \leq i \leq r$, 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 centigrade.

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 g to 9.40 g. Peak trawl recoveries at Chipps Island ranged from two to five days after release at Chipps Island.

Table 1 near here

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.

Figure 1 near here

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)
$$\pi_i = \pi(m_i | n_i, \phi_i, p_i) = \binom{n_i}{m_i} (p_i\phi_i)^{m_i}(1 - p_i\phi_i)^{n_i - m_i}$$
$$\phi_i = \phi(T_i) = \frac{1}{1 + e^{-b_1 - b_2 T_i}}$$

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)
$$E[m_i] = p_i\phi_i n_i$$
$$V[m_i] = E[m_i] - \frac{1}{n_i}E[m_i]^2$$

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

A biologically natural alternative to the parameterization (b_1, b_2) of the survival curve is $(\mathrm{LT50}, \alpha)$, where LT50 is the temperature at which the predicted survival is 0.50, and α is the slope of the survival function at $T = \mathrm{LT50}$. 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, $\mathrm{LT50} = 23.12$, $\alpha = -0.1718$.

The Pearson chi-square for the fit is 104.5 with 13 degrees of freedom. The log-likelihood ratio statistic D, which is also approximately distributed as a chi-square 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 Figure 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.

Table 2 near here

Figure 2 near here

OVERDISPERSION

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

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

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

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 $\sigma^2 = X^2/\text{d.f.}$, where X^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 re-examined. 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 over-dispersion in these experiments: The probability of survival surely depends on factors other than water temperature; fish from different release groups have different histories; 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 channel cross section which 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 two-, three-, four-, and five-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 two-year-olds from the Ryde groups with the ocean recovery rates for two-year-olds from groups of similar smolts released near Chipps Island at about the same time, it is easy to obtain estimates of survival 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:

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

where n_{Ryde} is the number released at Ryde, n_{PC} is the number released at the Port Chicago, and m_{Ryde}, m_{PC} are the corresponding numbers recovered as two-year-olds in the ocean. These can be compared with simple estimates of survival from Ryde to Chipps Island for the same releases

$$S_{\text{Trawl}} = \frac{m_i}{n_i p_i}$$

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 Figure 3, that the hypothesis $S_{\text{Ocean}} = S_{\text{Trawl}}$ cannot be rejected at the 95% confidence level. Figure 3 near here
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 (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

$$
\begin{aligned}
\pi(m_i|n_i,\phi_i,p_i) &= \int_0^1 \binom{n_i}{m_i}(P\phi_i)^{m_i}(1-P\phi_i)^{n_i-m_i} f_i(P)\,dP \\
\phi_i = \phi(T_i) &= \frac{1}{1+e^{-b_1-b_2T_i}}
\end{aligned}
\tag{4}
$$

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

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

(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 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 delta 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

$$f_i(P) = \begin{cases} \frac{1}{2w}, & \text{if } |P - p_i| < w \\ 0, & \text{otherwise} \end{cases}, \qquad w = p_i\sqrt{3\rho^2}$$

and the triangular distribution

$$f_i(P) = \begin{cases} \frac{1}{w}(1 - \frac{1}{w}|P - p_i|), & \text{if } |P - p_i| < w \\ 0, & \text{otherwise} \end{cases}, \qquad w = p_i\sqrt{6\rho^2}$$

The largest value of ρ^2 consistent with the uniform distribution is 1/3, and the largest value consistent with the triangular distribution is 1/6. 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 chi-squared 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.

Table 3 near here

The results of the simulation are shown more vividly in Figure 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.

Figure 4 near here

THE QUASILIKELIHOOD-GENERATING MODEL

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

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

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 (5), so that it reasonable to call (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

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

and the quasilikelihood-generating distribution takes the form:

$$(8) \qquad \pi(m_i|n_i,\phi_i,p_i) = \begin{cases} \frac{(p_i\phi_i n_i)^{m_i}}{m_i!}e^{-p_i\phi_i n_i}, & \text{for } \gamma_i = 0 \\ \binom{-n_i/\gamma_i+m_i-1}{m_i}(-\gamma_i p_i\phi_i)^{m_i}(1-\gamma_i p_i\phi_i)^{n_i/\gamma_i-m_i}, & \text{for } \gamma_i < 0 \end{cases}$$

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

The second (negative binomial) distribution of (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. Figure 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 to 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 to 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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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. (From USFWS 1983–1992.)

i	Coded-Wire-Tag Number(s)	Date of Release	Average Weight(g)	Temperature (°C) T_i	Number Released n_i	Number Recovered m_i	Trawl Effort p_i
1	06-62-23	5/20/83	5.89	16.1	92 693	95	0.00083324
2	06-42-09 06-62-29	6/13/84	5.15	18.9	59 998	37	0.00088098
3	06-62-35	5/11/85	5.82	18.9	107 161	88	0.00106649
4	06-62-48	5/30/86	5.34	23.3	101 320	74	0.00112363
5	06-62-55	4/29/87	5.79	19.4	51 103	46	0.00105899
6	06-62-58	5/2/87	6.21	17.8	51 008	47	0.00107142
7	06-31-01	5/3/88	8.40	17.2	52 741	106	0.00213811
8	06-31-02	5/6/88	8.56	16.1	53 238	146	0.00214250
9	06-62-63	6/22/88	8.25	23.9	53 961	46	0.00213117
10	06-31-03	6/25/88	8.72	23.3	53 942	39	0.00212647
11	06-31-12	5/3/89	7.00	16.7	51 046	65	0.00107005
12	06-31-07	6/2/89	9.40	19.4	50 601	26	0.00107047
13	06-01-14-01-02	6/16/89	7.83	22.8	51 134	8	0.00097782
14	06-31-20	5/9/90	5.04	20.6	51 878	87	0.00103647
15	06-31-22	5/31/90	6.87	18.3	50 837	67	0.00105773

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

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
s.d.	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
s.d.	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

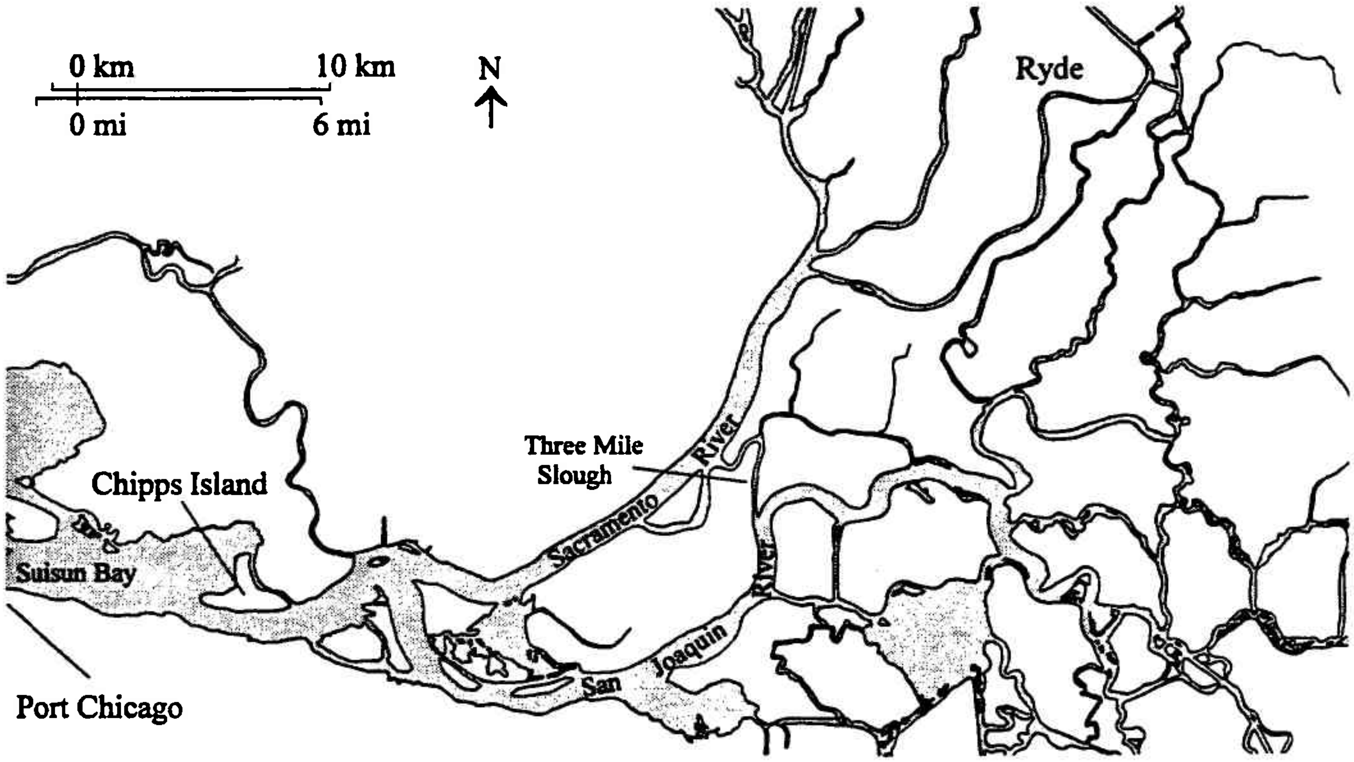
Figure 1. North-Central Region of the Sacramento - San Joaquin Delta.

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

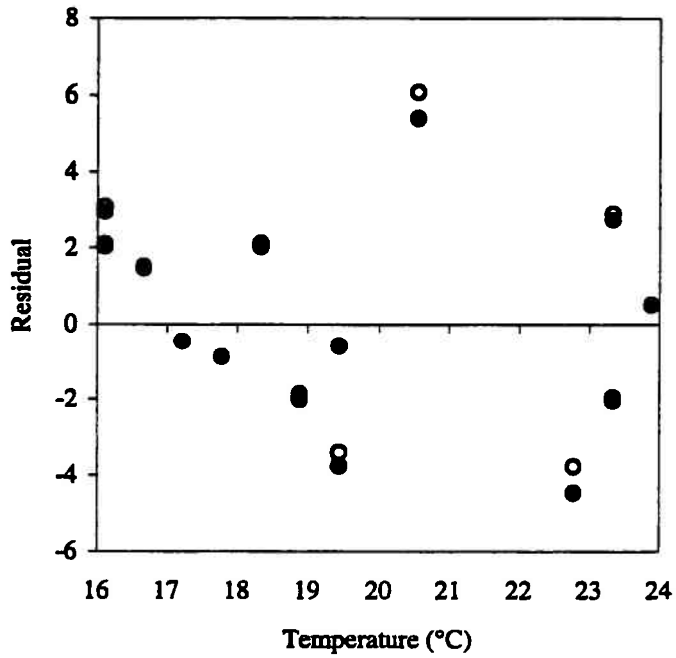
Figure 3. Two methods of estimating smolt survival from Ryde to Chipps Island. The diagonal line Trawl-based survival = Ocean-based survival is provided for reference.

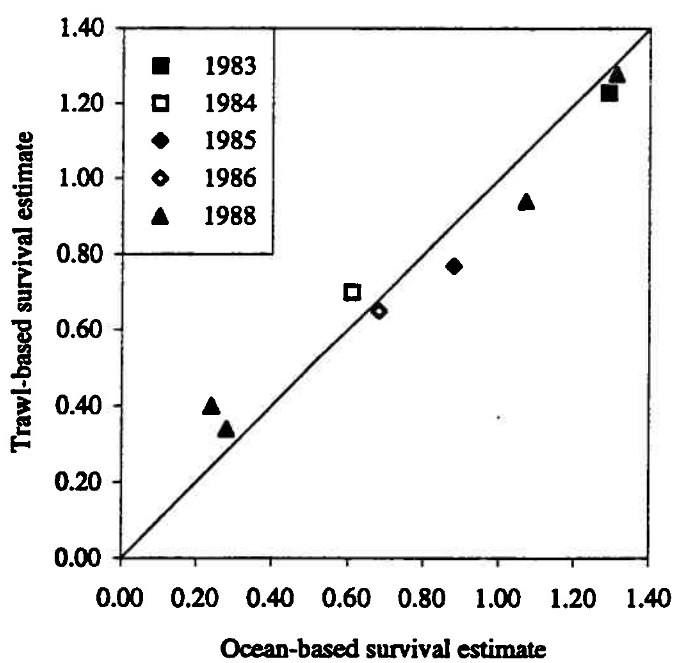
Figure 4. Distributions of quasilikelihood estimates of smolt survival from Ryde to Chipps Island, for the fitted model, assuming that the probabity of capture is drawn from (a) the uniform distribution and (b) the triangular distribution.

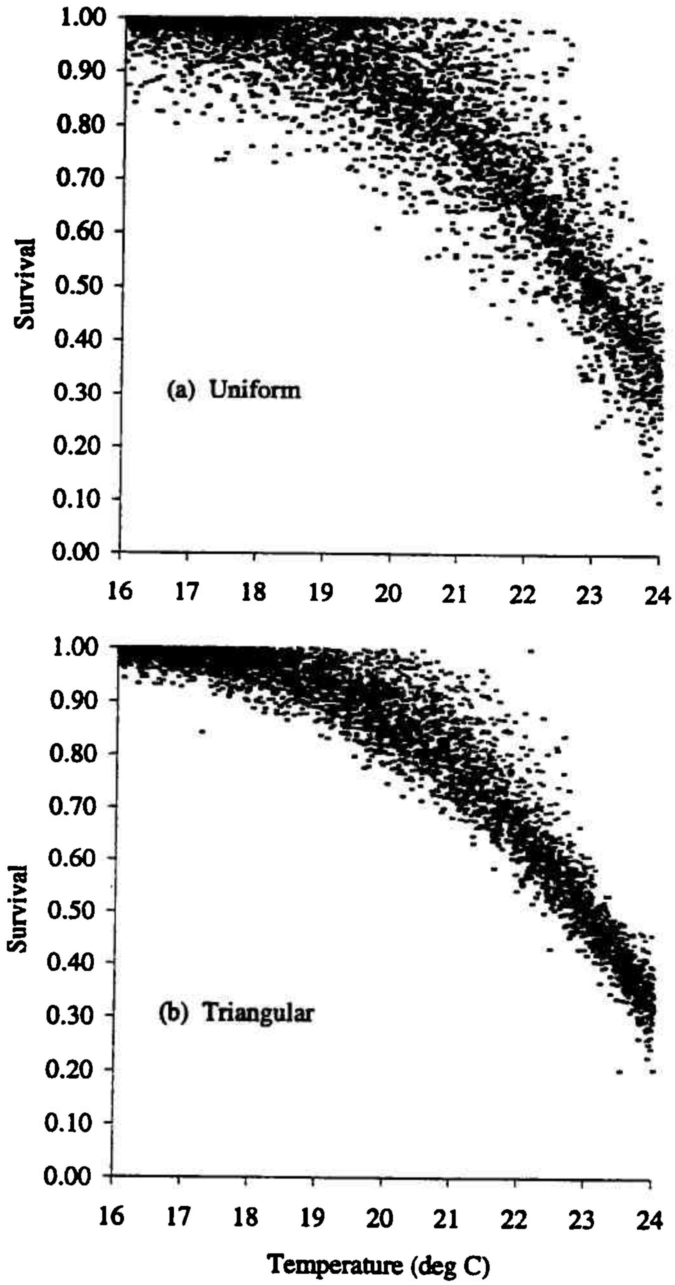
Figure 1



0 km
10 km
0 mi
6 mi
N
Ryde
Three Mile
Slough
Chipps Island
Sacramento
River
River
San
Joaquin
Suisun Bay
Port Chicago


8
6
4
2
0
-2
-4
-6
Residual
16
17
18
19
20
21
22
23
24
Temperature (°C)


1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
1983
1984
1985
1986
1988
Trawl-based survival estimate
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Ocean-based survival estimate


1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Survival
(a) Uniform
16 17 18 19 20 21 22 23 24
(b) Triangular
Temperature (deg C)

Remarks on the document "The Development of a refined San Joaquin Delta Salmon Smolt Model" (Brandes 5/31/94)

by
Terence P. Speed[1]

1. Introduction

It is the view of this writer that the statistical analysis in the above report has main significant shortcomings, anyone of which could have major implications for the regulatory use of the models obtained. Without presenting an alternative, more appropriate analysis, however, it is impossible to be specific about the regulatory consequences of a better analysis of the data. There has been insufficient time since we became aware of this report to provide such an analysis, although we have begun to do so. In the interim, we offer a brief critique of the report, highlighting three of the major shortcomings. Reference will be made to the paper Baker et al (1994) which is shortly to be published, in which a method of analysis of smolt survival data of this kind is explained and applied to smolt release data from the Sacramento River.

2. Dealing with "survival" apparently exceeding one (1)

In the present report, as in a number of preceding reports on the same topic, Brandes deals with observed counts being greater than "expected" by dividing all observed proportions by 1.8, a number obtained in a quite *ad hoc* manner in the course of analyzing smolt survival data from the Sacramento River. The concern over apparent survival proportions exceeding 100% is quite misplaced: it need be nothing more than chance variation, observing over (as in this case) or under what is expected, by chance alone. There is no difficulty dealing with this chance variation by standard statistical methods, as has been demonstrated in our paper Baker et al. (1994). Of course, in any particular case, there may be a special reason other than chance error, which causes an unusually high survival, errors in key variables such as % time trawling, counting the smolts release, trawl efficiency etc., but none of this necessitates a wholesale scaling by 1/1.8. Furthermore, as remarked in Baker et al. (1994), the unscaled Delta survival values are quite consistent with those obtained from ocean recoveries.

3. Effectively utilizing data from all release points

The report by Brandes estimates mortalities separately fro each of four reaches, using data from different release points and algebraic relationships. This is neither necessary, nor the most efficient way to combine all the data, and, as was found in the report, can lead to negative estimates of what should be non-negative quantities. Within the framework of a multiplicative model survival, with independent contributions from distinct release groups, a combined analysis of the data is possible using the method of maximum likelihood. This is the standard statistical approach to such problems.

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4. Modeling the effect of environmental variable

There is no sound basis for modeling the effect on survival or mortality of continuous environmental variables such as temperature, flow, or exports by using multiple linear regression. Not only does such a relation fail to guarantee that estimated values lie within the interval [0,1], but also it does not adequately reflect the changes in expected variability that occur as the expected values change. One standard approach to this issue is to make use of multiple linear logistic relations connecting survival or mortality to the environmental variable.

A further point needs making here. The practice of using a backwards selection procedure and a generous alpha value (0.15) is extremely likely to result in what is known as overfitting, that is, in producing apparent relationships which do not hold up when additional data are obtained. With such small sample sizes, the issue is complicated, but as illustrated in Baker et al. (1994), simulation (parametric bootstrapping) can be used to obtain realistic measures of the real uncertainty.

5. Other issues

A number of other aspects of the analysis of these data by Brandes warrant a more careful treatment. These include the issue of discordant observations (so-called outliers, p.5); the possible impact of the hatchery from which released salmon originate; and the appropriate way to compare observed with predicted survival (Figure 7 and the correlation cited are quite misleading). Such issues will be fully dealt with in our analysis of these data.

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October 14, 1994

Curriculum Vitae

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SAN JOAQUIN TRIBUTARY AGENCIES

SALMON ALTERNATIVE[1]

Salmon Smolt Outmigration Pulse Flows

- Two seven-day pulses:
  - one in mid-April
  - one in mid-May
- Pulses at Vernalis to total at least:
  - Critical year - 1,000 cfs
  - Dry year - 2,000 cfs
  - Below normal year - 3,000 cfs
  - Above normal year - 3,000 cfs
  - Wet year - 4,000 cfs
- Old River Barrier must be installed.
- Exports limited to 1,500 cfs from April 15 to May 15 or 2 to 3 days after second pulse.

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[1] Presented at the State Water Resources Control Board Workshop, October 19, 1994.

MODELED SAN JOAQUIN CHINOOK SALMON ESCAPEMENT UNDER SELECTED PULSE FLOW ALTERNATIVES

EACH for Windows 8.5.3, runs of 11 October 1994

	Percentage Increase over Modeled Historical Escapement					
	With Old River Barrier			Without Old River Barrier		
	DFG	JP	SJT	DFG	JP	SJT
1982	812	688	494	201	153	67
1983	547	489	488	117	91	61
1984	518	460	542	111	81	73
1985	450	349	457	89	45	60
1986	392	238	289	86	23	40
1987	293	202	222	60	21	25
1988	200	144	196	24	-1	15
1989	217	180	201	34	14	20
1990	305	311	231	75	72	36
1991	375	372	262	106	100	50
1982–1991	*394*	*315*	*360*	*81*	*45*	*45*

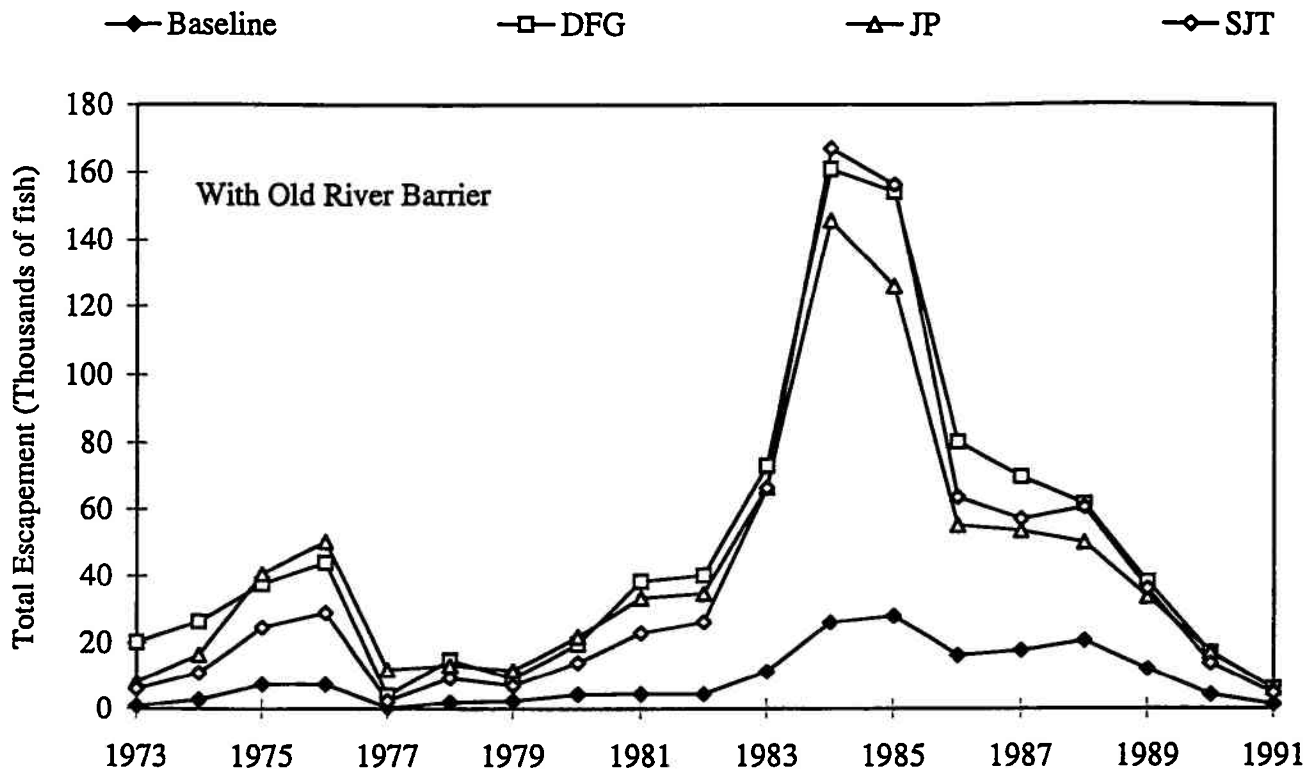
DFG: SWRCB Alternative 4.

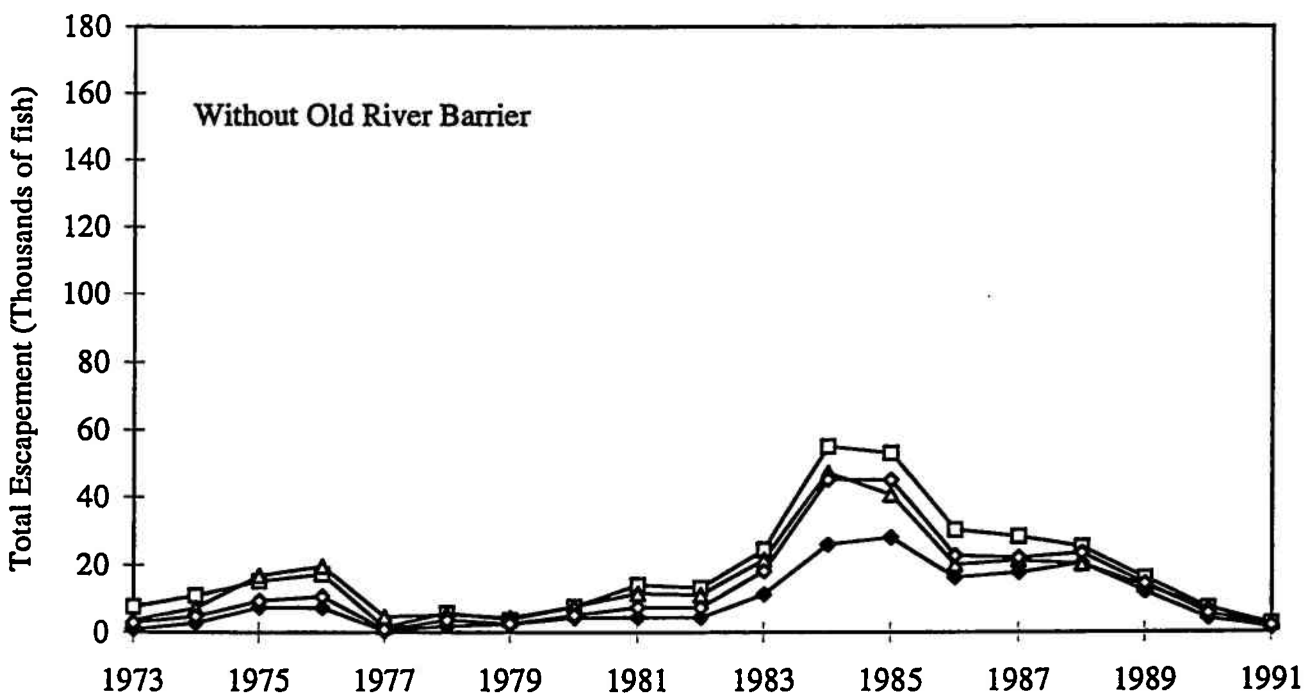
JP: Water Users Joint Proposal.

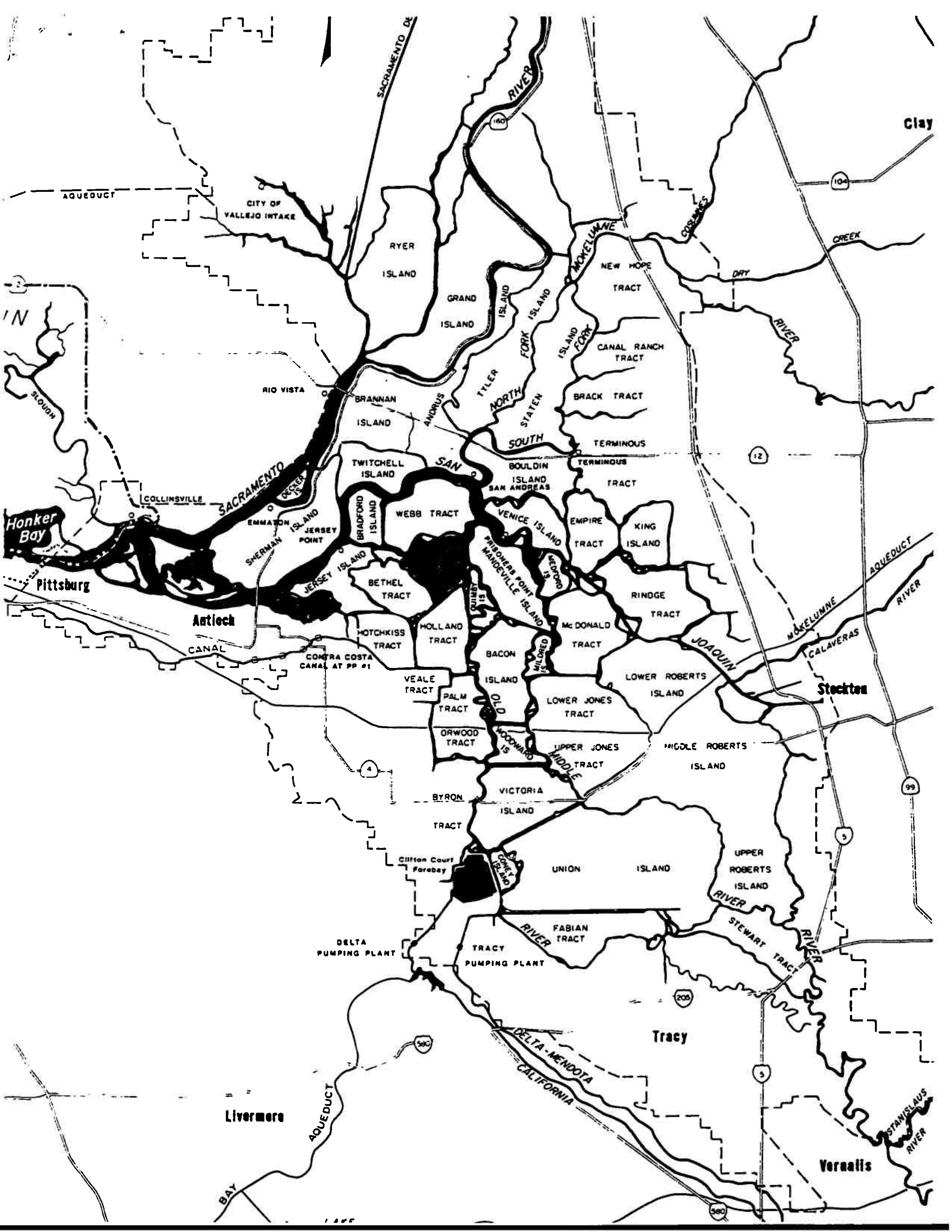
SJT: San Joaquin Tributary Agencies. (Export limited to 1,500 cfs from 15 April through 15 May. Two seven-day pulses, one in mid-April and one in mid-May. Pulses to total at least 1,000 cfs at Vernalis in Critical water-years, 2,000 cfs in Dry years, 3,000 cfs in Below Normal and Above Normal years, and 4,000 cfs in Wet years.)

MODELED SAN JOAQUIN CHINOOK SALMON ESCAPEMENT
UNDER SELECTED PULSE FLOW ALTERNATIVES

EACH for Windows 8.5.3, runs of 11 October 1994







AQUEDUCT
CITY OF VALLEJO INTAKE
RYER ISLAND
GRAND ISLAND
RIO VISTA
BRANNAN ISLAND
ANDRUS
TYLER ISLAND
NORTH FORK
STATEN ISLAND
SOUTH
TWITCHELL ISLAND
SAN
BOULDIN ISLAND
SAN ANDREAS
SACRAMENTO
SACRAMENTO RIVER
DECKER IS.
COLLINSVILLE
Honker Bay
EMMATON
SHERMAN ISLAND
JERSEY POINT
BRADFORD ISLAND
WEBB TRACT
VENICE ISLAND
JERSEY ISLAND
BETHEL TRACT
PRISONERS POINT
MANDEVILLE ISLAND
MEDFORD IS.
Pittsburg
Antioch
CANAL
CONTRA COSTA CANAL AT PP #1
HOTCHKISS TRACT
HOLLAND TRACT
QUIMBY IS.
BACON ISLAND
MILDRED IS.
McDONALD TRACT
VEALE TRACT
PALM TRACT
OLD
LOWER JONES TRACT
ORWOOD TRACT
WOODWARD IS
UPPER JONES TRACT
MIDDLE
BYRON TRACT
VICTORIA ISLAND
Clifton Court Forebay
CONEY ISLAND
UNION ISLAND
DELTA PUMPING PLANT
TRACY PUMPING PLANT
FABIAN TRACT
RIVER
Tracy
DELTA-MENDOTA
CALIFORNIA
AQUEDUCT
Livermore
BAY
SLOUGH
MOKELUMNE
NEW HOPE TRACT
COSUMNES
DRY CREEK
RIVER
ISLAND
CANAL RANCH TRACT
BRACK TRACT
TERMINOUS
TERMINOUS TRACT
EMPIRE TRACT
KING ISLAND
RINDGE TRACT
JOAQUIN
LOWER ROBERTS ISLAND
MIDDLE ROBERTS ISLAND
UPPER ROBERTS ISLAND
STEWART TRACT
MOKELUMNE AQUEDUCT
CALAVERAS RIVER
Stockton
Clay
STANISLAUS RIVER
Vernalis
160
104
12
4
99
5
205
580

The Salinity Barrier and Striped Bass Ecology: an Evaluation[1]

The San Joaquin Tributary Agencies do not believe that there is a scientific basis for setting a salinity standard in the san Joaquin River to allow the upstream spawning migration of striped bass. We believe that (1) there is no real evidence that a salinity barrier to migration exists; (2) even if such a barrier did exist, it would not affect the production of striped bass, because as broadcast spawners they are not spawning-habitat limited; and (3) if striped bass could be induced to spawn farther upstream in the San Joaquin this would be to their detriment, as it would increase the potential entrainment of eggs and larvae into the state and federal export facilities. Finally, from a policy standpoint it seems inappropriate to be setting standards to enhance an exotic species that is known threat to an endangered native species, the Sacramento winter run chinook salmon.

The San Joaquin River, especially in years of low flow, has a high concentration of total dissolved solids due primarily to saline agricultural discharges, creating a reverse salinity gradient in the region upstream of the mouth of the Mokelumne River. It has been suggested that striped bass are often restricted from using spawning areas in the San Joaquin River by a salinity barrier beyond which migrating adult bass will not pass.

The basis for this belief rests upon inconclusive evidence obtained in the 1960s from field observations of adult striped bass distribution during the spawning season. Radtke and Turner (1967), sampling adult bass throughout the reverse salinity gradient, found the highest numbers of fish in TDS concentrations between 250 and 300 ppm. They found lower numbers both below 200 and above 350 ppm TDS. On the basis of these observations, they concluded that 350 ppm TDS formed a barrier to striped bass movement. This occurred in the vicinity of Venice Island.

Such anecdotal evidence in no way proves that a salinity barrier exists. It might lead one to hypothesize that salinity can prevent upstream migration and then one could go on to test that hypotheses experimentally. However, no such tests have been conducted. An alternative hypothesis would be that the fish stopped near Venice Island for any one of a number of other reasons having nothing to do with salinity. There are data that support this second hypothesis.

Striped bass in the Sacramento-San Joaquin system spawn primarily the Sacramento River from Colusa to Sacramento and in the San Joaquin Delta from Antioch to Venice Island. There is considerable evidence that striped bass spawn in the same area of the San Joaquin River year after year, regardless of flow. The three-dimensional bar graph of striped bass spawning locations vs. flow shows that negligible spawning occurs in the vicinity of Venice Island regardless of flow. One would expect that if salinity was preventing upstream migration fish would spawn farther upstream in years of higher flow.

Striped bass in the Delta have been shown to spawn in salinities of up to 1, 500 microsiemens

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[1] Prepared by EA Engineering, Science and Technology for San Joaquin Tributary Agencies.

(approximately 1,000 ppm TDS) and greater in years of low flow when ocean salinities intrude in to the western Delta. Such conditions in 1972 were not shown to adversely affect egg survival (Turner 1976), and laboratory studies have corroborated that these levels of salinity are not harmful to egg survival (Turner and Farley 1971). Water quality records dating from about 1929 show that salinities in the San Joaquin River in los flow years have exceeded those felt to constitute a barrier to striped bass migration even during the period when the bass population was flourishing (Paterson 1989).

There is no evidence that striped bass populations are limited by area available for spawning. In fact, there are several reasons why this is highly unlikely. The species is a mass spawner that spawns in groups of fish of from 5 to 30 individuals. There is no territorial behavior that would translate into a "carrying capacity" of the area to accommodate spawning adults. Historically, bass presumably spawned in much higher numbers and densities in the same areas when their populations were at a higher level, with no attendant ill effects on egg or larval survival. Eggs do not remain in the spawning area but are immediately carried by the current to downstream nursery areas; the actual area in which they were spawned is only inhabited for a short period of time. There is no evidence showing that egg or larval survival is related to density-dependent effects on the spawning grounds.

To conclude, we feel that there is no evidence to support the belief that a salinity barrier restricts striped bass from spawning in the San Joaquin River above Venice Island. In addition, even if such a barrier existed and spawning habitat area was reduced in size, there is no evidence that a reduction in area available for spawning would adversely affect the bass population. We have reviewed almost 400 articles on striped bass ecology and management and have found no evidence of salinity barriers or spawning habitat limitations.

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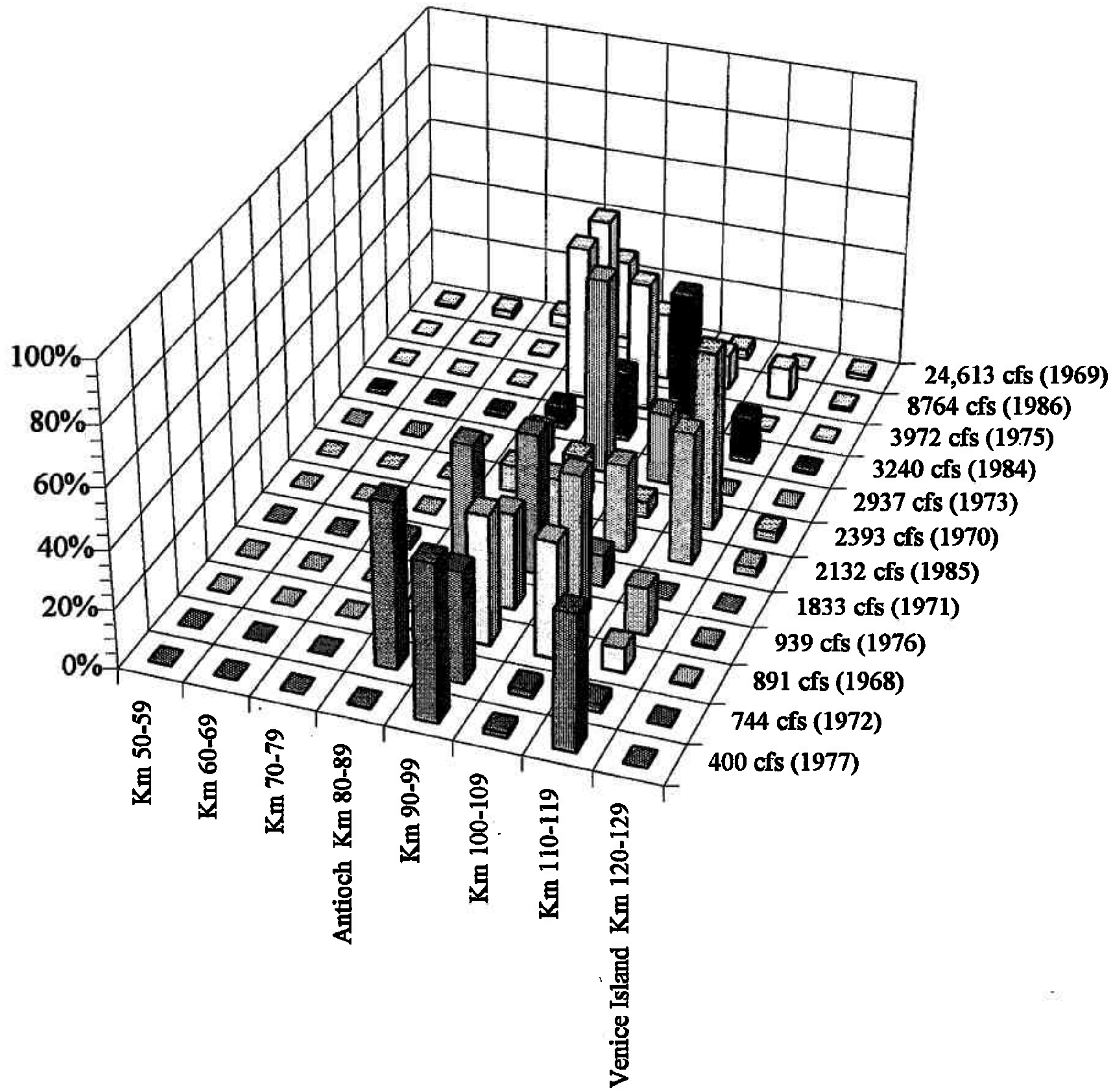

Percentages of striped bass eggs between 0 and 8 hours old collected in segments of the Sacramento-San Joaquin Delta and Suisun Bay at different flows (San Joaquin River mean May flow at Vernalis), for the years 1968-1973, 1975-1977, and 1984-1986. (Km 0 is the Golden Gate.)

Source: California Department of Fish and Game. 1987. Factors affecting striped bass abundance in the Sacramento-San Joaquin river system. San Francisco Bay/Sacramento-San Joaquin Delta Estuary Water Quality\Water Rights Hearings Phase I, Exhibit 25. CDFG, Region 4, Fresno.

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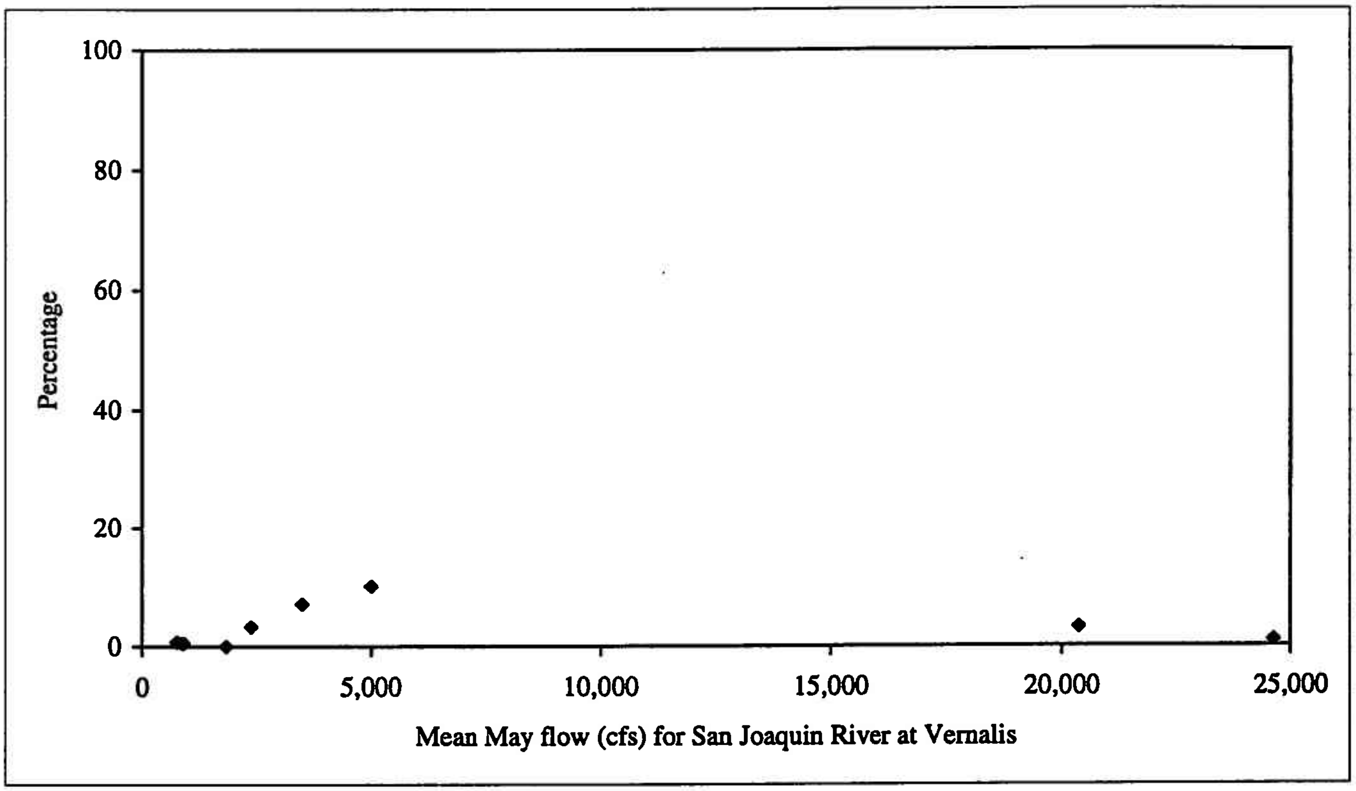
Table 8. Percentages of striped bass eggs between 0 and 8 hours old in 10 km (6.2 mile) segments of the Delta and Suisun Bay. River km (mile) 0 is at the Golden Gate. * = Not Sampled.

Area	River Kilometer (Miles)	Year 1968	1969	1970	1971	1972	1973	1975	1976	1977	1984	1985	1986
Suisun Bay[1/]													
	50-59 (31.1-36.7)	0	0.7	0	0	0	0	0	*	*	0.1	*	0.1
	60-69 (37.3-42.9)	0	2.5	0	0	0	0	0	*	*	0	0	0
	70-79 (43.5-49.1)	0	4.5	0.2	2.3	0	0	0.2	0	0	0.5	0	0.3
San Joaquin River[2/]													
Antioch	80-89 (49.7-55.3)	6.5	27.8	9.0	39.6	55.5	10.0	52.8	1.5	0.1	6.9	0.9	52.2
	90-99 (55.9-61.5)	43.9	13.3	16.6	46.9	37.6	66.2	43.9	32.4	52.8	22.9	20.3	22.8
	100-109 (62.1-67.7)	39.5	3.3	5.0	10.8	2.4	23.9	1.8	49.3	1.6	53.9	29.3	11.8
	110-119 (68.4-73.9)	8.3	0	59.8	0	2.7	0	0.2	16.2	45.5	15.0	44.2	10.7
Venice Island	120-129 (74.6-80.2)	0.5	1.9	3.2	0	0.2	0	0.1	0.6	0.1	0.5	3.0	1.1
Sacramento River[3/]													
Collinsville	80-89 (49.7-55.3)	0	43.5	0.1	0	0	0	0.3	0	0	0.1	0.1	0.2
	90-99 (55.9-61.5)	0.3	2.6	5.3	0.4	1.3	0	0.4	*	0	0.1	2.1	0.9
Rio Vista	100-109 (62.1-67.7)	0.9	0	0.9	0	0.3	0	0.2	*	0	0	0.1	0

1/ Based on sampling of DFG striped bass egg and larvae survey stations from Martinez to Collinsville.

2/ Based on sampling of DFG striped bass egg and larvae survey stations from Broad Slough to Mandeville Cutoff.

3/ Based on sampling of DFG striped bass egg and larvae survey stations from Collinsville to Rio Vista.



Percentage of striped bass eggs collected above Venice Island at various spawning flows, 1966-1972.

TABLE 1. OBSERVATIONS IN LITERATURE OF STRIPED BASS SPAWNING UPSTREAM OF VENICE ISLAND AND/OR STOCKTON

Year	Flow (cfs)[1]	Spawning Activity Upstream of Venice Island
1946	13,058	striped bass in spawning condition u/s of Stockton (Woodhull 1947)
1948	5,001	~ 10% of eggs originated upstream of Stockton (Erkkila et al. 1950)
1949	3,520	7% of eggs collected at Mossdale site (Erkkila et al. 1950)
1952	27,639	eggs and larvae collected in Old River from Frank's Tract to Coney Island (USBR & USFWS 1957, as cited in Paterson 1989)
1963	9,339	many eggs collected from Stockton to Mossdale (Farley 1966)
1964	703	very few eggs collected from Stockton to Mossdale (Farley 1966)
1966	863	0.5% of eggs collected above Venice Island (Turner 1976)
1967	20,365	3.1% of eggs collected above Venice Island (Turner 1976)
1968	891	0.5% of eggs collected above Venice Island Turner 1976)
1969	24, 613	0.9% of eggs collected above Venice Island (Turner 1976)
1970	2,393	3.2% of eggs collected above Venice Island (Turner 1976)
1971	1,833	0.0% of eggs collected above Venice Island (Turner 1976)
1972	744	0.7% of eggs collected above Venice Island (Turner 1976)

[1] Mean San Joaquin River discharge at Vernalis for month of May

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HISTORIC SPAWNING LOCATIONS OF STRIPED BASS IN THE SACRAMENTO-SAN JOAQUIN DELTA

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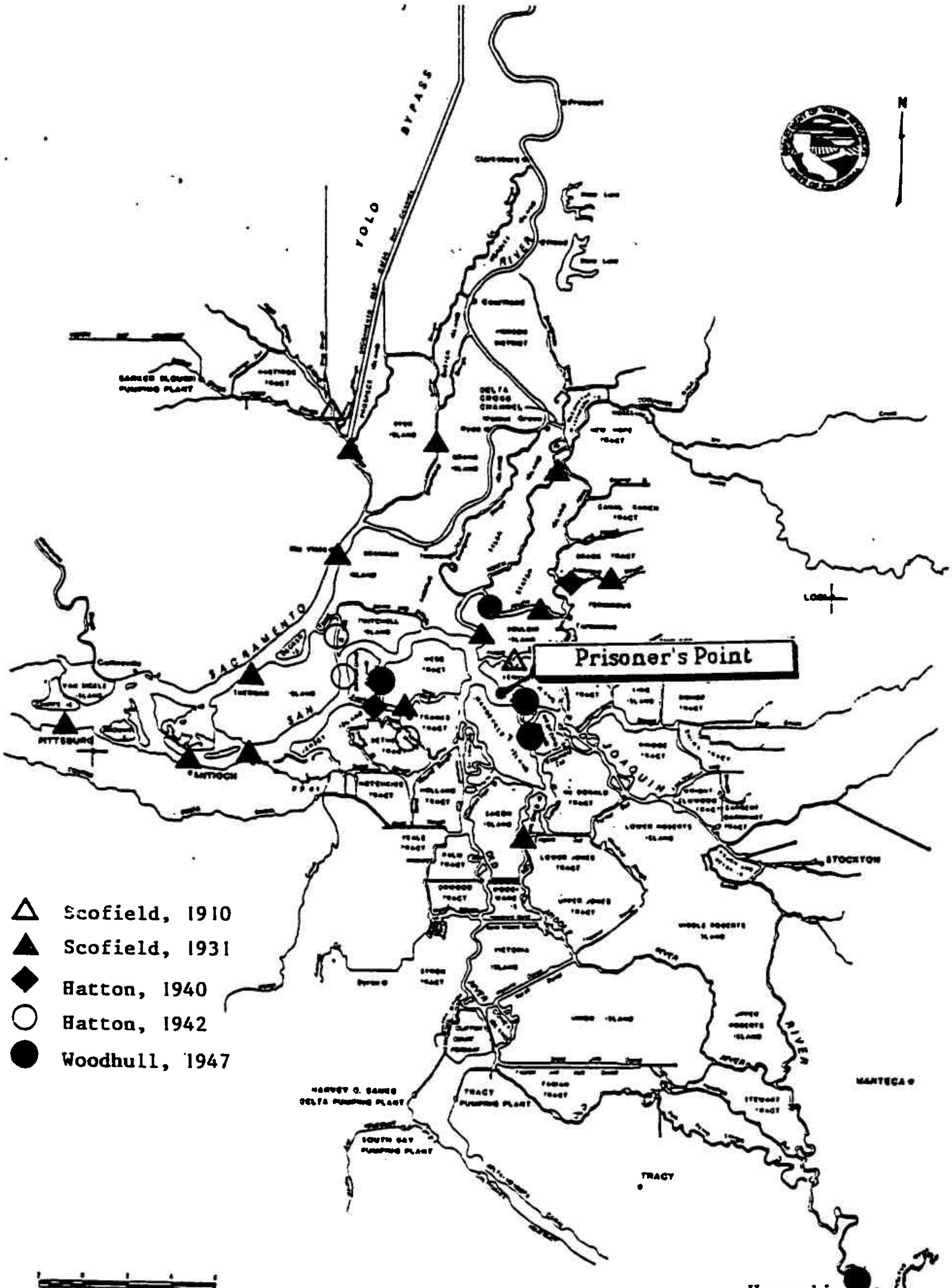
CONCLUSION

For almost ninety years, biologists have sought to find out where striped bass spawn. During that time, the most important change appears to be the establishment of the Sacramento River spawning run.

Much of the early evidence is anecdotal in nature, but it is far from unimportant. Fishery experts, and fishermen, looked where experience and observation told them spawning stripers were most likely to be found. In the Delta, those locations were in the San Joaquin River from the vicinity of Bouldin and Venice islands downstream, and in adjacent channels.

Although the best known and probably most important spawning area was in the central and western Delta, observational evidence suggested that striped bass spawned farther up the San Joaquin River. The work of the U.S. Fish and Wildlife Service in 1948 and 1949 demonstrated that, in some years at least, spawning striped bass were widely distributed in the San Joaquin Delta. However, their results also suggested that the most consistently important Delta spawning area was west of Venice Island. Subsequent tag return and spawning surveys by DFG tended to confirm that the principal Delta spawning area remained in approximately the same location it had been in since the turn-of-the-century.

REPORTED STRIPED BASS SPAWNING LOCATIONS IN THE SACRAMENTO-SAN JOAQUIN DELTA, 1903-1946



Base Map by DWR