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ISOHALINE POSITION AS A HABITAT INDICATOR FOR ESTUARINE POPULATIONS[1]

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Abstract. Populations of native and introduced aquatic organisms in the San Francisco Bay/Sacramento–San Joaquin Delta Estuary ("Bay/Delta") have undergone significant declines over the past two decades. Decreased river inflow due to drought and increased freshwater diversion have contributed to the decline of at least some populations. Effective management of the estuary's biological resources requires a sensitive indicator of the response to freshwater inflow that has ecological significance, can be measured accurately and easily, and could be used as a "policy" variable to set standards for managing freshwater inflow. Positioning of the 2‰ (grams of salt per kilogram of seawater) bottom salinity value along the axis of the estuary was examined for this purpose.

The 2‰ bottom salinity position (denoted by X_2) has simple and significant statistical relationships with annual measures of many estuarine resources, including the supply of phytoplankton and phytoplankton-derived detritus from local production and river loading; benthic macroinvertebrates (molluscs); mysids and shrimp; larval fish survival; and the abundance of planktivorous, piscivorous, and bottom-foraging fish. The actual mechanisms are understood for only a few of these populations.

X_2 also satisfies other recognized requirements for a habitat indicator and probably can be measured with greater accuracy and precision than alternative habitat indicators such as net freshwater inflow into the estuary. The 2‰ value may not have special ecological significance for other estuaries (in the Bay/Delta, it marks the locations of an estuarine turbidity maximum and peaks in the abundance of several estuarine organisms), but the concept of using near-bottom isohaline position as a habitat indicator should be widely applicable.

Although X_2 is a sensitive index of the estuarine community's response to net freshwater inflow, other hydraulic features of the estuary also determine population abundances and resource levels. In particular, diversion of water for export from or consumption within the estuary can have a direct effect on population abundance independent of its effect on X_2. The need to consider diversion, in addition to X_2, for managing certain estuarine resources is illustrated using striped bass survival as an example.

The striped bass survival data were also used to illustrate a related important point: incorporating additional explanatory variables may decrease the prediction error for a population or process, but it can increase the uncertainty in parameter estimates and management strategies based on these estimates. Even in cases where the uncertainty is currently too large to guide management decisions, an uncertainty analysis can identify the most practical direction for future data acquisition.

Key words: fish; freshwater flow; habitat indicator; interannual variability; mollusc; phytoplankton; Sacramento–San Joaquin Delta; salinity distribution; San Francisco Bay; statistical models.

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INTRODUCTION

Much of the spatial distribution of estuarine organisms can be understood in terms of the salinity gradient between the landward and seaward boundaries of the estuary (Boesch 1977). The salinity field also embodies other information not directly or solely related to the chemical properties of water. The amount of freshwater flow into an estuary, for example, is reflected in the salinity distribution, which in turn may determine the geographic location of estuarine turbidity maxima, entrapment phenomena, or null zones (Peterson et al. 1975). Both freshwater inflow and entrapment have profound biological consequences through their effects on loading of nutrients and organic matter, as well as on the residence time of planktonic organisms and detrital particles. The salinity distribution therefore contains much information regarding habitat conditions for the estuarine biota, and, in particular, temporal variability in the salinity field reflects changing habitat conditions.

Habitat variability is of particular interest for the San Francisco Bay/Sacramento–San Joaquin Delta Estuary ("Bay/Delta") because of striking long-term trends and interannual variability in the abundances of many estuarine populations (Herbold et al. 1992). Populations of aquatic organisms in the upper estuary (Sacramento–San Joaquin Delta; Fig. 1) and upper portions of San Francisco Bay have undergone significant declines over the past several decades. Declining populations include many rotifers (e.g., *Keratella* spp.); native copepods (*Eurytemora affinis*); mysids (*Neomysis mercedis*); shrimp (*Crangon franciscorum*); and fishes of economic interest (chinook salmon, *Oncorhynchus tshawytscha*), recreational interest (striped bass, *Morone saxatilis*), and of interest due to biodiversity (delta smelt, *Hypomesus transpacificus*). Reductions in these populations have led to public concern about the conditions of the estuarine system, petitions for endangered species status, and curtailed fishing seasons.

In response to these developments, the San Francisco Estuary Project, part of the National Estuary Program of the U.S. Environmental Protection Agency

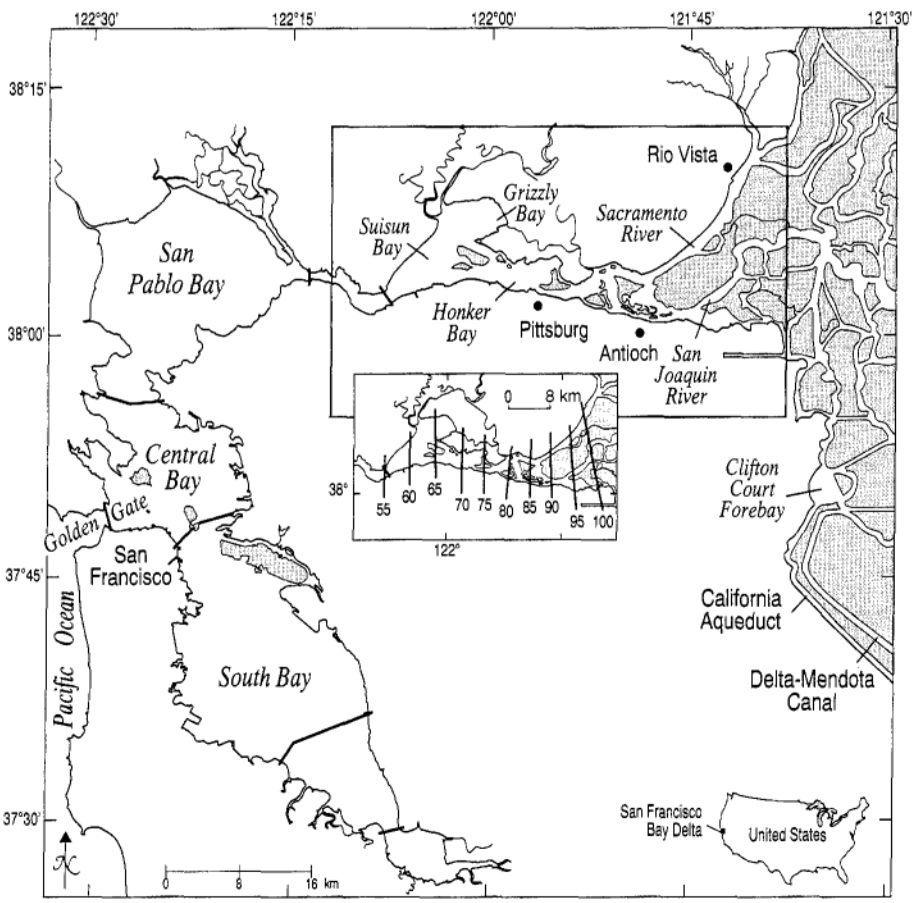

FIG. 1. Map of San Francisco Bay/Sacramento-San Joaquin Delta Estuary. The portion of the estuary upstream of the confluence of the Sacramento and San Joaquin rivers is known as the "Delta"; the portion downstream of the confluence, called "San Francisco Bay", is composed of four main subembayments: Suisun, San Pablo, Central, and South bays. Grizzly and Honker bays, in turn, are subembayments of Suisun Bay. *Inset,* Suisun Bay and the western portion of the Delta, with lines positioned at nominal distances (in kilometres) from the Golden Gate along the axis of the estuary.

(USEPA), convened a series of workshops in 1991 and 1992 to develop a strategy for protecting estuarine populations in the Bay/Delta (Schubel 1993). The simultaneous declines in many estuarine species suggest that they are responding to common stresses. The evidence indicates that decreased river inflow due to drought and increased freshwater diversion have contributed to reductions in at least some populations (CDFG 1987*a,b*, IESP 1990). Drought conditions persisted from 1987 through most of 1992; diversion of freshwater from the estuary has frequently exceeded 50% of inflows since 1977. A major goal of the workshops was, therefore, to select a "policy" variable that could be used to set standards for managing freshwater inflow; difficulties with the measurement of net freshwater inflow itself in a strongly tidal environment (see Discussion) motivated the search for some surrogate policy variable. Workshop participants recommended that standards should be based at least in part on the estuary's physical response to fluctuations in freshwater input, i.e., on some "habitat indicator" (sensu Messer 1990, who defines habitat indicator as a "physical attribute measured to characterize conditions necessary to support an organism, population, or community in the absence of pollutants"). The salinity field was of particular interest because it is well-defined and measurable, has ecological significance, integrates a number of important estuarine properties and processes, and is meaningful to a large number of constituencies. Participants eventually decided on a scalar index consisting of the position of a particular near-bottom isohaline, measured as distance (kilometres) from the Golden Gate along the axis of the estuary (Fig. 1). The position of a near-bottom isohaline depends primarily on net freshwater inflow (and secondarily on tidal stage) and therefore can be managed by regulating freshwater diversions from the estuary.

Workshop participants chose the 2‰ near-bottom isohaline in particular for further exploration. Position of this particular isohaline, denoted here by X_2, has varied historically between ≈50 km to 100 km (see Results). The choice of the 2‰ value was based on two separate observations: (1) X_2 is a useful length scale for parameterizing the spatial structure of the salt field in the northern estuary. A series of vertical salinity profiles collected from January 1990 through February 1992 (Wienke et al. 1991, 1992, 1993) illustrates the point. In Fig. 2a, the mean (depth-averaged) salinity is plotted as a function of distance from the Golden Gate, X. In Fig. 2b, the same quantity is plotted as a function of X/X_2. Comparing these figures, it is apparent that, apart from scatter due probably to tidal variation, scaling by X_2 nearly "collapses" the data about an equilibrium mean salinity distribution. Knowing only X_2, one can recreate the entire mean salt field. However, given that the scaling works well for all salinities <4‰ (Fig. 2b), other isohaline positions such as X_1 or X_3 could also serve in this regard. (2) X_2 also describes

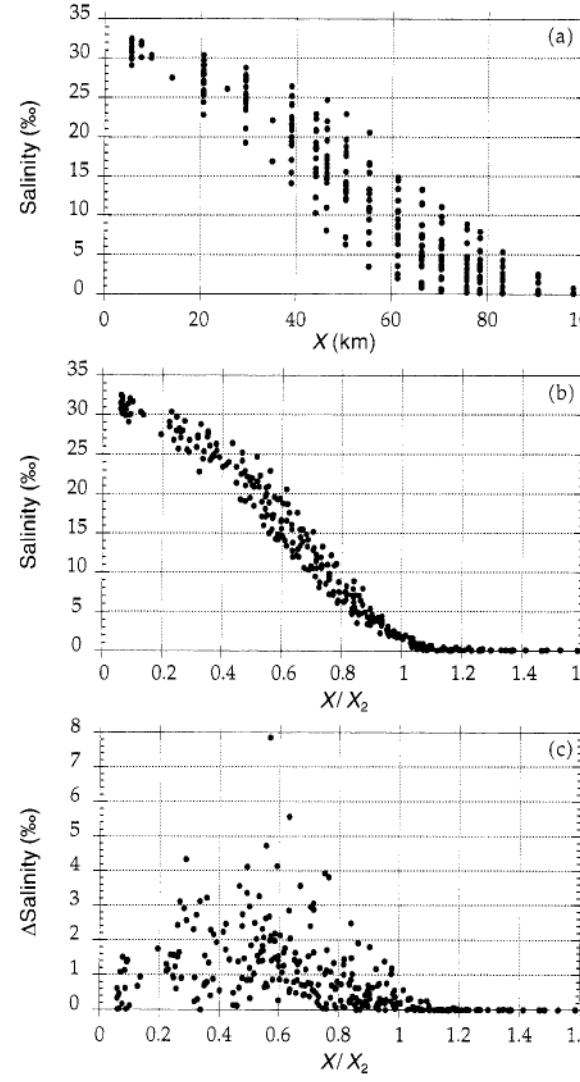

FIG. 2. (a) Vertically averaged salinity vs. distance from the Golden Gate (X) along the axis of the estuary, based on salinity profiles collected from January 1990 through February 1992; (b) the same data as in (a), but distances from the Golden Gate are scaled by X_2; (c) bottom minus top salinity values for each vertical profile vs. distance from the Golden Gate, again scaled by X_2.

the boundary between a downstream reach characterized by strong baroclinic pressure gradients and density stratification from an upstream reach of weak pressure gradients and little or no stratification. In Fig. 2c, the difference between top and bottom salinity is plotted as a function of X/X_2, illustrating the stratification differences up- and downstream of X_2. In view of the traditional model for entrapment zone dynamics (Arthur and Ball 1979), X_2 should therefore be a good measure of entrapment location. Indeed, X_2 often occurs in the vicinity of the estuarine turbidity maximum (ETM), as well as near spatial maxima in abundance of zooplankton species that are historically important

as food sources (*Eurytemora affinis* and *Neomysis mercedis*), and near a spatial maximum in abundance of larval striped bass (Kimmerer 1992). The location of X_2 in this estuary therefore has *both* physical and ecological meaning, a property not shared with other near-bottom isohaline positions.

Here, we examine the hypothesis that position of a near-bottom isohaline can be used to index response of the estuarine community to freshwater inflow and, more generally, as a policy variable to manage population abundances. Although the utility of the 2‰ value may be peculiar to this estuary, we emphasize that the concept of using isohaline position for management purposes and the methods for selecting a particular isohaline value on the basis of physical and ecological criteria are more general. The hypothesis is accordingly of interest for other estuaries as well. Our examination of X_2 has four parts: (1) First, we ask how pervasive the empirical relationships are between X_2 and various biological resources. Do they extend across trophic levels? Do they pertain for species at the same trophic level but with different life habits? An extensive historical database on population abundances is used to address these questions, and we also briefly review the causal mechanisms believed to underlie the relationships. Although associations between estuarine resources and freshwater inflow to the Bay/Delta have been noted before (Turner and Chadwick 1972, Stevens 1977*a*, Herrgesell et al. 1981, Armor and Herrgesell 1985, Stevens et al. 1985), previous studies concentrated on only a few fish species, most notably striped bass. (2) Next, we summarize a number of additional reasons why a near-bottom isohaline is a suitable habitat indicator for setting estuarine standards, and why it might be preferable to freshwater inflow in this context. Of course, freshwater inflow estimates are required for many other purposes, such as water allocation, and in no way can isohaline position be a substitute in these other contexts. (3) We then raise some caveats against blind adherence to the use of X_2 when predictions can be improved by including or even substituting other variables. Models based on X_2 alone may lead to misleading management conclusions if additional variables not highly correlated with X_2 have large enough effects. In order to explore this possibility, we examine a simple statistical model for striped bass survival (from egg to young-of-the-year) that incorporates both X_2 and freshwater diversion. (4) Finally, this same model will be used to illustrate a related important point: statistical models with fairly low residual variance may nevertheless have high uncertainty for setting management goals. An explicit estimate of this uncertainty is always required to determine if existing data are adequate for a meaningful data-based policy.

Site description

The Bay/Delta is a complex system consisting of a landward, tidal freshwater region known as the Delta and a seaward region known as San Francisco Bay (Fig. 1). The Delta is a highly dissected region of channels and islands where the Sacramento, San Joaquin, and other rivers coalesce and narrow as they approach the sea. The outflow from the Delta passes through a narrow notch in the Coast Range into a series of subembayments and ultimately through a narrow, deep trough—the Golden Gate—into the Pacific Ocean. Four major subembayments of San Francisco Bay can be recognized: South, Central, San Pablo, and Suisun bays. Together they constitute the largest coastal embayment on the Pacific coast of the United States (Conomos et al. 1985). Ninety percent of the freshwater input to the Bay flows through the Delta, the remainder supplied by local tributaries. The Sacramento–San Joaquin drainage basin encompasses 40% of California's land area. River inputs are highly seasonal, consisting of rainfall during winter and snowmelt during spring and early summer; almost no precipitation falls for half the year. A series of reservoirs regulates river flows for irrigated agriculture, hydroelectric power, flood control, and the repulsion of salinity intrusions into the Delta during the dry summer and autumn months. A large portion of the water flowing into the Delta is diverted from the estuary, mostly for agriculture, before it can flow into the Bay. Most of this water is drawn from the estuary into canals of the federal Central Valley Project (Delta–Mendota Canal) and the State Water Project (California Aqueduct) by facilities in the southern Delta (Fig. 1). Additional freshwater diversion takes place within the Delta through ≈1800 unscreened siphons used to irrigate farmlands on Delta islands. The remainder flows through the Delta into San Francisco Bay. Interannual variability in river inflow to the estuary and diversion is extremely high; in recent decades, annual discharge from the Delta into the Bay has varied by as much as a factor of 25.

METHODS

X_2 *time series*

We estimated X_2, the monthly mean position of 2‰ near-bottom salinity, using historical data from several sources. The principal source was a record of daily mean specific conductance at the surface for six fixed stations throughout the estuary, maintained by the U.S. Bureau of Reclamation (USBR; J. Arthur, *personal communication*). As no equivalent long-term record of bottom salinity is available, we first determined the relationship between bottom and surface salinity using a smaller record from the USBR (J. Arthur, *personal communication*), the California Department of Fish and Game (CDFG; J. Orsi and C. Armor, *personal communication*), and the U.S. Geological Survey (J. Cloern, *personal communication*) monitoring programs. Where the bottom salinity was near 2‰ (specifically, between 1.5 and 2.5‰), the difference between bottom and surface salinity was unrelated to

TABLE 1. Data used for testing relationships between various biological resources and the position of the 2‰ isohaline (X_2): the biological resource, the quantitative measure of the resource, the geographic location of measurements, the averaging period for X_2, and the years for which observations are available.*

Resource	Measure	Location	X_2 averaging period	Observation years
Particulate organic carbon (POC) supply	annual primary production plus river load of algal-derived POC (Gg/yr)	Suisun Bay	Jan–Dec	1975–1989
Eurytemora affinis	Mar–Nov abundance index (no. individuals)	Suisun Bay, Delta	Mar–Nov	1972–1982, 1984–1990
Neomysis mercedis	Mar–Nov abundance index (no. individuals)	Suisun Bay, Delta	Mar–Nov	1972–1982, 1984–1990
Crangon franciscorum	annual abundance index (no. individuals)	South Bay through Suisun Bay	Mar–May	1980–1990
Delta smelt (*Hypomesus transpacificus*)	fall midwater trawl index (no. individuals)	San Pablo Bay through Delta	Apr–Jul	1968–1973, 1975–1978, 1980–1991
Longfin smelt (*Spirinchus thaleichthys*)	annual abundance index (no. individuals)	San Pablo Bay through Delta	Jan–Jun	1968–1973, 1975–1978, 1980–1982, 1984–1991
Striped bass (*Morone saxatilis*) survival	38-mm index: Petersen egg production	eastern San Pablo Bay through Delta	Apr–Jul	1969–1982, 1984–1991
Striped bass (*Morone saxatilis*)	fall midwater trawl index (no. individuals)	San Pablo Bay through Delta	Jul–Nov	1968–1973, 1975–1978, 1980–1991
Molluscs	annual abundance (no. individuals/m^2)	Grizzly Bay	3-yr mean Jan–Dec	1981–1990
Starry flounder (*Platichthys stellatus*)	annual abundance index (no. individuals)	South Bay through Suisun Bay	previous year Mar–Jun	1980–1991

* Data were collected by the California Department of Water Resources and California Department of Fish and Game as part of the Interagency Ecological Studies Program.

flow, except at very high flow. The median difference (bottom minus surface) was 0.24 ± 0.06 (mean and 95% confidence interval), implying that a bottom salinity of 2‰ corresponded to a surface salinity of 1.76‰.

We then interpolated between fixed stations to determine the daily position of 1.76‰ at the surface, in the following manner. On the basis of both a steady-state diffusion equation and examination of the data, we determined that log S should be ≈ proportional to X/V_X, where S is salinity (‰), X is distance along the estuarine axis from the Golden Gate (kilometres), and V_X is the volume of the estuary between X and the 100-km position upstream (cubic metres). V_X was determined by trapezoidal integration of cross-sectional areas determined from nautical charts at 1-km intervals. For each day, we fit this linear relation to the data and used the resulting equation to interpolate the position of 1.76‰ surface salinity, i.e., of X_2. We were able to estimate X_2 for 7794 of the 8827 d from 1 October 1967 through 30 November 1991.

We filled in gaps (12% of the days) in the resulting X_2 series by constructing a time series-regression model relating the current X_2 to the previous day's X_2 and the current value of Q_{out} (cubic metres per second), the net outflow of water from the Delta into the Bay. The Q_{out} series is available as part of the California Department of Water Resources (CDWR) DAYFLOW program output, an accounting tool for determining Delta boundary hydrology (CDWR 1986); a correction was applied for updated estimates of water consumption within the Delta. Using the longest single unbroken record of ~1000 points, we identified the model using the prewhitening procedure described by Box and Jenkins (1976). The model was estimated iteratively using a Marquardt nonlinear least-squares algorithm. We then used the model, which was well-behaved according to conventional diagnostic criteria, to forecast the missing values of daily X_2.

From the resulting series of daily values for X_2, monthly means were calculated for use in the analyses of biological responses. To summarize the responsiveness of the monthly series of X_2 values to net Delta outflow, we built an additional time-series regression model with a 1-mo time step, using the same methods as for the daily series.

Biological resources

The response variables were chosen so that populations at a number of trophic levels would be repre-

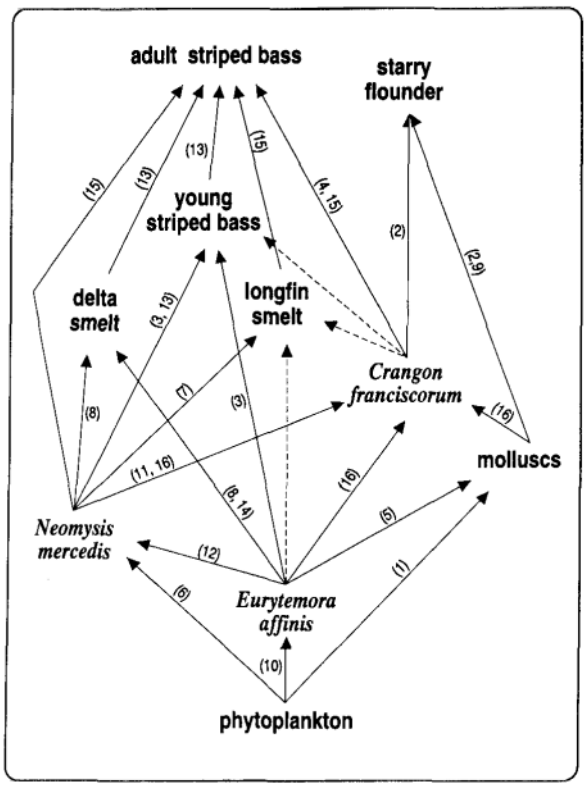

FIG. 3. Partial food web for the San Francisco Bay–Delta from various published sources, illustrating the trophic relationships among the populations and communities considered in this study. – – –; probable connections that have not actually been observed due to restricted sampling for stomach contents; ———; more substantiated connections. Numbers in graph refer to these references: (1), Alpine and Cloern 1992; (2), Boothe 1967; (3), Heubach et al. 1983; (4), Johnson and Calhoun 1952; (5), Kimmerer 1992; (6), Kost and Knight 1975; (7), Moyle 1967; (8), Moyle et al. 1992; (9), Orcutt 1950; (10), Orsi 1988; (11), Siegfried 1982; (12), Siegfried and Kopache 1980; (13), Stevens 1966; (14), Stevens et al. 1990; (15), Thomas 1967; (16), Wahle 1985.

sented (Table 1; Fig. 3). The base of the food web is represented by the supply of phytoplankton for Suisun Bay from local production and riverine inputs, expressed as particulate organic carbon (POC). Primary productivity values were based on estimates determined by Alpine and Cloern (1992), and loading of phytoplankton POC from the Delta was estimated using chlorophyll data collected by the CDWR Compliance Monitoring and Analysis Program (CDWR 1991); together, these constitute the main source of organic carbon for Suisun Bay (Jassby et al. 1993).

Data for *Neomysis mercedis* and *Eurytemora affinis* were collected by the CDFG *Neomysis*/Zooplankton Study (Knutson and Orsi 1983). Oblique tows from the bottom to the surface were taken with a plankton net at 35 stations throughout Suisun Bay and the western and central Delta. Samples were collected monthly in March and November, and twice-monthly in the intervening months. The number of mysids ≥4 mm in length and the number of adult *Eurytemora* were both weighted by the estimated volume of water associated with a given station, and averaged over the sampling period. Boundaries separating the areas associated with adjacent stations were placed either midway between the stations or determined by prominent topographic features.

Data for *Crangon franciscorum* and starry flounder were collected by the CDFG Delta Outflow/San Francisco Bay Study (Armor and Herrgesell 1985). Samples were collected monthly with an otter trawl from 35 open water sites throughout San Francisco Bay. Abundance indices were calculated by correcting catches for effort, weighting by the area associated with each station, and averaging for the relevant time period. The *Crangon franciscorum* index is based on the May–October catch of immature shrimp. The starry flounder index is based on the February–May catch of fish >1 yr old.

The striped bass survival index measures the proportion of eggs that develop and survive to become young-of-the-year bass; it is calculated as the ratio of the 38-mm index to the Petersen egg production estimate. The 38-mm index is based on the CDFG Summer Tow-Net Survey (Turner and Chadwick 1972, Stevens 1977*b*). Each survey consisted of three to five subsurveys conducted between June and August. Depth-integrated tows were made at each of 30 sampling stations between eastern San Pablo Bay and the eastern Delta. For each subsurvey, the number of captured fish was weighted by the volume of water associated with each station. An index of annual abundance was obtained by plotting total number against mean length for each subsurvey and interpolating abundance for 38-mm fish. Petersen egg production (Stevens et al. 1985) is based on mark–recapture estimates of adult striped bass and age-specific fecundity data (Stevens 1977*a*). The abundance of each age class from age 4 to age 8 and >age 8 yr is multiplied by the estimated fecundity for the appropriate age and corrected for age-specific maturity. The annual index of total eggs spawned is the sum of these products.

Data for delta smelt, longfin smelt, and striped bass were collected by the CDFG Fall Midwater Trawl Survey (Stevens 1977*b*). Depth-integrated tows with a midwater trawl were made at each of 87 sampling sites from San Pablo Bay through the Delta. Monthly surveys started in August or September and continued through March of the following year. For each of 17 groups of stations, mean catches were weighted by the total volume of water associated with each group. These means were summed to obtain monthly abundance indices, and the annual index is the total of these monthly values.

The benthic macrofauna are represented by total mollusc abundance in Grizzly Bay, a subembayment of Suisun Bay (Fig. 1). Bottom grab samples were col-

lected monthly by the CDWR Compliance Monitoring and Analysis Program (CDWR 1991), and organisms retained on a 0.5-mm sieve were identified and enumerated.

Statistical models using X_2 alone as a predictor

We expressed the associations between estuarine resources and X_2 with generalized linear models, which are flexible extensions of classical linear models (McCullagh and Nelder 1989). If Y is the response variable, the Z_i are predictor variables, and $E(Y) = \mu$, a generalized linear model takes the following form:

$$g(\mu) = \alpha + \sum_{i=1}^{p} \beta_i Z_i, \quad (1)$$

where g is a *link* function describing how the mean depends on the linear combination of predictors, and α and the β_i are constants; g can be any monotonic differentiable function. The dependence of the variance of Y on the mean μ is specified independently of the link function by a *variance* function $V(\mu)$, i.e., the variance is not assumed to be homogeneous. Once a link and variance function have been chosen through some sort of exploratory data analysis, the parameters α and β_i are estimated by maximum-likelihood, using an iteratively reweighted least-squares algorithm. Nonlinear biological phenomena are often expressed as classical linear models by transforming the response (e.g., with a log transform), but the transformation often leads to unnatural scales, does not necessarily result in homogeneity of variance, and may not even be defined for certain response values. Generalized linear models avoid these problems, yet remain almost as tractable as classical linear models with regard to summary statistics and hypothesis testing.

For each biological resource, we estimated the averaging period over which X_2 was likely to be related to the resource (Table 1). In the case of POC, *Eurytemora, Neomysis,* and molluscs, we simply used the same interval as the period of standing stock measurements. The remaining periods were chosen by CDFG specialists, who were asked to decide when flow and the salinity field were most critical to the abundance of each population. The averaging periods were therefore chosen on the basis of biological and ecological judgement, not by trying to optimize some statistic. Only one averaging period was explored for each organism. In the case of *Neomysis,* striped bass survival, and longfin smelt, the observation corresponding to 1983 flows was eliminated. The El Niño-Southern Oscillation (ENSO) event of 1983 resulted in the largest freshwater inflows of the century and, for the cases noted, a significant portion of the population may have been displaced seaward of the sampling stations, causing an underestimate of the annual abundance.

Because the number of observations was ≤ 22 (years), models requiring estimation of more than two parameters (aside from the intercept) were not considered. For each resource, two types of models were estimated: (1) using X_2 alone, averaged over some suitable period, and (2) using a natural spline in X_2 with one interior knot (two degrees of freedom; Hastie and Tibshirani 1990). Generally speaking, a natural spline is superior to a polynomial for representing nonlinearities; with the few degrees of freedom permitted here, however, the difference between the two may be unimportant. If more than one model was "well-behaved" (each coefficient individually significantly different from 0 at the $P < 0.05$ level and residuals consistent with model assumptions), the final model was selected on the basis of the AIC statistic (Hastie and Tibshirani 1990). If a nonlinear relationship was indicated, a log link was tested before deciding on the degrees of freedom for X_2, in order to ensure that fitted population abundances would not be negative. The variance function was chosen iteratively by examining plots of residuals vs. fitted values. The overall value of including X_2 in each model was assessed with an approximate F test (McCullagh and Nelder 1989).

Statistical models using multiple predictors

We further examined striped bass survival as an example of interannual biological variability in which freshwater diversion, in addition to X_2, has been hypothesized to play a role. We assumed that egg survival is independent of egg number (spawning stock). The survival index should then be independent of the population's history and we can exclude previous values of the index from the set of predictor variables. The monthly series for freshwater diversion (DIV) was calculated as the portion (percentage) of monthly river inflow that is used either for within-Delta consumption (mostly for irrigation) or export to water projects (CDWR 1986). We used the same averaging period for DIV as the period previously chosen for X_2 on the basis of life history and behavior (April–July). Because of the small number of data points, no additional predictors were considered. The nature of the relationship incorporating X_2 and DIV was explored with generalized additive models (Hastie and Tibshirani 1990). These are extensions of generalized linear models in which the effects of individual predictor variables are additive, but the form of each effect is relatively unconstrained and determined by a smoothing of the data. Eq. 1 is still appropriate but the Z_i are replaced by $f_i(Z_i)$, where the f_i are cubic splines:

$$g(\mu) = \alpha + \sum_{i=1}^{p} \beta_i f_i(Z_i).$$

The parameters are chosen through an iterative smoothing process. The algorithm cycles through each variable i in turn and smooths the partial residuals obtained by subtracting from $g(\mu)$ current estimates for all additive terms $j \neq i$, resulting in updated estimates of β_i and f_i. Because of the number of observations, only two degrees of freedom were permitted for each smoothing

spline. Once a form has been established for each effect, the individual effects can be parameterized and their significance tested exactly in more conventional ways. In the case of striped bass survival, we constructed a classical linear model using the generalized additive model results as a guide.

We examined how our ability to predict striped bass survival changed with models of increasing complexity. Models were compared on the basis of their prediction squared error (PSE):

$$\mathrm{PSE} = E\{Y - \hat{Y}(\boldsymbol{X})\}^2,$$

where Y is the response, $\hat{Y}$ is the predicted value for the vector-valued predictor variable $\boldsymbol{X}$, and the expectation is over new realizations of the joint distribution $(Y, \boldsymbol{X})$. We estimated PSE using the ".632" bootstrap method of Efron (1983). In this method, a given model is refit using bootstrap samples of the original observations, and the observations *not* included in the bootstrap sample are compared with model predictions. In each case, we estimated PSE with 250 bootstrap samples.

The S–Plus language and functions (Statistical Sciences 1993) were used for the generalized linear and additive models, as well as for all bootstrap calculations.

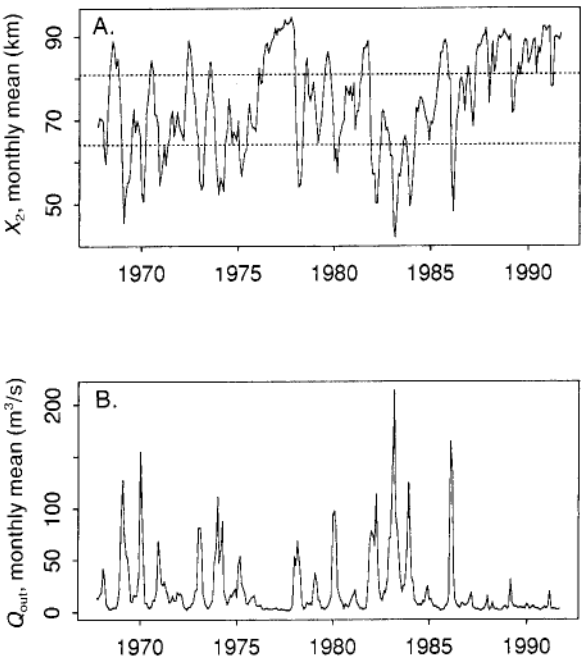

FIG. 4. (A) monthly mean of X_2, the location of the 2‰ bottom isohaline along the axis of the estuary (distance from the Golden Gate) vs. time (years). The dashed lines indicate the mean maximum and minimum monthly X_2 for 1968–1990; (B) monthly mean of Q_{out}, net Delta outflow vs. time (years).

RESULTS

X_2 *time series*

The daily time series for X_2 (mean distance of the 2‰ near-bottom isohaline from the Golden Gate in kilometres) is related to that of Q_{out} (mean net Delta outflow, in cubic metres per second) by:

$$X_2(t) = \theta_0 + \theta_1 X_2(t-1) + \gamma \log Q_{out}(t),$$

where t is the time in d; $\theta_0 = 8 \pm 1$ (mean $\pm$ 1 SE); $\theta_1 = 0.945 \pm 0.007$; and $\gamma = -1.5 \pm 0.2$. The coefficient of determination $R^2 = 0.99$, and the standard error of estimate $s = 1.3$ km, less than the semidiurnal tidal excursion of 5–10 km. No important structure is present in the residuals or the cross-correlogram between residuals and prewhitened input. This time-series regression model was used to fill in data gaps in the long-term X_2 record.

The monthly time series for X_2 has the same form as the daily series:

$$X_2(t) = \omega_0 + \omega_1 X_2(t-1) + \delta \log Q_{out}(t), \quad (2)$$

where X_2 and Q_{out} are now monthly averages and t is the time in months; $\omega_0 = 95 \pm 3$ (mean $\pm$ 1 SE); $\omega_1 = 0.33 \pm 0.02$; and $\delta = -17.6 \pm 0.5$. The coefficient of determination $R^2 = 0.96$, and the standard error of estimate $s = 2.3$ km. No structure is present in the residuals or the cross-correlogram between residuals and prewhitened input.

Although X_2 is not equivalent to flow (Eq. 2), it still reflects the large interannual variability in river flow (Fig. 4). Notable are the extreme low in 1983, an unusually wet ENSO year, and the extreme high in 1977, an unusually dry ENSO year. These are the two most extreme years of the century, as far as inflow into the estuary is concerned. Also of interest is the low of 1969, another ENSO year, and the low of 1986, in which the largest single monthly precipitation of the century occurred in February. From March 1986 through most of 1992, X_2 never advanced further downstream that the long-term mean minimum, and most of the time it was upstream of the long-term mean maximum, symptomatic of the protracted drought conditions and relatively high diversion levels during that period.

Biological resources

Except for *Eurytemora* and delta smelt, each biological variable exhibits a statistically verifiable relationship with X_2 (Table 2; Figs. 5 and 6). An (approximate) F test for the value of including X_2 is significant in each case ($P < 0.01$) and residuals are consistent with the variance function selected in each case. In all cases but for molluscs, no autocorrelation is present in the respective X_2 series. In the case of molluscs, the 3-yr running mean (Table 1) introduces autocorrelation into the X_2 series (at both lags 1 and 2), but the mollusc series itself exhibits no autocorrelation. The significance tests are therefore not compromised by autocorrelation in the data (Jassby and Powell 1990).

Except for mollusc density in Grizzly Bay, all sig-

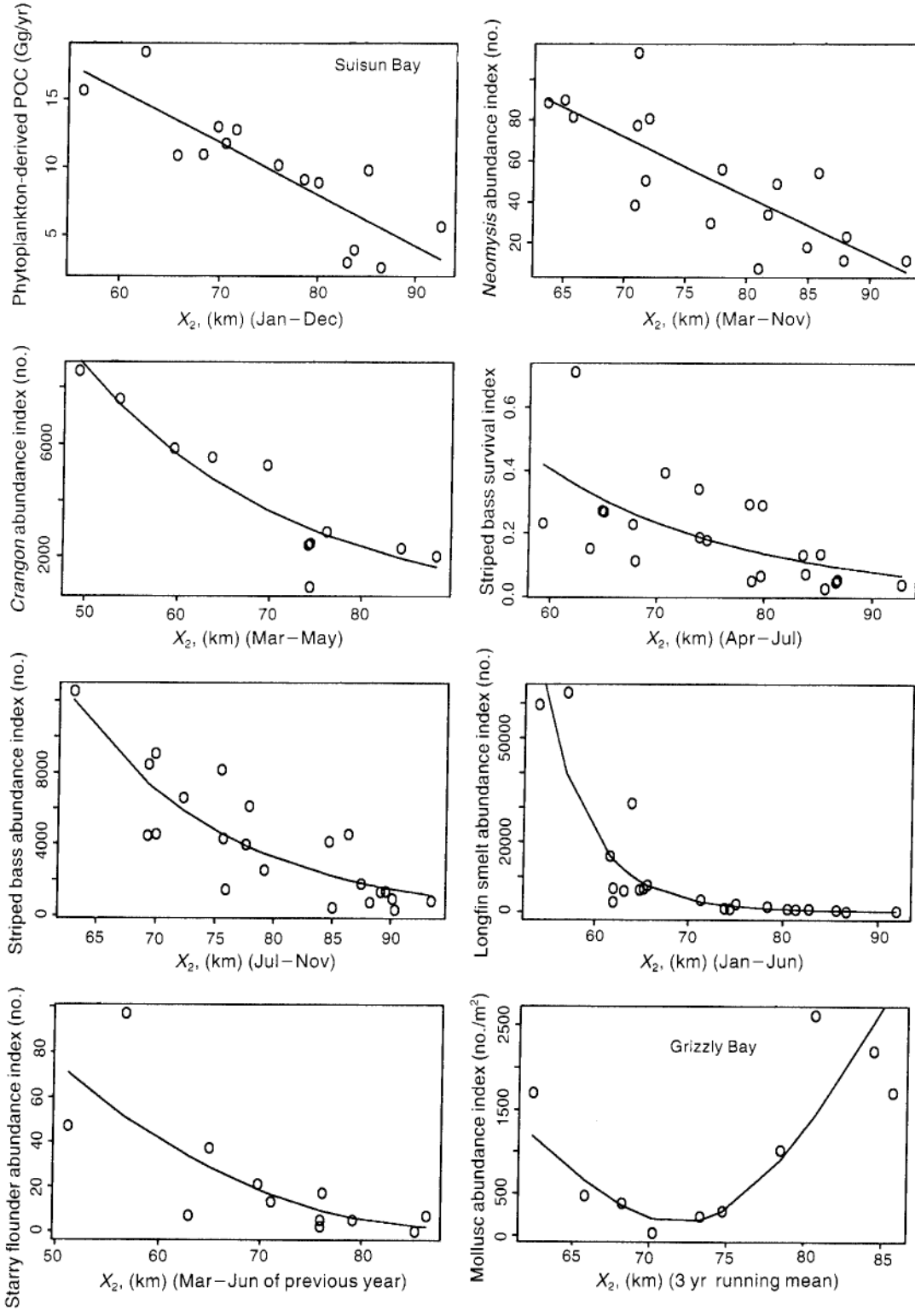

FIG. 5. Relationships between various biological variables and X_2, the position of the 2‰ isohaline. ———; fitted values using the generalized linear models summarized in Table 2 (POC: particulate organic carbon). Months refer to averaging intervals.

TABLE 2. Summary of relationships between response variable Y and predictor variable X_2: n, number of observations (years); g, link function; V, variance function; df, degrees of freedom for X_2 in model (1 = linear, 2 = natural spline with one interior knot); r, correlation between Y and the fitted values; $s/\bar{Y}$, square root of mean squared residual as proportion of mean response.

Y	n	g	V	Spline df	r	$s/\bar{Y}$
POC supply	15	I	1	1	0.85	0.26
Neomysis	18	I	1	1	0.79	0.39
Crangon	11	log	1	1	0.93	0.23
Longfin smelt	21	log	μ	2	0.89	0.85
Striped bass survival	22	log	μ	1	0.59	0.66
Striped bass	22	log	1	1	0.85	0.45
Molluscs	10	I	μ	2	0.80	0.65
Starry flounder	12	log	μ	2	0.76	0.94

nificant relations show a decline as X_2 increases. Molluscs exhibit an increase at extreme values of X_2, whether high or low. Two of the variables—POC supply and *Neomysis*—were linear in X_2. The others required some form of nonlinearity, either by transforming the response variable (*Crangon* and striped bass), the predictor variable (molluscs), or both (longfin smelt and starry flounder). Interannual variability in *Eurytemora* and delta smelt could not be described with a generalized linear model in X_2, at least for the averaging periods used here.

The correlation r between the response variable and fitted values (Table 2) is simply the multiple correlation coefficient in the case of classical linear models; its square is therefore a guide to the proportion of variability attributable to the model. Similarly, s is the standard error of estimate for classical linear models and is a guide to the precision of predictions.

Multiple predictors for striped bass survival

Generalized additive modelling was used to explore the simultaneous effects of X_2 and the monthly series for freshwater diversion (DIV) on striped bass survival. The link function was taken to be g = log, and the variance function $V = \mu$. Survival appeared to have a nonlinear dependency on X_2, but a more or less linear dependency on DIV (Fig. 7). The X_2 effect was unimodal with a peak between 70 and 80 km, while DIV had a monotonic negative effect. The correlation between response and fitted values increased substantially to 0.74 (cf. Table 2). The dependence of the variance on the mean was consistent with assumptions, and the residuals exhibited no autocorrelation. Only 1 yr, 1982, was not fit well by the model.

In order to quantify the relationship in more familiar terms, a classical linear model was constructed using the generalized additive model results as a guide. The response was log-transformed and the nonlinearity in X_2 was represented with a quadratic term:

$$\ln B = \alpha + \beta_1 X_2 + \beta_2 X_2^2 + \beta_3 \mathrm{DIV}. \qquad (3)$$

where B = striped bass survival index; $\alpha = -38 \pm 15$; $\beta_1 = 1.0 \pm 0.4$; $\beta_2 = -0.0064 \pm 0.0024$; and $\beta_3 = -7.3 \pm 3.3$ (mean ± 1 SE). The diagnostic plots were essentially unchanged, once again showing consistency with the underlying assumptions. The multiple correlation coefficient between the untransformed survival index and the predictors was $r = 0.71$ ($P < 0.001$), almost as high as the generalized additive model that used an additional degree of freedom for the DIV effect.

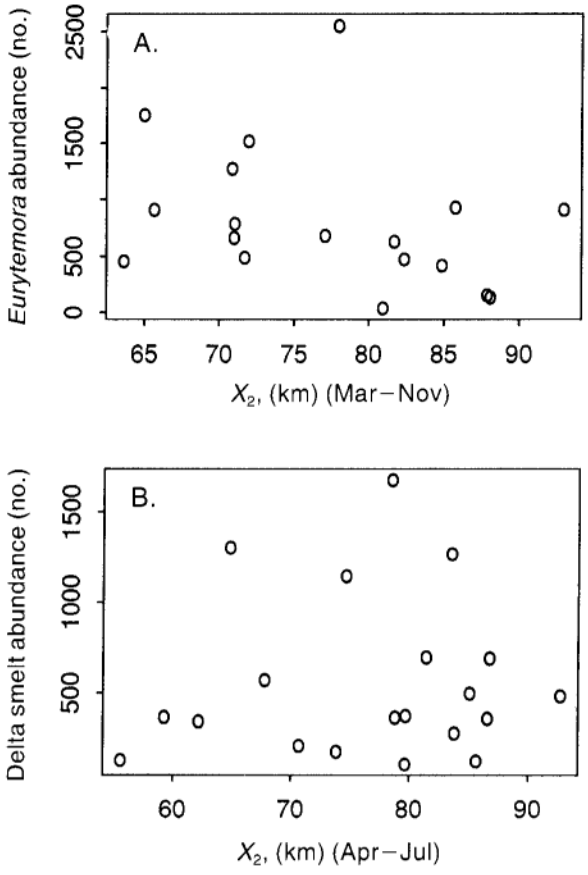

FIG. 6. (A), *Eurytemora affinis* abundance index vs. X_2; (B), delta smelt (*Hypomesus transpacificus*) abundance index vs. X_2. Months refer to averaging intervals.

Further linear models were constructed with subsets of predictor variables and their PSE values compared (Table 3). On the basis of PSE, as well as traditional statistics such as the adjusted coefficient of determination and standard error of estimate, the full model appeared superior. Also on the basis of PSE, the predictive capabilities of all remaining models were similar, except for one inferior to the others that used a linear term only for both X_2 and DIV.

DISCUSSION

Why estuarine resources are associated with X_2

This study demonstrates that X_2 has extensive relationships with estuarine resources in the Bay/Delta es-

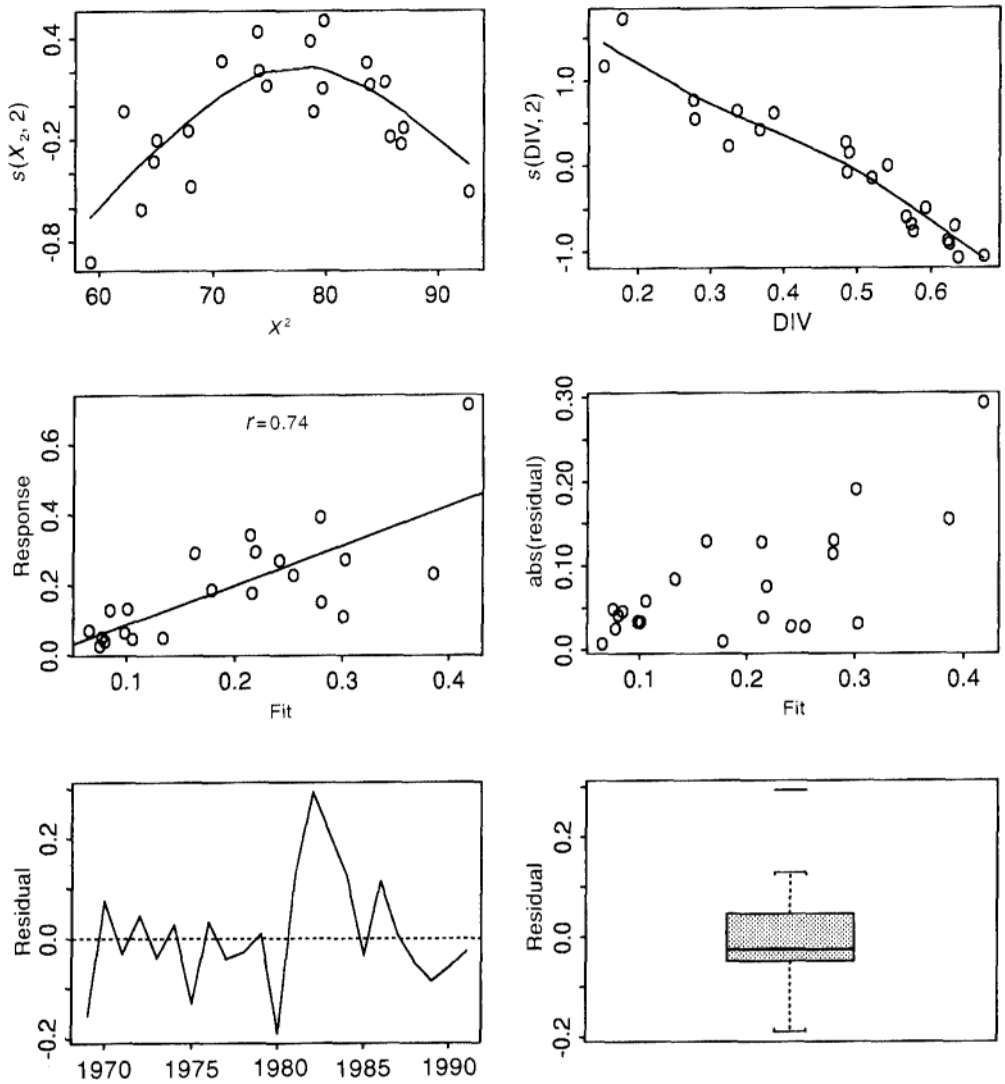

FIG. 7. Diagnostics for generalized additive model of striped bass survival index with link function g = log and variance function $V = I$: *top panels,* partial residual plots for X_2 and DIV (Freshwater diversion), [$s(X_2, 2)$ and s(DIV, 2) refer to smoothing splines with two degrees of freedom]; *middle panels,* response and absolute value (abs) of residuals vs. fitted values from the survival model; *bottom panels,* time and box plots of residuals (see Fig. 8 caption for a description of box plot).

tuary. The associations exist for benthic and pelagic organisms, planktivorous and piscivorous organisms, and a range of taxa from algae through molluscs and crustaceans to fishes. What are the causal mechanisms underlying these relationships? A variety of potential mechanisms deserves a detailed consideration that is beyond the scope of this study, but a summary is in order here.

In the case of phytoplankton POC, several flow- and salinity-related effects are at work. First, phytoplankton tend to concentrate in the vicinity of the ETM, the upstream boundary of which is marked approximately by X_2 (Kimmerer 1992). If the ETM is positioned in the channels upstream of Suisun Bay, phytoplankton receive insufficient light for the development of blooms; a necessary condition appears to be the positioning of the ETM downstream near the broad, shallow expanses of Suisun Bay where phytoplankton growth rates are higher (Arthur and Ball 1979, Ball and Arthur 1979, Cloern et al. 1983). Second, persistent low flows of ≥2 yr create equable salinity conditions and result in colonization of Suisun Bay by marine suspension-feeding bivalves, increasing losses of phytoplankton (Nichols 1985, Alpine and Cloern 1992). Finally, under low flow conditions, the input of fluvial phytoplankton from upstream areas into Suisun Bay is diminished (Jassby et al. 1993). At high flows, the ETM may be positioned in channels downstream of Suisun Bay (Carquinez Strait), once again leading to severe light-limitation (Cloern et al. 1983). High flows also increase washout of chlorophyll from the ETM (Peterson and Festa 1984). Furthermore, if these high flows

TABLE 3. Five linear models relating the logarithm of striped bass survival index to the position of the 2‰ isohaline (X_2) and DIV (Diversion) (based on 250 bootstrap replications for each model). Symbols: PSE, prediction squared error; R_a^2, adjusted coefficient of determination; $s/\bar{Y}$, standard error of estimate as proportion of mean response.

Predictors	PSE	R_a^2	$s/\bar{Y}$
X_2, X_2^2, DIV	0.017	0.60	0.28
X_2	0.020	0.49	0.32
X_2, X_2^2	0.020	0.51	0.31
DIV	0.021	0.42	0.34
X_2, DIV	0.023	0.46	0.32

are persistent, high densities of *freshwater* suspension-feeding bivalves can develop in Suisun Bay. Although these phenomena can lead to depressed production *within* Suisun Bay at high flows, just as they can at low flows, the increased loading from the Delta more than offsets this depression, and so the overall phytoplankton POC supply continues to increase. Export of phytoplankton from the Delta to state and federal water projects also influences the phytoplankton POC supply in Suisun Bay but we do not consider its separate effects in the present study (cf. Jassby and Powell 1994).

The response of the mollusc community is distinctive: it has a clear minimum at intermediate values of X_2 compared to the other variables examined. As mentioned previously, persistent high values of X_2 (persistent low flows) permit the colonization of Suisun Bay by marine benthic macroinvertebrates. The 3-yr averaging period for X_2 was chosen to take into account the time necessary for colonization. In times past, the main colonizing species was *Mya arenaria,* but this role was usurped by the invader *Potamocorbula amurensis* during the drought period of 1987–1992. In a similar manner, persistent low values of X_2 (persistent high flows) lead to colonization by freshwater benthic macroinvertebrates, particularly *Corbicula fluminea.* The net effect of these "high-density" colonizations from both the seaward and landward directions under persistent low or high flows, respectively, is a minimum in mollusc density at intermediate values of X_2. The response to high X_2 may be accentuated in recent years because of the high densities achieved by *Potamocorbula* (Nichols et al. 1990).

Mechanisms governing interannual variability in the remaining organisms are less certain. Because of the relation between primary production and fisheries yield that holds for many aquatic systems (Nixon 1988), one could postulate that variability of populations at higher trophic levels simply reflects "bottom-up" control by the food supply. However, the correlation of every population abundance with X_2 prevents a simple statistical evaluation of the relationship among populations. In particular, the spatial-temporal coincidence of *Neomysis* and phytoplankton abundance (measured as chlorophyll *a*) can be attributed to similar salinity and seasonal responses (Kimmerer 1992); trophic relations need not be invoked. Alternative explanations for the historical decrease in *Neomysis* include the negative effect of temperature, which increases at low flows, on brood size (Orsi 1993). The problem, however, remains unresolved.

The response of *Crangon franciscorum* has been attributed to two flow-related mechanisms (IESP 1990). First, higher river inflows result in larger landward-flowing gravitational currents, transporting the small post-larval shrimp into the Bay and dispersing them upstream. Second, higher river inflows reduce Bay salinity and increase the amount of suitable nursery habitat for juvenile shrimp. Food scarcity in Suisun Bay during low flows has also been suggested as a factor in the decline of *C. franciscorum* (Herbold et al. 1992); *Neomysis mercedis,* for example, is a common food item.

In the case of striped bass, laboratory experiments demonstrate that the food density for larval fish in the estuary is sometimes low enough to have an effect on both growth and mortality rates (IESP 1990). Food concentrations for striped bass in Chesapeake Bay, the major striped bass habitat on the east coast of the U.S., are much higher than in the Bay/Delta estuary (Miller 1991). The main mechanism behind long-term variability of striped bass populations, however, is postulated to be export to the water projects and entrainment within local water intakes. Losses to export and entrainment are in turn controlled by freshwater diversion, specifically by the *proportion* of water diverted for export and within-Delta use. This proportion increases as X_2 decreases (or net Delta outflow increases), possibly giving rise to the relationships portrayed here for striped bass. Herbold et al. (1992) review the significance of freshwater diversion for longfin smelt abundance as well.

Young starry flounder (>1 yr old) are usually found in Suisun Bay and downstream. Although young-of-the-year can be found further upstream, especially in years of low flow, their overall distribution is such that diversion plays a minor role, if any, in their variability. As in the case of *Crangon,* reproduction takes place in near-shore areas and bottom currents transport the young into the Bay (Wang 1986). Higher net Delta outflows can therefore be expected to result in higher abundance of 1-yr-old fish the following year.

The lack of a simple relationship between *Eurytemora affinis* and delta smelt, on the one hand, and X_2 on the other, is not well understood. The distribution of *Eurytemora* is definitely affected by X_2 position: it tends to be most common in or near the ETM (Orsi and Mecum 1986). X_2 alone, however, cannot explain the abundance of *Eurytemora* in the estuary, which therefore must depend on other factors as well. Declines in food levels and the introduction of the copepod *Sinocalanus doerrii* have been suggested as pos-

sible factors (CDFG 1987*c*). Delta smelt distribution is also determined by X_2, but population abundance depends in part on the presence of shallow habitat at a preferred salinity range (Moyle et al. 1992). As a result, the highest abundance levels are attained at intermediate values of X_2, i.e., when X_2 is in Suisan Bay. As low abundance has also been observed when X_2 is in Suisun Bay other mechanisms must be operating as well. For both organisms, an effect of X_2 position on abundance cannot be ruled out; its role may simply be masked by the presence of additional mechanisms. Alternatively, abundance of either organism may be related to some other functions of X_2, rather than the averaging periods used here.

Relationships between X_2 (or freshwater discharge) and year-to-year variability in estuarine resources are not unique to the Bay/Delta, particularly if we include coastal currents and marginal seas. Chapman (1966) published one of the earliest of these studies for U.S. waters, showing that fish and shellfish catch in seven Texas estuaries was higher in a wet year than a dry one. In two influential papers, Sutcliffe (1972, 1973; cf. Drinkwater and Myers 1987) described correlations between St. Lawrence River discharge and Quebec landings of haddock, halibut, lobster, and soft-shell clams. Yáñez-Arancibia et al. (1985) showed that fish capture per unit area was correlated with river discharge in Mexican coastal lagoons and estuaries in the southern Gulf of Mexico. Similarly, variations in the annual catch of shallow-water shrimp (*Penaeus indicus*) on the Sofala Bank in Mozambique can be predicted on the basis of Zambezi River runoff (Gammelsrød 1992), and flows in the Apalachicola–Chattahoochee–Flint River system are associated with the Apalachicola Bay oyster catch (Wilber 1992). A number of other studies have treated this issue, many of which are referred to in a symposium on the subject (Skreslet 1985). Most of these studies, however, either address shorter time scales or are qualitative. Kaartvedt (1985) summarized the discussions of the symposium work group on zooplankton and fish: "A lot of speculation on mechanisms and responses may [be] undertaken, but to surpass pure theoretical and nonquantitative statements a search for documented covariations between freshwater discharge and biological variables is needed." Nowhere have the connections between river inflow or salinity distribution and estuarine resources been shown to be operative for so many types of organisms over such a long time period as in the San Francisco Bay/Sacramento–San Joaquin Delta Estuary. However, the causal mechanisms—particularly the importance of trophic linkages versus direct effects of flows—remain in large part unresolved.

X_2 *compared to net Delta outflow*

Relationships between estuarine resources and net Delta outflow Q_{out} can also be demonstrated and, considering the close association between X_2 and net Delta outflow, these relationships may be as broad as those with X_2. One could expect, however, an advantage to using X_2 instead of net Delta outflow in the future. The latter is estimated as follows (CDWR 1986):

$$Q_{out} = Q_{tot} + Q_{prec} - Q_{depl} - Q_{exp},$$

where Q_{tot} = total Delta inflow; Q_{prec} = runoff within the Delta; Q_{depl} = depletions (within-Delta consumption); and Q_{exp} = exports. Q_{depl} in particular is a significant quantity in the estimate of net Delta outflow, but it is impractical to measure because of the large numbers of locations at which water is withdrawn. As a result, a fixed value is assigned for each month of the year. Similarly, many assumptions enter into the estimate of Q_{prec}, although its magnitude is small compared to the other terms. Certain components of Q_{tot} are estimated as well. On some days, the inputs Q_{tot} + Q_{prec} are similar in magnitude to Q_{depl} + Q_{exp}. The difference between them, Q_{out}, is then a relatively small number with a relatively high uncertainty. More formally, by making the conservative assumption that errors in each of the other daily flows have a coefficient of variation (CV) of 10%, and that they are uncorrelated, we can estimate the CV in daily Q_{out} by propagating the uncertainty (Bevington 1969). We examined both lower and higher flow conditions separately, dividing the days from 1956–1991 into two equal groups based on whether Q_{out} was smaller or larger than its median, 356 m³/s (Fig. 8). The uncertainty is large under the lower flow conditions; the middle half of the data has CVs of 20–40%, with much higher uncertainties occurring at

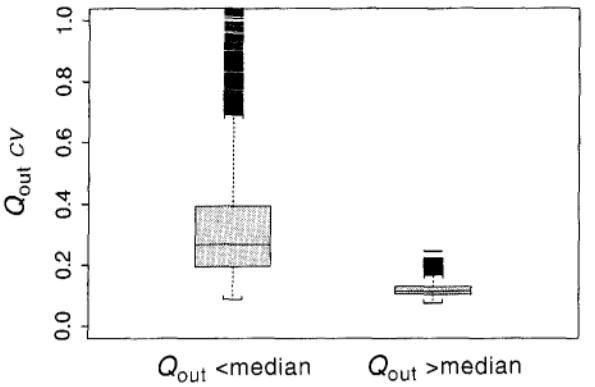

FIG. 8. Coefficient of variation (CV, expressed as a fraction) in daily Q_{out} (net Delta outflow) estimated by propagating uncorrelated fluctuations of 10% in each of Q_{tot}, Q_{prec}, Q_{depl}, and Q_{exp} (Q_{tot}, total Delta inflow; Q_{prec}, runoff within the Delta; Q_{depl}, depletion [consumption within the Delta], Q_{exp}, exports). Values for each term were taken from the DAYFLOW data set for 1956–1991. Median Q_{out} during this period was 356 m³/s. The center horizontal line in each box is the median. The lower and upper edges of each box, called *hinges*, mark the first and third quartiles. The *whiskers*, dashed lines emanating from each box, show the range of values falling within 1.5 times the interquartile distance from the nearest hinge. The remaining horizontal lines mark *outside values* that fall beyond the whiskers.

times. Even under the higher flow conditions, uncertainties of >20% can occur.

Estimates of X_2 with a well-chosen series of monitoring stations, although requiring interpolation between stations, can certainly be accomplished with less uncertainty. The more noise in the predictor variables, the weaker the apparent relationship between the response and predictors; we are thus more likely to discover subtle relationships when using measured X_2 than when using outflow, particularly at low flows. This difference between the precision of X_2 and Q_{out} is most important at short time scales (days), as the fluctuations will compensate to some extent on monthly scales. On the other hand, these short scales may be of interest for some organisms, particularly those that can be affected by pulse flows at certain points in their life cycles.

Utility of X_2 *as a habitat indicator*

Messer (1990) discusses a number of criteria for selection of indicators in environmental monitoring and assessment. These criteria represent the consensus of various working groups convened under the USEPA Environmental Mapping and Assessment Program and provide a useful context in which to assess the utility of X_2. The critical criteria include:

(1) correlation with changes in ecosystem processes or components. Our results demonstrate that X_2 has a clear and pervasive relationship with estuarine biological properties. Relationships exist between X_2 and an important component of the food web base in Suisun Bay (phytoplankton POC), zooplankton consumers (*Neomysis*), epibenthic crustaceans (*Crangon*), a major group of benthic consumers in Suisun Bay (molluscs), bottom-foraging fish (starry flounder), and both survival (striped bass) and abundance (longfin smelt and striped bass) of fish that feed in the water column.

(2) regional applicability. Our results do not bear directly on this issue. However, the statistical associations reflect, at least in part, general estuarine processes. Moreover, similar associations, albeit with river flow as the predictor, exist for other estuaries. Isohaline position, therefore, probably has widespread utility as an estuarine habitat indicator. The applicability of a particular isohaline value will differ from one estuary to the next, depending on both the physiography and water management patterns. Isohaline positions other than X_2 may be more appropriate choices for other estuaries; even in this estuary, isohaline positions other than X_2 could be expected to exhibit the same close relationships with estuarine resources (Fig. 2). Nevertheless, the concept of using isohaline position and the criteria for choosing a physically or ecologically meaningful value can be generalized to other estuaries.

(3) integration of effects over space and time. X_2 certainly integrates over space, acting as a scalar representation of the entire salinity field. It also integrates over time, as only the mean value needs to be known for periods of several months to 3 yr. Some judgments are required in selecting averaging periods, requiring an understanding of life histories and basic biology.

(4) unambiguous and monotonic relation with a habitat variable. X_2, in fact, has unambiguous relationships with many habitat variables including the salinity distribution and net outflow from the Delta. The salinity distribution in turn determines several habitat characteristics such as the position of an ETM, the mean depth and surface area between any two salinities, and the geographic location of aquatic habitat. Net Delta outflow and the salinity distribution together affect residence times for particles in the estuary.

(5) quantifiable by automated or synoptic monitoring. X_2 can be measured by the strategic placement of automated sensors over its range. Participants at the technical workshops giving rise to this study recommended that the salinity distribution be monitored continuously at a series of at least six stations spaced ≈5 km apart (the tidal excursion distance), spanning the range of most historical X_2 observations (Fig. 1). The data would be telemetered to a suitable location for timely analysis and interpretation.

Other desirable, but not critical, criteria for habitat indicators include: (6) importance to ecological structure and function; (7) responsiveness to stressors and management strategies; (8) existence of a standard method; (9) low measurement error; (10) existence of a historical data base; and (11) cost-effectiveness (Messer 1990). All of these criteria can be satisfied by X_2 (although cost-effectiveness depends on the alternatives under consideration). X_2 is clearly a viable candidate for indexing estuarine habitat conditions.

Complications caused by variables additional to X_2

As the previous discussion implies, X_2 or net Delta outflow is not the only variable affecting estuarine resources. The history of the resource, as well as other environmental forces, may exert some influence. In some cases, the unexplained variability is high, and predictions based on X_2 alone would be uncertain. Also in certain cases, variables correlated with X_2 or net Delta outflow are thought to be important causal factors. These correlations may not persist into the future if the estuary is managed in a different fashion, and the utility of X_2 as a predictor may no longer hold.

For a simple demonstration of these difficulties, we chose the striped bass survival index. Much of its variability cannot be accounted for by X_2 (Fig. 5; Table 2). Moreover, ecological considerations suggest that freshwater diversion is important to survival as well. The relation between survival and X_2 therefore suffers from both of the difficulties mentioned above. In practice, the proportion of river inflow diverted for within-Delta consumption and export (DIV), is correlated with X_2, but it is nevertheless an independent variable in principle and could become uncorrelated in the future.

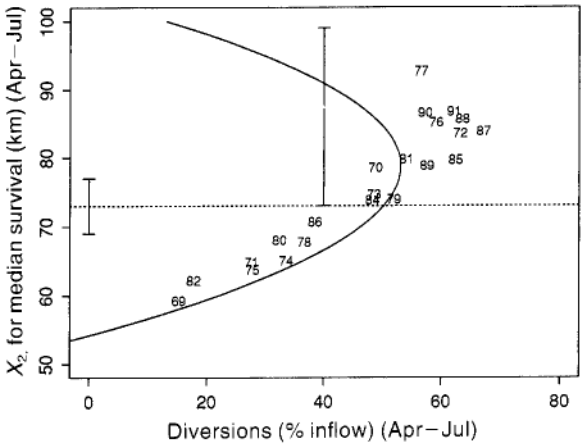

FIG. 9. Value of X_2 (the position of the 2‰ isohaline) needed to ensure median survival of striped bass, as a function of DIV (Freshwater diversion). Status for individual years also indicated on the plot. – – –; from model using X_2 only as predictor; ———; from model using X_2 and DIV as predictors; *vertical lines,* bootstrap percentile estimates of 0.95 confidence intervals. Months refer to averaging intervals.

When both X_2 and DIV were used as predictors, maximal survival was attained at intermediate values of X_2, while survival always decreased as DIV increased (Fig. 7). Both forms are consistent with the probable mechanisms at work. X_2 may indicate the *susceptibility* of a population to entrainment; the further downstream the larval bass population (which tends to track X_2), the less the effect of a given DIV. If X_2 is pushed too far downstream, however, the implied higher flows result in a lower flushing time, and larvae are washed out of the sampling area at increasing rates. DIV, on the other hand, represents the relative *intensity* of forces entraining the larvae in local intakes or export flows. For a fixed value of X_2, any increase in diversion should result in lower survival for striped bass.

How does DIV complicate the choice of some management target for X_2, for example, the value of X_2 that results in the long-term median survival index? Suppose we wish to ensure that

$$B \geq B_{\text{med}}, \tag{4}$$

where B_{med} is the median survival value. For the simple model of Table 2, $\ln B = \eta + \beta X_2$, where η and β are constants, so Eq. 4 implies that

$$X_2 > \frac{\ln B_{\text{med}} - \eta}{\beta} = 73 \text{ km}.$$

X_2 therefore has to be kept downstream of the 73-km position in order to achieve a survival of at least B_{med}, regardless of the value of DIV (dashed line of Fig. 9).

In the case of the model incorporating DIV, Eqs. 3 and 4 imply that X_2 must lie within the parabola (solid curved line of Fig. 9)

$$\text{DIV} = -\frac{1}{\beta_3}[\beta_2 X_2^2 + \beta_1 X_2 + (\alpha - \ln B_{\text{med}})].$$

One obvious implication is that too high an X_2 may *depress* survival, a feature not present in the single-predictor model using only X_2. Furthermore, as long as DIV is $< \approx 55\%$ (which is the case for 12 of the 22 yr plotted in Fig. 9), an X_2 of 78 km is sufficient to ensure the median survival value. For DIV $> 55\%$, on the other hand, no X_2 position can ensure that B_{med} will be achieved.

By ignoring variables other than X_2 (or Q_{out}) we could therefore be in danger of imposing inappropriate standards, either too stringent or too lenient. The mere fact of a correlation between some ecosystem property and an indicator such as X_2 is therefore not sufficient grounds for using the indicator as a policy variable. The presence of much unexplained variation is one signal that an existing model can lead to unacceptably biased management policies, and should result in a search for alternative and additional variables.

Uncertainties in policy variables

It is important to distinguish the problem of predicting a resource level from that of setting a management goal for that resource. In the case of striped bass survival, for example, the problem of predicting survival is different from that of choosing X_2 to attain some target survival value. As Walters (1986) concludes: ". . . it is quite possible for a very good "predictive" model (low s^2) to give very poor (highly uncertain) estimates for key variables of policy interest." In order to evaluate the utility of a particular model for pursuing policies, one must therefore examine the uncertainty in choosing a management goal and not simply how well the model accounts for variability in the resource level.

To illustrate this point, we once again considered the problem of maintaining striped bass survival above a certain minimum level (the long-term median) by manipulating X_2 and DIV. We computed bootstrap percentile interval estimates of the 0.95 confidence interval for "median-survival" X_2, both for the simple model using X_2 alone and the more complex model incorporating DIV. As an example, we set DIV to a typical value of 40%. For the simpler model, the 0.95 confidence interval was 69–77 km, independent of diversion level. For the more complex model, the 0.95 confidence intervals were 54–68 km for the downstream boundary and 73–99 km for the upstream boundary (Fig. 9). The confidence intervals for the more complex model are therefore larger, despite its lower PSE (Table 3).

As the number of parameters increases in a model, the uncertainty in parameter estimates tends to increase. This increase may be sufficient to offset a superior specification, that is, a specification that better describes the underlying dynamics (Linhart and Zuc-

chini 1986). One is therefore faced with the problem of determining an "optimum complexity" (Walters 1986), below which incomplete structural specification introduces too much bias and above which parameters cannot be estimated with sufficient certainty on the basis of available data. What constitutes optimum complexity is highly dependent on the nature of the resource and the available data. No general (rigorous) rules can be given; nonetheless, it is important to recognize the concept. Too often, managers are presented with highly complex models that are based on a knowledge of the essential dynamics but eventually fail as guides to policy. The fact that models accurately embody underlying mechanisms cannot be taken as complete evidence of their utility if the parameters are estimated on the basis of too few data.

As fish recruitment is among the most unpredictable ecological phenomena and represents one of the most severe challenges to the modelling process, we can expect to have more success (less uncertainty) with resources other than striped bass survival. As an example, consider the *Neomysis mercedis* abundance index (Table 1; Fig. 5). Loss through export and entrainment of water is not considered to be a factor in *Neomysis* variability (Kimmerer 1992) and so we base the analysis on the simple relationship with X_2 (Table 2). Using bootstrap percentile intervals, we again computed bootstrap estimates of the 0.95 confidence interval for the X_2 value (March–November mean) corresponding to long-term median abundance. The confidence interval was 75–80 km. Although the difference between these two boundaries still represents a large difference in water requirement, the analysis offers a much more exact prescription for management of water flow, permitting a leeway of only 5 km for X_2, compared to 26 km for striped bass survival. In the case of *Neomysis,* then, existing data can provide a useful statistical touchstone for water management policies.

Even in the case of striped bass survival, where the confidence interval is so large as to provide little guidance for optimal positioning of X_2, the uncertainty analysis performs a useful function. By demonstrating that the upstream boundary is particularly uncertain, reflecting the almost complete lack of actual data points in the vicinity of this boundary, the analysis suggests combinations of X_2 and DIV that might be chosen for a "bold management experiment" (Walters and Collie 1988). The analysis therefore guides future data acquisition, as well as providing a much truer picture of the sufficiency of a given data set for management purposes.

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Literature Cited

Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography **37**:946–955.

Armor, C., and P. L. Herrgesell. 1985. Distribution and abundance of fishes in the San Francisco Bay estuary between 1980 and 1982. Hydrobiologia **129**:211–227.

Arthur, J. F., and M. D. Ball. 1979. Factors influencing the entrapment of suspended material in the San Francisco Bay-Delta Estuary. Pages 143–174 *in* T. J. Conomos, editor. San Francisco Bay: the urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California, USA.

Ball, M. D., and J. F. Arthur. 1979. Planktonic chlorophyll dynamics in the northern San Francisco Bay and Delta. Pages 265–286 *in* T. J. Conomos, editor. San Francisco Bay: the urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California, USA.

Bevington, P. R. 1969. Data reduction and error analysis for the physical sciences. McGraw-Hill, New York, New York, USA.

Boesch, D. F. 1977. A new look at the zonation of benthos along an estuarine gradient. Pages 245–266 *in* B. C. Coull, editor. Ecology of the marine benthos. University of South Carolina Press, Columbia, South Carolina, USA.

Boothe, P. 1967. The food and feeding habits of four species of San Francisco Bay fish. MRO Reference Number 67-13. Bodega Marine Laboratory, University of California, Bodega Bay, California, USA.

Box, G. E. P., and G. M. Jenkins. 1976. Time series analysis: forecasting and control. Revised edition. Holden-Day, San Francisco, California, USA.

CDFG (California Department of Fish and Game). 1987*a*. Associations between environmental factors and the abundance and distribution of resident fishes in the Sacramento-San Joaquin Delta. Exhibit Number 24, 1987 Water Quality/Water Rights Proceedings on San Francisco Bay/Sacramento-San Joaquin Delta, State Water Resources Control Board, Sacramento, California, USA.

CDFG (California Department of Fish and Game). 1987*b*. Delta outflow effects on the abundance and distribution of San Francisco Bay fish and invertebrates. Exhibit Number 60, 1987 Water Quality/Water Rights Proceedings on San Francisco Bay/Sacramento-San Joaquin Delta, State Water Resources Control Board, Sacramento, California, USA.

CDFG (California Department of Fish and Game). 1987*c*. Long-term trends in zooplankton distribution and abundance in the Sacramento-San Joaquin estuary. Exhibit Number 28, 1987 Water Quality/Water Rights Proceedings on San Francisco Bay/Sacramento-San Joaquin Delta, State Water Resources Control Board, Sacramento, California, USA.

CDWR (California Department of Water Resources). 1986. DAYFLOW program documentation and data summary user's guide. California Department of Water Resources, Sacramento, California, USA.

CDWR (California Department of Water Resources). 1991. Water quality conditions in the Sacramento-San Joaquin Delta during 1989. Report to the State Water Resources

Control Board in accordance with Water Right Decision 1485, Order 4(f). California Department of Water Resources, Sacramento, California, USA.

Chapman, C. R. 1966. The Texas basins project. Pages 83–92 *in* R. Smith, A. Swartz, and W. Massmann, editors. A symposium on estuarine fishes. Special Publication Number 3, American Fisheries Society, Washington, D.C., USA.

Cloern, J. E., A. E. Alpine, B. E. Cole, R. L. J. Wong, J. F. Arthur, and M. D. Ball. 1983. River discharge controls phytoplankton dynamics in Northern San Francisco Bay estuary. Estuarine, Coastal and Shelf Science **12**:415–429.

Conomos, T. J., R. E. Smith, and J. W. Gartner. 1985. Environmental setting of San Francisco Bay. Hydrobiologia **129**:1–12.

Drinkwater, K. F., and R. A. Myers. 1987. Testing predictions of marine fish and shellfish landings from environmental variables. Canadian Journal of Fisheries and Aquatic Sciences **44**:1568–1573.

Efron, B. 1983. Estimating the error rate of a prediction rule: improvements on cross-validation. Journal of the American Statistical Association **78**:316–331.

Gammelsrød, T. 1992. Variation in shrimp abundance on the Sofala Bank, Mozambique, and its relation to the Zambezi River runoff. Estuarine, Coastal and Shelf Science **35**:91–103.

Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. Chapman and Hall, London, England.

Herbold, B., A. D. Jassby, and P. M. Moyle. 1992. Status and trends report on aquatic resources in the San Francisco Estuary. San Francisco Estuary Project, U.S. Environmental Protection Agency, San Francisco, California, USA.

Herrgesell, P., D. Kohlhorst, L. Miller, and D. Stevens. 1981. Effects of freshwater flow on fishery resources in the Sacramento-San Joaquin Estuary. Pages 71–108 *in* R. Cross and D. Williams, editors. Proceedings of a national symposium on freshwater inflow to estuaries. Publication Number FWS/OBS-81/04, U.S. Fish and Wildlife Service, Washington, D.C., USA.

Heubach, W., R. J. Toth, and A. M. McCready. 1963. Food of young-of-the-year striped bass (*Roccus saxatilis*) in the Sacramento-San Joaquin River system. California Fish and Game **49**:224–239.

IESP [Interagency Ecological Studies Program]. 1990. 1989 annual report: Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary. California Department of Water Resources, Sacramento, California, USA.

Jassby, A. D., J. E. Cloern, and T. M. Powell. 1993. Organic carbon sources and sinks in San Francisco Bay: variability induced by river flow. Marine Ecology Progress Series **95**: 39–54.

Jassby, A. D., and T. M. Powell. 1990. Detecting changes in ecological time series. Ecology **71**:2044–2052.

Jassby, A. D., and T. M. Powell. 1994. Hydrodynamic influences on interannual chlorophyll variability in an estuary: upper San Francisco Bay-Delta (California, U.S.A.). Estuarine, Coastal and Shelf Science, *in press*.

Johnson, W. C., and A. J. Calhoun. 1952. Food habits of California striped bass. California Fish and Game **38**:531–534.

Kaartvedt, S. 1985. Oceanographic functions of freshwater discharge and consequences of change. Zooplankton and fish. Pages 410–415 *in* S. Skreslet, editor. The role of freshwater outflow in coastal marine ecosystems. Proceedings of the NATO Advanced Research Workshop, Bodø, Norway, May 21–25, 1985. Springer-Verlag, New York, New York, USA.

Kimmerer, W. 1992. An evaluation of existing data in the entrapment zone of the San Francisco Bay Estuary. Technical Report 33, Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary, California Department of Water Resources, Sacramento, California, USA.

Knutson, A. C., and J. J. Orsi. 1983. Factors regulating abundance and distribution of the shrimp *Neomysis mercedis* in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society **112**:476–485.

Kost, A. B., and A. W. Knight. 1975. The food of *Neomysis mercedis* Holmes in the Sacramento-San Joaquin River system. California Fish and Game **49**:224–239.

Linhart, H., and W. Zucchini. 1986. Model selection. John Wiley and Sons, New York, New York, USA.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, London, England.

Messer, J. J. 1990. EMAP indicator concepts. Pages 2.1–2.26 *in* C. T. Hunsaker and D. E. Carpenter, editors. Ecological indicators for the environmental monitoring and assessment program. EPA 600/3-90/060, U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, North Carolina, USA.

Miller, L. 1991. Concentration of food in the Sacramento-San Joaquin estuary compared with other estuaries inhabited by striped bass. Pages 45–48 *in* D. Kelley, editor. 1990 working papers of the food chain group. Interagency Ecological Studies Program, California Department of Water Resources, Sacramento, California, USA.

Moyle, P. B. 1967. Inland fishes of California. University of California Press, Berkeley, California, USA.

Moyle, P. B., B. Herbold, D. E. Stevens, and L. W. Miller. 1992. Life history and status of the Delta smelt in the Sacramento-San Joaquin estuary, California. Transactions of the American Fisheries Society **121**:67–77.

Nichols, F. H. 1985. Increased benthic grazing: an alternative explanation for low phytoplankton biomass in Northern San Francisco Bay during the 1976–77 drought. Estuarine, Coastal and Shelf Science **21**:379–388.

Nichols, F. H., J. K. Thompson, and L. E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. Marine Ecology Progress Series **66**:95–101.

Nixon, S. W. 1988. Physical energy inputs and the comparative ecology of lakes and marine ecosystems. Limnology and Oceanography **33**:1005–1025.

Orcutt, H. G. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallus). California Fish and Game, Fish Bulletin **78**:1–64.

Orsi, J. J. 1988. Food habits of zooplankton important in the diet of young striped bass in the Suisun Bay and Delta areas of the Sacramento-San Joaquin Estuary. State Water Resources Control Board, Sacramento, California, USA.

———. 1993. *Neomysis*/zooplankton. Page 4 *in* Interagency Ecological Studies Program, Newsletter, Winter 1993. California Department of Water Resources, Sacramento, California, USA.

Orsi, J. J., and W. Mecum. 1986. Zooplankton distribution and abundance in the Sacramento-San Joaquin Delta in relation to certain environmental factors. Estuaries **9**:326–339.

Peterson, D. H., T. J. Conomos, W. W. Broenkow, and P. C. Doherty. 1975. Location of the nontidal current null zone in Northern San Francisco Bay. Estuarine and Coastal Marine Science **3**:1–11.

Peterson, D. H., and J. F. Festa. 1984. Numerical simulation of phytoplankton productivity in partially mixed estuaries. Estuarine, Coastal and Shelf Science **19**:563–589.

Schubel, J. R. 1993. Managing freshwater discharge to the San Francisco Bay-Delta Estuary: the scientific basis for an estuarine standard. San Francisco Estuary Project, U.S.

Environmental Protection Agency, San Francisco, California, USA.

Siegfried, C. A. 1982. Trophic relations of *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* Rathbun: predation on the opossum shrimp, *Neomysis mercedis* Holmes. Hydrobiologia **89**:129–139.

Siegfried, C. A., and M. E. Kopache. 1980. Feeding of *Neomysis mercedis* (Holmes). Biological Bulletin **159**:193–205.

Skreslet, S. 1985. The role of freshwater outflow in coastal marine ecosystems. Proceedings of the NATO Advanced Research Workshop, Bodø, Norway, May 21–25, 1985. Springer-Verlag, New York, New York, USA.

Statistical Sciences, Incorporated. 1993. S-PLUS for UNIX 3.1 and S-PLUS for Windows 3.1. Seattle, Washington, USA.

Stevens, D. E. 1966. Food habits of striped bass (*Roccus saxatilis*) in the Sacramento-San Joaquin Delta. Pages 68–96 *in* J. L. Turner and D. W. Kelley, editors. Ecological studies of the Sacramento-San Joaquin Delta, Part II, Fishes of the Delta. Fish Bulletin 136. California Department of Fish and Game, Sacramento, California, USA.

———. 1977*a*. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento-San Joaquin Estuary, Calif. Transactions of the American Fisheries Society **106**:34–42.

———. 1977*b*. Striped bass (*Morone saxatilis*) monitoring techniques in the Sacramento-San Joaquin Estuary. Pages 91–109 *in* W. Van Winkle, editor. Proceedings of the conference on assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, New York, New York, USA.

Stevens, D. E., D. W. Kohlhorst, L. W. Miller, and D. W. Kelley. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society **114**:12–30.

Stevens, D. E., L. W. Miller, and B. C. Bolster. 1990. A status review of Delta Smelt (*Hypomesus transpacificus*) in California. Candidate Species Status Report 90-2. California Department of Fish and Game, Sacramento, California, USA.

Sutcliffe, W. H. 1972. Some relations of land drainage, nutrients, particulate material, and fish catch in two eastern Canadian bays. Journal of the Fisheries Research Board of Canada **29**:357–362.

———. 1973. Correlations between seasonal river discharge and local landings of American lobster (*Homerus americanus*). Journal of the Fisheries Research Board of Canada **30**:856–859.

Thomas, J. L. 1967. The diet of juvenile and adult striped bass, *Roccus saxatilis*, in the Sacramento-San Joaquin river system. California Fish and Game **53**:49–62.

Turner, J. L., and H. K. Chadwick. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society **101**:442–452.

Wahle, R. A. 1985. The feeding ecology of *Crangon franciscorum* and *Crangon nigricauda* in San Francisco Bay, California. Journal of Crustacean Biology **5**:311–326.

Walters, C. J. 1986. Adaptive management of renewable resources. McMillan, New York, New York, USA.

Walters, C. J., and J. S. Collie. 1988. Is research on environmental factors useful to fisheries management? Canadian Journal of Fisheries and Aquatic Sciences **45**:1848–1854.

Wang, J. C. S. 1986. Fishes of the Sacramento-San Joaquin estuary and adjacent waters, California: a guide to the early life histories. Technical Report No. 9. Interagency Ecological Studies Program, California Department of Water Resources, Sacramento, California, USA.

Wienke, S. M., B. E. Cole, and J. E. Cloern. 1991. Plankton studies in San Francisco Bay, XII. Chlorophyll distributions and hydrographic properties of San Francisco Bay, 1990. Open-File Report 91-476. Water Resources Division, United States Geological Survey, Menlo Park, California, USA.

Wienke, S. M., B. E. Cole, and J. E. Cloern. 1992. Plankton studies in San Francisco Bay, XIII. Chlorophyll distributions and hydrographic properties of San Francisco Bay, 1991. Open-File Report 92-158. Water Resources Division, United States Geological Survey, Menlo Park, California, USA.

Wienke, S. M., B. E. Cole, and J. E. Cloern. 1993. Plankton studies in San Francisco Bay, XIV. Chlorophyll distributions and hydrographic properties of San Francisco Bay, 1992. Open-File Report 93-423. Water Resources Division, United States Geological Survey, Menlo Park, California, USA.

Wilber, D. H. 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. Estuarine, Coastal and Shelf Science **35**:179–190.

Yáñez-Arancibia, A., G. Soberón-Chavez, and P. Sánchez-Gil. 1985. Ecology of control mechanisms of natural fish production in the coastal zone. Pages 571–594 *in* A. Yáñez-Arancibia, editor. Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. Editorial Universitaria, UNAM-PUALICML, Mexico, D.F., Mexico.