Estuaries Vol. 24, No. 4, p. 557–575 August 2001

Analysis of an Estuarine Striped Bass Population: Effects of Environmental Conditions During Early Life

William J. Kimmerer[1,*], James H. Cowan, Jr.[2], Lee W. Miller[3], and Kenneth A. Rose[4]

[1] *Romberg Tiburon Center, San Francisco State University, 3152 Paradise Drive, Tiburon, California 94920*
[2] *University of South Alabama, Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528*
[3] *California Department of Fish and Game, 4001 North Wilson Way, Stockton, California 95205*
[4] *Coastal Fisheries Institute and Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana 70803*

ABSTRACT: Estuarine fish populations are exposed to a variety of environmental conditions that cause both short-term variability and long-term trends in abundance. We analyzed an extensive data set for striped bass (*Morone saxatilis*) in the San Francisco Estuary to refine our understanding of how environmental variability influences recruitment. We examined the effects of environmental variability during early life stages on subsequent recruitment (age 3 yr), and the degree to which conditions in early life may have contributed to a long-term decline in abundance of adult striped bass in the San Francisco Estuary. Survival from egg to young-of-the-year varied strongly with freshwater flow; this effect apparently occurred within the first week or two of life, a time period that encompasses transport of eggs and larvae from the rivers to rearing areas and the onset of feeding. The rate of freshwater flow to pumping facilities that export freshwater from the system had small or sporadic effects on survival during the first month or two of life. Although many young striped bass between ages 2 and 8 mo were entrained in export pumping facilities, the resulting high mortality was unrelated to total mortality rates determined from field data on young striped bass. This lack of effect was apparently due to strong density-dependent mortality occurring between ages 1 mo and 3 yr (Kimmerer et al. 2000). The available data do not support previously suggested relationships between recruitment and freshwater flow during early life, or between gross estimates of pesticide input and survival of early life stages. We used a simple life-cycle model to show that various combined factors could have led to a decline in adult abundance, particularly a large and increasing adult mortality, but that events early in life probably did not contribute substantially to the decline. These results demonstrate that several decades of monitoring data from numerous life stages are needed to distinguish among alternative hypotheses about environmental influences on populations of estuarine fish.

Introduction

The economic value of many estuarine fisheries emphasizes the importance of understanding the roles of environmental and human impacts in regulating recruitment and population abundance. Fishery scientists need to determine the causes of long-term trends in abundance or production, and identify the effects of environmental, including anthropogenic, perturbations on year-class strength. Striped bass is an important fishery species in many estuaries in North America, with a long history of scientific investigation. Variability in year-class strength of striped bass populations has been attributed to effects of freshwater flow (Turner and Chadwick 1972), egg supply (Olney et al. 1991), temperature (Secor and Houde 1995), food supply (Rutherford et al. 1997), and combinations of interacting factors (Cowan et al. 1993; Bennett and Moyle 1996). The objectives of this paper are to examine the evidence for environmental influences, particularly freshwater flow effects, on the early life history of striped bass in the San Francisco Estuary, and to evaluate the likelihood that these influences have contributed significantly to a substantial decline in population abundance (Stevens et al. 1985).

The San Francisco Estuary (Fig. 1) is a complex, dynamic system with widely-varying river flow, a large urban population, and numerous sources of stress including frequent droughts and floods, diversions of freshwater at many locations, a variety of toxic contaminants, and frequent introductions of exotic species (e.g., Conomos 1979; Cloern and Nichols 1985; Nichols et al. 1986; Hollibaugh 1996). Several of these stresses have changed substantially in recent decades. Exports of freshwater from pumping plants in the southern Sacramento-San Joaquin delta (Fig. 1) increased during the 1960–1970s (Nichols et al. 1986). Concerns over

---

[*] Corresponding author: tele: 415/338-3515; fax: 415/435-7120; e-mail: kimmerer@sfsu.edu.

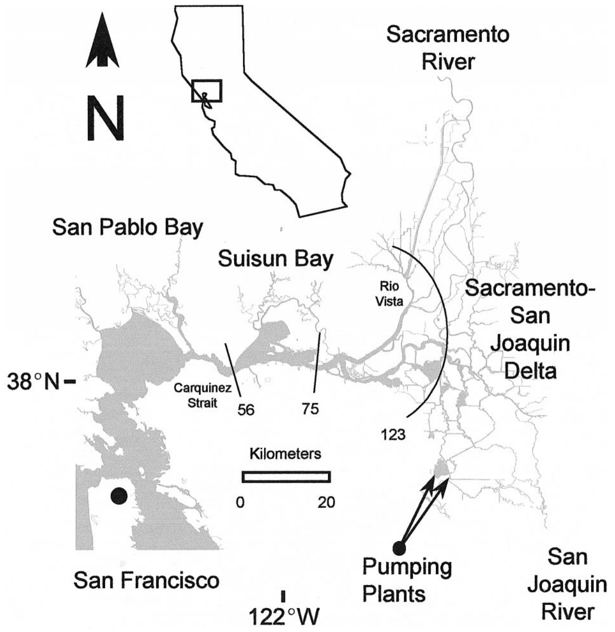

Fig. 1. Map of the northern San Francisco estuary and Sacramento-San Joaquin delta with the location of the major export pumping plants. Lines indicate selected river kilometer indices.

declines in abundance of several estuarine fish species led to establishment of standards to control freshwater flow (or salinity distribution) within the estuary (Jassby et al. 1995; Arthur et al. 1996). Declines in abundance of planktonic organisms important as food for young striped bass accelerated following the introduction of the clam *Potamocorbula amurensis,* which spread throughout the northern part of the estuary in 1986–1988 (Nichols et al. 1990; Alpine and Cloern 1992; Werner and Hollibaugh 1993; Kimmerer et al. 1994; Orsi and Mecum 1996; Kimmerer and Orsi 1996). Application rates of pesticides used in rice cultivation, much of which occurs near striped bass spawning habitat, increased substantially in the late 1970s (Bailey et al. 1994). All of the major changes in potential stresses coincided, more or less, with both the decline in striped bass (Kimmerer et al. 2000) and decadal-scale changes in conditions in the coastal Pacific Ocean (Mantua et al. 1997).

Striped bass were introduced to the San Francisco Estuary in 1879 and have since supported an active recreational fishery, although the commercial fishery for striped bass was closed in 1935 (Calhoun 1949; Chadwick 1962). The population has been in a state of decline for the last 2 to 3 decades (Stevens et al. 1985). Numerous potential influences on abundance of striped bass have been identified (Radovich 1963; Turner and Chadwick 1972; Stevens 1977; Whipple et al. 1981; Stevens et al. 1985; White 1986; Bailey et al. 1994; Bennett 1994; Young et al. 1994; Bennett et al. 1995; Kimmerer et al. 2000). Many reports have emphasized the potential roles of reduced freshwater flow and high export pumping rates in reducing survival during the first 2–8 mo of life, thereby limiting recruitment (e.g., Turner and Chadwick 1972; Stevens 1977; Stevens et al. 1985). We have presented evidence for density-dependent mortality occurring after the first few months of life, potentially offsetting some or all of the effects of flow (Kimmerer et al. 2000). The multiple, confounded patterns of variability in potential environmental influences on striped bass present a major challenge in identifying causal links.

Figure 2 illustrates some of the complexity of the issues involved with striped bass, and provides a map to our key results. We focus here primarily on the interval between spawning and the time when the young-of-the-year (YOY) index is determined, about 1–2 mo, with a secondary focus on the interval between 1–2 mo and either the end of the first calendar year (about 8 mo) or recruitment (3 yr of age). Spawning occurs in freshwater, after which eggs and larvae drift downstream until they reach the low-salinity zone of the estuary. The influence of pesticides used in Central Valley agriculture should be most strongly felt during egg and early larval development. Freshwater flow may affect the speed of downstream transport of larvae and possibly their survival, or the proportion of larvae entrained in export pumps. Larvae and juveniles in the low-salinity zone may be affected by changes in retention due indirectly to changes in flow (e.g., Kimmerer et al. 1998). Export pumping may affect eggs and early larvae during transport to the estuary, and juveniles throughout development when they stray landward from their rearing area in the low-salinity zone. Only the juveniles are captured at the export pumping facilities, so entrainment of eggs and larvae is unobserved.

We examined patterns of abundance and survival from several different sampling programs to separate short-term environmental effects from those factors potentially contributing to the long-term decline in abundance. The principles that guided these analyses were: because each life stage is influenced by the abundance of the previous stage, analyses should focus on estimates or indices of survival or reproductive rate, which should be less ambiguous and less likely to be contaminated by autocorrelation than estimates or indices of abundance; and because the data record includes a period before the decline, factors contributing to the decline should contain observable time trends.

Methods

Data were obtained mainly from the California Department of Fish and Game (CDFG) and the

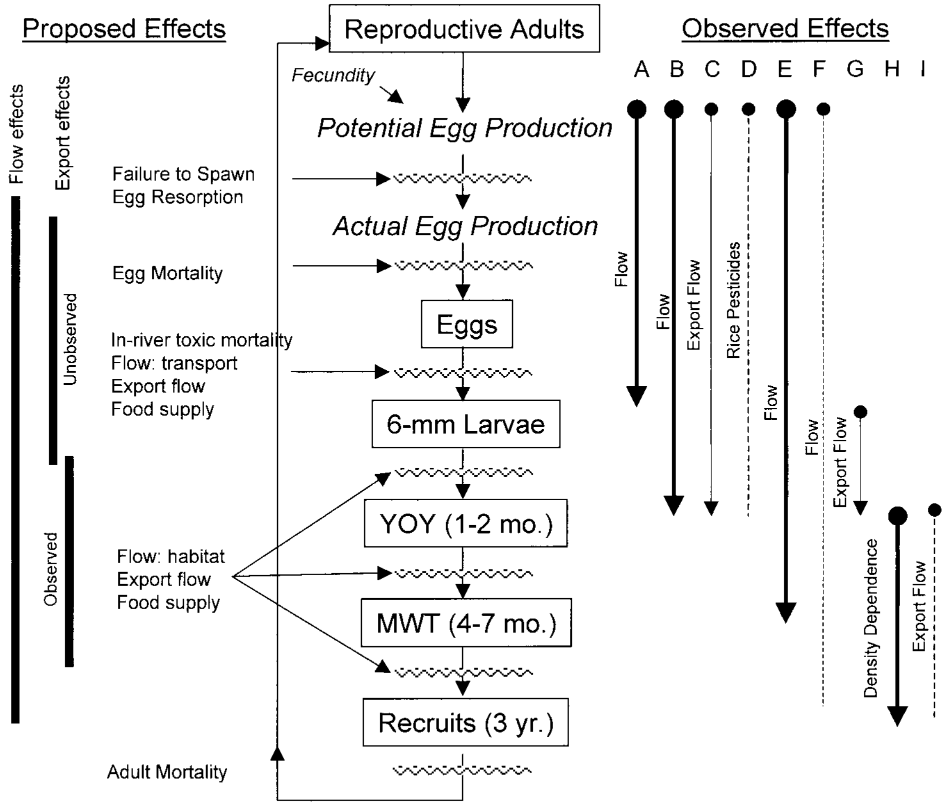

Fig. 2. Schematic diagram of the life cycle of striped bass with predicted environmental effects and results of this study. Previous analyses and conclusions about the important environmental effects of striped bass are summarized on the left, and our key findings are summarized and indexed on the right. In the center of the diagram, life stages are indicated in boxes to represent quantities that are measured or estimated. Exceptions are potential egg production, which is calculated from age-specific abundance and fecundity, and actual egg production, which is unobserved. Wavy lines between boxes indicate potential barriers to development from one stage to the next, identified by the list at the left. Also on the left are vertical bars indicating the range of life stages over which freshwater flow or export effects can be expected or have been proposed; export effects are unobserved for small fish that cannot be effectively screened in the water diversion facilities. Observed effects on the right indicate results of this study and those of Kimmerer et al. (2000). Effects were significant (heavy arrow), significant but weak and ambiguous (thin arrow), or not detected (dashed line). Letters link this diagram with results: A) Table 2 item 6; B) Table 2 items 2, 3, 5, Fig. 7; C) Table 2 item 2 and 3; D) Fig. 8; E) Table 2 item 4; F) Fig. 4; G) Table 2 items 7 and 8; H) Kimmerer et al. (2000), also Table 4; and I) Table 4, Fig. 10.

Interagency Ecological Program for the San Francisco Estuary (IEP). Most of these data are available in raw form on the IEP web site (http://www.iep.water.ca.gov).

ENVIRONMENTAL VARIABLES

The principal environmental factors considered include freshwater flow into the estuary and into export pumps, mortality due to entrainment in the export facilities, and application rates of pesticides used on rice fields. Flow variables obtained from California Department of Water Resources included flow in the Sacramento River, export flow rates, and calculated net delta outflow (i.e., freshwater flow into the estuary). A related variable used extensively in these analyses is the mean position of the 2 pss near-bottom isohaline in kilometers from the mouth of the estuary (X_2; Jassby et al. 1995). X_2 is a useful integrator of flow conditions over a time scale of weeks, and provides a geographic context in that many estuarine species are abundant near 2 pss (Kimmerer and Orsi 1996; Kimmerer et al. 1998; this paper). X_2 has also been used in setting standards for freshwater flow into the estuary for the protection of aquatic resources (Jassby et al. 1995). X_2 was determined for 1968–1992 by interpolation between fixed salinity monitoring stations, and for other years by a lagged regression with net delta outflow (Jassby et al. 1995). Temperature was obtained from a continuous-monitoring station at Rio Vista (Fig. 1) from 1983–1995; data from 1972 to 1982 were obtained from the IEP zooplankton monitoring sample set, corrected upward by the mean difference of 0.6°C;

the corrected and measured temperatures were closely correlated where they overlapped (r = 0.95, 91 df for monthly mean values).

Numerous issues related to toxic contaminants in the San Francisco Estuary exist, but in only two cases have contaminants been linked to population-level effects on striped bass. Egg resorption in females was weakly related to tissue concentrations of petroleum hydrocarbons (Whipple et al. 1981; Knudsen and Urquhart 1988). We have no data to assess time trends in this factor. Pesticides applied to rice fields in the Sacramento Valley have been linked to high mortality in bioassays (Finlayson and Faggella 1986) and liver damage in larval striped bass (Bennett et al. 1995); application rates of rice pesticides increased substantially in the late 1970s (see Results). A previous analysis claimed to show a relationship between an index of pesticide concentration in the rivers and the abundance of young striped bass (Bailey et al. 1994). Pesticides are applied to rice fields in early spring, held on the fields for a period of time, and discharged into the river. Annual application rates of chemicals used in rice cultivation were obtained from the California Department of Pesticide Regulation. Following Bailey et al. (1994), we calculated estimated instream concentrations (EIC) by dividing application rates by the mean Sacramento River flow in May measured at U.S. Geological Survey gages. These variables were used in analyses of early survival, because early life stages are most exposed, and there is evidence that pesticides can cause abnormalities in striped bass larvae (Bennett et al. 1995). Pesticide concentrations, which have not been measured routinely in the rivers or estuary, declined following a change in rice-field management practices, after which the level of abnormalities in young striped bass decreased (Lee et al. 1993).

STRIPED BASS VARIABLES

Variables for striped bass (Table 1) included both estimates of abundance and indices, which are assumed to be proportional to actual abundance, for eggs, larvae, juveniles, and recruits (age 3 yr). Survival estimates or indices were calculated as ratios of abundance estimates or indices between successive stages, or as slopes of abundance with time or length.

Variables for adult striped bass included Petersen mark-recapture estimates of annual adult abundance by age, which included recruitment defined as abundance at age 3 yr (Stevens et al. 1985; Kimmerer et al. 2000). Petersen estimates were obtained through tagging of fish captured by fyke traps and gill nets during spawning migrations and recaptured either in creel surveys or during subsequent spawning migrations. Methods have remained consistent throughout the period reported here except that gill-netting effort was reduced in 1977–1978, the fyke net sites were moved in 1990, and creel surveys before 1988 were conducted from mid-June to mid-December, and all year starting in 1988. A party-boat recruitment index was calculated as the difference between annual catch per unit effort (CPUE) from reports by a recreational party-boat fishery, and CPUE during the previous year multiplied by the mean survival of adult striped bass (Stevens 1977).

Potential egg production was calculated for each year from the Petersen estimates of abundance of female striped bass multiplied by age-specific fecundity estimates and corrected for maturity and proportion migrating to the spawning grounds as described by Kimmerer et al. (2000). Potential egg production values with and without the maturity correction were closely correlated r = 0.997, 24 df).

Abundance data for eggs and larvae were taken from surveys performed every 2–4 d during and after the spawning season using 10-min oblique tows with a 0.4-m^2 mouth area, 505-μm mesh net. Before 1975 a 930-μm mesh net was used, and data were corrected using size-specific ratios determined with paired tows of the two nets (CDFG 1987, see below). We used abundance of eggs and larvae in 1-mm intervals from 6 to 14 mm, calculated for each survey as the catch per volume at each station times the volume represented by that station, then summed across surveys. Egg abundance data were available for 10 yr during 1968–1993, and larval abundance data for all length classes for 14 yr. Eggs are large enough (> 3 mm) to be unaffected by the change in net mesh size, but abundance of smaller larvae may have been biased before 1975 by the correction for differences in net efficiency. We used abundance of larvae at 6-mm length in several survival indices (below). To account for the potential bias identified above we calculated an alternative abundance estimate for 6-mm larvae as the predicted value at 6 mm of a regression of log abundance on length for each year. Results using the two alternative estimates of 6-mm abundance were very similar, suggesting that the bias in abundance of small larvae did not materially affect our results.

Abundance data for juvenile striped bass were obtained from surveys conducted by CDFG. The summer tow-net survey is used to obtain a YOY index of abundance at 38 mm mean length (Turner and Chadwick 1972), based on 2 to 5 surveys conducted during 1959–1995 (except 1966) at approximately 2-wk intervals starting in June. No substantive changes have been made to this program.

TABLE 1. Striped bass abundance and mortality variables used in the analysis. Indices refer to unitless values believed to be proportional to population size. Abundance refers to an estimate of total population size, although some of these estimates are based on unknown, but assumed, sampling efficiencies. Items 1–9 are abundance indices or estimates derived from field data; the remainder were calculated.

	Variable Name	Frequency	Source	Estimate
1	Adult abundance by age	Annual	Tagging survey	Petersen mark-recapture estimates by age and sex or aggregated; includes recruitment as abundance at age 3 yr
2	Recruitment index	Annual	Party-boat catch data	Interannual change in CPUE for the party-boat fishery adjusted by average annual mortality
3	Potential egg production	Annual	1 and fecundity data	Sum of age-specific fecundity times abundance
4	Egg and larva abundance	Every 2–4 d	Egg and larval survey	Abundance of eggs and of larvae in 1-mm size intervals
5	6-mm larval abundance index	Annual	Egg and larval survey	Larval abundance in 6-mm length class, summed over stations; alternatively calculated as predicted value at 6 mm from regression of abundance on length
6	YOY Index	Annual	Summer tow-net survey	Index of abundance interpolated to mean length of 38 mm
7	YOY abundance	Variable	Summer tow-net survey	Sum of catch/volume times volume weighting factor
8	MWT Index	Annual	Fall midwater trawl survey	Sum of catch times volume weighting factor
9	MWT abundance	Monthly	Fall midwater trawl survey	Sum of catch/volume times volume weighting factor
10	Median position	Survey	Summer and fall surveys	Median position of the young striped bass population as river kilometer
11	Larval mortality rate	Annual	Item 4	Slope of log of larval abundance versus length in mm
12	Egg-to-YOY and egg-to-MWT survival indices	Interval	Items 3 and 6 or 8	Ratio of YOY or MWT, respectively, to potential egg production
13	Egg-to-6 mm survival index	Interval	Items 3 and 4	Ratio of 6-mm abundance index to potential egg production
14	6 mm-to-YOY survival index	Interval	Items 4 and 6	Ratio of YOY index to 6-mm abundance index
15	Young striped bass apparent mortality rate	Annual	Kimmerer et al. (2000)	Estimated mortality rates from declining abundance between 1 mo and 8–12 mo of age from 3 sets of data
16	Proportion transported by numbers	June–December	Export flow rate, field abundance estimates	Estimated monthly flux of fish to export facilities, divided by estimated population size (Eqs. 1 and 2)
17	Proportion transported by biomass	June–December	From item 16 and estimated weight	Estimated monthly biomass flux of fish to export facilities, divided by estimated population biomass
18	Proportion lost by biomass	June–December	From item 17 and proportion salvaged	Entrainment transport by biomass times proportion not successfully salvaged

The median number of stations used was 27. The YOY index was not calculated in 1983, when high flow moved the striped bass population downstream of the sampled area. In 1995, flow was nearly as high as in 1983 and the mean length of captured fish never reached 38 mm, so we estimated the index for 1995 as the prediction of a regression of the YOY index in previous years on the catch of striped bass in the last two tow-net surveys of each year. Estimates of abundance were determined by dividing raw catches by estimates of volume sampled and weighting the resulting abundance values by habitat volume represented by each station (Kimmerer et al. 2000).

The fall midwater trawl survey (MWT; see Moyle et al. 1992) has been used to calculate an index of abundance for 1967–1995 (except 1974 and 1979) based on monthly surveys at 88 stations (median). Abundance estimates were determined as for the summer tow-net index above.

Several additional variables were calculated for young striped bass (Table 1). Larval mortality (mm^{-1}) was estimated as the slope of a regression of the natural log of larval abundance on larval length for each year. Indices of survival from egg to YOY, egg to 6-mm larvae, and 6-mm larvae to YOY were calculated as ratios of the respective indices or estimates. Apparent mortality rates of young striped bass were calculated as described by Kimmerer et al. (2000) for the combined summer tow-net and fall midwater trawl surveys, and separately for midwater trawl and otter trawl sample data from San Pablo Bay eastward taken by the San Francisco Bay study since 1980 (Armor and Herrgesell 1985). The San Francisco Bay study included 19 stations within the region in our analysis, but 3 stations were added in 1988 and 4 stations in 1990. We also calculated median position of the striped bass population in terms of distance up the axis of the estuary from the summer tow-net and fall midwater trawl survey data. Length-frequency distributions for juvenile striped bass were determined by aggregating length data from the San Francisco Bay study for all stations within major regions of the estuary.

Striped bass and other fish are salvaged at fish-collection facilities at state and federal export pumping plants in the southern delta (Fig. 1; Brown et al. 1996). In general, fish larger than about 20–30 mm are retained by fish screens, collected, and periodically loaded into tanker trucks and released into the western delta. During collection and transport striped bass suffer mortality due to handling, and they may also be consumed by predators in the waterways leading to the pumping plants, particularly at the state facility (Brown et al. 1996). Three estimates were made of losses during June–December due to entrainment in these facilities. One estimate of the proportion of fish transported to the pumping facilities was calculated over the 7-mo period from June through December. Estimates of proportion transported by numbers were calculated for each survey as:

$$PT_{surv} = \frac{Q_{exp} \times A_{sd}}{N_{tot}} \tag{1}$$

where Q_{exp} is export flow rate in $m^3\ d^{-1}$, A_{sd} is abundance m^{-3} from the summer tow-net and fall midwater trawl samples in the southern delta closest to the pumping facilities, and N_{tot} is the estimated total population size from the same surveys. The survey values were averaged where needed within each month, and seasonal transport was calculated as:

$$PT_{seas} = 1 - \prod_{seas} (1 - PT_{surv}) \tag{2}$$

where PT_{seas} is the seasonal value of proportion transported, i.e., the estimated total proportion of the population transported to the export facilities during June to December. The second estimate of losses, proportion transported by biomass, was calculated as in Eq. 1 multiplied by the ratio of median weight in the export facilities to that in the population, using the length-weight relationship in Rose et al. (1993), then multiplied out as in Eq. 2. The underlying assumption is that larger fish have a greater probability of contributing to recruitment, so the smaller fish are discounted based on their estimated weight. The third estimate of losses, proportion lost by biomass, is an estimate of actual losses after salvage, calculated as in Eq. 2 above except that the monthly transport rate was first multiplied by screening efficiency by size class (Skinner 1973) and median survival during trucking and handling (Raquel 1989). This represents our best estimate of the biomass of striped bass >20 mm length removed from the population during this period. Losses of smaller striped bass are not quantified, and must be inferred from export flow rates.

STATISTICAL ANALYSES

Results are presented here from a variety of regression analyses using independent variables either selected to match previously reported analyses or based on aspects of striped bass life history. We re-examined the relationship of freshwater flow to the recruitment index as in Stevens (1977), extending the time period and also using the Peterson estimate of abundance at age 3 yr as an alternative to the recruitment index. We examined time trends and flow influences in potential egg production, egg abundance, and mortality of striped bass larvae. Several survival indices for early life were examined for relationships with flow variables (Table 2). We also examined the position of the young striped bass population in summer and fall as a function of X_2, and the spread of the population as the inter-quartile range of abundance-weighted position in kilometers up the axis of the estuary, to determine whether the population was more geographically dispersed under high-flow versus low-flow conditions.

We used an adjusted export flow variable as a predictor variable in analyses of egg-to-YOY survival. Previous analyses had revealed a strong dependence of egg-to-YOY survival index on freshwater flow or X_2 and export flow (Stevens et al. 1985; CDFG 1987; Jassby et al. 1995). Export flow is related nonlinearly to X_2, but with no underlying model for the relationship (see below). We fit a natural spline with 2 degrees of freedom (Venables and Ripley 1997) to the relationship between X_2 and export flow, assuming only that the underlying function is smooth. The residuals from the spline

TABLE 2. Regression statistics for various models for young striped bass variables. (1) is for export flow rate ($m^3 s^{-1}$) versus natural spline in X_2 (2 degrees of freedom); (2) log egg-to-YOY survival index versus X_2 and the residual from the export flow-X_2 relationship in (1); (3) has 1994 eliminated; (4) log egg-to-MWT survival index versus X_2; (5) log egg-to-YOY survival index versus X_2 for years with 6-mm larval data; (6) log egg-to-6 mm survival index; (7) and (8) log 6 mm-to-YOY survival index versus export flow in two different time periods; robust regression.

	Dependent Variable	df	Independent Variable	Slope	95% Conf. Interval	p	r^2
1	Export flow	22	X_2 (April–June)	—	—	0.017	0.25
2	Log egg-to-YOY survival index	22	X_2	−0.027	0.0109	< 0.0001	0.59
			Residual from (1)	−0.0038	0.0029	0.012	
3	Log egg-to-YOY survival index	21	X_2	−0.029	0.0109	< 0.0001	0.59
4	Log egg-to-MWT survival index	22	X_2	−0.023	0.014	0.003	0.33
5	Log egg-to-YOY survival index	12	X_2	−0.032	0.016	0.0016	0.58
6	Log-egg-to-6 mm survival index	12	X_2	−0.032	0.014	0.0003	0.67
7	Log 6 mm-to-YOY survival index	12	Export Flow (April–June)	−0.0046	0.0042	0.03	0.37
8	Log 6 mm-to-YOY survival index	12	Export Flow (May–June)	−0.0028	0.0045	0.20	—

curve were then used as a measure of export flow that was independent of X_2, allowing for clear interpretation of results.

All analyses were conducted after graphical exploratory analyses (Cleveland 1993) using the S-Plus statistical language (Venables and Ripley 1997). Regressions were by ordinary least squares if the data met assumptions of normality, homoscedasticity, and lack of autocorrelation in residuals, and were not unduly influenced by single points. These assumptions were tested by examining various diagnostic plots. None of the models reported here contained significant autocorrelation in the residuals. When the other assumptions of linear regression were not met, we used a robust linear model procedure (function rlm, Venables and Ripley 1997) or a generalized linear model with variance increasing in proportion to the mean squared. In cases requiring regressions of two variables both measured with substantial error we applied geometric mean regression (Ricker 1973), under the assumption that errors in both variables were of similar relative magnitude (see Prairie et al. 1995). In a few instances we used tree regression (Venables and Ripley 1997) to separate time series data into two segments, which were then fitted to step functions for statistical evaluation.

LIFE CYCLE MODEL ANALYSES

We used the results of this study and our previous work (Kimmerer et al. 2000) to construct a simple Monte Carlo life cycle model to explore alternative mechanisms for the decline in striped bass abundance. The main purpose of the model was to investigate major intervals in the life cycle to assess their potential for producing the observed pattern of decline in abundance of various life stages.

The life cycle model consisted of a series of five equations describing egg production and survival over 4 intervals for which analysis revealed some uncertainty about the influence of environmental effects on the life cycle, and for which data were adequate. These life-history intervals were from egg to 6-mm larva, egg to YOY, and YOY to recruit (age 3), and throughout adult life. We did not consider larva-YOY because of the smaller amount of data for larval abundance than for eggs or YOY. Although the intervals from egg to 6-mm larva and egg to YOY overlap partially, we included both because they were based on different field samples and might be expected to vary somewhat in response; survival from egg to 6-mm larva was used only to predict larval abundance, not to provide input to the next life stage in the model.

Each equation had the form:

$$X_{i,t_i} = f_i(X_{i-1,t_{i-1}}) \pm SD_i \qquad (3)$$

where the X values are abundance indices or estimates, in some cases log-transformed, for life stage i at time t_i. The functions f could be either functions linking the two X values, survival indices, or age-specific fecundity estimates in the case of adult stages. The SD_i were either standard deviations of residuals from regressions, or of single parameter estimates, in both cases calculated from the data.

For each run the model was initialized using the observed age-specific abundance from 1969. Potential egg production was then calculated using the estimates of age-specific fecundity with associated standard deviations. Abundance of 6-mm larvae and the YOY index were then calculated using one of several alternative algorithms (the f in Eq. 3). Recruitment was then calculated from YOY, after which adult age classes were advanced after mortality had been applied. This process was repeated for the duration of the data.

In all cases the f functions were determined by analysis of the available data, and several of these functions had alternative formulations (Table 3).

TABLE 3. Summary of alternative formulations for the life cycle model. Alternatives used in the base run are listed in **bold.** Error terms, either standard deviations of the data or of the residuals from regressions, establish the scatter used in repeated simulations. ResidExp in 2C refers to the residual export flow used in the regression model in Fig. 7b and Table 2 items 1–2.

	Functional Relationship	Alternative
1	Egg-to-6 mm survival index	**A Log S = (6.18 − 0.032 X_2) ± 0.22**
2	Egg-to-YOY survival index	A Log S = −0.77 ± 0.40
		B Log S = (1.3 − 0.029 X_2) ± 0.25
		C Log S = (1.18 − 0.027 X_2 − 0.0036 ResidExp) ± 0.26
3	Recruitment as a function of YOY	A Recruits = (0.018 × YOY) ± 0.30 (in millions)
		B Beverton-Holt function, constant carrying capacity (Eq. 4): b1 = 0.25, b2 = 0, a = 8.07, predicted value ± 0.25
		C Beverton-Holt function, declining carrying capacity (Eq. 4): b1 = 2.69, b2 = −0.022, a = 8.07, predicted value ± 0.22
4	Adult annual mortality	A Mean from combined data in Kimmerer et al. 2000 (Fig. 3) for years 1970–1994: M = 0.70 ± 0.17
		B Linear increase from Kimmerer et al. 2000 (Fig. 3) for years 1970–1994: M = (−0.36 + 0.013 Year) ± 0.17
		C Step increase from Kimmerer et al. (2000, Fig. 3): M = (0.59, Year ≤ 1970; 0.78, Year > 1970) ± 0.13

These were either constants or functions developed here or in Kimmerer et al. (2000). The appropriate error term SD_i was used to generate normally-distributed errors that were truncated to match the range of the observed error distributions. For the relationship of YOY to recruitment we used the Beverton-Holt relationship developed by Kimmerer et al. (2000). To reflect the decline in carrying capacity evident in the data from that relationship (Kimmerer et al. 2000, Fig. 5b) we took the original Beverton-Holt equation and modified it to include a carrying capacity declining over time:

$$\text{Recruits} = \frac{(\text{b1} - \text{b2 YearClass})\text{YOY}}{\text{a} + \text{YOY}} \tag{4}$$

where YearClass is the calendar year of hatching (e.g., 67 for 1967), b1 and b2 were fit by nonlinear least squares, and a was a constant 8.07 (from Table 3 in Kimmerer et al. 2000).

We conducted 100 simulations of each of the 27 combinations of alternatives in Table 3 for the 26 years from 1969 to1994. We then narrowed the results down to a base run and a series of deviations from the base run. The base run was chosen as most representative of conclusions from analyses here and in Kimmerer et al. (2000). It included egg-to-YOY survival based on X_2 but not export flow, recruitment according to a Beverton-Holt function with a declining carrying capacity, and a step increase in adult mortality. Model results were compared on the basis of mean square deviations from the 26 yr of annual data, and the base run had the lowest grand mean. Data used for comparison included potential egg production, 6-mm larval abundance (n = 14 yr), YOY index, and recruitment.

Results

Flow in the Sacramento River and net delta outflow in April–June were highly variable, including drought periods in 1976–1977 and 1985–1992 and heavy floods in 1982–1983 and 1995 (Fig. 3a). X_2 was farthest landward during droughts and farthest seaward during floods (Fig. 3b). Export flow increased until the mid-1970s as additional pumping capacity was brought on line (Fig. 3c). Export pumping since 1972 has been high except during some drought years (because water is unavailable for export) and high-flow periods (because demand is reduced). Temperature averaged 17°C during April–June of 1972–1995, with minima and maxima averaging 15.5°C and 18°C, respectively (Fig. 3d). None of these variables had significant trends over the time period for which most of the striped bass data are available, i.e., 1967–1995.

Recruitment at age 3 yr, previously shown to depend on freshwater flow during the first spring (Stevens 1977), had no relationship with flow in the more recent data. The party-boat recruitment index of year-class strength for year-classes 1956–1971 was positively related to the logarithm of freshwater flow into the estuary during June and July lagged 3 yr (robust regression slope = 110 ± 59, 95% confidence interval, $p < 0.01$, 14 df). That relationship changed after 1971, with a weaker fit, spreading residuals, and the data falling below the fitted line (Fig. 4a). Using only the data from after 1971, there was no significant relationship between recruitment index and log of flow (robust slope = 7 ± 43, $p > 0.1$, 19 df) or export flow (robust slope = 25 ± 44, $p > 0.1$, 19 df). Recruitment measured as Petersen abundance estimates of 3-yr-old fish (year-classes 1966–1989) was unrelated to flow (Fig. 4b).

Potential egg production, calculated from age-

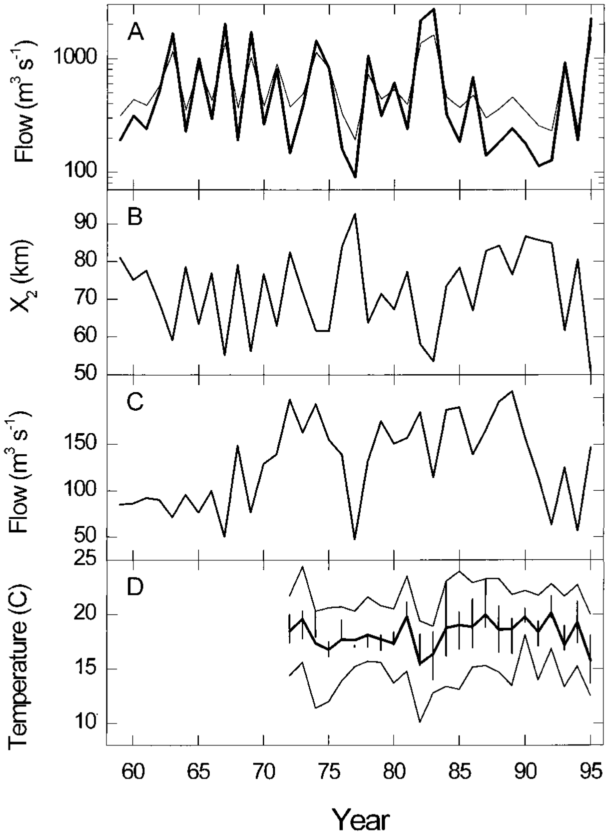

Fig. 3. Time course of key environmental variables averaged over April–June of each year: A) Freshwater outflow (heavy line) and Sacramento River flow; B) X_2, the distance up the axis of the estuary to where tidally-averaged salinity is 2 (practical salinity scale); C) Combined flow from federal and state export facilities; D) temperature at Rio Vista on the lower Sacramento River (Fig. 1): lines are mean, minimum, and maximum for April–June, and vertical bars are ranges for May.

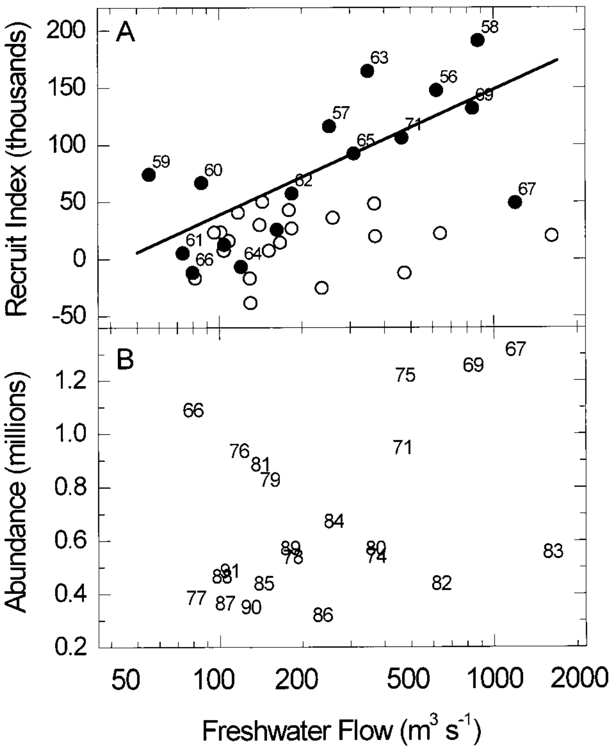

Fig. 4. Recruitment versus net delta outflow three years earlier. A) Recruitment index for 1956–1971 (solid circles) and 1972–1994 (open circles); numbers are years; solid line, prediction of robust regression model using only year-classes up to 1971. B) Petersen abundance estimate at age 3 years; numbers are years.

specific fecundity and abundance, declined sharply in the late 1970s, primarily because of declines in the abundance of larger adults (Fig. 5a). Although confidence limits on potential egg production were large, a regression of potential egg production on a step change in 1976–1977 explained 78% of the variance in annual means ($p < 0.0001$, 24 df) and the residuals had no time trend. Egg abundance (Fig. 5a), available for 10 yr from the egg and larval survey, was related to potential egg production but much lower: the median ratio between the two values was only 2.7% (range 1.7–8.6%), and the slope of the geometric mean regression of egg abundance on potential egg production was 0.06 ± 0.015 ($r = 0.68$, $p = 0.029$, $n = 9$). This ratio was unrelated to flow conditions in the river or in the estuary, and did not have a significant time trend, although the lowest values occurred in the last four surveys, in 1990–1993 (Fig. 5a). Abundance of young fish in the summer tow-net survey and fall midwater trawl survey showed the influence of reduced potential egg production after 1976–1977 (Fig. 5b).

Larval mortality rates, estimated as rate of decline of larval abundance with length, did not have a trend through years, although mortality was generally higher during the 1980s than earlier or later (Fig. 6a, $p > 0.1$, linear regression, 13 df). Larval mortality rate was unrelated to X_2 ($p > 0.7$). Abundance of 6-mm larvae declined over time (Fig. 6b) and declined with increasing X_2. Tree regression showed that a step occurring in 1976 effectively split the 6-mm abundance data into two groups. A linear regression with this step and X_2 as independent variables and 6-mm larval abundance as the response variable was highly significant (Fig. 6b) with significant coefficients for both independent variables: -0.025 ± 0.013 for X_2 and -0.46 ± 0.27 for the step change (with 95% confidence intervals, 12 df). This relationship has few degrees of freedom for the number of independent variables, but the prediction mean square error (determined by predicting each data point from the relationship not including that point) was 0.27, only slight-

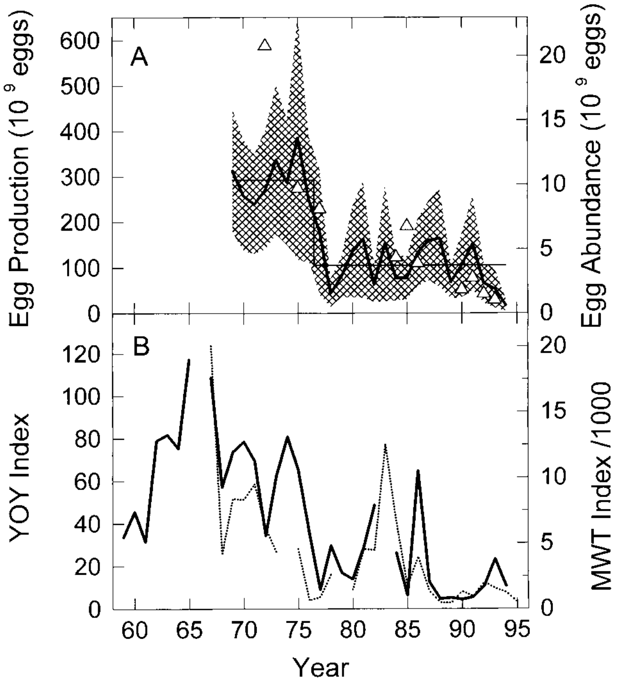

Fig. 5. Time course of abundance of early life stages. A) Two estimates of egg production: potential egg production as estimated by the Petersen mark-recapture estimate and age-specific fecundity (heavy line), with 90% confidence limits (shaded), and egg abundance estimates (triangles, right axis, scaled by the mean ratio of egg abundance to potential egg production). The thin line is a step function fit to the potential egg production data. B) YOY (solid line) and MWT (dashed line) indices of young striped bass abundance.

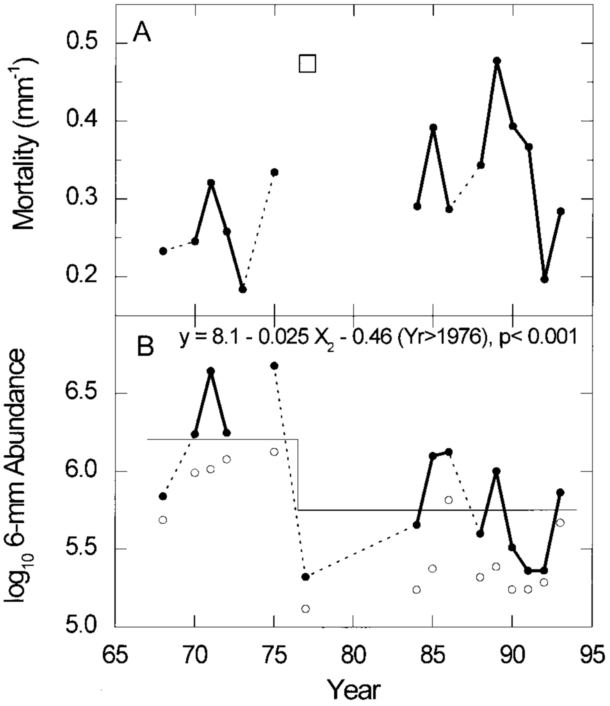

Fig. 6. Striped bass larval abundance and survival. A) Larval mortality plotted against year; the open square indicates data from 1977 which were available only from 6–9 mm; B) Log_{10} 6-mm larval abundance plotted against year: solid circles and lines, measured values; open circles, values calculated from annual regressions of log abundance on length. The thin solid line indicates a step regression with the mean value of X_2 (75.2 km) inserted in the equation shown.

ly larger than the variance of the residuals from the linear regression using all data (0.21). The same regression with log larval abundance predicted by regression of log abundance versus length (open circles in Fig. 6b) gave similar results, with coefficients of -0.016 ± 0.008 for X_2 and -0.50 ± 0.17 for the step change. These alternative estimates were highly correlated ($r = 0.89$, 12 df). These comparisons give us confidence that the step change in Fig. 6b is a robust description of the underlying variability in abundance of early larvae.

The egg-to-YOY survival index, encompassing roughly the first month of life, was related to both X_2 and export flow. Export flow in April through July had a significant curvilinear relationship with X_2 (Fig. 7a, Table 2 item 1), mainly because export flow was lower in several drought years and in several years of higher than normal flow (low X_2). The residuals from that relationship, together with X_2, were used as independent variables in a linear regression with log of survival index as the response variable. This regression explained 59% of the variance (Fig. 7b, Table 2 item 2). Neither the egg-to-YOY survival index nor the residuals from the regression of log survival index on residual export flow and X_2 had a significant time trend (Fig. 7c,d). The data point for 1994 had excessive influence on the regression, and when that point was removed, the term for export flow was no longer significant and the regression with X_2 alone explained 59% of the variance in log survival index (Table 2 item 3).

Alternative analyses to those in the previous paragraph were attempted to ensure that evidence for export flow effects was not being overlooked. An analysis similar to that in Table 2 (items 1 and 2) was performed using the log of total freshwater flow into the delta instead of X_2 as the predictor variable for export flow. In that case, the residual of export flow was not a significant contributor to the egg-to-YOY survival index (linear regression, 22 df, slope $= -0.28 \pm 0.41$, $p > 0.1$), and only X_2 contributed to the regression (23 df, slope $= -0.026 \pm 0.006$, $p = 0.0003$). Second, the log of egg-to-MWT survival index was related only to X_2 with no export effect (Table 2 item 4). None of the survival indices for young striped bass was sig-

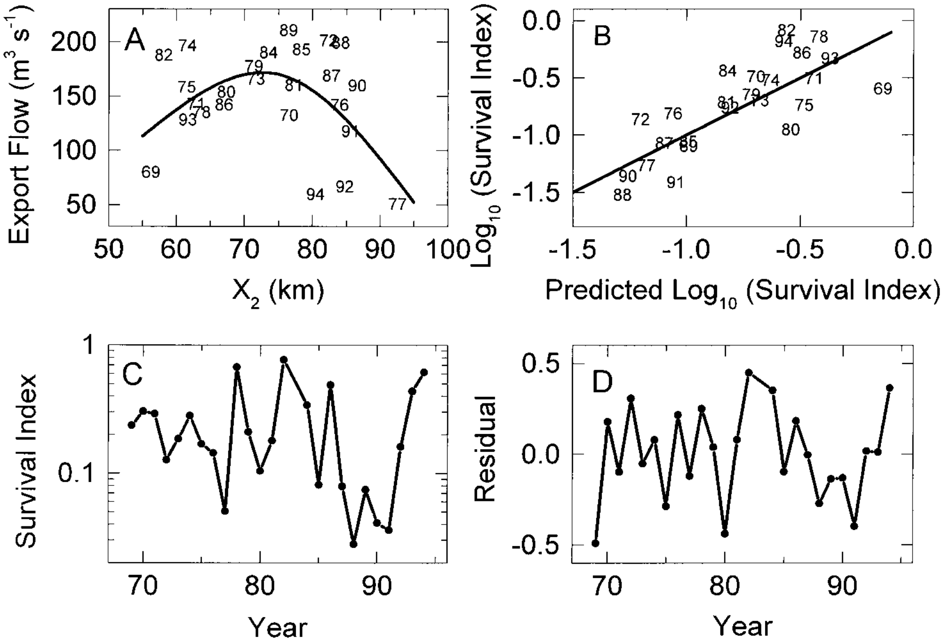

Fig. 7. Egg-to-YOY survival index. A) Relationship of X_2 to export flow in April–June fitted with natural spline with two degrees of freedom (Table 2 item 1); numbers are years; B) Predicted versus observed log survival index for the model in Table 2 item 2; numbers are years; C) Time trend of survival index; D) Time trend of the residual from B.

nificantly related with temperature, nor were residuals from the above relationships related to temperature (linear regression, $p > 0.1$ and by inspection).

Effects of freshwater flow apparently occurred early in the egg-to-YOY interval. The egg-to-6 mm survival index and the egg-to-YOY survival index had nearly identical relationships to X_2 when the same set of years was included (Table 2 items 5 and 6). Plots of egg-to-6 mm survival index suggested no effect of export flow. Log 6 mm-to-YOY survival index was unrelated to X_2 but had a significant but weak negative relationship with export flow rate in April to June, although not in May to June (robust regression, Table 2 items 7 and 8).

Pesticide application rates increased in the late 1970s to early 1980s, roughly coincident with the decline in YOY index (Fig. 8a), and the EIC of molinate was correlated with the YOY index (Bailey et al. 1994). EIC of molinate was uncorrelated with log of egg-to-YOY survival index (Fig. 8b; $r = -0.2$, $p \sim 0.3$, Pearson correlation). Application rates and EIC of other rice chemicals had lower correlations with the log of egg-to-YOY survival index than those for molinate.

Median positions of young striped bass expressed as river kilometer were closely related to X_2 (Fig. 9). Under low-flow conditions the striped bass distribution reached well into the delta (river kilometer 81). The distribution of striped bass in the fall midwater trawl survey was further seaward than their distribution in the summer tow-net survey, although part of the difference could be attributed to a more seaward sampling effort in the fall survey. For both surveys combined, the log of the ratio of monthly mean abundance at sampling stations near the export facilities to monthly mean population size was positively related with X_2 (slope = 0.014 ± 0.009, 95% CL, 137 df). The proportion of the young striped bass population entrained in the export facilities was related to proximity of the population to the facilities and therefore indirectly to freshwater flow. The longitudinal spread of the population, as measured by the interquartile range of position in the same surveys as in Fig. 9, was unrelated to X_2 for the summer tow-net survey ($p > 0.2$, 129 df), and had a weak but significant positive relationship for the fall midwater trawl survey (slope = 0.35 ± 0.21, 95% CL, $p < 0.001$, 95 df). These results indicate that the population was more spread out when it was concentrated in the delta than when it was further seaward.

The three measures of losses of juvenile striped bass to delta export pumping facilities (Table 1 items 16–18) were unrelated to apparent mortality rates during the summer-fall (Fig. 10). The estimated proportion of fish transported to the two export facilities during June through December varied with flow conditions and was as high as 99%

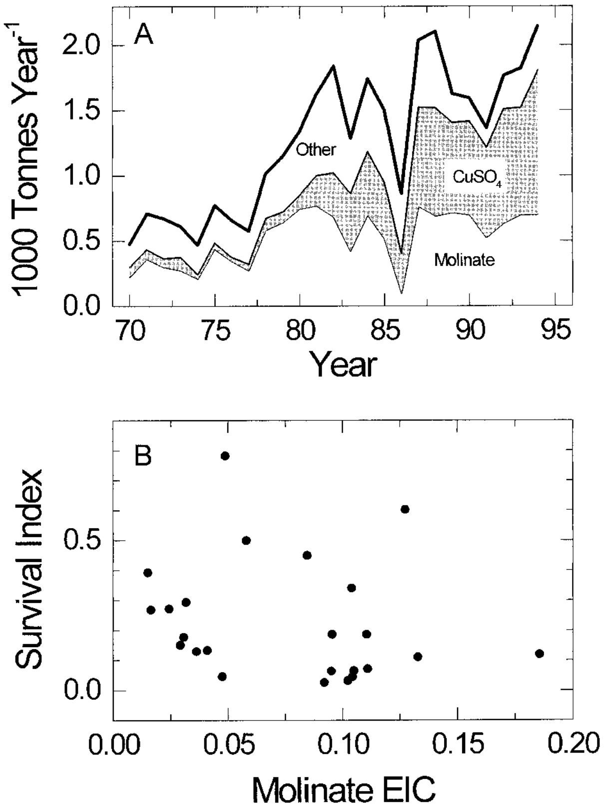

Fig. 8. Data on application rates of chemicals to rice fields and their relation to striped bass YOY index. A) Application rates of pesticides and herbicides plotted as cumulative tons yr^{-1} for molinate, copper sulfate, and all other chemicals; B) Egg-to-YOY survival index versus EIC of molinate.

(Fig. 10a). The proportion transported by biomass was somewhat lower (Fig. 10b) because the fish exposed to export pumping were smaller (median length) than those in the population as a whole. The proportion lost by biomass (i.e., the proportion not salvaged and returned to the estuary) had a median value of 33% and ranged from 4% to 95% (Fig. 10c). Correlations between these export losses and apparent mortality rates from three young striped bass sampling programs (combined summer-fall surveys, San Francisco Bay study midwater trawl and otter trawl; Kimmerer et al. 2000) were negative (Fig. 10a–d, Table 4). Two of the three export loss estimates were positively related to X_2 (generalized linear model with variance increasing with mean squared; 21 df, $p = 0.026$, 0.007, and 0.10 corresponding to Fig. 10a–c). This indicates that young striped bass were more vulnerable to export pumping when the salt field, and therefore the striped bass population, was upstream, and is therefore consistent with the interpretation of Fig. 9.

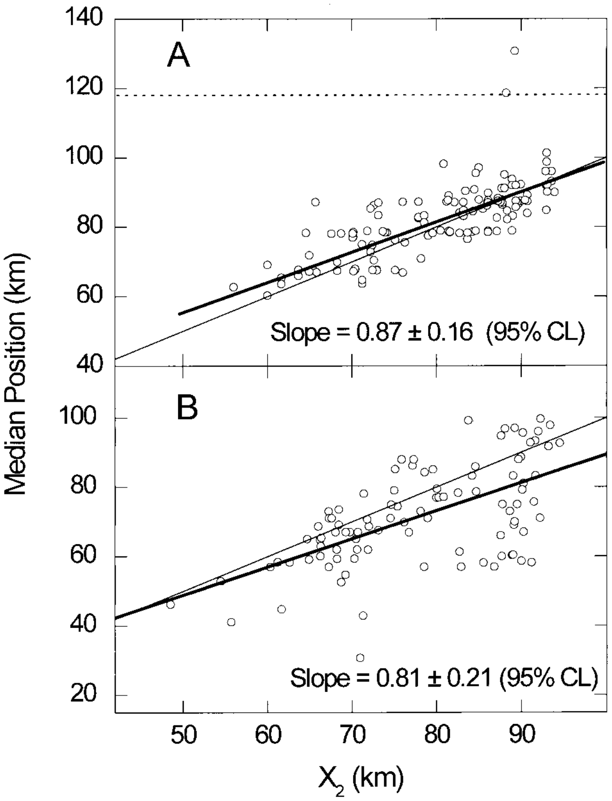

Fig. 9. Median position of young striped bass in river kilometer for each survey plotted against mean X_2 for each month: A) Summer tow-net survey; B) Fall midwater trawl survey. Heavy line, significant ($p < 0.001$) linear regressions; thin line, 1:1 line. Y axes are scaled to encompass approximately the range of the sampling stations in each survey. Horizontal dashed line indicates the position in river kilometer of the junction of Old River and the San Joaquin River (Fig. 1), where vulnerability to export pumps probably increases.

LIFE CYCLE MODEL ANALYSES

All model runs showed declining abundance in all life stages over the 26 yr of the modeled period, as demonstrated in the example runs (Fig. 11), although the patterns of the decline differed sharply among the various alternative model formulations. The base run, using the functions represented in bold in Table 4, gave the best fit overall, while mean square errors from the other runs were slightly to substantially larger.

The results of 7 sets of model runs, incorporating all alternative model formulations, are summarized in Fig. 12. The base run and the run with constant carrying capacity in the Beverton-Holt relationship were indistinguishable, except that recruitment had a slightly greater mean square error with constant carrying capacity than in the base run (Fig. 12a). Eliminating density dependence resulted in large deviations from the data in recruitment (Fig. 12a) and in potential egg production

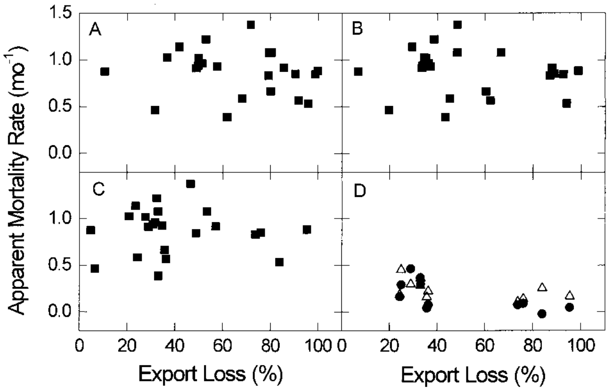

Fig. 10. Relationships between measures of transport and loss to export facilities and apparent mortality rates of young striped bass (Kimmerer et al. 2000). A) Proportion transported by numbers of young striped bass (Table 1 item 16) versus apparent mortality rate in combined summer-fall surveys; B) as in A for proportion transported by biomass (Table 1 item 17); C) as in B for proportion lost by biomass (Table 1 item 18); D) as in A except the y values are apparent mortality rates using data from the San Francisco Bay Study midwater trawl (solid circles) and otter trawl (open triangles).

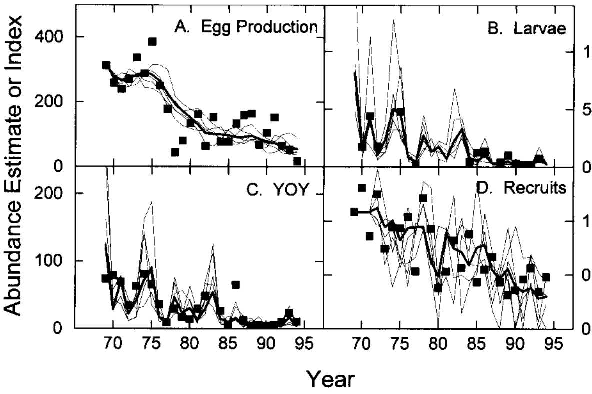

Fig. 11. Example model runs for effects of selected mortality factors for the base model run (Table 3). Squares, original data; thin lines, results of single model runs; heavy lines, median values from 100 model runs. A) Potential egg production; B) Abundance of 6-mm larvae; C) YOY index; and D) Recruitment as abundance at age 3 yr.

(Fig. 12b). Model runs with constant or steadily-increasing adult mortality generated larger mean square errors than obtained in the base run because these runs failed to replicate the high potential egg production in the mid-1970s followed by the sharp drop observed in the data. These errors propagated forward into larval abundance (Fig. 12c) and to some extent into the YOY stage (Fig. 12d). Either including exports in the egg-to-YOY model (as in Fig. 7b) or eliminating all environmental influences on the egg-to-YOY survival index resulted in greater error in the YOY, but had almost no effect on the other life stages (Fig. 12d).

Discussion

This study demonstrates the value of long-term, comprehensive, consistent ecological monitoring. In the Hudson River estuary (Pace et al. 1993), patterns of striped bass abundance were weakly related among stages and to environmental conditions. We believe that the strong relationships between environmental conditions and striped bass survival in the San Francisco Estuary result from the duration, breadth, and intensity of monitoring, as well as from the large variations in flow and striped bass abundance providing a high signal-to-noise ratio. Two to three decades of intense monitoring on multiple life stages appear to be required to allow the dissection of the complex web of causal linkages between striped bass and their environment.

In the Chesapeake Bay (Secor and Houde 1995; Rutherford et al. 1997), survival of larval striped bass appeared to be related to food supply and temperature, and larval abundance was a good predictor of the juvenile index, which is roughly comparable to our YOY index. We found a good correspondence between the flow responses of egg-to-6 mm and egg-to-YOY survival indices. None of the measures of early survival was related to temperature, possibly because temperatures during larval development (Fig. 3d) were within the range of minimum larval mortality reported by Secor and Houde (1995).

We distinguish between two modes of variability in striped bass abundance: interannual variability related to environmental conditions, and the observed long-term decline. We can separate these modes based on the detection of long-term trends.

TABLE 4. Effects of export losses during June to December (Table 1 items 17 and 18) on apparent mortality (Table 1 item 15) during the same period. Values given are Pearson correlation coefficients for each pair of values with 95% confidence limits, which either include 0 or do not include any positive values. Also given are correlation coefficients between apparent mortality rates and mean abundance from Kimmerer et al. (2000), all of which have 95% confidence intervals excluding zero.

Apparent Mortality from Sampling Program	Proportion Transported by Biomass	Proportion Lost by Biomass	Mean Log_{10} Abundance
Summer–Fall (YOY)	−0.18 (0.43)	−0.06 (0.43)	0.56 (0.43)
Bay Study Midwater Trawl	−0.81 (0.68)	−0.66 (0.68)	0.72 (0.68)
Bay Study Otter Trawl	−0.71 (0.68)	−0.54 (0.68)	0.74 (0.68)

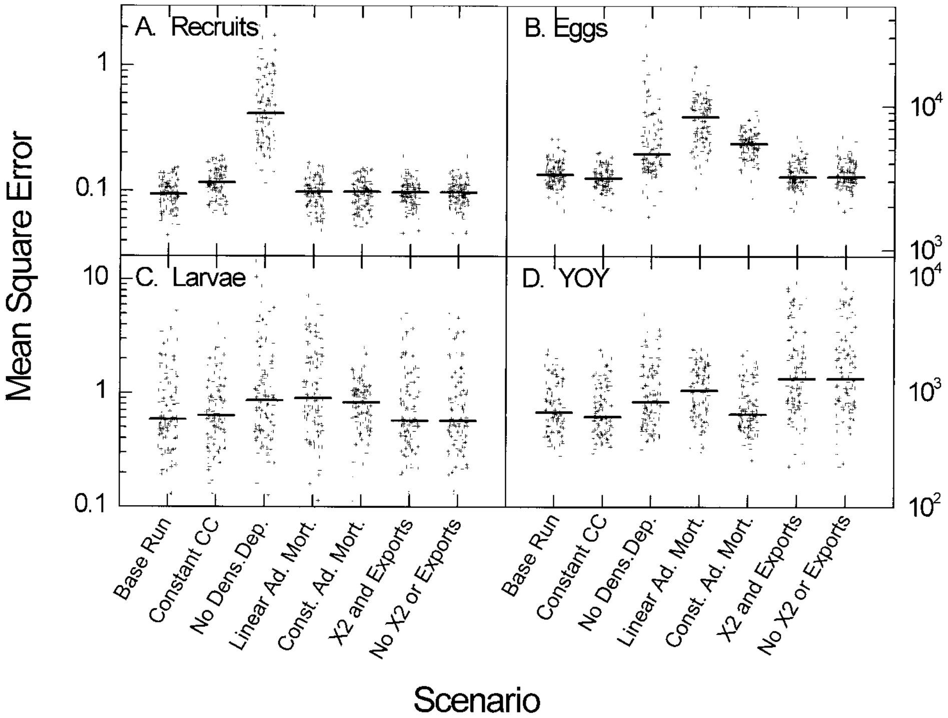

Fig. 12. Summary of results of model study of effect of selected mortality factors for life stages in Fig. 11a-d. Each point in each panel shows the mean square error for a single simulation, with median values depicted by horizontal bars. Model runs differed from the Base Run by only one of three characteristics at a time. Scenarios depicted are: Base Run (Table 3); Constant CC, with constant carrying capacity (Table 3 item 3B); No Dens. Dep., where recruitment had a constant ratio to YOY (Table 3 item 3A); Linear Ad. Mort., with linearly declining adult mortality (Table 3 item 4B); Const. Ad. Mort., constant adult mortality (Table 3 item 4A); X2 and Exports, egg-to-YOY survival with export term included (Table 3 item 2C); and No X2 or Exports, egg-to-YOY survival was by a constant ratio (Table 3 item 2A).

YOY indices provide accurate forecasts of future recruitment for striped bass populations in the Chesapeake Bay, so environmental variability early in life can strongly influence adult abundance (Polgar 1981; Goodyear 1985). Results presented here and in a previous paper (Kimmerer et al. 2000) show that little of the substantial flow-related variability in YOY propagates into variability in recruitment. We interpret these results to mean that the interannual mode of variability in YOY related to freshwater flow conditions is related only weakly, if at all, to the long-term decline in abundance.

EFFECTS OF FRESHWATER FLOW AND EXPORTS

Our conceptual model for interannual variation of survival of young striped bass with flow is as follows. High flow moves larvae rapidly down the river as they hatch, and also shifts the low-salinity rearing habitat seaward. The higher the freshwater flow, the more rapidly the larvae move to their rearing habitat, although this movement slows as the larvae encounter increasing tidal influence. Larvae reach the rearing area at about the onset of exogenous feeding (Eldridge et al. 1982) and development of the swim bladder, so rapid transport may be advantageous. In addition a seaward position of 2 pss salinity, and therefore the rearing area of young striped bass, is associated with lower exposure to export pumping at the large pumping plants and the numerous smaller agricultural diversions in the Sacramento-San Joaquin delta (but see below).

Flow-related variability in YOY index is unlikely to be an artifact of the sampling or analytical methods. As X_2 moves seaward, the center of mass of the population of young striped bass also moves (Fig. 9), moving part of the population out of the region sampled by the summer tow-net survey (Stevens et al. 1985). This could bias abundance estimates downward, but not upward, under high-flow conditions.

Jassby et al. (1995) concluded that the ratio of export flow to total river flow had a significant influence on egg-to-YOY survival that changed the response of survival to X_2. The denominator in this ratio is closely and negatively related to X_2. Using X_2 and export flow rate instead of percent exported, we also found a significant negative effect of export flow on survival; this relationship was complicated by the curvilinear relationship of X_2 to export flow (Fig. 7a) and the excessive influence of a single data point (1994), without which the effect of export flow in the relationship vanished. Although there is no justification for removing the data point for 1994, these results suggest the export effect may be sporadic.

A weak effect of export flow was detected in the 6 mm-to-YOY survival index but only if April export flow was included (Table 2 items 7 and 8). In most years larvae are absent or not abundant until May (Miller unpublished data). These results suggest that variability in export flow has a weak, possibly sporadic effect on survival over the first 1 to 2 mo of life. This is surprising given the large proportion of freshwater flow exported during summer (up to 50% of flow into the Sacramento-San Joaquin delta). This result contrasts with previous analyses (Stevens et al. 1985; CDFG 1992) and to some degree with recent studies using an individual-based model of striped bass population dynamics (Rose unpublished data).

Proportional entrainment of young striped bass at the export pumping facilities is only partially represented by export flow or by the residual export flow used in the analysis of egg-to-YOY survival (Table 2 item 2). The movement of the young striped bass population with the salt field of the estuary (Fig. 9) would vary their degree of exposure to export pumping even if export flow rate were constant. The effect of X_2 appeared during the egg-to-6 mm stage (Table 2 items 5 and 6), which encompasses a portion of the period of transport from the river to the low-salinity zone of the estuary, when the young fish might be most vulnerable to export pumping. The weak and inconsistent effect of export flow occurred after the 6-mm larval stage (Table 2 items 7 and 8), suggesting that the effects of X_2 and exports occurred through different mechanisms. The X_2 effect could also have to do with swim bladder formation, the onset of position maintenance, and the ability of the fish to find suitable food resources. An alternative possibility for the X_2 effect is that the spatial extent of physical habitat for rearing increases as X_2 moves seaward (Turner and Chadwick 1972; Jassby et al. 1995). The spread of the population in both summer and fall surveys of young striped bass did not increase as X_2 moved seaward, so it seems unlikely that the areal extent of habitat is involved in the mechanism for variation of early survival with X_2. We are unable to distinguish among the remaining possibilities with the available data.

During and after the YOY stage, apparent mortality rates (Kimmerer et al. 2000) were not positively correlated with the estimated rates of loss to the export pumps, in spite of the sometimes high values of those rates (Fig. 10; Table 4). This does not mean that losses to the export facilities are unimportant sources of mortality, but that variation in export losses does not contribute to variation in recruitment. Variation in this source of mortality could have been swamped by variation from other sources. As with other striped bass populations, the bulk of the losses of each year's potential egg production occurs within days to weeks after spawning, with much lower but still substantial mortality in the juvenile stage (Olney et al. 1991; Rose et al. 1993). Based on Fig. 7 in Rose and Cowan (1993) and striped bass length data (Kimmerer unpublished data), we estimate that total mortality from June through December averaged about 76%. By comparison, the median losses to pumping were estimated at 33%, a substantial fraction of the total mortality, and were often much higher than estimated total mortality. Variability in total mortality, and possibly also in the success of the salvage operations, may have obscured any effect of exports on subsequent recruitment of striped bass. Alternatively, the fish remaining in the tidal freshwater region of the estuary may not contribute significantly to recruitment in most years irrespective of export pumping effects. High mortality due to pumping losses may be partially offset by density-dependent effects occurring during and after the YOY stage (Kimmerer et al. 2000). These compensatory effects presumably have less effect when YOY is very low than they did in the past; recruitment of striped bass may now be sensitive to flow conditions in early life.

Stevens (1977) reported that the party-boat recruitment index during 1956–1969 was positively related to freshwater flow into the estuary during June and July 3 years earlier. This relationship has apparently deteriorated starting with the 1971 year-class, and since then has not been significant. The lack of a relationship between the Petersen estimate of abundance at age 3 and flow three years earlier suggests that this relationship did not exist for year-classes after 1966. The Petersen estimate may be more reliable than the recruitment index, as its assumptions are more realistic. The previous relationship of recruitment index to flow may have collapsed because of declining spawning stock, although changes in fishery practices also may have contributed. That relationship shows an influence of flow on early survival that existed when export pumping was considerably lower than in years since 1971, suggesting that varying exposure to export pumping is not the mechanism underlying the relationship between early survival of striped bass and X_2.

POTENTIAL CAUSES OF LONG-TERM TRENDS

Previous analyses have attempted to explain the downward trend in striped bass abundance as a result of reduced egg supply and the effects of flow and exports on young fish (Stevens et al. 1985; CDFG 1992) or contaminants (Bailey et al. 1994). Results presented here and in Kimmerer et al. (2000) support mechanisms for the decline occurring later in life, but fail to support mechanisms occurring during the larval to early juvenile stage. Failure to support these mechanisms does not rule them out, and may indicate merely that the power of the tests is low. Our results provide alternative explanations of the observed patterns that are well supported by the available data.

Despite the long-term decline in abundance of all life stages, and the increasing trend in export flows up to the early 1970s, no comparable temporal trends could be seen in survival indices for egg-to-6 mm or egg-to-YOY, or mortality of larval stages. No trend was seen in X_2, the principal explanatory variable for early survival, or in export flows after the early 1970s. Removing the effect of exports actually improved the fit of our simple model, and removing the X_2 effect had little influence on predicted recruitment or subsequent egg production. Although we are unable to rule out an early effect of exports on recruitment, no such effect is evident in the data presented here. The lack of time trend in any of these variables fails to support, but does not rule out, an influence on subsequent recruitment and on the decline. Recent individual-based modeling studies show that exports alone are unable to explain the observed decline, despite apparent negative effects of removal of tens of millions of young striped bass (Rose unpublished data).

High concentrations of contaminants could have negative effects on striped bass populations (Hall et al. 1985; Stevens et al. 1985). Contaminant effects on biological populations in the San Francisco Estuary and watershed are the subject of considerable recent and ongoing research. Although there may be such effects on striped bass, our analyses do not support the theory that rice pesticides are implicated in the population decline. Evidence of toxicity of water to striped bass in the Sacramento River and in agricultural drains based on bioassays (Finlayson and Faggella 1986; Bailey et al. 1994) and histopathology (Bennett et al. 1995) suggested individual-level effects on striped bass survival of pesticides used on rice. Extrapolation of these results to effects on the striped bass population is not supported by the available data. Effects of these chemicals would most likely occur when rice fields are drained and the fish are in the river, where they would be exposed to high concentrations of agricultural chemicals. This time coincides with reproduction and early development. Any substantial population-level effect on reproduction or egg or larval survival should therefore appear in the egg-to-YOY survival index. That index was unrelated with estimated instream concentrations (EIC) of any of the rice pesticides. Increased retention of water on the rice fields in the 1980s apparently reduced pesticide concentrations and toxicity in water discharged to the Sacramento River without changing EIC (Lee et al. 1993), but there was no corresponding increase in the egg-to-YOY survival index (Fig. 7). The previously-reported correlations (Bailey et al. 1994) were apparently the result of the increase in application rates which were coincidental with, but unrelated to, the decline in potential egg production of striped bass.

Potential egg production showed a clear step change in the late 1970s attributed to a decline in abundance of older, more fecund females. The cause of the lower abundance of older striped bass may be traceable to effects of an increasing frequency of warm ocean conditions, occurring with El Niño events, on the migratory patterns and survival of striped bass (Bennett personal communication). Our analysis assumed that age-specific fecundity and maturity did not change during the period when the data were collected. This assumption is supported by the step change apparent in egg abundance, larval abundance, and YOY index.

The low ratio of egg abundance to potential egg production could be due to incomplete sampling, failure to spawn, egg resorption (Whipple et al. 1981), poor egg quality (Zastrow et al. 1989), or other sources of egg mortality. Olney et al. (1991) found mortality of striped bass eggs to average 68% d^{-1}, which would be nearly high enough to account for the low egg abundance in our study. In any case, egg production was clearly lower later than earlier in the data record.

The results of our simple simulation model can be used to infer the relative importance of various alternative scenarios for survival. The fit of the model to recruitment data was unaffected by any change in functional relationships used except the removal of density dependence or, to a lesser extent, setting carrying capacity constant (Fig. 12a). The fit for potential egg production (Fig. 12b) was affected most by a change in adult mortality from a step increase to a constant value or to a linear increase over time. These effects were weakly visible in the 6-mm larval abundance data (Fig. 12c), whereas the fit to the YOY index data (Fig. 12d) was most severely degraded by the addition of export flow to, or the removal of X_2 from, the model for egg-to-YOY survival. The export effect was surprising since it was the opposite to that expected if export flows were an important predictor of early survival. Neither the X_2 effect nor the export effect propagated to recruitment. The best model fits to recruitment and potential egg production were obtained with realistic descriptions of survival from YOY to recruit and within the adult stages, and conditions early in life had little effect on these fits.

Our analyses suggest different causes of the long-term decline in striped bass than previously considered. We interpret these results to mean that the decline in striped bass was more likely related to events happening later in life, and further seaward, than previously thought. Earlier analyses (Stevens et al. 1985; CDFG 1992; Bailey et al. 1994) focused on larval and YOY life stages in the rivers and as far seaward as the low-salinity zone. We found that survival in early life was highly sensitive to freshwater inflow (or its surrogate, X_2) while the response to export flow was weak or sporadic. We found no temporal trends in survival indices over these life stages, or in X_2 or export flow, during the time period examined. Our previous analyses showed evidence of density-dependent compensation between YOY and recruitment with a declining carrying capacity, as well as an increase in adult mortality (Kimmerer et al. 2000). The life-cycle model runs showed that these influences were important in determining recruitment and egg production. The declining carrying capacity may be related to changes in the estuarine foodweb (Kimmerer et al. 2000). Although fishing effort appears not to have increased (CDFG 1987, 1992), the cause of the increase in adult mortality remains to be demonstrated.

ACKNOWLEDGMENTS

We gratefully acknowledge funding by the California Urban Water Agencies and the Interagency Ecological Program for the Sacramento-San Joaquin Delta. We thank Dave Kohlhorst, Scott Barrow, Ken Miller, Karl Jacobs, and Phyllis Fox for providing data; Bill Bennett for thoughtful and stimulating discussions throughout this study; members of the Interagency Ecological Program Estuarine Ecology Team for ongoing discussions on striped bass; Randy Brown for continuing support of this research; and Don Stevens for helpful comments and thoughtful discussion at several stages in development of this paper. B. J. Miller and Elaine Archibald were instrumental in obtaining funding for this study. We thank all of our many reviewers, particularly Phyllis Fox and Ed Houde, for helpful comments on previous versions of this paper.

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., M. D. BALL, AND S. Y. BAUGHMAN. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta Estuary, California, p. 445–495. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The Ecosystem. American Association for the Advancement of Science, San Francisco.

BAILEY, H. C., C. ALEXANDER, C. DIGIORGIO, M. MILLER, S. I. DOROSHOV, AND D. E. HINTON. 1994. The effect of agricultural discharge on striped bass (*Morone saxatilis*) in California's Sacramento-San Joaquin drainage. *Ecotoxicology* 3:123–142.

BENNETT, W. A. 1994. Interactive influence of starvation and size-selective predation on larval striped bass (*Morone saxatilis*). Ph.D. Thesis, University of California, Davis, California.

BENNETT, W. A. AND P. B. MOYLE. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento-San Joaquin Estuary, p. 519–542. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The Ecosystem. American Association for the Advancement of Science, San Francisco.

BENNETT, W. A., D. J. OSTRACH, AND D. E. HINTON. 1995. Larval striped bass condition in a drought-stricken estuary: Evaluating pelagic food-web limitation. *Ecological Applications* 5:680–692.

BROWN, R., S. GREENE, P. COULSTON, AND S. BARROW. 1996. An evaluation of the effectiveness of fish salvage operations at the intake to the California Aqueduct, 1979–1993, p. 497–518. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The Ecosystem. American Association for the Advancement of Science, San Francisco.

CALHOUN, A. J. 1949. California striped bass catch from the party boat fishery: 1938–1948. *California Fish and Game* 35:211–253.

CALIFORNIA DEPARTMENT OF FISH AND GAME. 1987. Factors affecting striped bass abundance in the Sacramento-San Joaquin River system. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary Technical Report 20. Sacramento, California.

CHADWICK, H. K. 1962. Catch records from the striped bass sportfishery in California. *California Fish and Game* 48:153–177.

CLEVELAND, W. S. 1993. Visualizing Data. Hobart Press, Summit, New Jersey.

CLOERN, J. E. AND F. H. NICHOLS. 1985. Temporal Dynamics of an Estuary: San Francisco Bay. Kluwer, Dordrecht, The Netherlands.

CONOMOS, T. J. (ED.). 1979. San Francisco Bay: The Urbanized Estuary. Pacific Division, American Association for the Advancement of Science, San Francisco.

COWAN, J. H., K. A. ROSE, E. S. RUTHERFORD, AND E. D. HOUDE. 1993. Individual-based model of young-of-the-year striped bass population dynamics. 2. Factors affecting recruitment in the Potomac River, Maryland. *Transactions of the American Fisheries Society* 122:439–458.

ELDRIDGE, M. B., J. A. WHIPPLE, AND M. J. BOWERS. 1982. Bioenergetics and growth of striped bass, *Morone saxatilis,* embryos and larvae. *Fishery Bulletin* 80:461–474.

FINLAYSON, B. J. AND G. A. FAGGELLA. 1986. Comparison of laboratory and field observations of fish exposed to the herbicides molinate and thiobencarb. *Transactions of the American Fisheries Society* 115:882–890.

GOODYEAR, C. P. 1985. Relationship between reported commercial landings and abundance of young striped bass in Chesapeake Bay, Maryland. *Transactions of the American Fisheries Society* 114:92–96.

HALL, JR., L. W., A. E. PINKNEY, L. O. HORSEMAN, AND S. E. FINGER. 1985. Mortality of striped bass larvae in relation to contaminants and water quality in a Chesapeake Bay tributary. *Transactions of the American Fisheries Society* 114:861–868.

HOLLIBAUGH, J. T. (ED.). 1996. San Francisco Bay: The Ecosystem. Further Investigations into the Natural History of San

Francisco Bay and Delta with Reference to the Influence of Man. American Association for the Advancement of Science, San Francisco.

Jassby, A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J. R. Schubel, and T. J. Vendlinski. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5:272–289.

Kimmerer, W. J., J. R. Burau, and W. A. Bennett. 1998. Tidally-oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnology and Oceanography* 43:1697–1709.

Kimmerer, W. J., J. H. Cowan, Jr., L. W. Miller, and K. A. Rose. 2000. Analysis of an estuarine striped bass population: Influence of density-dependent mortality between metamorphosis and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 57:478–486.

Kimmerer, W. J., E. Gartside, and J. J. Orsi. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. *Marine Ecology—Progress Series* 113:81–93.

Kimmerer, W. J. and J. J. Orsi. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987, p. 403–424. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The Ecosystem. American Association for the Advancement of Science, San Francisco.

Lee, J. M., L. J. Ross, and R. G. Wang. 1993. Integrating environmental toxicology and monitoring in the development and maintenance of a water quality program: California's rice herbicide scenario, p. 211–224. *In* R. L. Jolley and R. G. M. Wang (eds.), Effective and Safe Waste Management. Interfacing Sciences and Engineering with Monitoring and Risk Analysis, Lewis, Boca Raton, Florida.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:6.

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., J. Cloern, S. Luoma, and D. Peterson. 1986. The modification of an estuary. *Science* 231:567–573.

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.* 2. Displacement of a former community. *Marine Ecology Progress Series* 66:95–101.

Olney, J. E., J. D. Field, and J. C. McGovern. 1991. Striped bass egg mortality, production, and female biomass in Virginia rivers, 1980–1989. *Transactions of the American Fisheries Society* 120: 354–367.

Orsi, J. J. and W. L. Mecum. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin estuary, p. 375–401. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The Ecosystem. American Association for the Advancement of Science, San Francisco.

Pace, M. L., S. B. Baines, H. Cyr, and J. A. Downing. 1993. Relationships among early life stages of *Morone americana* and *Morone saxatilis* from long-term monitoring of the Hudson River Estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1976–1985.

Polgar, T. T. 1981. Larval retention: Transport and behavior, or differential mortality? *Estuaries* 4:276–277.

Prairie, Y. T., R. H. Peters, and D. F. Bird. 1995. Natural variability and the estimation of empirical relationships: A reassessment of regression methods. *Canadian Journal of Fisheries and Aquatic Sciences* 52:788–798.

Radovich, J. 1963. Effect of ocean temperature on the seaward movements of striped bass, *Roccus saxatilis,* on the Pacific coast. *California Fish and Game* 49:191–205.

Raquel, P. F. 1989. Effects of handling and trucking on chinook salmon, striped bass, American shad, steelhead trout, threadfin shad, and white catfish salvaged at the John E. Skinner Delta Fish Protective Facility. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary Technical Report 19. Sacramento, California.

Ricker, W. E. 1973. Linear regression in fishery research. *Journal of the Fisheries Research Board of Canada* 30:409–434.

Rose, K. A. and J. H. Cowan. 1993. Individual-based model of young-of-the-year striped bass population dynamics. 1. Model description and baseline simulations. *Transactions of the American Fisheries Society* 122:415–438.

Rose, K. A., J. H. J. Cowan, E. D. Houde, and C. C. Coutant. 1993. Individual-based modeling of environmental quality effects on early life stages of fishes: A case study using striped bass. *Transactions of the American Fisheries Society* 14:125–144.

Rutherford, E. S., E. D. Houde, and R. M. Nyman. 1997. Relationship of larval-stage growth and mortality to recruitment of striped bass, *Morone saxatilis,* in Chesapeake Bay. *Estuaries* 20:174–198.

Secor, D. H. and E. D. Houde. 1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). *Estuaries* 18:527–544.

Skinner, J. E. 1973. Evaluation testing program report for Delta Fish Protective Facility. State Water Facilities, California Aqueduct, North San Joaquin Division Memorandum Report. California Resources Agency, Sacramento, California.

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

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.

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.

Venables, W. N. and B. N. Ripley. 1997. Modern Applied Statistics with S-plus, 2nd edition. Springer-Verlag, New York.

Werner, I. and J. T. Hollibaugh. 1993. *Potamocorbula amurensis*—Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. *Limnology and Oceanography* 38:949–964.

Whipple, J. A., M. B. Eldridge, and P. E. J. Benville. 1981. An ecological perspective of the effects of monocyclic aromatic hydrocarbons on fishes, p. 483–551. *In* S. J. Vernberg, A. Calabrese, F. P. Thurberg, and W. B. Vernberg (eds.), Biological Monitoring of Marine Pollutants. Academic Press, New York.

White, J. R. 1986. The striped bass sport fishery in the Sacramento-San Joaquin Estuary, 1969–1979. *California Fish and Game* 72:17–37.

Young, G., C. L. Brown, R. S. Nishioka, L. C. Folmar, M. Andrews, J. R. Cashman, and M. Bern. 1994. Histopathology, blood chemistry, and physiological status of normal and moribund striped bass (*Morone saxatilis*) involved in summer mortality (''die-off'') in the Sacramento-San Joaquin Delta of California. *Journal of Fish Biology* 44:491–512.

Zastrow, C. E., E. D. Houde, and E. H. Saunders. 1989. Quality of striped bass (*Morone saxatilis*) eggs in relation to river source and female weight. *Rapports et Proces-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 191: 34–42.

SOURCES OF UNPUBLISHED MATERIALS

BENNETT, W. A. personal communication. Bodega Marine Laboratory, Bodega Bay, California 94923.

CALIFORNIA DEPARTMENT OF FISH AND GAME. 1992. A re-examination of factors affecting striped bass abundance in the Sacramento-San Joaquin estuary. Unpublished testimony to the State Water Resources Control Board. Sacramento, California.

KNUDSEN, D. L. AND K. A. F. URQUHART. 1988. Striped bass health monitoring 1988 final report. California Department of Fish and Game Unpublished Report.

Received for consideration, March 25, 2000
Accepted for publication, February 13, 2001