

**Analysis of the Striped Bass  
Population  
of the  
San Francisco Estuary:**

**Effects of Freshwater Flow Mitigated  
by Density-dependent Mortality**

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**Prepared for  
California Urban Water Agencies**

**October 1997**

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October 9, 1997

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## Abstract

Among the numerous challenges facing fisheries scientists are determining causes of long-term trends, assessing environmental effects on populations, and detecting compensatory mechanisms within populations. In this paper we address all three issues through analysis of an extensive data set on striped bass (*Morone saxatilis*) in the San Francisco estuary. A long-term decline in abundance has apparently been caused by increasing adult mortality, sporadic losses of older adults, and a declining carrying capacity of the estuary for age 0<sup>+</sup>-3 fish. Survival during early life had no time trend, but was positively related to freshwater flow into the estuary. However, flow effects were nearly eliminated during the first 1-3 years of life through density-dependent mortality. Several lines of evidence are consistent with density dependence: apparent mortality rates were positively related to abundance in three different sets of data on age 0<sup>+</sup> fish; recruitment at age 3 had a saturating relationship to a young-of-the-year (YOY) abundance index; and survival from egg to recruit was negatively related to the YOY index.

## Introduction

The causes of variability in fish recruitment have been the central theme of fisheries research over the last several decades (Sissenwine 1984; Shepherd and Cushing 1990). The economic value of many commercial and recreational fisheries emphasizes the importance of understanding the roles of environment and human impacts, including fishing mortality, in regulating recruitment and population size. In particular, fisheries scientists need to: determine the causes of long-term trends in abundance or production; assess the effects of environmental, including anthropogenic, perturbations; and determine the influence of feedback loops including density-dependent effects on the population trajectory. In this paper we attempt to address these issues with regard to striped bass in the San Francisco estuary.

Striped bass (*Morone saxatilis*) are an important fish to recreational and some commercial fisheries along the east and west coasts of North America. They are among the most-studied estuarine fish species: long-term data records are available for the Hudson River (Barnthouse et al. 1984; Connell 1987), Chesapeake Bay (Polgar 1981; Goodyear et al. 1985; Goodyear 1985), and San Francisco Bay (Chadwick et al. 1977, Stevens 1977; Stevens et al. 1985). Much of the emphasis in research on striped bass has been on early life stages (e.g. Chadwick 1964; Turner and Chadwick 1972; Eldridge et al. 1982; Martin et al. 1985; Chesney 1989; Breitburg 1988; Cowan et al. 1993; Rose et al. 1993; Pace et al. 1993; Secor and Houde 1995; Rutherford et al. 1997). Year-class strength appears to be set early in life (Stevens 1977, Ulanowicz and Polgar 1980). Indices of young-of-the-year (YOY) can be useful predictors of recruitment (Polgar 1981; Goodyear 1985), and have been used to establish management goals for fishing effort and freshwater flow.

The life history of striped bass is complex. Estuarine populations of striped bass spawn in freshwater during spring, annually or less often (Calhoun 1952; Turner 1976). Negatively-buoyant, free-floating eggs drift downstream as they develop, suffering high mortality (Olney et al. 1991). Late larval and early juvenile stages occur mainly in brackish regions of the estuary (Turner and Chadwick 1972), where they feed on small zooplankton including copepods, mysids, and amphipods, shifting toward piscivory late in the first year (Heubach et al. 1963; Stevens 1966; Thomas 1967). Striped bass mature at 4-5 years of age and can live to over 30 years, migrating to brackish or salt water during summer and returning to freshwater in fall to winter (Calhoun 1952). Some adult striped bass, particularly the older ones, enter the ocean and undergo extensive coastal migrations (Orsi 1971; Coutant 1985; Secor and Piccoli 1996).

Factors shown to be related to the abundance or condition of striped bass include egg quality (Zastrow et al. 1989), freshwater flow (Stevens 1977, Turner and Chadwick 1972; Stevens 1977), water diversions (Chadwick et al. 1977; Stevens et al. 1985), temperature (Coutant 1985), food supply (Martin et al. 1985; Breitburg 1988) and toxic contamination (Hall et al. 1985, 1987; Palawski et al. 1985; Connell 1987; Bailey et al. 1994; Young et al. 1994; Bennett et al. 1995).

Striped bass in the San Francisco estuary have undergone a substantial decline in abundance over the last 3 decades, prompting investigations into the causes (Stevens et al. 1985). Potential influences on abundance and survival of striped bass include concentrations of food and contaminants, river flow, and amount of water exported from the Sacramento-San Joaquin River delta for urban and agricultural use (Turner and Chadwick 1972, Stevens et al. 1985). YOY abundance and survival from egg to YOY are strongly related to river flow, salinity, and export flow, and spatial distribution of young striped bass follows that of salinity (Turner and Chadwick 1972; Stevens et al. 1985; Jassby et al. 1995). Adult striped bass abundance and recruitment have also been related to river flow (Stevens 1977). Striped bass larvae are rarely found to be starving in the estuary (Bennett et al. 1995), an observation that has been used incorrectly to reject food limitation as an influence on survival (see Bennett 1994). Estimated concentrations of agricultural chemicals used on rice, much of which is cultivated near the major spawning areas, have also been correlated with YOY index (Bailey et al. 1994). Bioassay experiments (Bailey et al. 1994), and histopathological studies (Bennett et al. 1995) suggested toxicity to striped bass larvae in Sacramento River water. An annual die-off of adult striped bass in early summer may be related to tissue concentrations of contaminants and frequency of lesions (Young et al. 1994). Egg resorption in females has been related to tissue concentrations of petroleum hydrocarbons (Whipple et al. 1981), although more recent analyses did not support that relationship (Knudsen and Urquhart 1988). Radovich (1963) showed that the proportion of adult striped bass migrating to the coastal ocean was influenced by ocean temperature, and Coutant (1985) speculated that adult striped bass are confined by a "thermal niche" to certain parts of the estuary, possibly affecting their survival.

The California Department of Fish and Game (CDFG 1987, 1992) has summarized the evidence on the decline in striped bass and concluded the following. Mortality of adult striped bass has increased, while growth rates have not changed. The abundance of young striped bass is related to river flow and the amount of water exported from the estuary, but this relationship has changed due to a decline in egg supply over time. The principal cause of the decline in adults is the decline in production of young striped bass,

driven largely by losses at export facilities. Finally, contaminant levels are high and may be causing harm.

With the variety of potential influences on striped bass populations, it is tempting to assume that any or all of these factors are affecting or limiting production of striped bass in this estuary (Bennett and Moyle 1996). However, a very large and rich database is available to analyze the effects of environment on different parts of the life cycle. The purpose of this paper is to examine the available data for evidence of environmental influences and long-term changes in survival of striped bass at various life stages. To address the long time lags and autocorrelation inherent in this long-lived population, our analysis emphasizes survival through selected portions of the life cycle rather than time trends in abundance. We focus mainly on the period 1969-1995, for which most of the data are available.

The San Francisco estuary (or Sacramento-San Joaquin Delta estuary) is a complex, dynamic system with widely varying river flow, a large urban population, and numerous sources of stress including frequent droughts and floods, withdrawal 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). Significant changes in recent decades include increasing exports of freshwater from the Sacramento-San Joaquin delta (Figure 1) during the 1960s-70s (Nichols et al. 1986), the establishment of standards to control freshwater flow or salinity distribution within the estuary (Jassby et al. 1995, Arthur et al. 1996), and the introduction of the clam *Potamocorbula amurensis*, which spread throughout the northern estuary in 1986-88 with consequent severe effects on lower trophic levels (Nichols et al. 1990, Alpine and Cloern 1992, Werner and Hollibaugh 1993, Kimmerer et al. 1995, Kimmerer and Orsi 1996). Striped bass were introduced successfully to the San Francisco estuary in 1879 (Radovich 1963). Spawning occurs about 200 km up the Sacramento River, and in the delta in the lower San Joaquin River, in April-June (Figure 1) (Turner 1976).

## Methods

**Striped bass data sources** Data were obtained mainly from the California Department of Fish and Game (CDFG) and from the California Interagency Ecological Program (IEP) databases<sup>1</sup>. Data from CDFG included raw data and several indices as indicated below. Ongoing sampling programs gather data on abundance and distribution of striped bass at nearly all stages in the life cycle (Figure 2). Methods of collection are described briefly in the following paragraphs; see references for full descriptions.

Abundance data used (Table 1) were either indices or estimates of size of the entire population, or estimates of abundance per unit area or volume that were then used to calculate population size. Mortality estimates were calculated generally as the slope of log abundance over time (Table 2). Survival estimates or indices were calculated as the log ratio of abundance indices or estimates at two successive life stages (Table 2). To reduce confusion about the numerous variables analyzed, names of variables in Tables 1 and 2 are used consistently throughout the text. The years included in each data set are given in Figure 2. Environmental variables used in analyses are listed in Table 3.

*Adult abundance* Gill nets and fyke traps were used to capture and tag striped bass during their spring spawning migrations (Stevens et al. 1985). The population was resampled during a year-round census of angler catches and during subsequent spring tagging. About 75-90% of the censused fish were sexed and aged (3-7 and 8+ years old). The remainder of censused fish were assumed to have the same sex ratio as this sample, and ages as determined from an age-length key. Data were provided by CDFG as total fish marked, recaptured, and recaptured with tags for each age and sex. Age-3 fish, particularly females, are not fully vulnerable to capture, so age-3 female abundance was estimated from that of males assuming a 1:1 sex ratio. The Petersen estimate of abundance was determined using the unbiased method of Bailey (1951). This estimate is valid, although with wide confidence limits, when there are no recaptures of tagged fish, as has happened in recent years for ages 7 and 8+. To adjust for the effect of hatchery production we reduced abundance data by the proportion of fish of each age-class that were of hatchery origin as determined by recovery of tags applied at the hatchery. Recruitment was taken as the Petersen abundance estimate at age 3.

Variables related to adult abundance included total abundance, abundance by age, and recruitment, which

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<sup>1</sup>

Most of these data are available in raw form on the IEP web site at <http://www.iep.water.ca.gov>

was taken as abundance at age 3, with results checked using abundance of age-4 fish from the same year-class. Three alternative adult abundance indices provided by CDFG were used in analysis. The San Francisco Bay party-boat fishery has provided a long record of catch-per-unit-effort (CPUE) data that was used to index total abundance (Stevens 1977). A party-boat recruit index was calculated as the difference between abundance in a year and abundance in the previous year times the mean survival of adult striped bass (Stevens 1977). CPUE data were also obtained from a recreational fishery in Carquinez Strait (Figure 1), which targets mainly ages 3-5.

Adult mortality rate was calculated by year-class as the slope of the natural log of the Petersen abundance estimate vs. age, not including age 8+ fish. A tagging estimate of mortality rate by year was obtained from CDFG's tagging program as  $-\ln(\text{survival})$ , where survival was calculated using Ricker's (1975) Equation 5.1 (Stevens et al. 1985). The Petersen mortality estimate emphasizes all age classes equally, while the tagging estimate puts more emphasis on younger, more abundant age classes.

Potential egg production was calculated from the Petersen estimates of abundance of female striped bass using fecundity estimates developed as follows. Raw fecundity in eggs per fecund female were obtained from reports of a striped bass health monitoring study for 8 years in 1978-88 (Knudsen and Urquhart 1988). Differences among years were significant (analysis of variance,  $p < 0.01$ ), but there was no time trend. Because data were not available for all years or for all ages over 8 years, we pooled the fecundity data for all years and calculated egg production as the prediction of a regression with age as the independent variable. Mean fecundity of age 8+ fish was calculated from age-specific fecundity from the model, weighted by abundance of ages 8-11. Two corrections were applied to obtain actual fecundity: a correction for the proportion of females migrating to the spawning grounds, and a correction for the proportion that was mature. The migration correction was calculated using data from the annual tagging survey as the sex ratio (female to male) for ages 4 and 5, divided by the sex ratio of ages 6 and older. Sex ratios did not change with age after age 5. The maturity correction was obtained from Scofield (1931); population egg production with and without this correction was correlated at  $r = 0.998$ . Resulting fecundity estimates are close to those used by Stevens et al. (1985) based on fewer years of fecundity data (Table 4). Egg production estimates include confidence intervals based on propagation of error from Petersen estimates and from variability in fecundity. An egg-recruit survival estimate was calculated as the ratio of the 3-year-old Petersen estimate of abundance to potential egg production.

*Egg and larval surveys* The purpose of this survey series is to determine the abundance and distribution of eggs and larvae of striped bass and to estimate growth and mortality rates (CDFG 1987). Surveys were taken every 2-4 days during and after the spawning season. Ichthyoplankton were sampled in 10-minute oblique tows with a 0.4 m<sup>2</sup> mouth area, 505 µm mesh net mounted on skis. We used abundance of eggs and 6-14mm larvae in 1mm intervals, 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 from 9 years, and larval abundance data from 16 years, but for 1973 and 1977 data were available for only a limited range of lengths.

Larval mortality was estimated as the slope of the natural log of larval abundance vs. size for each year. Production of 6mm larvae was calculated as the intercept of those fitted lines at length 6mm, and an egg-6mm survival index was calculated as the ratio of 6mm larval production to potential egg production.

*Summer townet surveys* The original purpose of this survey series was to obtain a young-of-the-year (YOY) index of abundance when the catch averages 38 mm in mean length (Chadwick 1964). Two to five surveys have been conducted during 1959-1995 except 1966 at approximately two-week intervals starting in June or early July, and ending when the mean fork length of striped bass in the catch reached at least 38.1 mm. Two or three 10-minute tows were made at 31 stations using a 1.5 m<sup>2</sup> frame on skis fitted with a net of 1-inch stretch mesh in the forward half and 2.5 mm nylon mesh in the back half. Stations have changed since the program began (Chadwick 1964). All striped bass caught are measured currently to the nearest millimeter; measurements made in tenths of inches prior to 1969 have been converted to mm. The YOY index was calculated for each survey as the sum of catches at each station times the volume represented by that station. The final YOY index was interpolated to the date when the mean size was estimated to be 38.1 mm. The YOY index was considered invalid in 1983, when high flow moved the striped bass population downstream of the sampled area. In 1995, mean size of the captured fish never reached 38.1 mm. We used YOY indices provided by CDFG but 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 townet surveys of each year.

We computed YOY abundance from catch per volume, assuming a nominal towing speed of 0.8 m/s and 100% net efficiency for a volume sampled of 720 m<sup>3</sup>. Total population size was computed by summing the catch at each station times a volume weighting factor for each station. Length frequency distributions

were determined by aggregating length data from all stations within major regions of the estuary.

Indices of survival from egg to YOY and 6-mm larva to YOY were calculated as ratios of the YOY index to potential egg production and 6-mm production respectively. YOY - recruit survival index was examined using plots of YOY index vs. abundance at age 3.

*Fall midwater trawl surveys* The purpose of this survey series is to monitor the abundance and distribution of striped bass and other fish during the fall of their first year. Surveys were taken in 1967-1995 except 1974 and 1979, monthly from September to December (data from other months sampled before 1980 were not used) at 45-124 (median 94) stations. Ten-minute oblique tows from near the bottom to the surface were taken with a 3.7 m x 3.7 m midwater trawl with a 2.5 cm stretch mesh body and a 1.3 cm stretch mesh cod end. The midwater trawl index (MWT) was calculated for each survey as the mean catch per tow over each of 19 regions multiplied by the volume in that region, summed over all regions. We converted catch per tow to abundance estimates by using a volume sampled of 7000 m<sup>3</sup>, the median value based on flowmeter readings taken since 1985, and calculated population size as for the summer townet survey except that the volume weighting factor was by region rather than station.

Apparent mortality rate for the combined summer YOY and fall MWT surveys was calculated as the mean rate of decline of log abundance from July to November. Mortality rate appeared to decrease during this time, resulting in a curved trajectory of log abundance. To avoid potential bias due to this curvature, log abundance data for each year were fit to a quadratic function in time (based on mortality rate decreasing linearly with time). Residuals from this fit had no apparent time trend within years, suggesting this was an appropriate model. The apparent mortality rate was calculated for each year as the negative slope of the fitted curve between months 7 and 11. This decline includes mortality and decreasing catchability, but we assumed that variation among years was due solely to variation in mortality.

*San Francisco Bay study* The purpose of this survey series (called the Bay study here) is to assess the effects of freshwater outflow on the abundance and distribution of fish and crustaceans in the San Francisco estuary (Armor and Herrgesell 1985). Surveys have been taken monthly all year starting in 1980, except in winter months since 1989. At each of 35-52 stations, one 5-minute tow each was taken with an otter trawl with a 4.9 m headrope, and a 12-minute oblique tow was made with a 3.7 m x 3.7 m square midwater trawl with mesh graduating from 20.3 cm stretch mesh at the mouth to 1.3 cm at the cod

end. All fish and crustaceans were identified and random samples of up to 50 were measured to the nearest millimeter.

Data used from this study comprised catch per effort and length data from the otter trawls (catch per 1000 m<sup>2</sup>) and midwater trawls (catch per 1000 m<sup>3</sup>) for 1980-1992. Stations sampled in most or all surveys in San Pablo Bay (8 stations), Suisun Bay (9 stations), and the western delta (2 stations) were included; stations in south and central San Francisco Bay were eliminated since catches of striped bass there were usually negligible. Estimates of population abundance were calculated from the Bay study separately for otter and midwater trawls. Expansion of catch rates was the same as for the fall midwater trawl survey; expansion of the otter trawl data was by area rather than by volume. A potential for bias exists when the young bass population is centered in the delta because no samples are taken in the central and southern delta. We estimated the effect of that bias for each month in summer-fall by dividing abundance estimates from the Bay study by the proportion of the population west of the delta, determined from the YOY and MWT abundance data.

Apparent mortality was estimated as the slope of the linear regression of log population size vs. month from July-April for each sample set from the Bay study. Curvature was not evident in these data. Again we assumed that variation among years was due solely to variation in mortality. Median lengths by survey were calculated from the combined Bay study midwater and otter trawl data for July-April after length frequency distributions had been truncated at 180 mm to eliminate most age-1 fish. Growth rates were determined by fitting data to a von Bertalanffy curve using a nonlinear least-squares method (Venables and Ripley 1994). Residuals from this analysis for each year were examined for mean and trend to assess interannual variation in growth rate.

*Salvage data* Striped bass and other fish were collected at fish-collection facilities at the State Water Project (SWP) and Central Valley Project (CVP) pumping plants in the southern delta (Figure 1). See Brown et al. (1996) for a complete discussion of salvage operations at the SWP fish facility. In general, fish larger than about 20-30 mm were retained by fish screens, collected, and periodically loaded into tanker trucks and released into the western delta. During this process they suffer mortality due to handling, and may also be consumed by predators in the waterways leading to the pumping plants, which offer little refuge from predators (Brown et al. 1996). The SWP takes water from an intake basin that is filled tidally, possibly increasing predation risk, whereas water flows continuously to the CVP.

At intervals throughout the day and night, a subsample of the fish salvaged was collected and counted; before 1993, 20-50% of the fish counted were identified to species, and thereafter all fish have been identified and 20-40% measured. For all years counts were expanded to total by species and month, and abundance per unit volume of water was calculated by dividing by the export flow rate.

**Environmental variables** Several environmental variables were used as predictors in analyses of abundance or survival (Table 3). Averaging periods varied depending on the analysis, but were usually either April-June, encompassing spawning and early development (for analyses of larvae or YOY) or June-December to coincide with summer and fall sampling. Temperature data were obtained from the CDFG zooplankton survey, and checked against hourly data from the IEP continuous monitoring program at two estuarine stations from 1983-1995 (river kilometers 56 and 74). Flow variables used included Sacramento River flow rate at Grimes (200 river km from the confluence with the San Joaquin River) from the US Geological Survey, flow into and out of the delta, and CVP and SWP export flow rates from California Department of Water Resources (DWR). Delta outflow (i.e. freshwater flow into the estuary) is calculated by DWR from gaged and ungaged flows, export flows, and net consumption of water within the delta. a related variable used extensively in these analyses is the mean position of the 2 psu near-bottom isohaline in kilometers from the mouth of the estuary ("X<sub>2</sub>"; Jassby et al. 1995). X<sub>2</sub> is a useful integrator of recent flow conditions, and provides a geographic context in that many estuarine species are abundant near 2 psu (Kimmerer and Orsi 1996 and this paper). It has also been used in setting standards for freshwater flow into the estuary for protection of aquatic resources (Jassby et al. 1995). X<sub>2</sub> was determined for 1968-1992 by interpolation between fixed salinity monitoring stations, and for other years by a lagged regression with delta outflow (Jassby et al. 1995).

Annual application rates of chemicals used in rice were obtained from the California Department of Pesticide Regulation. Following Bailey et al. (1994), we calculated estimated instream concentrations (EICs) by dividing application rates by mean Sacramento River flow in May. These variables were used in analyses of survival from egg to YOY, since early life stages are most exposed, and there has been evidence of toxicant effects on early larvae (Bennett et al. 1995). The use of EIC's is somewhat misleading because changes in application and retention practices in the early 1990's may have reduced toxicity without appreciably changing EIC's ( ).

Abundance of mysid shrimp, *Neomysis mercedis* and *Acanthomysis* spp. (Orsi and Mecum 1996), was obtained from the IEP zooplankton monitoring study as an indicator of food availability to young striped bass (Heubach et al. 1963, Stevens 1966).

**Data consistency and analyses** Where possible we compared results using alternative estimates of abundance or survival to assess consistency. For example, we used CPUE data to evaluate the time trends in Petersen estimates of abundance; tagging mortality to compare with adult mortality from Petersen estimates; egg abundance as a check on egg production; Bay study otter trawl vs. midwater trawl, and both vs. summer townet and fall midwater trawl data; and abundance of age-4 adults as a check on recruitment at age 3. We compared the abundance per unit volume from the export salvage facilities with abundance values calculated from the summer townet and fall midwater trawl samples from stations in the southern delta. In addition we examined differences in length distributions among these data, since potential sources of bias (net avoidance and predation) are size-selective. We also conducted simulations when needed to check on suitability of data for analyses.

Estimates of entrainment in the CVP and SWP pumping plants were made using both the summer townet and fall midwater trawl data. We multiplied export flow by the abundance in the net samples at stations in the southern delta to estimate entrainment rate, then divided by total population size to get the proportion transported to the facilities. This calculation eliminates bias due to net efficiency, although it requires an assumption that abundance in the southern delta is the same as that in water taken in by the export facilities. This assumption is discussed further below. Length distributions of fish in the salvage facilities had smaller medians than those from the net samples. To account for the smaller size of fish near the pumping plants we also calculated a transport rate in terms of biomass, using the length-weight relationship in Rose et al. (1993); the underlying assumption is that larger fish have a greater probability of contributing to recruitment so the smaller fish are discounted by using their estimated weight. Actual loss rate of fish is a function of size; total screen efficiency exceeds 90% at a length above about 50 mm (Brown et al. 1996). Midpoints of data on screening efficiency by size class (Skinner 1973) were combined with data on survival during trucking and handling (Raquel 1989) to obtain overall survival, which was multiplied by the biomass-specific transport rate to derive an estimate of total losses to exports. Pre-screen losses to predation can be as high as 99%, and were assumed to average 75%, for young chinook salmon (Brown et al. 1996); these losses were not included in this estimate, but are discussed below.

Evidence of density dependence was developed in three ways. First, we fit a Beverton-Holt curve to recruitment vs. YOY index:

$$\text{Recruits} = \frac{b \text{ YOY}}{a + \text{YOY}} \quad (1)$$

The choice of this curve over a straight line or other relationship was dictated by the requirement that the line go through the origin. The asymptote  $b$  of the Beverton-Holt curve can be interpreted as carrying capacity, and we also examined the residuals from this curve for evidence that carrying capacity had declined. The second way of demonstrating density dependence was by analysis of the influence of YOY on egg-recruit survival. The third method was by regression of apparent mortality rates from the three surveys (Table 2) on mean log abundance for the same surveys; a positive relationship, indicating high mortality when fish are abundant, was taken as evidence of density dependence, the expectation in the absence of density dependence being a slope of zero.

Data analysis used the S-Plus statistical language (Venables and Ripley 1994). We emphasized graphical techniques for exploring raw data before developing models to fit the data (Cleveland 1993). 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 plots of residuals, including plots of autocorrelation functions in which we used the approximate 5% significance level as a criterion for the presence of autocorrelation. None of the models reported here contained significant autocorrelation in the residuals. When the other assumptions of linear regression were not met, we used robust fitting techniques (generalized linear model with robust fit, Venables and Ripley 1994) which do not require those assumptions and are less influenced by outliers than least-squares regression. 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 1994) to separate time series data into two segments, which were then fitted to step functions for statistical evaluation. In fitting a relationship of export flows to  $X_2$ , curvature was evident in the relationship but there was no underlying model of the expected relationship. In that case we fit a natural spline with 2 degrees of freedom (Venables and Ripley 1994), assuming only that the underlying function is smooth.

## Results

**Consistency of Data** Patterns of abundance differed somewhat between the YOY and MWT indices (Figure 3a, B). The YOY index reached a record low value in 1977 and has remained below the pre-1977 median in every subsequent year except 1986. The MWT index roughly paralleled the YOY index except that it was relatively high in 1983, when no YOY index was computed because of incomplete sampling. Adult abundance and CPUE indices also have declined more-or-less in parallel (Figure 3C, D). Correlations between the CPUE indices and the abundance estimates were 0.89 ( $p=0.001$ ) for the Carquinez Strait troll fishery (ages 3-5; Figure 3C) and 0.74 ( $p<0.001$ ) for the party boat fishery (all ages; Figure 3D). By contrast, correlations of the party-boat recruit index with the Carquinez Strait CPUE was 0.50, and with the recruitment estimate at age 3 it was 0.31.

Values of population size were correlated between the Bay study otter and midwater trawl data ( $r=0.65$  for log-transformed values), and did not differ significantly (Wilcoxon sign-rank test,  $p=0.1$ ). Values from the Bay study midwater trawl samples taken in fall were correlated with those from the fall midwater trawl surveys ( $r=0.52$  for log-transformed values) and not significantly different (Wilcoxon sign rank test,  $p>0.4$ ). Values from the Bay study in summer were considerably lower than those from the summer townet survey, presumably because the smaller fish were not vulnerable to the trawls and because the Bay study does not sample in the interior delta.

The summer townet survey, fall midwater trawl survey, and CVP and SWP salvage facilities provide independent estimates of abundance for the southern delta. Differences in log values between the net samples and salvage samples were significant in 2 of the 4 cases: values from the federal facility were lower than those from the summer townet survey and higher than those from the fall midwater trawl survey (Table 5). Values from the SWP facility did not differ significantly from either set of net sampling data (Table 5). Sampling practices at the CVP and SWP facilities have changed over time; the only apparent result of that change is a significant decline in the ratio of abundance at the SWP facility to that in the MWT data ( $p=0.014$ ,  $n=70$ , robust regression). Otherwise there was no trend in these ratios.

Comparisons of median lengths from the summer and fall surveys at stations near the CVP and SWP export facilities with the salvage data revealed a moderately good fit to a 1:1 line. Median lengths at the SWP facility were not significantly different from median lengths in the net samples during summer or fall

(Wilcoxon sign-rank test on the differences,  $p \sim 0.1$ ). However, median lengths at the CVP facility were higher in general, and had numerous high values relative to the net samples (Wilcoxon sign-rank test,  $p < 0.001$ ). Median lengths were also higher at the CVP facility than the SWP facility.

Egg abundance 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 egg production was  $0.06 \pm 0.015$  ( $r = 0.68$ ,  $p = 0.029$ ,  $n = 9$ ). 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 from 1990 to 1993.

We analyzed for several potential sources of bias in the apparent mortality data. One possible source of bias is distortion of abundance distributions by large numbers of zeros in samples (the median percent zeros in the samples was 47% for both of the Bay study data sets). Simulations with synthetic data showed that slopes of abundance were not strongly affected by the frequency of zeros, suggesting that this source of bias was negligible. Bias in the Bay study data, resulting from inadequate sampling in the delta, was insufficient to alter substantially any results using those data.

**Environmental conditions** Summer temperatures in the estuary were always higher in the delta ( $> 120$  river kilometer from the mouth of the estuary) than further down the estuary, and lowest in the furthest seaward samples (Figure 4a). Flow in the Sacramento River and outflow from the delta in April-June were highly variable, including drought periods in 1976-77 and 1985-92 and heavy floods in 1982-83 and 1995.  $X_2$  varied inversely, being furthest landward during droughts and seaward during floods (Figure 4B). Export flow increased until the mid-1970s as additional pumping capacity was brought on line (Figure 4C). 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).

**Striped bass abundance and distributions** The variability in log-transformed abundance indices can be compared directly since they describe relative changes in abundance. Table 6 lists variance of log abundance indices or estimates truncated to the time period (1969-1994) for which adult abundance estimates were available. Variance was highest for the YOY and MWT indices, and lowest for fish aged 3-5 years. The variance of adult abundance increased with age because of a decrease in the number of marked fish recaptured. Variance for Bay study and egg abundance data were intermediate, partly

reflecting fewer data points in those series. The variance of the YOY and MWT indices was about 5-6-fold higher than that for adults in the first few years of life, and nearly twice that for potential egg production. Much of this higher variance may be due to higher sampling variability in the surveys of early life stages.

All age-classes of adults have declined over the last several decades, based on total abundance and CPUE data (Figure 3) and abundance by age (Figure 5). Figure 5 reveals a difference in the patterns of change between the younger adults age 3-5 and the fish 6 years old and greater: while the former have declined more-or-less continuously over the period of record, the latter have declined more than the younger fish, particularly in 1977-78, 1984, and 1993-94. The declines in abundance appear to have affected older ages in individual years rather than individual age-classes: for example, the decline in age 6 in 1978 did not follow a proportional reduction in age 3 in 1975. Although the low abundance values for older fish are based on few recaptures, with resulting wide confidence intervals, the nearly-simultaneous declines in more than one age class (Figure 5a) and the overall step decrease in older relative to younger fish (Figure 5B) probably reflect real abundance patterns. Neither the abundance of older fish nor the ratio of older to younger fish was related to water temperature in the bay ( $p > 0.2$ , linear regression).

Potential egg production declined sharply in the late 1970s (Figure 6). Confidence limits on potential egg production were large, owing partly to the small number of recaptures; in particular, no marked fish in the 7-year or 8+-year age-classes were recaptured in 5 out of 26 years of the survey, all in 1977 and later. A regression of potential egg production on a step change in 1976.5 explained 78% of the variance ( $p < 0.0001$ , Figure 6) and the residuals had no time trend or autocorrelation.

Distributions of young striped bass were more closely related to salinity than to geography. Median positions expressed as river kilometer were closely related to  $X_2$  (Figure 7). Both regressions are highly significant with slopes of  $0.87 \pm 0.16$  (95% confidence limits) for the YOY abundance and  $0.81 \pm 0.21$  for MWT abundance. Under low-flow conditions the freshwater limb of the striped bass distribution reaches well into the delta (River kilometer 81, Figure 7). The distribution of striped bass in the fall midwater trawl survey was further seaward than that in the summer townet survey, although part of the difference could be attributed to weighting of the sampling effort further downstream in the fall survey.

Length data were available from the YOY and MWT surveys, the Bay study, and salvage data from the

CVP and SWP facilities. The first two surveys gave the best spatial picture of length distributions. In both surveys there was a tendency for striped bass to be larger at higher salinity, i.e., down-estuary, than in the delta: mean length in the townet survey was 25 mm at salinity < 0.25 psu, and 38 mm at salinity > 6 psu, while in the midwater trawl survey these values were 79 and 91 mm, respectively. These patterns were consistent among years. Median length of striped bass from Bay study stations in the northern estuary increased with age during each year. The fit of these data to a von Bertalanffy growth curve gave the following parameters: initial growth rate  $k = 0.29 \pm 0.03 \text{ month}^{-1}$ , asymptote  $L_{\infty} = 104 \pm 2.3 \text{ mm}$ , and time at zero length on April  $25 \pm 3$  days. Residuals from this curve for each year had no apparent or significant trend; residuals differed among years mainly in the timing of the growth curve.

The party boat recruit index was positively related to the logarithm of freshwater flow into the estuary during June and July 3 years earlier for year-classes from 1956 to 1971 (Figure 8a). We fit a series of straight lines to data from 1956 to each year in succession, and found that error variance increased starting with year-class 1971. The fit to the data up to 1971 was significant ( $r^2 = 0.46$ ,  $p = 0.002$ , 14 df, generalized linear model with robust fit), but there was also a declining trend in the residuals ( $p = 0.014$ , linear regression). After 1971 there was no relationship with log of flow. Recruitment as Petersen abundance estimates for 3-year-old fish (year-classes 1966-1989) was unrelated to flow, either with all years or restricted to year-classes before the 1980s (Figure 8B).

**Striped bass survival** Here we examine survival or mortality estimates and indices for the various life stages, in the order listed in Table 2, and relate them to environmental conditions.

Tagging and Petersen estimates of mortality (Table 2) differ somewhat in perspective: the tagging estimate gives mortality in a given year, while the Petersen estimate gives mortality in a year-class. Therefore differences between the patterns for particular years are less informative than the overall trends, which are similar (Figure 9). The Petersen estimate of mortality did not have a significant linear trend ( $p > 0.2$ , 20 df), but fit a step function in year-class 1970.5 as determined by tree regression (robust linear regression on step function,  $p = 0.009$ ,  $r^2 = 0.29$ , 20 df, means  $0.59$  and  $0.79 \text{ y}^{-1}$  respectively). The linear trend in the tagging estimate of mortality is significant, even including the high mortality calculated in 1959 (robust linear regression,  $p = 0.001$ ,  $r^2 = 0.14$ , 35 df, slope =  $0.008 \pm 0.002 \text{ y}^{-1}$ , standard error).

Larval mortality did not have a trend through years ( $p > 0.1$ , linear regression; Figure 10a, 1977 excluded),

nor was it related to  $X_2$  ( $p > 0.7$ , Figure 10B). Production of 6mm larvae declined over time (Figure 10C) and declined with increasing  $X_2$  (Figure 10D). Tree regression showed that a step occurring in 1976-77 split the data into two groups most effectively. a linear regression with this step and  $X_2$  as independent variables was highly significant ( $p = .0002$ , 12 df,  $r^2 = 0.76$ , 1973 excluded) with significant coefficients for both independent variables:  $-0.015 \pm 0.005$  for  $X_2$  and  $-0.38 \pm 0.10$  for the step change (standard errors). 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 0.19, only slightly larger than the variance of the residuals from the regression (0.16). This gives confidence that the relationship is a robust description of the underlying variability.

Previous analyses of survival have revealed a strong dependence of egg-YOY survival index on freshwater flow or  $X_2$  and export flows (Stevens et al. 1985, CDFG 1987, Jassby et al. 1995). Following Jassby et al. (1995) we used  $X_2$  and export flow as predictor variables. Export flow in April-July had a significant curvilinear relationship with  $X_2$  (Figure 11a, Table 7), mainly because export flow was lower in several drought years and also 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 on log of survival index, which explained 60% of the variance (Figure 11B, Table 7). Neither the egg-YOY survival index nor the residual from the regression in Table 7 had a significant time trend (Figure 11C, D).

Egg-YOY survival index was unrelated to application rates or estimated instream concentrations (EICs) of chemicals commonly applied to rice. Figure 12 shows the application rates of the most common chemicals and total chemicals, YOY index, and graphs of EIC for molinate vs. YOY index and egg-YOY survival index. Pesticide application rates increased in the late 1970s-early 1980s, roughly coincident with the decline in YOY index, and EIC of molinate was correlated with YOY index (Figure 12C). However, EIC of molinate was uncorrelated with log of survival index (Figure 12D;  $r = -0.2$ ,  $p \sim 0.3$ , Pearson correlation). Application rates and EICs of other rice chemicals had lower correlations with the log of egg-YOY survival index than that for EIC of molinate.

The egg-6mm survival index was related to  $X_2$  in a similar manner to the egg-YOY survival index. Linear regression slopes of both log-transformed survival indices were highly significant and almost identical (Figure 13, Table 8). Plots of egg-6mm survival index suggested no effect of export flow. Log 6mm-YOY survival index was unrelated to  $X_2$  (since it is nearly equal to the difference between the residuals of

the two regressions on  $X_2$  in Table 8) but had a significant negative relationship with export flow rate (robust regression, Table 8).

Plots of log of abundance in the combined summer and fall surveys vs. date showed a rapid decrease in the first few months that decelerated through fall and early winter (Figure 14). Similar plots of the Bay study midwater and otter trawl data (not shown) revealed a nearly linear change of log abundance with time from July to April. Presumably the initially steep decline seen in the summer townet survey data (Figure 14) is absent from the Bay study data because the townet more efficiently captures the smaller fish whose initial mortality rates are very high.

Apparent mortality rates for the three sets of data for juvenile fish (Table 2) were positively related to the mean log of abundance for each set of data (Figure 15, Table 9). Apparent mortality rates were unrelated to export flows but were related to  $X_2$  with negative slopes, i.e., higher  $X_2$  was associated with lower apparent mortality, presumably because abundance of young striped bass in summer varied negatively with  $X_2$  and positively with apparent mortality rate (Table 10).

The estimated proportion of fish transported to the two export facilities over the 7-month period from June through December varied with flow conditions and was as high as 99% (Figure 16a). The proportion of biomass transported is somewhat lower (Figure 16a) because the fish exposed to export pumping were smaller (median value) than those in the population as a whole. The proportion of biomass estimated to be lost to the population through export pumping (i.e. the proportion not salvaged and returned to the estuary) had a median value of 33% and a range of 4-95% (Figure 16a). Correlations between these export losses and the three measures of apparent mortality (Figure 16C-D) were not significantly positive for any combination of survey data and estimate of loss; for the Bay study surveys these correlations were negative (Table 11).

The Beverton-Holt curve appeared a reasonable description of the relationship between recruitment and YOY index, albeit with considerable residual variation (Figure 17a). Parameters were carrying capacity  $b = 0.98 \pm 0.11$  and half-saturation constant  $a = 8.1 \pm 4.0$  (standard errors;  $r^2 = 0.37$ ,  $p < 0.001$ , 22 df). Most of the data points were on the saturated portion of the curve, at which further increases in YOY index do not result in consistent increases in recruitment. The residuals from this curve had a downward time trend that was significant when the points were weighted by the value of the YOY index (Figure 17B;

slope =  $-0.028 \pm 0.008$ ,  $p \sim 0.002$ , 22 df). This weighting was used to distinguish temporal changes in carrying capacity from changes occurring because of low abundance of young fish. Similar, significant downward trends were obtained when the regression was unweighted but included only those points with YOY index above the half-saturation constant, or when 1986 was eliminated because of its influence on the slope. The residuals were uncorrelated with  $X_2$ , export flow, or summer-fall abundance of the mysid shrimp *Neomysis mercedis* ( $p > 0.3$  in all cases).

Egg-recruit survival was not simply related to environmental variables, but a significant relationship was obtained between the logarithm of egg-recruit survival and  $X_2$  in April-July, YOY index, and the interaction between  $X_2$  and YOY index (Figure 18a, Table 12). Fitted values from this model projected on the plot of  $X_2$  vs. YOY index (Figure 18B) illustrate that, at low values of the YOY index, egg-recruit survival increases with decreasing  $X_2$ , while at low  $X_2$  it is negatively influenced by variation in YOY index.

## Discussion

Our analyses indicate that the long-term decline in all life stages of the striped bass population in the San Francisco estuary is likely related to changes in adult mortality and declining carrying capacity. Year-to-year variability in early survival is affected by flow and export rates, but this variation is dampened by density-dependent survival from YOY to recruitment.

**Long-term trends** We have attempted to unravel the causes of the long-term decline by examining indices or estimates of survival rather than abundance. This avoids most problems with autocorrelation and limits the range of possible causes to those associated with declining survival.

Previous analyses have attempted to explain the downward trend in striped bass abundance as a result of effects of flow and exports on young fish (Stevens et al. 1985; CDFG 1992). Despite the long-term decline in abundance at all life stages, and the increasing trend in export flows, no comparable temporal trend could be seen in survival indices for egg to 6mm, egg to YOY, egg to recruit, or larval stages, or any of the apparent mortality rates for age 0+ striped bass. Also, modeling studies have shown that it is unlikely that flows and exports alone could explain the observed decline (Rose et al. in prep.).

Effects of contaminants have been hypothesized as potentially detrimental to striped bass populations (Hall et al. 1985; Stevens et al. 1985). Bailey et al. (1994) reported close correlations between YOY index and the estimated instream concentrations (EICs) of several pesticides commonly applied to rice. Evidence of toxicity to striped bass of water 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. Although it is tempting to extrapolate to the striped bass population as a whole, this extrapolation is not supported by the population-level data. These chemicals would be most likely to affect the striped bass either during reproduction or during early larval survival, when the fish are in the river during the time of application, and would therefore be exposed to high concentrations of agricultural chemicals. Any substantial population-level effect should therefore manifest itself in the egg-YOY survival index, but that index was unrelated with EIC's of any of the rice pesticides.

Another possibility to explain the decline in YOY index is the reduction in organic loading presumed to have resulted from the increase in degree of sewage treatment throughout the system (Stevens et al. 1985; see Rose et al. in prep.). Although the lack of a time trend in early survival does not reflect a significant role of declining organic input in producing fewer young fish, the reduction in carrying capacity for striped bass between age 0<sup>+</sup> and 3 suggest a lower overall system productivity, the cause of which is unknown.

Mortality of adults increased through the 1970s as shown by tagging studies and the Petersen estimates (Figure 9). In addition, on at least two occasions (1976-77 and 1992-94) there has been a downward step in abundance of the larger striped bass, with the result that the proportion of the larger, more fecund striped bass in the population has declined. Increasing adult mortality could result from increasing fishing pressure: declining stock size and recruitment in the Chesapeake Bay in the 1970s and early 1980s apparently resulted from increased fishing mortality (Goodyear et al 1985). However, there is no evidence from the San Francisco estuary that increased fishing effort has caused increased adult mortality; if anything, effort in the bay sport fishery has probably decreased due to progressively poorer catches, and CDFG estimates of legal fishing effort show a decline (CDFG 1987). The effect of illegal fishing is unknown.

The step changes that apparently reduced the abundance of larger striped bass may result from the difference in migratory patterns with age. Older striped bass migrate to sea more than younger ones (Orsi 1971, Secor and Piccoli 1996), and the ocean fishery takes larger striped bass than the fisheries in the bay

(White 1986). Radovich (1963) found that an index of seaward migration was strongly related to sea surface temperature at Pacific Grove or La Jolla, with striped bass migrating more toward sea when surface temperature was high. Coutant (1985) hypothesized that large striped bass are "squeezed" by a shrinking thermal niche in the bay, and that migration to sea can be viewed as a search for a suitable temperature. However, temperature in the bay (Figure 4) was unrelated to abundance of adult bass. The 2 psu isohaline was anomalously far upstream in the summer of 1977, and also during the protracted drought of the late 1980s-early 1990s (Figure 4C), when abundance of larger striped bass also declined; however, migration patterns of striped bass are believed to be more attuned to temperature than salinity (Coutant 1985; Secor and Piccoli 1996).

Nevertheless, White (1986) reported that catches of large striped bass in the ocean fishery were unusually high in 1977, the year preceding the biggest decline in fish older than 5 years (Figure 5). Although he could not identify a cause of the high catch, he suggested that this harvest could have been "detrimental". Furthermore, Bennett and Howard (submitted) found that catches of striped bass in the ocean fishery were high relative to those in the bay starting in 1977, and this trend appeared to be related to increasing frequency of El Niño events and step changes in other variables in the Pacific (Ebbesmeyer et al. 1991). Thus, although the temperature data do not suggest that the "thermal niche" was moving more striped bass offshore, a greater proportion seems to be in the ocean since 1977 than before.

Primarily because of the loss of older, more fecund fish, potential egg production of the striped bass population declined sharply in the late 1970s (Figure 6). Abundance of eggs and all stages of young striped bass (Figure 3) declined at the same time. This decline in abundance of young striped bass was most likely a result of the decline in potential egg production.

Our analyses are consistent with changes in adult mortality resulting in lower egg production and ultimately the long-term decline of the population, although we recognize that correlative analyses have inherent weaknesses. Other proposed explanations for the decline require early survival to have declined, for which we found no evidence. There was also no time trend in the explanatory variables for early survival,  $X_2$  and export flow (Figure 4), during the time period of the analyses presented here. Egg-YOY survival index may have been higher before 1969, when SWP pumping began.

**Year-to-year variability** Interannual variability in the San Francisco Bay striped bass population offers a

contrast to patterns described in east coast estuaries (Pace et al. 1993, Secor and Houde 1995, Rutherford et al. 1997). In those locations, correspondence among life stages was relatively poor. The San Francisco Bay population showed considerable coherence among patterns observed in different sampling programs at different life stages, both in responses to flow and in evidence of density dependence.

*Flow effects* Variability in year-class strength of striped bass populations has been variously attributed to effects of flow (Turner and Chadwick 1972), egg supply (Olney et al. 1991), temperature (Secor and Houde 1995), and food supply (Rutherford et al. 1997). Interannual variability of early survival of striped bass in the San Francisco Estuary was primarily influenced by flow conditions (Turner and Chadwick 1972, Stevens et al. 1985, and this paper). An effect of river flow on abundance or production of fish or invertebrate stocks has been observed in numerous estuaries (e.g. Sutcliffe 1972, but see Sinclair et al. 1986; Gammelsrød 1992; Montagna and Kalke 1992; Wilber 1992; Longley 1994; Jassby et al. 1995). Rose and Summers (1992) analyzed catch data for a variety of estuarine fish and invertebrate species and found both positive and negative relationships to flow.

Our conceptual model for the influence of flow on striped bass is as follows. First, high flow moves eggs and larvae rapidly down the river and causes a seaward shift in  $X_2$ . Larvae generally move through the delta before they reach 6 mm length (Turner 1976), and develop near 2 psu salinity (L.W. Miller, unpublished data, see also Figure 7). The rate of movement is slower under the influence of tides than in the river, since residual velocity due to freshwater flow is small in the tidal channels. The larger the freshwater flow, the more rapidly the larvae move out of the delta, and the further west they go to their rearing habitat. Seaward position of 2 psu salinity, and therefore the population center of young striped bass, is associated with lower exposure to export pumping at the CVP and SWP facilities and the numerous smaller diversions in the Sacramento-San Joaquin delta, and possibly to more favorable rearing habitat than the Delta (Turner and Chadwick 1972).

It seems unlikely that the flow-related variability in YOY index is an artifact of the sampling or analytical methods. First, as  $X_2$  moves seaward the center of mass of the population of young striped bass also moves (Figure 7), such that some of them move out of the region sampled by the townet survey (Stevens et al. 1985). Second, five different sampling programs (larval surveys, summer townet, fall midwater trawl, Bay study, and export salvage) show grossly similar patterns of abundance.

Jassby et al. (1995) analyzed the data on egg - YOY survival index, and concluded that the percentage of inflow to the delta that is exported (referred to in that paper as "diversions") had a significant influence on survival that changed how survival responded to  $X_2$ . However, the denominator in the calculation of percent exported is inflow, which is closely correlated with outflow, itself the predictor variable for  $X_2$ . Using  $X_2$  and export flow rate instead of percent exported, we also found a significant negative effect of export flow on survival, but this relationship was complicated by the curvilinear relationship of  $X_2$  to export flow (Figure 11A). The egg - YOY survival index was negatively and linearly related both to  $X_2$  and to the component of export flow that is unrelated to  $X_2$ .

It is useful to examine the time sequence of the effects of  $X_2$  and exports to attempt to unravel the causes. Egg abundance was low compared to potential egg production, but the ratio of the two was unrelated to  $X_2$  or export flow. This low ratio could be due to incomplete sampling, failure to spawn, egg resorption (Whipple et al. 1981), poor egg quality (Zastrow et al. 1989), or egg mortality. Olney et al. (1991) found mortality of striped bass eggs to average 68%  $d^{-1}$ , which alone would be nearly high enough to account for the low egg abundance.

The influence of  $X_2$  on survival occurs mostly between hatching and the 6-mm larval stage, based on the similarity of relationships of egg-6mm and egg-YOY survival indices to  $X_2$  (Table 8, Figure 13) and the lack of relationship of larval mortality to  $X_2$  (Figure 10). This stage encompasses a portion of the period of transport from the river to the low-salinity zone of the estuary, but also the onset of exogenous feeding, which occurs at about 5mm length (Eldridge et al. 1982).

The influence of export pumping could account for both the significant relationship to export flow and the relationship to  $X_2$ , since the proportion of striped bass lost to pumping may depend as much on the vulnerability of the population as the rate of export flow. The significant effect of export flow occurred between the 6-mm larval stage and YOY (Table 8). This suggests that the effect of  $X_2$  may not be related to vulnerability to exports, since it occurred at a different part of the life cycle; however, that conclusion may not be warranted given the variability in the data.

There are no reliable data on the gross rate of water withdrawal of the small diversions. Net rates calculated from cropping patterns, evapotranspiration, and precipitation approach the rates of export at the combined state and federal pumping facilities (California Department of Water Resources data). Gross

rates (more relevant to these analyses) would exceed net rates by an unknown amount. This potentially significant source of mortality remains unexplored. However, mortality due to these diversions would probably be related to the degree of exposure of the striped bass population as influenced by  $X_2$ .

Survival from the first summer through the rest of the first year was related to abundance (see below) but if anything was positively related to  $X_2$  and export flow. Furthermore, the apparent mortality rates were not positively correlated with the estimated loss rate to the export pumps (Figure 16, Table 11). The implication is that the actual mortality of the fish exposed to pumping is small (because of successful salvage) or that background mortality is much higher. Daily mortality rates generally fit the relationship determined by Rose et al. (1993), with mortality decreasing sharply during the first few months of life (Figure 19). 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 (Olney et al. 1991, Rose et al. 1993). Based on the mortality curve and on growth rate data, we estimate that total mortality from June through December should be about 76%. By comparison the median losses to pumping were estimated at 33%, a substantial fraction of the 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. Alternatively, high mortality due to pumping losses may be offset by density-dependent effects, as discussed below.

Stevens (1977) reported that the CPUE recruit index from the party-boat fishery in 1956-1969 was positively related to freshwater flow into the estuary during June and July 3 years earlier. The relationship was apparently linear and strong ( $r=0.83$ ,  $n=13$ ; Stevens 1977), although the data point for 1967 was omitted without explanation. This relationship has apparently deteriorated starting with year-class 1971 and since then has not been significant. In addition, the lack of a relationship between the Petersen estimate of abundance at age 3 and flow 3 years earlier suggests that this relationship did not exist for year-classes after 1966. The Petersen estimates may be more reliable in requiring fewer assumptions, and in their higher correlation with the CPUE index from the Carquinez Strait fishery, which targets young fish. The explanation for the collapse of the relationship of recruit index to flow may be that this relationship fails to take into account the effects of spawning stock size.

*Effects of food* Covariation of food supply with freshwater flow has been suggested as a potential mechanism for increased survival of young striped bass with increased flow (Turner and Chadwick 1972; Stevens et al. 1985; Martin et al. 1985; Rutherford et al. 1997). Striped bass larvae are resistant to

starvation (Eldridge et al. 1981, 1982), and starvation has been virtually ruled out for field-caught striped bass larvae in the San Francisco estuary (Bennett et al. 1995). However, reduced growth rate caused by low food supply can reduce survival through prolonged high vulnerability to predation (Bennett 1994). Furthermore, zooplankton abundance in the striped bass rearing area is much lower in the San Francisco estuary (Orsi and Mecum 1986, Kimmerer and Orsi 1996) than in Chesapeake Bay and its sub-estuaries (Heinle 1966; Rutherford et al. 1997). Modeling studies (Rose et al., in prep.) showed that food concentrations in the San Francisco estuary were probably frequently limiting the growth of larval striped bass.

The mechanism often proposed for flow effects on food is that increased nutrients entering the estuary with freshwater stimulate primary production, resulting in higher secondary production and higher food concentration for larval striped bass (Rutherford et al. 1997). This mechanism may not work in the San Francisco estuary. Productivity of the estuary was previously highest when  $X_2$  and the estuarine turbidity maximum or entrapment zone were in Suisun Bay, owing primarily to physical mechanisms (Arthur and Ball 1979, Cloern et al. 1983). Chlorophyll and presumably primary productivity of Suisun Bay declined drastically in 1987 because of intense grazing by the introduced clam *Potamocorbula amurensis* (Alpine and Cloern 1992). Likewise, abundance of the mysid *Neomysis mercedis*, previously correlated with  $X_2$  (Jassby et al. 1995), declined about 10-fold and lost its dependence on  $X_2$  in 1988, presumably because of the reduction in primary production (Orsi and Mecum 1996, Kimmerer and Orsi 1996). The changes in chlorophyll and *N. mercedis* due to this event overshadowed the previous, relatively weak, responses to  $X_2$ .

In spite of the decline in food supply, egg - YOY survival index did not change after 1987. Either the striped bass switched to other food sources, or the influence of flow occurs through some other mechanism than food availability. Carrying capacity for young striped bass between YOY and age 3 appears to have declined over the same time frame (Figure 17B), but there is no apparent relationship between carrying capacity and abundance of *N. mercedis*, the principal food of striped bass during their first year (Heubach et al. 1963; Stevens et al. 1966). Mysids underwent a near-collapse in abundance in 1988 (Orsi and Mecum 1996), but this collapse is not reflected in the time trend of carrying capacity.

**Density dependence** Several lines of evidence indicate density-dependent survival between the first summer and recruitment: the saturating YOY-recruit relationship, the negative relationship between egg-

recruit survival and YOY index, and the correlation of mortality rates to mean log abundance in the combined summer-fall data and the Bay study midwater trawl and otter trawl data. This density-dependent survival nearly eliminates the flow effect on the abundance of young fish.

Density dependence is a necessary condition for, and a fundamental assumption of, a fishery (Sissenwine 1984; Jones 1989): without compensatory effects, removal of adult fish would result in a decline in reproduction and eventual collapse of the population. Nevertheless, evidence of density dependence is infrequently seen in stock-recruit or similar relationships, presumably because of the overwhelming influence of environmental factors that cause density-independent variation in survival (Shepherd and Cushing 1990). The influence of density dependent survival may be too subtle, short-lived, or infrequent to be detected in most sampling programs (Houde 1989).

Density dependence is most often demonstrated where space can be a limiting factor. For example, spawning of salmonids in stream beds can reach a saturation point when the most favorable habitat is occupied first (Neilson and Banford 1989); similarly, survival of young salmonids can be space-limited and therefore compensatory (Elliott 1989). Fish of coral reefs can experience density-dependent survival either during or shortly after settlement into spatially limited habitats (e.g Jones 1984). Density-dependent survival of rockfish (*Sebastes* spp.) off the California coast occurred between settlement onto the rocky bottom and recruitment to the fishery (Ralston and Howard 1995).

Examples of density-dependent effects on fish populations in pelagic or soft-bottom demersal habitats of estuaries or marine waters are much less common. Lockwood (1980) presented evidence of density dependence in plaice. Although fish larvae are not often concentrated enough to affect their prey resource (Cushing 1983), Jenkins et al. (1991) showed that growth of larval tuna in the Indian Ocean was inversely related to density of larvae. Growth rates of silver hake on Georges Bank (Ross and Almeida 1986) and sockeye salmon in the Gulf of Alaska (Peterman 1984) were inversely related to population size. Recruitment of American shad was heavily influenced by environmental factors that tended to obscure significant density-dependent effects (Crecco et al. 1986).

Other striped bass stocks do not appear to undergo detectable density-dependent mortality (Ulanowicz and Polgar 1980; Logan 1985; Rutherford et al. 1997). However, juvenile abundance in the Hudson River estuary was relatively invariant over a wide range of larval abundance (Pace et al. 1993 Figure 6),

suggesting density dependence in this part of the life cycle, i.e., earlier than observed in this study.

The mechanism for the density dependent survival of striped bass in the San Francisco estuary can only be guessed. Reasonable candidates include food limitation, cannibalism, and response of predators. The density-dependent effects occur during the time after the YOY index is determined, when feeding rate of the population is at its maximum (Rose et al. in prep.). However, any presumed single mechanism for density dependence would have to explain also the apparent decrease in carrying capacity (Figure 17). Food limitation does not appear to meet that criterion. Although some zooplankton species have declined in abundance over the same time frame, others have increased (Kimmerer and Orsi 1996). We found no relationship between declines in *Neomysis mercedis* and the decline in carrying capacity. Furthermore, there is no report of declines in abundance of small fish on which the striped bass would begin feeding late in their first year (Heubach et al. 1963).

Predation by conspecifics or others would also appear not to explain the observed data. As the population declined, the effect of predators should also have declined as the predators switched to other, more abundant prey. This mechanism would require an additional condition: either a reduction in alternative prey, or a reduction in available habitat for the young striped bass, as the population decreased. The spatial extent of the population does not appear to have changed as the population shrank, so the striped bass do not appear to have become more concentrated and therefore more vulnerable to predators.

This study demonstrates some of the pitfalls but also the great value of long-term, comprehensive, consistent monitoring. In the Hudson River estuary (Pace et al. 1993) and Chesapeake Bay (Rutherford et al. 1997), patterns of abundance were weakly related among stages and to environmental conditions. We believe that the apparently stronger relationships found in the San Francisco estuary results from the duration, breadth, and intensity of monitoring, as well as the large variation in flow and striped bass abundance providing a high signal-to-noise ratio.

Several questions remain open. First, we have not addressed the potential influence of annual die-offs in Carquinez Strait in late spring-summer (Young et al. 1994). Data on interannual variability and the extent of this event may not be adequate to resolve this. Second, we have not examined the available data on the forage base for young striped bass, which could reveal trends to help in interpreting the pattern of density

dependence and the declining carrying capacity.

### Acknowledgments

We gratefully acknowledge funding by the California Urban Water Agencies and by 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; Chris Foe and the Interagency Ecological Program Contaminants Project Work Team for helpful insights on potential effects of contaminants; 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.

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Table 1. Abundance indices and estimates 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 efficiency.

Variable Name	Frequency	Source	Estimate
Adult abundance	Annual	Tagging survey	Petersen mark-recapture estimates by age and sex or aggregated
Recruitment	Annual	Tagging survey	Petersen estimates of abundance at age 3 years excluding hatchery fish
Party-boat CPUE	Annual	Party boat fishery records	Catch per effort
Party-boat recruit index	Annual	Party boat fishery	Abundance in year $i$ less abundance in year $i-1$ times mean survival
Carquinez Strait CPUE	Annual	Carquinez Strait recreational fishery	Catch per effort, mainly age 3-5 fish
Potential egg production	Annual	Annual tagging survey, fecundity estimates	Petersen estimates $\times$ age-specific fecundity $\times$ maturity/migration corrections
Egg abundance	Annual	Egg and larval surveys	Annual abundance estimate
Larval abundance	Annual	Egg and larval surveys	Annual abundance estimate by 1-mm length intervals
6-mm larval production	Annual	Egg and larval surveys	Intercept of larval abundance graph at length=6 mm
Young-of-Year (YOY) Index	Annual	Summer townet survey	Index of abundance interpolated to mean length of 38mm
YOY abundance	Variable	Summer townet survey	Sum of catch/volume times volume weighting factor
Midwater Trawl (MWT) Index	Annual	Fall Midwater Trawl	Index of abundance from average over months
MWT abundance	Monthly	Fall Midwater Trawl	Sum of catch volume times volume weighting factor
Bay Study Midwater Trawl abundance	Monthly	San Francisco Bay Study	Sum of catch volume times volume weighting factor
Bay Study Otter Trawl abundance	Monthly	San Francisco Bay Study	Sum of catch volume times volume weighting factor
Salvage abundance	Monthly	Salvage data from export pumping plants	Data expanded from samples for abundance by species and length, calculated as fish per unit volume

Table 2. Survival, mortality, and growth indices and estimates used in the analysis. Survival was calculated for specified interval in the life cycle, e.g., egg to recruit. Mortality was calculated when it could be evaluated per unit time, either month or year. The exception is larval mortality, for which mortality was evaluated over growth increments, which could vary among years.

Variable Name	Time period	Estimate
Petersen estimate of adult mortality	Year	Slope of Petersen estimates of log abundance vs. age up to age 7, by year-class
Tagging estimate of adult mortality	Year	From annual party boat tag returns using Ricker 1975 equation 5.1 and converting to instantaneous mortality, by year for all ages
Egg-recruit survival	Interval	Ratio of recruitment to egg production
Larval mortality	1mm growth increment	Slope of log larval abundance vs. length
Egg-6mm survival index	Interval	Ratio of 6mm production to egg production
Egg-YOY survival index	Interval	Ratio of YOY index to egg production
6mm -YOY survival index	Interval	Ratio of YOY index to 6mm production
YOY-recruit survival	Interval	Graph of recruit abundance vs. YOY index
Summer-fall apparent mortality rate	Monthly	Log of summer and fall abundance fit to a quadratic curve (implying linearly decreasing mortality rate with age); slope evaluated between months 7 and 11 for consistency
Bay Study Midwater Trawl apparent mortality rate	Monthly	Slope of log abundance over time from July to April
Bay Study Otter Trawl apparent mortality rate	Monthly	Slope of log abundance over time from July to April
YOY growth rate	Month	Fit of von Bertalanffy growth curve to data on length by month from combined Bay study samples
Transport rates	Monthly, accumulated summer-fall	Proportion of fish transported to CVP and SWP export facilities (pumping rate times abundance in southern delta divided by total abundance), with adjustments for size and for proportion returned to the estuary by salvage operations.

Table 3. Environmental variables used in the analysis. IEP is the California Interagency Ecological Program, USGS is US Geological Survey, and DWR is the California Department of Water Resources.

Variable Name	Frequency	Source	Estimate
Temperature	Monthly	IEP surveys, continuous monitoring stas.	Mean summer temperature by region from IEP zooplankton surveys, validated using continuous data
Sacramento River flow	Monthly	USGS	Flow at Grimes (100 km upriver from Sacramento)
Export flow	Monthly	DWR	Gaged flows leaving Delta in federal, state, and local pumping facilities
Delta outflow	Monthly	DWR	Flows into the Sacramento-San Joaquin Delta (most gaged, some estimated) minus export flow minus estimated net consumption in Delta
X <sub>2</sub>	Monthly	Calculated from DWR data	Distance in river kilometer to 2 psu isohaline, either interpolated from fixed monitoring stations or calculated as lagged function of outflow (Jassby et al. 1995)
Pesticide application rate	Annual	CA Dept. of Pesticide Regulation	Total pounds applied of selected chemicals
Pesticide EIC	Annual	Calculated	Estimated instream concentration (EIC) = Application rate divided by Sacramento River flow

Table 4. Fecundity values (thousands of eggs per female) used in this study with factors included in the calculation, and values reported by Stevens et al. (1985, Table 2).

Age	Raw Fecundity	Mean Migration Correction	Maturity Correction	Mean Fecundity	Stevens
3	0	--	--	0	0
4	260	0.20	0.35	18	14
5	470	0.76	0.87	310	350
6	670	1	1	670	652
7	880	1	1	880	856
8+	1260	1	1	1260	1427

Table 5. Comparison of abundance at salvage facilities with data from net samples taken close to the facilities during the same month. Data presented are geometric mean ratios of the salvage abundance estimates to those taken in the net samples with 95% confidence limits (CL). Asterisks denote mean log ratios significantly different from zero at  $p < 0.05$  (\*) or  $p < 0.01$  (\*\*) (t- test, 85 df for townet and 70 df for midwater trawl data).

Survey data	Federal Facility	State Facility
Summer Towntet (YOY)	0.47 (CL = 0.34 to 0.65)**	1.2 (CL = 0.9 to 1.7)
Fall Midwater Trawl (MWT)	1.3 (CL = 1.0 to 1.8)*	1.3 (CL = 0.8 to 2.2)

Table 6. Variance in log of abundance measures of striped bass life stages.

Variable	Number of Points	Variance
Abundance at age 3	26	0.04
Abundance at age 4	26	0.04
Abundance at age 5	26	0.03
Abundance at age 6	26	0.09
Abundance at age 7	26	0.14
Abundance at age 8+	26	0.16
Carquinez Strait CPUE	19	0.06
Party Boat CPUE	26	0.12
Potential egg production	26	0.11
Egg abundance	10	0.16
YOY index	25	0.19
MWT index	24	0.18
Bay study MWT abundance	11	0.10
Bay study otter trawl abundance	11	0.06

Table 7. Regression statistics: (1) export flow rate ( $m^3s^{-1}$ ) vs. natural spline of  $X_2$  (2 degrees of freedom); and (2) log egg - YOY survival index vs.  $X_2$  and the residual from the export flow- $X_2$  relationship. Partial  $R^2$  values for the independent variables in the second regression were 0.41 and 0.14 respectively.

Dependent Variable	Degrees of Freedom	Independent Variable	Slope	Standard Error	p	$R^2$
(1) Export Flow	22	$X_2$	--	--	0.017	0.25
(2) Log Survival	22	$X_2$	-0.027	0.005	<0.0001	0.59
		Residual from (1)	-0.0038	0.0014	0.012	

Table 8. Regression statistics: log of egg-YOY survival index vs.  $X_2$ , egg - 6mm survival index vs.  $X_2$ , and 6mm - YOY survival index vs. export flow (all April-June means).

Survival index	Independent variable	Degrees of Freedom	Slope	Standard Error	p	$R^2$
Egg-6mm	$X_2$	12	-0.032	0.006	0.0003	0.67
Egg-YOY	$X_2$	12	-0.032	0.008	0.0016	0.58
6mm-YOY	Export Flow	12	-0.0044	0.0016	0.02	0.37

Table 9. Regression statistics: Apparent mortality rate of young striped bass by month in three sampling programs vs. mean log abundance in the same programs. Slopes are geometric mean slopes (Figure 15), and statistics are based on linear regression.

Sampling Program	Degrees of Freedom	Slope	Standard Error	p	$R^2$
Summer-Fall (YOY/MWT)	21	0.48	0.09	0.006	0.31
Bay Study Midwater Trawl	9	0.50	0.12	0.012	0.52
Bay Study Otter Trawl	9	0.44	0.10	0.009	0.55

Table 10. Regression statistics: Apparent mortality rate of young striped bass by month in three sampling programs vs.  $X_2$  for April-December, linear regression. Probability values  $p$  were determined using a one-tailed distribution to determine significance for positive slopes only (i.e. increasing  $X_2$  associated with higher mortality).

Sampling Program	Degrees of Freedom	Slope	Standard Error	$p$
Summer-Fall (YOY/MWT)	21	-0.012	0.0056	>0.5
Bay Study Midwater Trawl	9	-0.012	0.004	>0.5
Bay Study Otter Trawl	9	-0.0075	0.0026	>0.5

Table 11. Percent of biomass transported to export facilities (Figure 16A, dotted line) and estimated percent of biomass lost (i.e. not salvaged; Figure 16A, lower solid line) vs. apparent mortality from three sampling programs (Figure 16B-D). Values given are Pearson correlation coefficients for each pair of values with 95% confidence limits. None of the correlation coefficients is significantly greater than zero; values significantly less than zero were not tested since that implies an increase in mortality with a decrease in export losses.

Apparent Mortality from Sampling Program	Percent Biomass Transported	Estimated Mortality (Biomass)
Summer-Fall (YOY)	-0.18±0.43	-0.06±0.43
Bay Study Midwater Trawl	-0.81±0.68	-0.66±0.68
Bay Study Otter Trawl	-0.71±0.68	-0.54±0.68

Table 12. Regression statistics: log of egg-recruit survival vs.  $X_2$ , YOY index, and the interaction.

Independent Variable	Parameter	Standard Error	$p$	$R^2$
Intercept	3.81	0.51	~0	0.62
$X_2$	-0.039	0.006	<0.0001	
YOY Index	-0.046	0.010	0.0007	
$X_2 \times$ YOY Index	0.00055	0.00013	0.0002	

## Figure Captions

1. Map of the San Francisco estuary and Sacramento-San Joaquin delta with the location of the major export pumping plants, and lines indicating selected river kilometer indices.
2. Schematic diagram of striped bass life cycle showing the sampling programs that track abundance of each life stage and the range of years for which data were used in this study. The dashed arrow shows the approximate segment of the life cycle in which density dependence seems to occur.
3. Time course of abundance indices of several life stages of striped bass. A, summer townet index of young-of-the-year (YOY); B, fall midwater trawl index (MWT); C, Age 3-5 abundance estimates (symbols) and Carquinez Strait CPUE index (solid lines) scaled by the mean ratio between the two values; D, total abundance estimate (symbols) and party-boat CPUE index (solid lines) scaled by the mean ratio between the two values.
4. Time course of several environmental variables: A, summer temperature in three regions of the bay based on river kilometer; B, April-June flow in the Sacramento River (thin line) and net outflow from the delta to the estuary (heavy line); C, mean  $X_2$  from April to June; D, mean export flow rate from April to June.
5. Time course of adult abundance by age-class. A, by age class; B, grouped age classes 3-5 years (heavy line, left axis) and 6 years and over (thin line, right axis), scaled so the mean of values before 1978 overlies each other.
6. Time course of potential egg production as estimated by the Petersen mark-recapture estimate and age-specific fecundity, with 90% confidence limits (shaded). The thin line is a step function fit to the data.
7. Median position of young striped bass in river kilometer for each survey plotted against mean  $X_2$  for each month: A, summer townet 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. The vertical bars represent the grand median (cross bar) and the medians of the 5th and 95th percentiles of position for each survey. Horizontal dashed line indicates the position in river kilometer of the junction of Middle River and the San Joaquin River (Figure 1), where vulnerability to export pumps probably increases.
8. Recruitment vs. net delta outflow three years earlier. A, recruit index from the party boat fishery (Stevens 1977) with solid symbols for year-classes up to 1971 (shown by numbers) and open

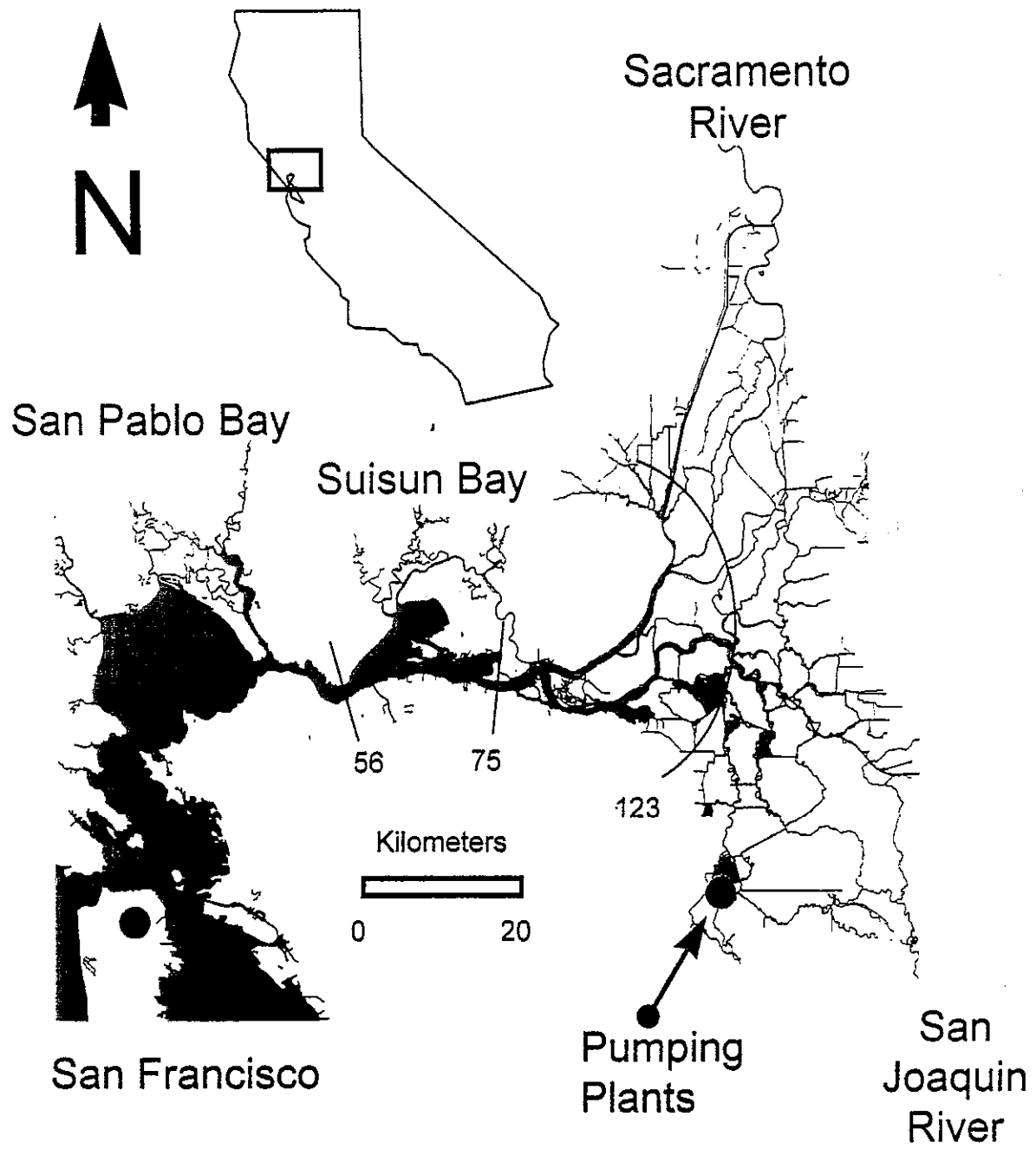
symbols for subsequent year-classes; B, Petersen estimate of abundance of 3-year-old striped bass; numbers are year-classes.

9. Tagging estimates of mortality by year (line), and Petersen estimates by year-class (symbols with 95% confidence limits). The year-class is shifted 4 years from the calendar year in which the mortality is considered to have occurred, because mean age of the striped bass is around 4 years.
10. Regression results for log abundance of larval striped bass vs. length (mm). A and B, slope of the regression plotted against year (A) and  $X_2$  (B). C and D, 6 millimeter intercept of the regression plotted against year (C) and  $X_2$  (D). Numbers in B and D are years. The line in D is a significant linear regression ( $y = 7.1 - 0.020x \pm 0.007$ , 14 df,  $p < 0.01$ ). Open squares indicate data points that were not included in the survival estimate (1977 had data only from 6-9 mm length) or the 6mm production estimate (1973 included data only from 9-14mm).
11. Egg - YOY survival index. A, relationship of  $X_2$  to export flow in April-June fitted with natural spline with two degrees of freedom. B, predicted vs. observed log survival index; prediction from a linear model including  $X_2$  and the residual from the natural spline curve in A. C, time trend of survival index; D, time trend of residual from B.
12. 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 tonnes per year for molinate, copper sulfate, and all other chemicals; B, time trend of YOY index over the same period; C, YOY index plotted against the estimated instream concentration (EIC) of molinate; D, egg-YOY survival index vs. EIC of molinate.
13. Survival indices vs.  $X_2$ : A, egg - YOY; B, egg - 6mm larvae, both for the same set of years. Numbers are years, and lines are significant linear regressions (Table 8).
14. Combined abundance data from the summer townet survey and fall midwater trawl survey (log scale) plotted against survey dates expressed as calendar month. Each line presents the data from a single year. Dotted lines and open symbols identify points not used to determine rates of decline. The heavy line is a quadratic function fit to all the remaining data.
15. Apparent mortality rate plotted against mean log population size for: A, combined summer and fall surveys; B, Bay study midwater trawl; and C, Bay study otter trawl. numbers are years and lines give geometric mean regression slopes (Table 9).
16. A, estimated percentage transport to the export facilities of young striped bass during June-December: Open circles, percentage by number; thin line, by weight; closed circles, estimated mortality by weight. B-D apparent mortality rate in three data sets depicted in Figure 15, with

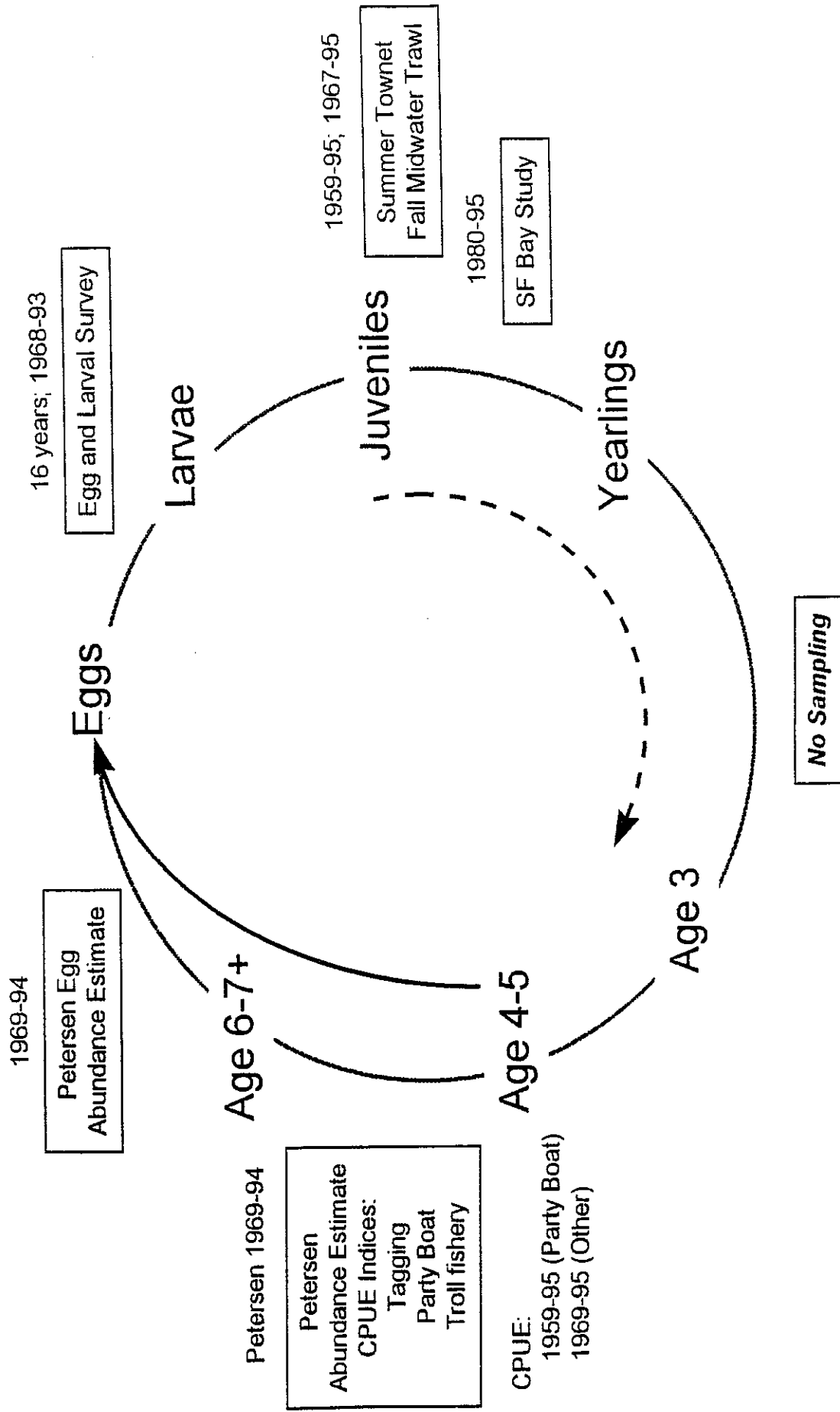
95% confidence limits.

17. A, Relationship between YOY and recruitment at age 3 fitted to a Beverton-Holt stock-recruit curve. Numbers are years, and horizontal and vertical lines give standard errors. B, time course of residual from A (line with symbols); sizes of symbols are scaled to the YOY index, and the straight line is fitted by linear regression weighted by the YOY index (see text).
18. Egg-recruit survival. A, Log of survival vs. that predicted from the a model including  $X_2$  and YOY index (Table 12), with the 1:1 line. B,  $X_2$  vs. YOY index with size of symbols representing relative magnitude of egg-recruit survival, and contour lines of survival determined by the model.
19. Mortality rate as a function of size of striped bass. The four values are for survival from egg to YOY abundance, survival from summer through fall from the combined summer townet and fall midwater trawl surveys, and the two Bay study datasets. Horizontal lines give the approximate range of lengths included and the median mortality rate, while vertical lines give the range (thin lines) and the upper and lower quartiles (thick lines) of the mortality rate. The curved line is that fit by Rose et al. (1993) to data from various sources:

$$Mortality = 0.003 + 0.295 e^{-0.075 L}$$



# Striped Bass Sampling



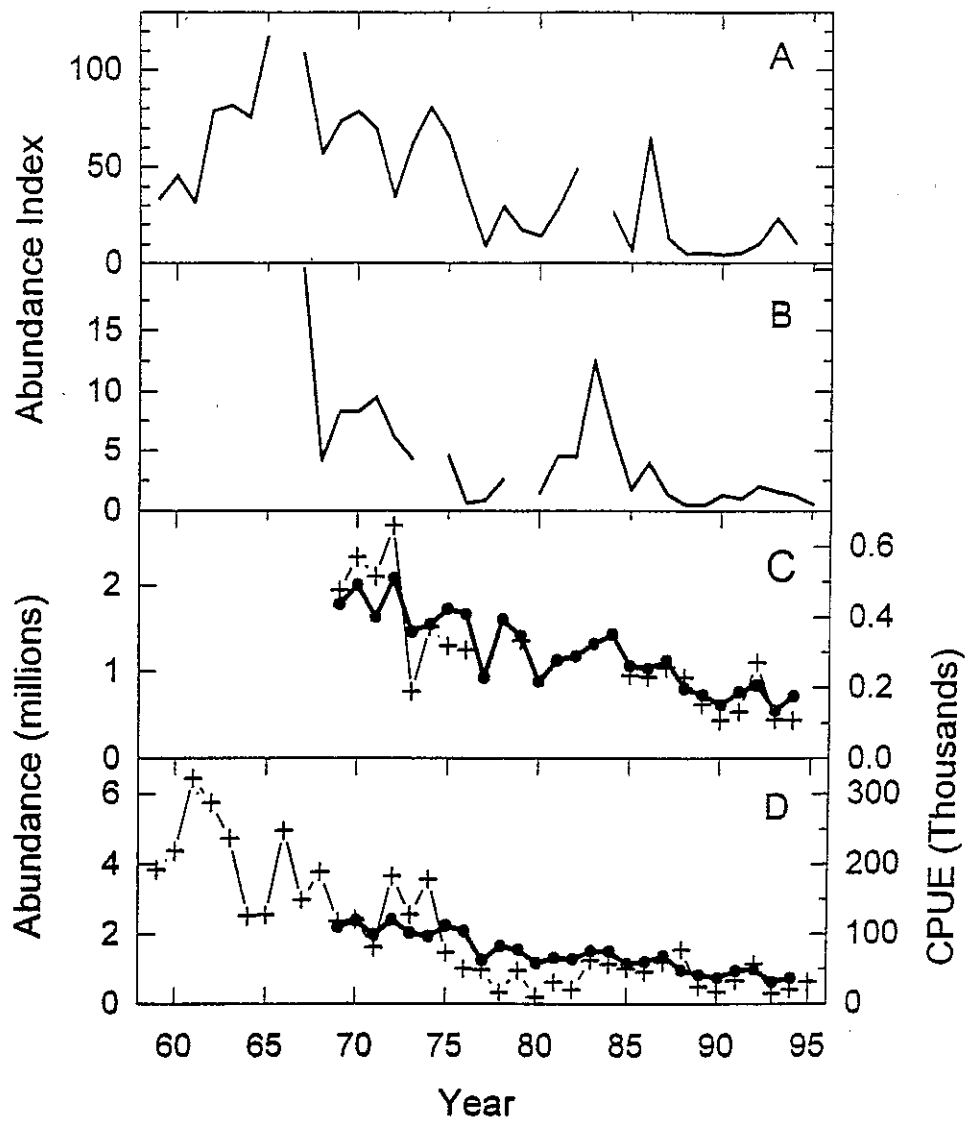


FIGURE 3

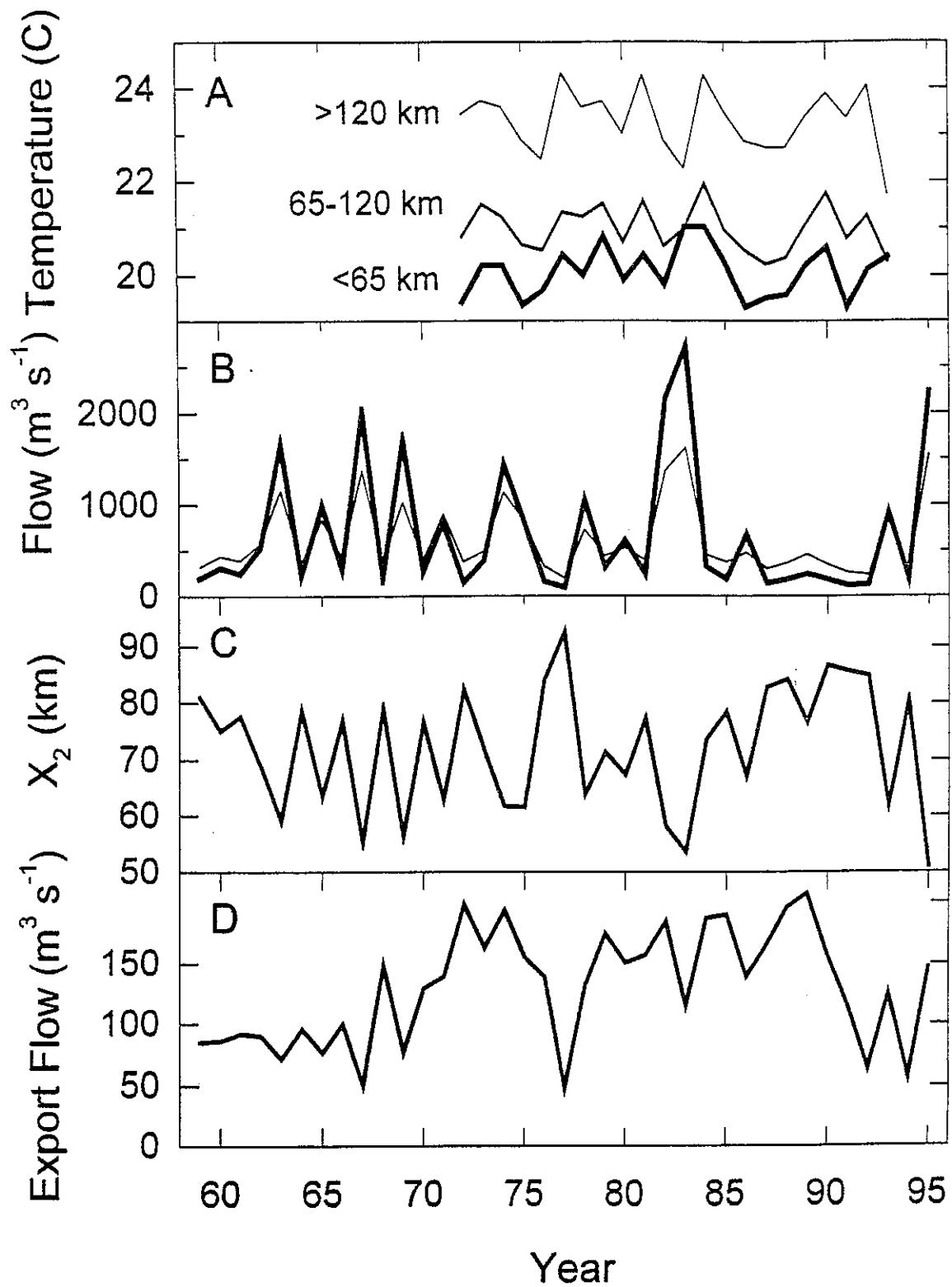


FIGURE 4

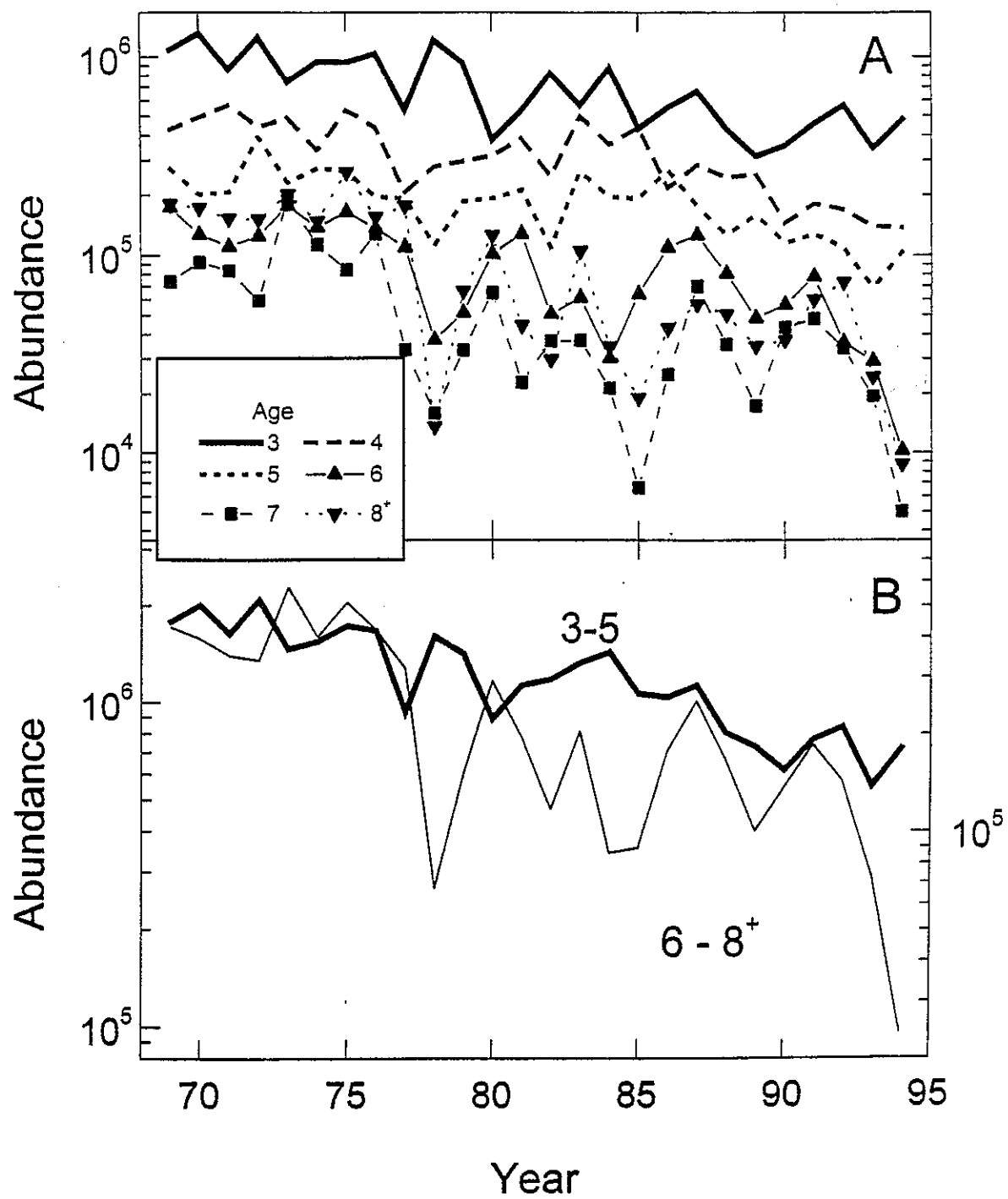
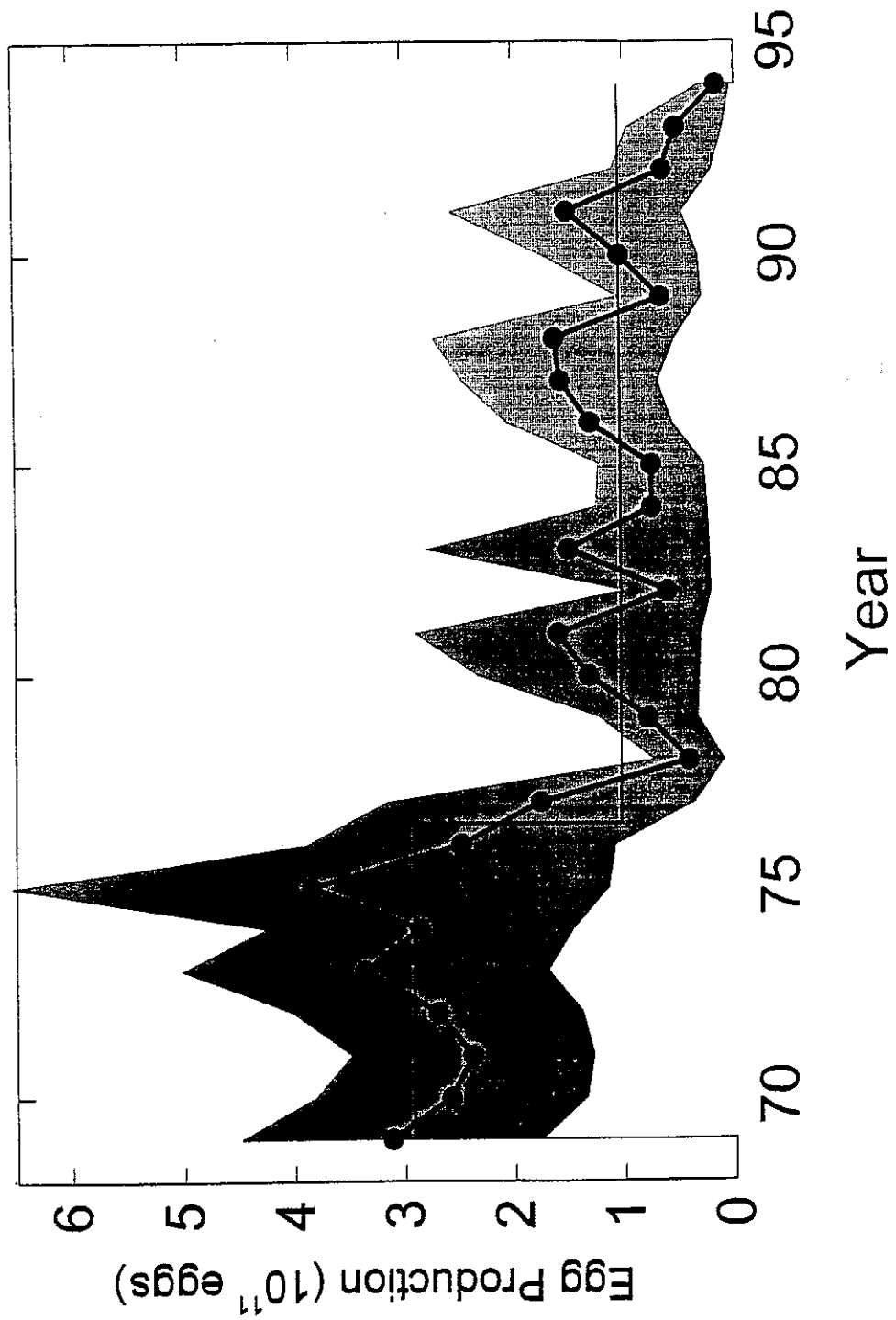


FIGURE 3



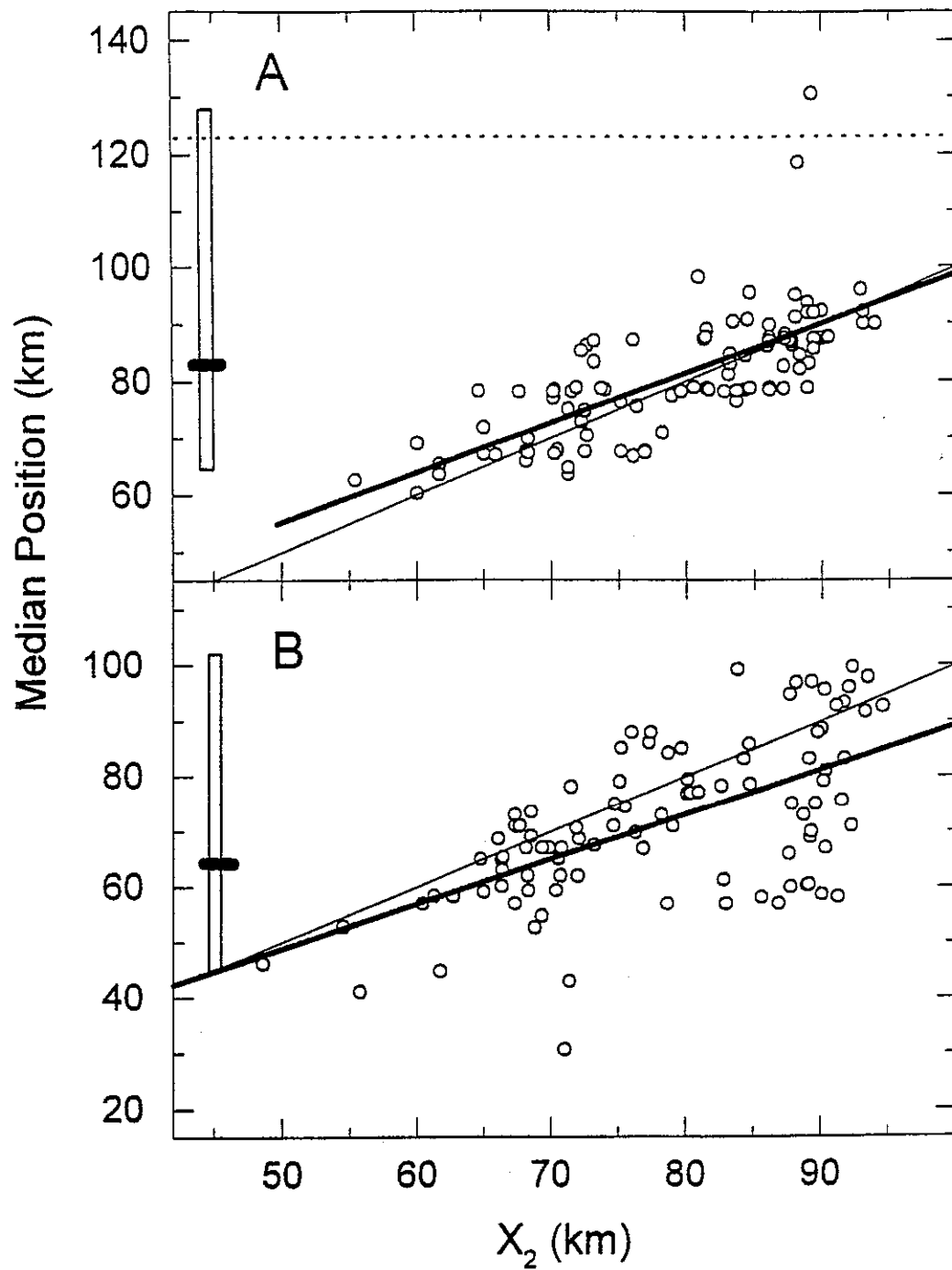


FIGURE 7

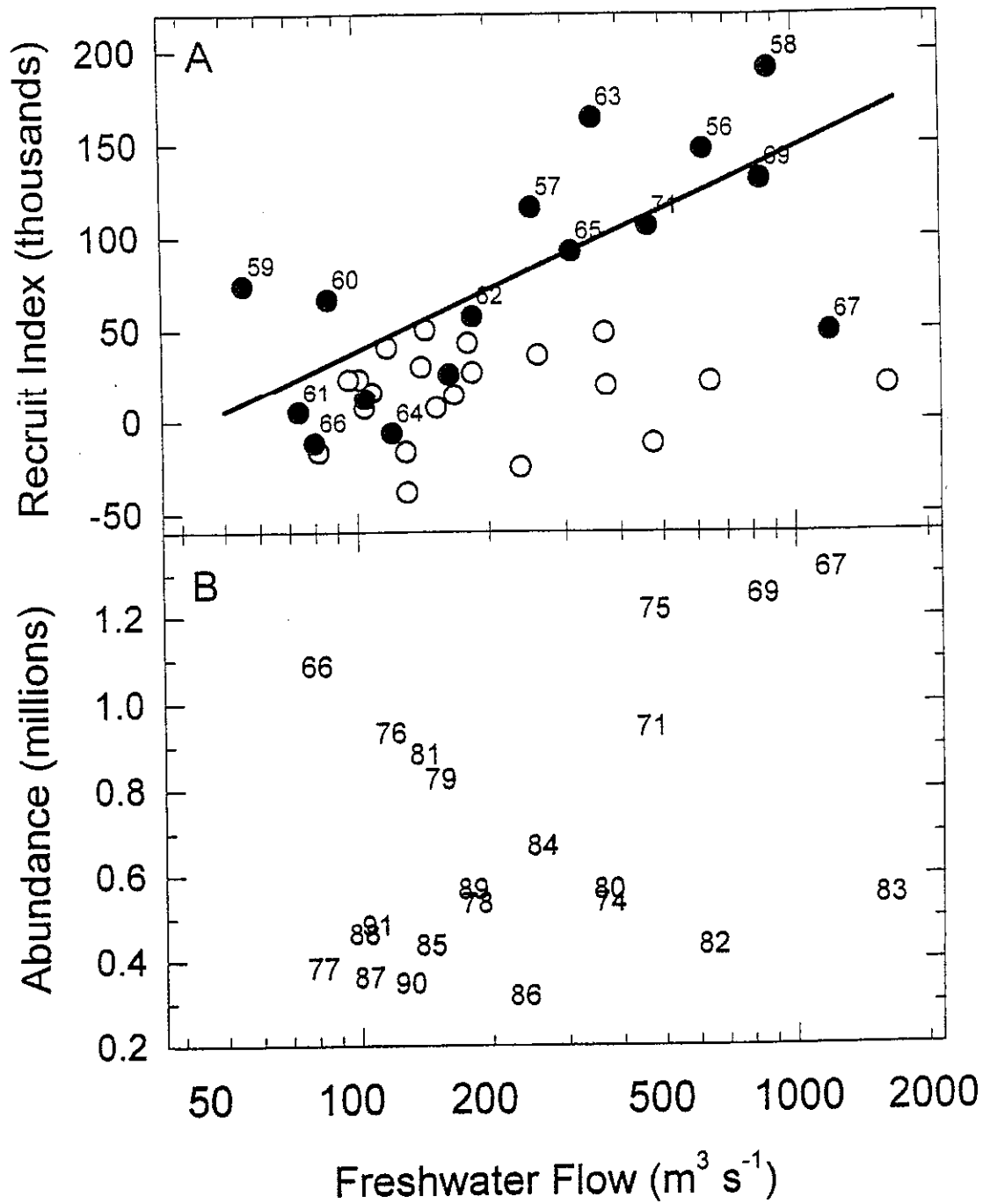


FIGURE 8

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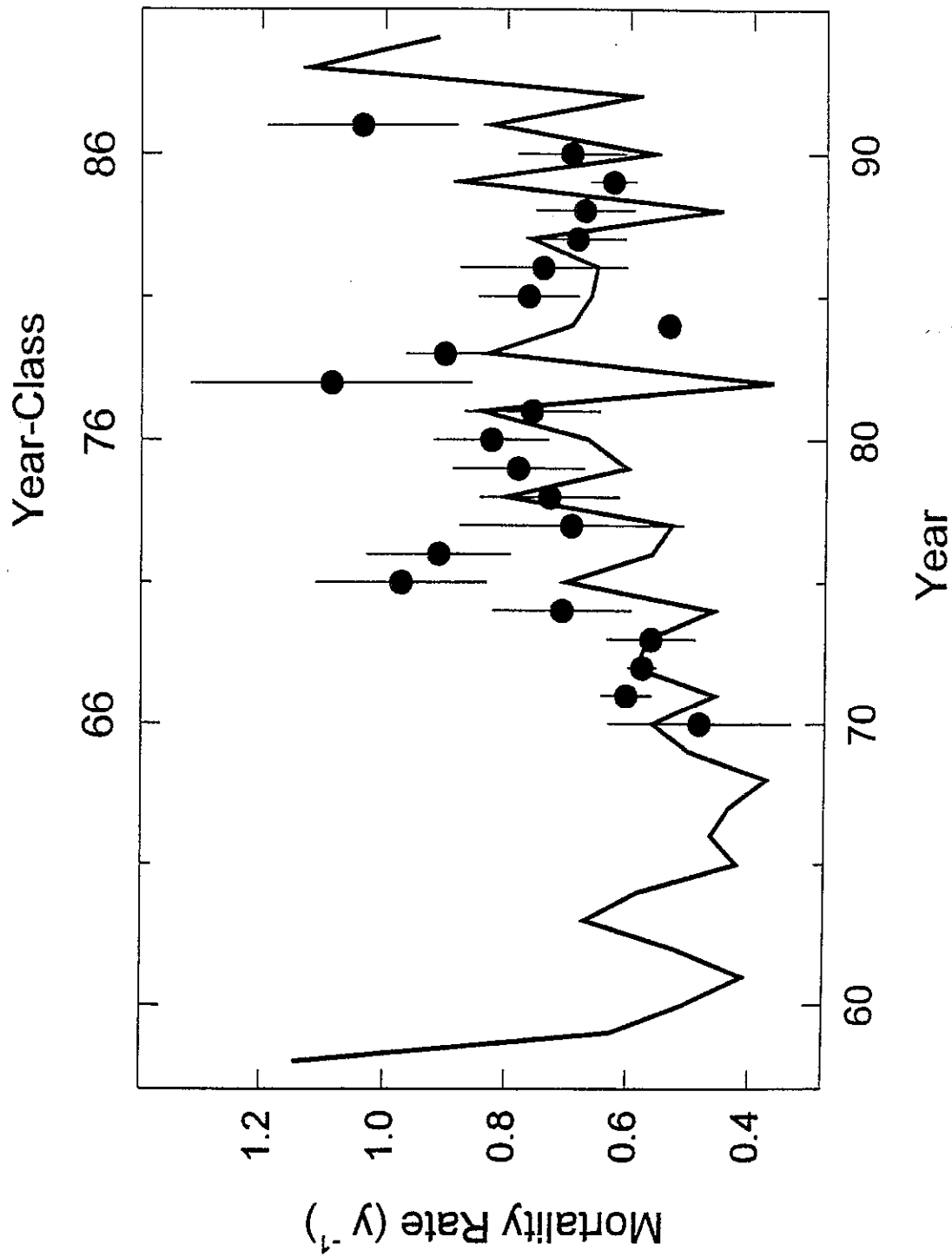


FIGURE 9

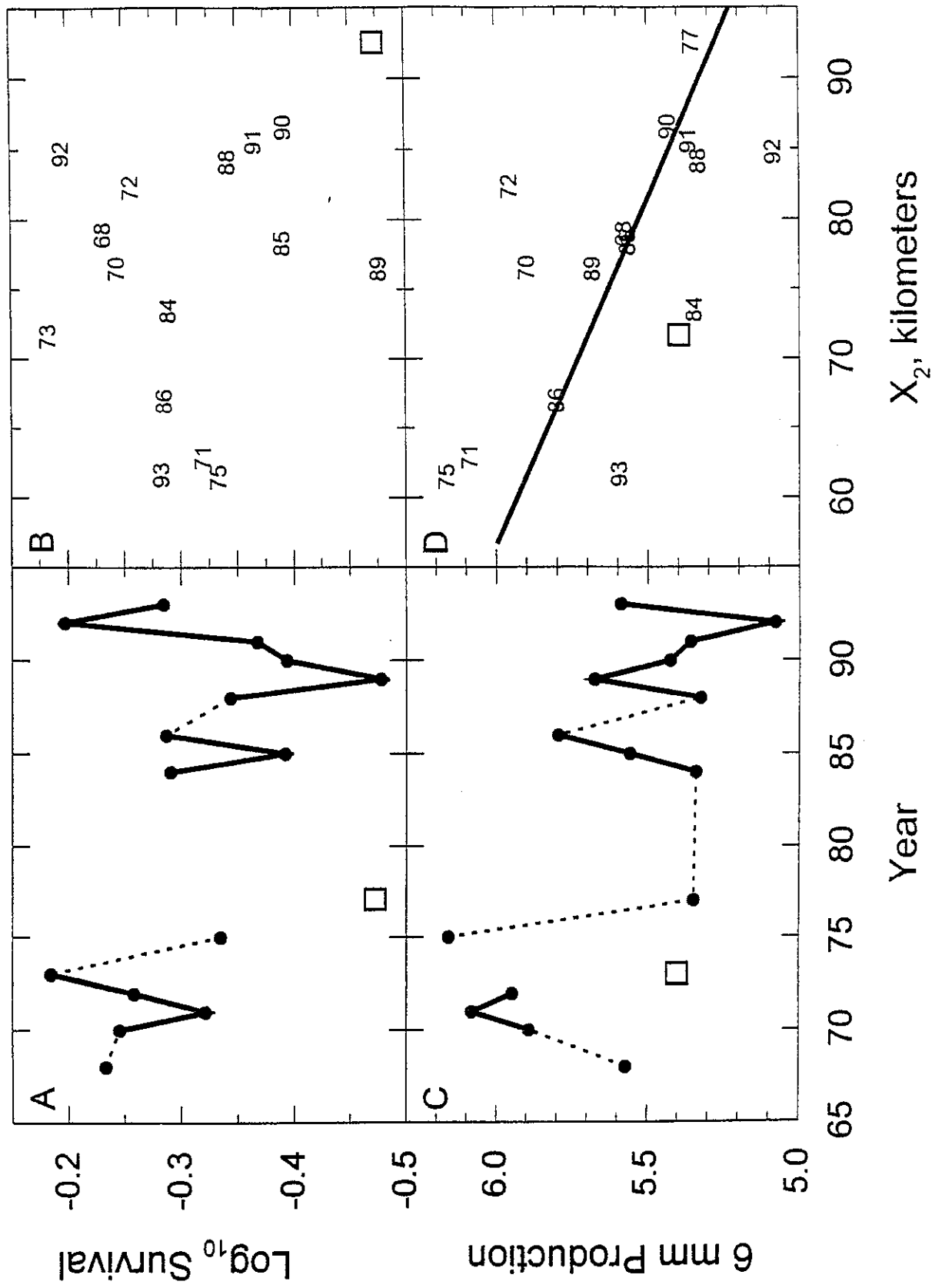


FIGURE 10

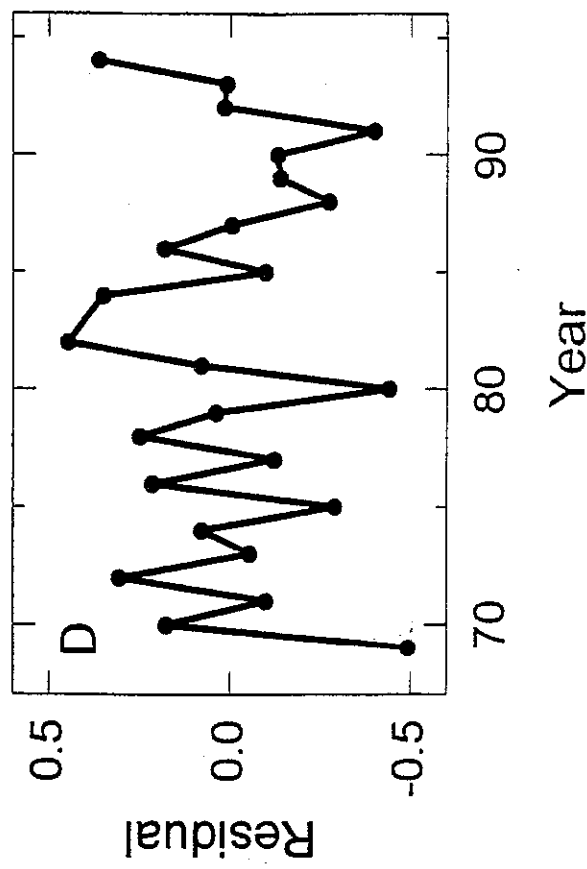
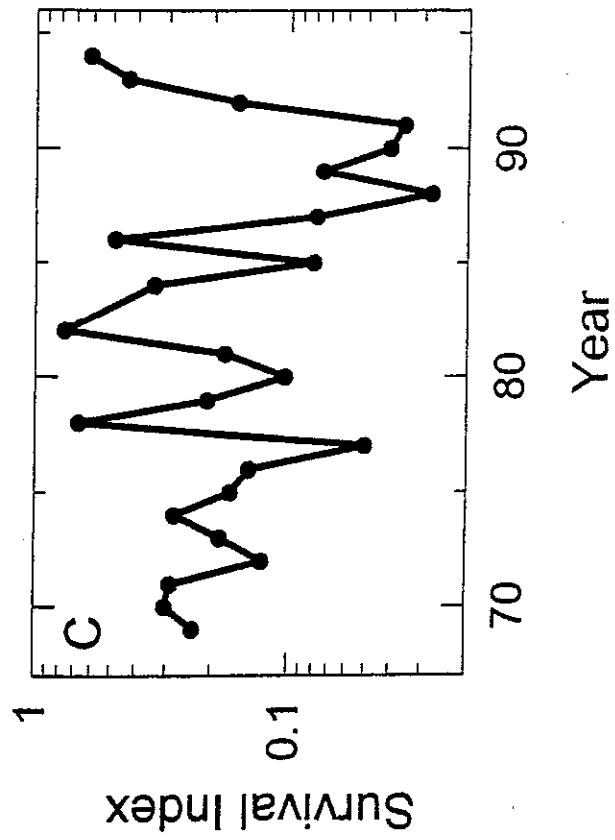
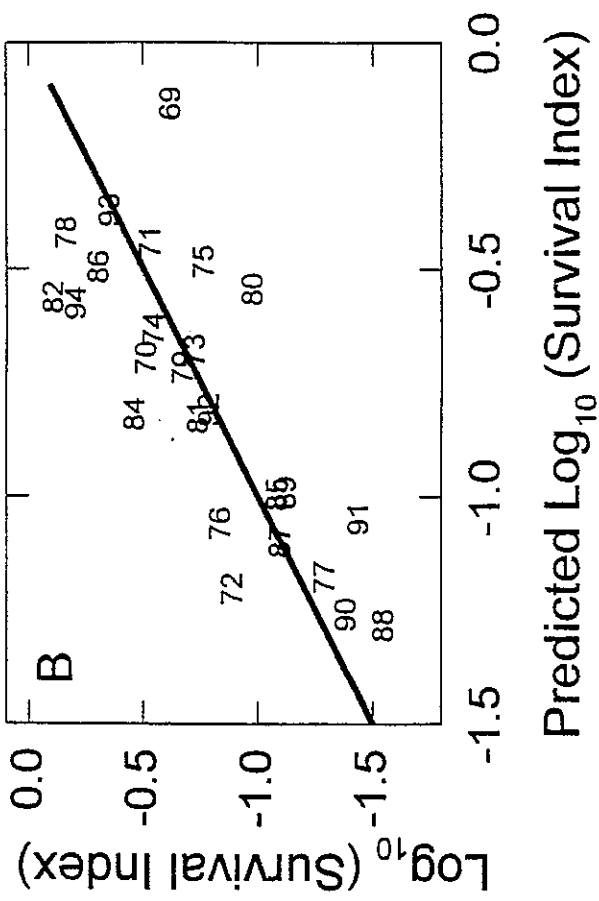
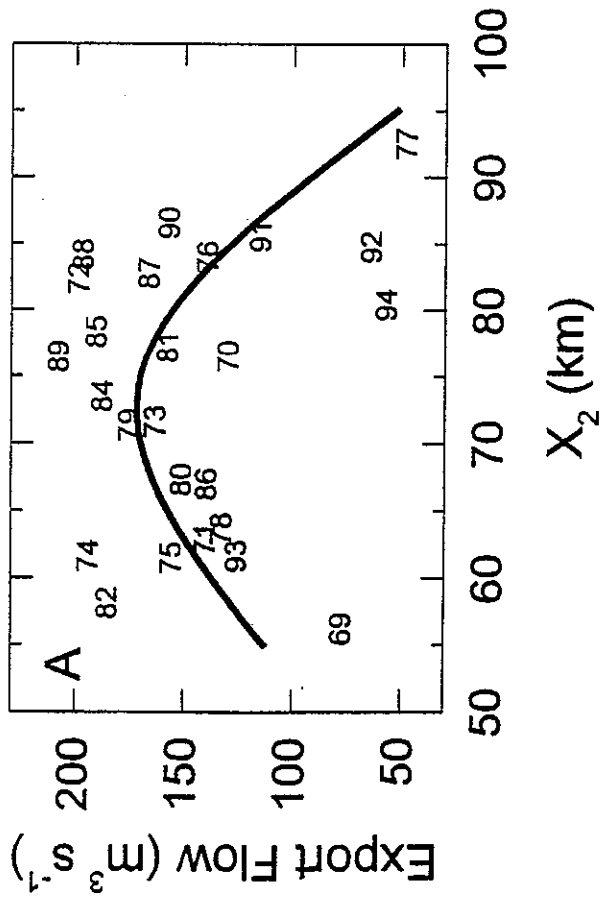


FIGURE 11

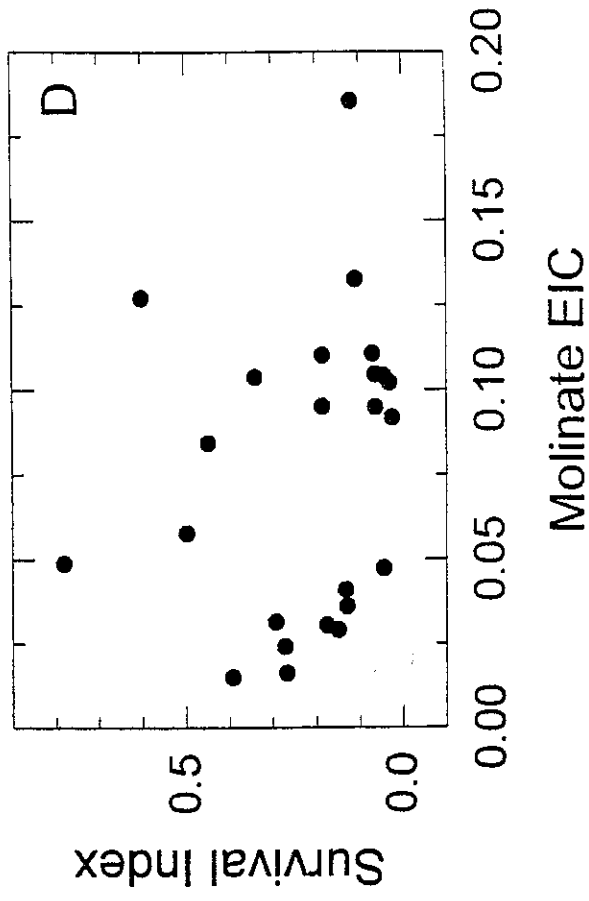
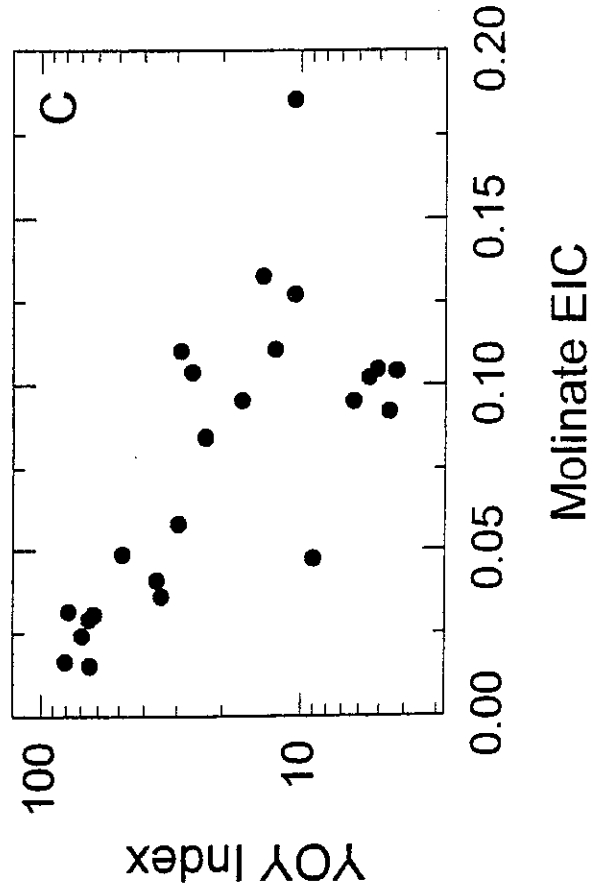
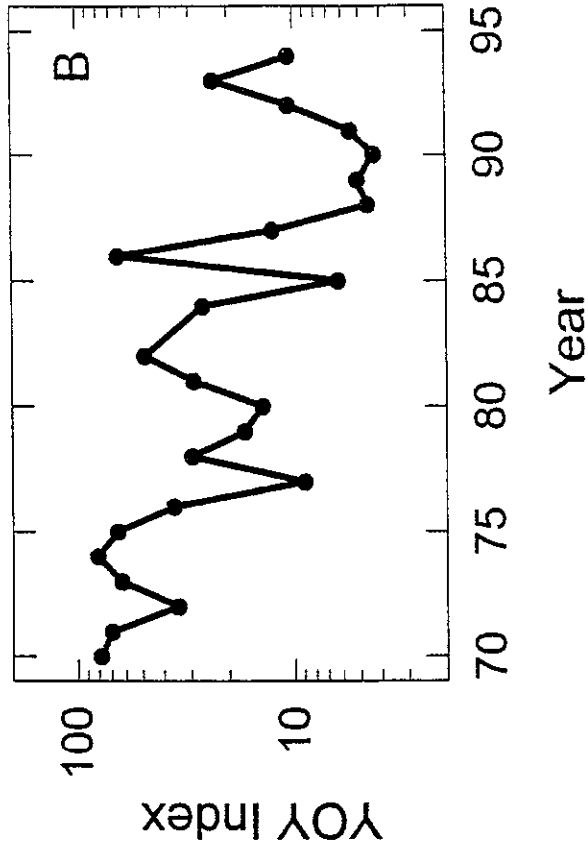
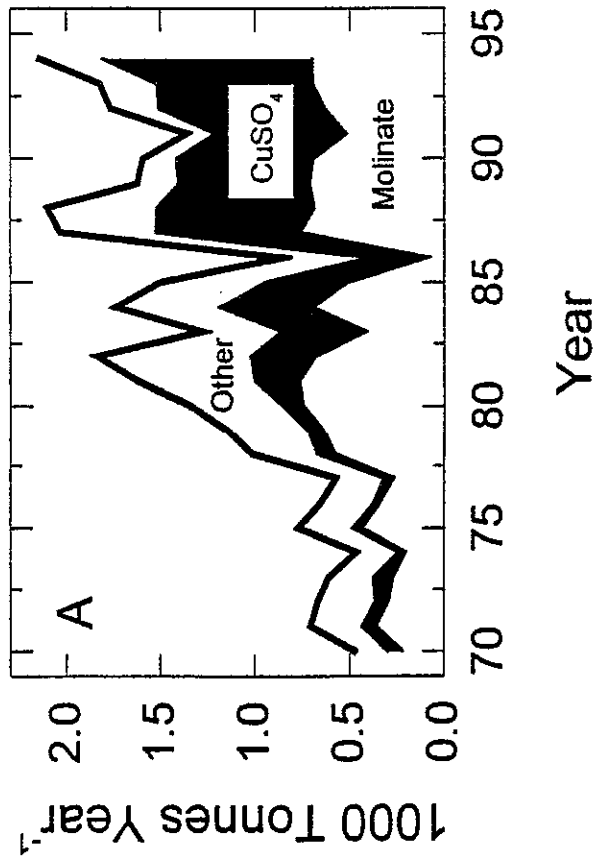


FIGURE 147 (2)

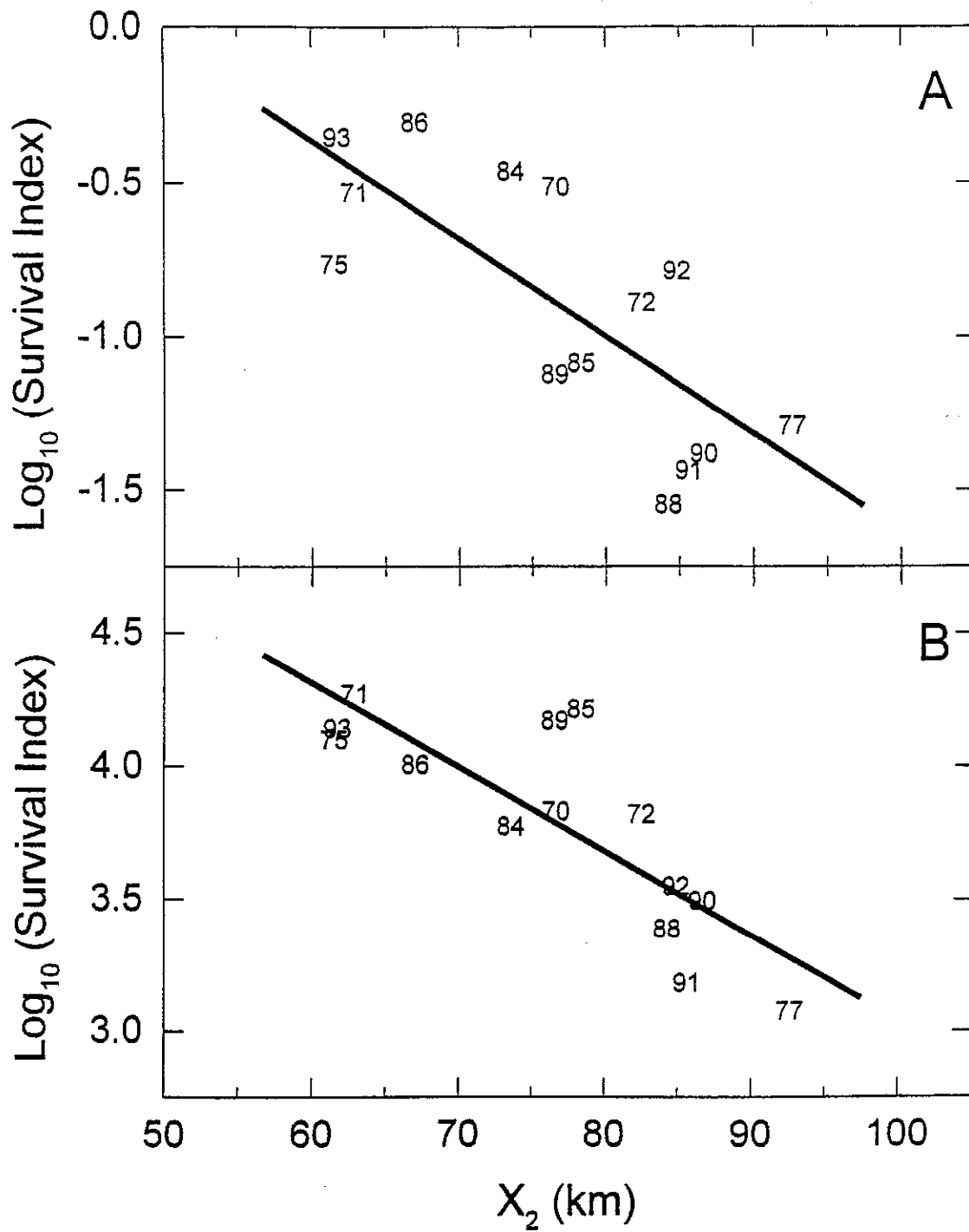


FIGURE 13

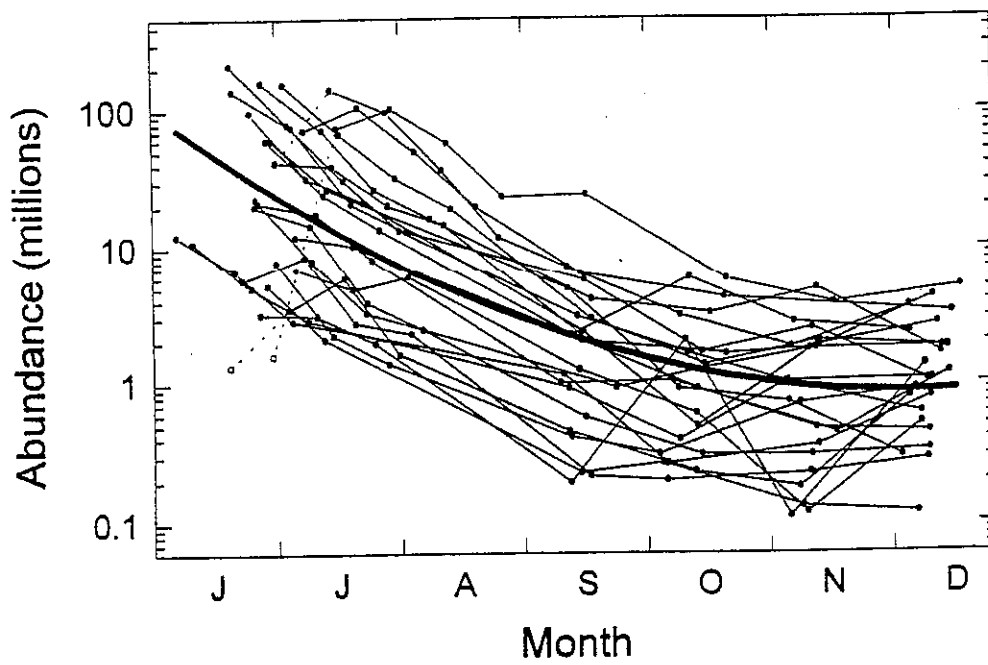
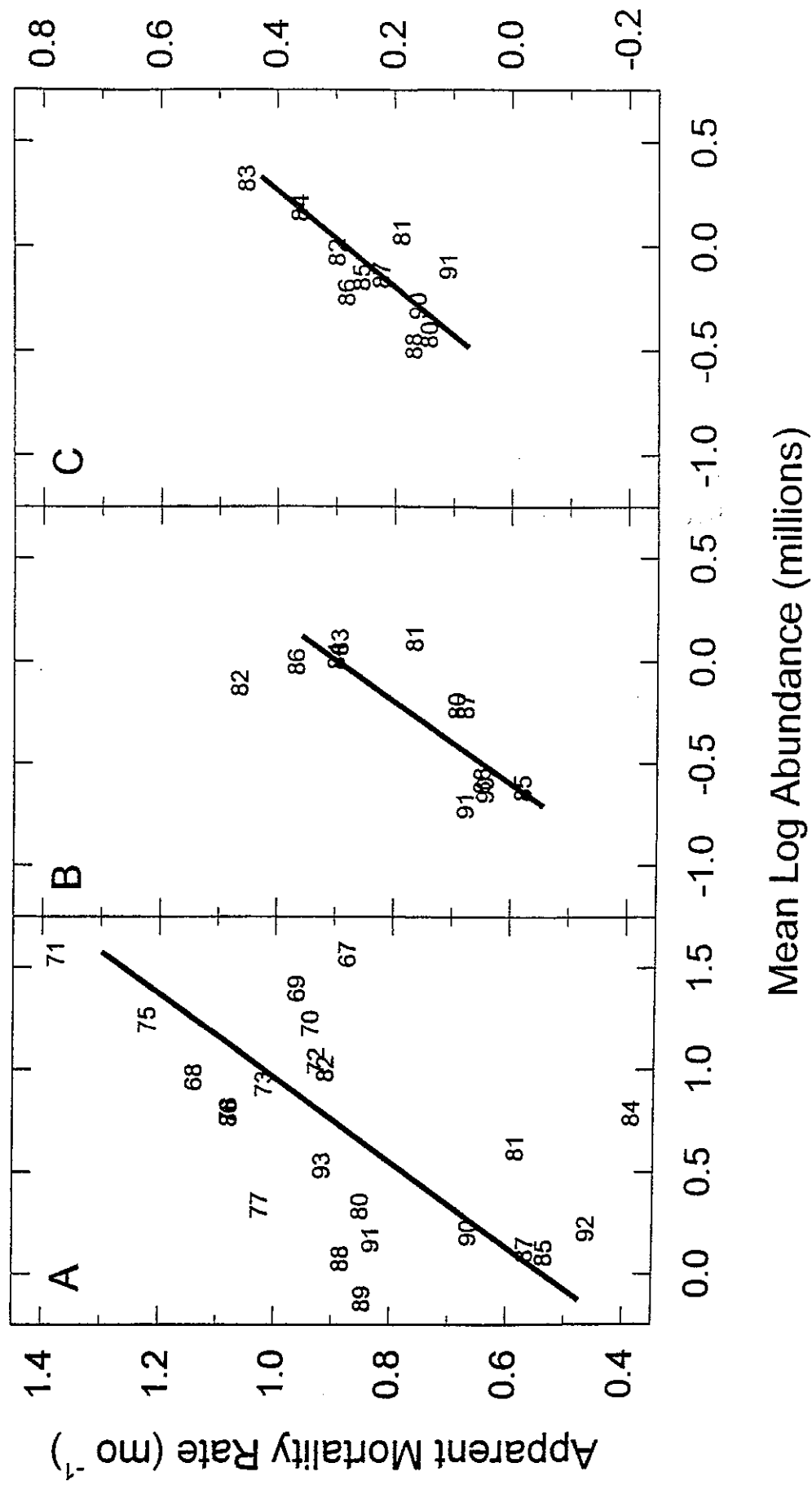


FIGURE 14



Mean Log Abundance (millions)

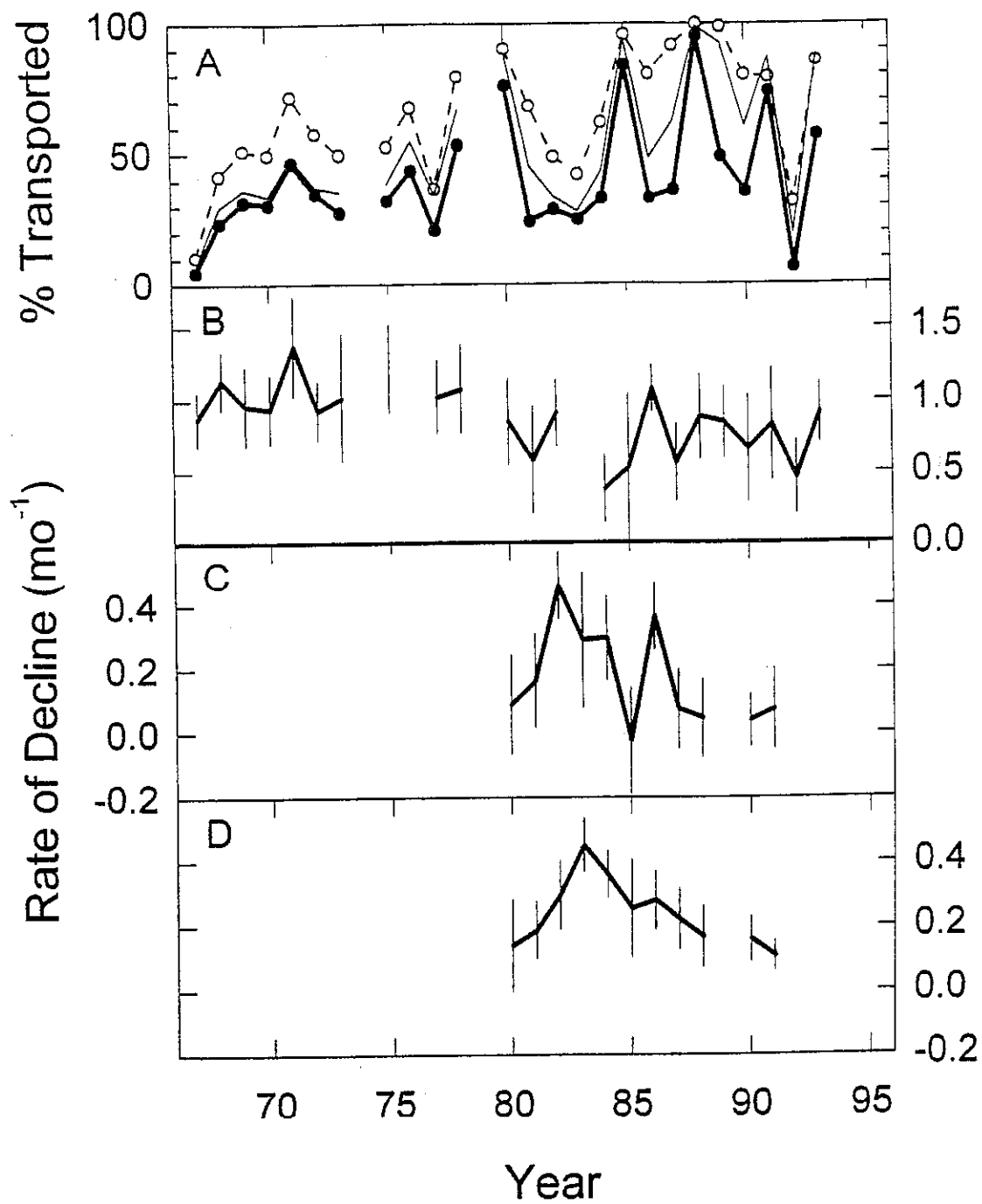
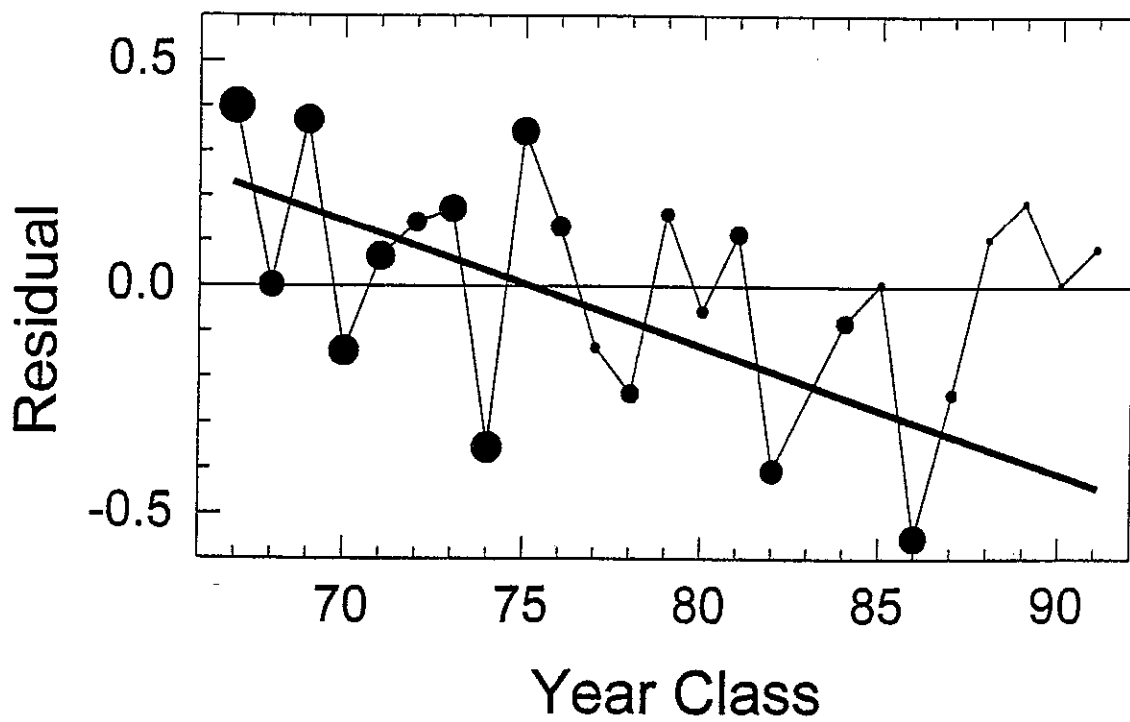
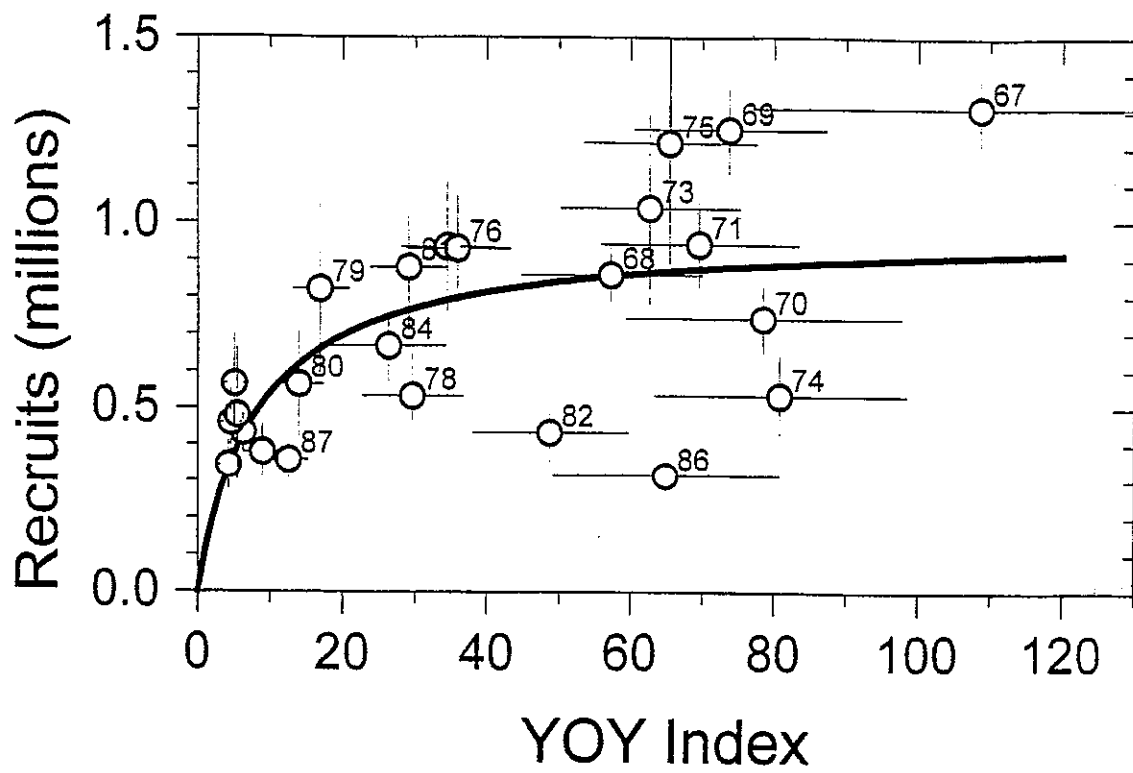
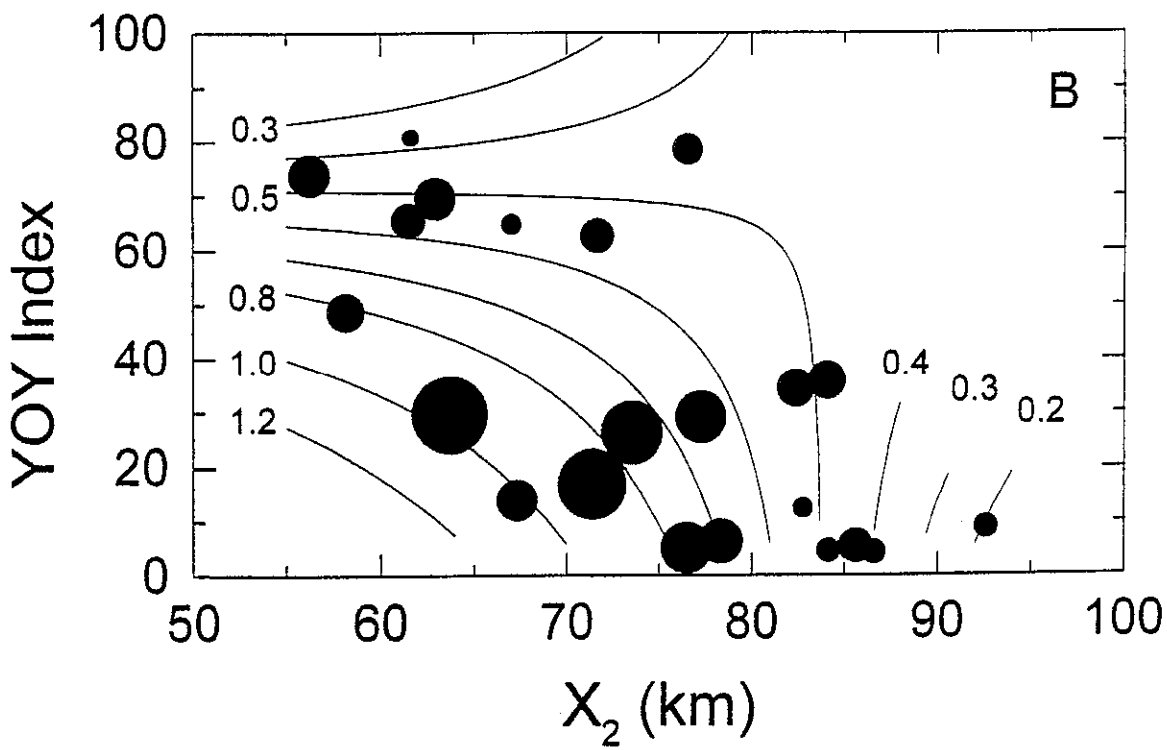
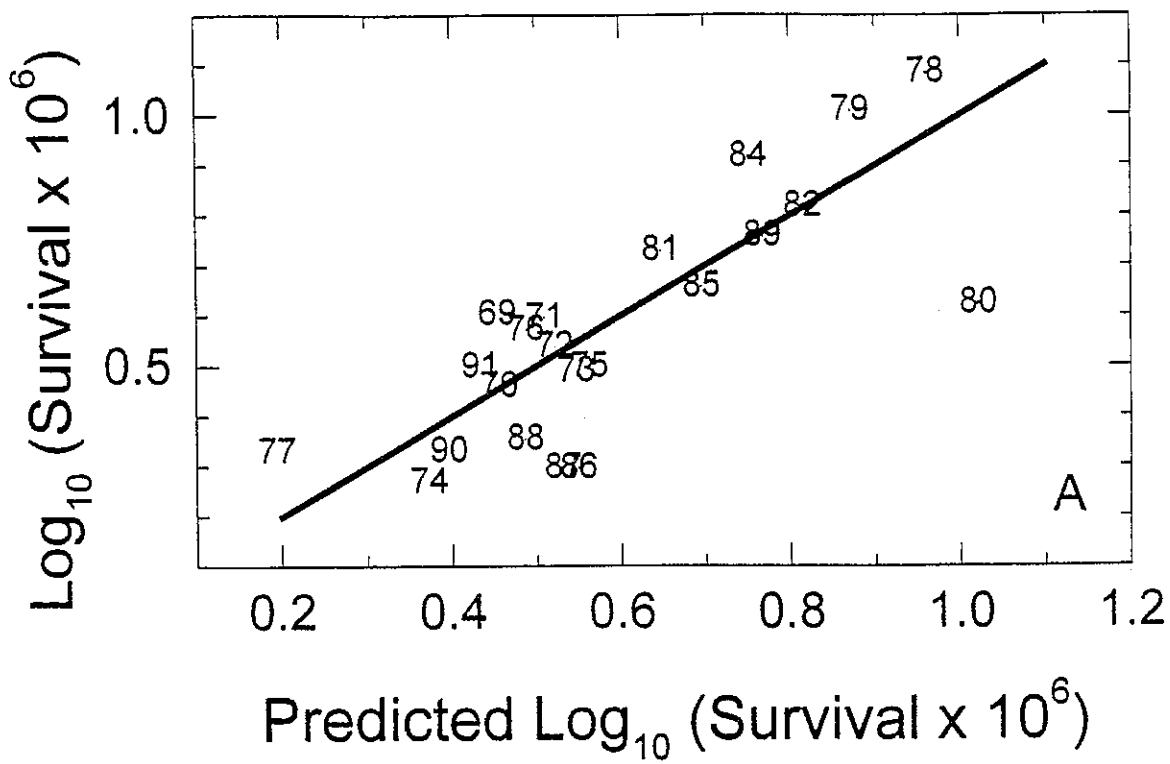


FIGURE 16





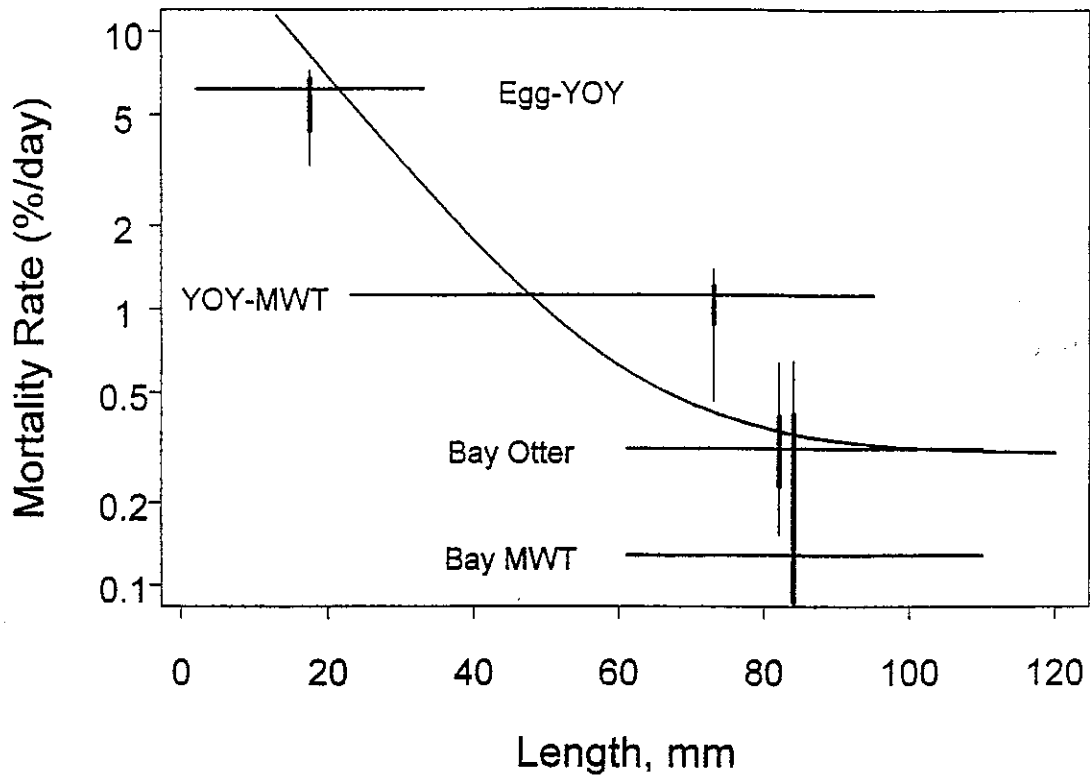


Figure 19

12/14/98B