Analysis of an estuarine striped bass (*Morone saxatilis*) population: influence of density-dependent mortality between metamorphosis and recruitment

W.J. Kimmerer, J.H. Cowan, Jr., L.W. Miller, and K.A. Rose

Abstract: Compensation due to density-dependent mechanisms is essential for the maintenance of an exploited fish stock. Understanding compensation is important for understanding population regulation and responses to added mortality. We examined possible density-dependent effects on striped bass (*Morone saxatilis*) in the San Francisco Estuary. Three sets of data from sampling programs for young striped bass showed density-dependent mortality between 1 month of age and 8–12 months. The relationships between two indices of young striped bass abundance and recruitment at age 3 fit a Beverton–Holt function, also indicating density dependence. The carrying capacity, as determined by the asymptote of the Beverton–Holt curves, has declined over the last two to three decades. These results are consistent with a compensatory mechanism based on food limitation occurring after metamorphosis and with the decline in food resources observed in the estuary over the same period. The decline in striped bass over the last two to three decades may be partly due to this declining carrying capacity.

Résumé : La compensation due à des mécanismes dépendants de la densité est nécessaire au maintien d'un stock de poissons exploité. Il est important de bien comprendre ce phénomène pour comprendre la régulation de la population et les réactions à la mortalité ajoutée. Nous avons examiné les effets possibles dépendants de la densité sur le bar rayé (*Morone saxatilis*) dans l'estuaire de San Francisco. Trois ensembles de données tirés de programmes d'échantillonnage de jeunes bars rayés ont montré que la mortalité entre 1 mois et 8 à 12 mois était fonction de la densité. Chez les jeunes bars rayés, le rapport entre les deux indices d'abondance et de recrutement à l'âge 3 correspond à une fonction de Beverton–Holt, ce qui indique également une dépendance à l'égard de la densité. La capacité limite, établie par l'asymptote des fonctions de Beverton–Holt, a diminué au cours des 20 à 30 dernières années. Ces résultats sont conformes à un mécanisme compensatoire fondé sur la quantité limitée de nourriture survenant après la métamorphose et concordent avec la diminution des ressources alimentaires observées dans l'estuaire pendant la même période. La diminution du nombre de bars rayés depuis 20 à 30 ans peut être attribuée en partie à une baisse de la capacité limite.

[Traduit par la Rédaction]

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). A key determinant of recruitment variability is density-dependent mortality. The compensatory effects of density-dependent mortality exerting a negative feedback on population abundance are fundamental to the long-term persistence of fish populations. Compensatory mortality is a necessary condition for, and a fundamental assumption of, fishery harvest (Sissenwine 1984): without compensatory effects, removal of adult fish would result in the eventual collapse of the population.

In spite of their importance, compensatory effects can be difficult to detect. Variability in recruitment may depend overwhelmingly on density-independent environmental factors (Shepherd and Cushing 1990), and density-dependent effects may be subtle (Houde 1989). This is particularly true for striped bass (*Morone saxatilis*), a highly fecund fish for which recruitment is generally thought to vary primarily with density-independent factors acting during larval and early juvenile stages (Ulanowicz and Polgar 1980; Polgar 1981; Goodyear 1985; Stevens et al. 1985).

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Table 1. Variables used in the analysis.

	Variable name	Frequency	Source	Estimate
1	Adult abundance (recruitment at age 3)	Annual	Tagging survey	Petersen mark–recapture estimates by age and sex or aggregated
2	Potential egg production	Annual	1 and fecundity data	Sum of age-specific fecundity times abundance
3	YOY index	Annual	Summer townet survey	Index of abundance interpolated to mean length of 38 mm
4	MWT index	Annual	Fall MWT survey	Index of abundance from average over months
5	YOY abundance	Variable	Summer townet survey	Sum of catch/volume times volume weighting factor
6	MWT abundance	Monthly	Fall MWT survey	Sum of catch/volume times volume weighting factor
7	San Francisco Bay study MWT abundance	Monthly	San Francisco Bay study	Sum of catch/volume times volume weighting factor
8	San Francisco Bay study otter trawl abundance	Monthly	San Francisco Bay study	Sum of catch/volume times volume weighting factor
9	Adult mortality	Annual	1 and tagging study	Rate of decline of adult abundance in a year-class; annual mortality from Ricker (1975, eq. 5.1)
10	Egg–YOY survival index	Interval	2 and 3	Ratio of YOY index to potential egg production
11	Egg–recruit survival	Interval	1 and 2	Ratio of recruitment to egg production
12	YOY–recruit survival	Interval	1 and 3	Graph of recruit abundance versus YOY index
13	Summer–fall apparent mortality rate	Monthly	5 and 6 combined	Log of abundance fit to a quadratic curve; slope evaluated between months 7 and 11 for consistency
14	MWT or otter trawl apparent mortality rates	Monthly	7 or 8 (one value for each)	Slope of log abundance over time from July to April

Note: 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. Items 1–9 are abundance indices or estimates and 10–14 are mortality or survival estimates based on abundance variables.

Striped bass is important to recreational and commercial fisheries along the east and west coasts of North America. Estuarine populations of striped bass spawn in freshwater during spring (Calhoun 1952). Negatively buoyant, free-floating eggs drift downstream as they develop, and late-larval and juvenile stages occur mainly in brackish regions of the estuary (Turner and Chadwick 1972). Larvae feed on small zooplankton starting with copepods and cladocerans; after metamorphosis, juveniles feed on copepods, switch to mysids and amphipods after several months, and become piscivorous late in the first year of life (Heubach et al. 1963; Stevens 1966). Striped bass mature at 4–5 years of age and can live to over 30 years. Mature individuals migrate to brackish or salt water during summer and return to freshwater during the fall and winter (Calhoun 1952). Year-class strength appears to be set early in life; indices of young-of-the-year (YOY) abundance can be useful predictors of recruitment (Polgar 1981; Goodyear 1985) and have been used to establish management goals for fishing effort (Field 1997) and freshwater flow (Jassby et al. 1995).

Abundance of striped bass in the San Francisco Estuary has declined substantially over the last three decades (Stevens et al. 1985). Possible environmental effects on young striped bass include effects of food on growth, contaminants on survival, river flow on transport or survival, and diversions of freshwater on survival (Turner and Chadwick 1972; Stevens et al. 1985). YOY abundance and survival from egg to YOY are strongly related to river flow, and the spatial distribution of young striped bass follows that of salinity (Turner and Chadwick 1972; Stevens et al. 1985; Jassby et al. 1995). These influences act on early life stages, and their effect would be partially mitigated by density-dependent mortality between the first summer and recruitment.

In this paper, we examine density-dependent survival of striped bass in the San Francisco Estuary through analysis of an extensive long-term data set on abundance of several life stages. We present several lines of evidence for compensation occurring between the end of the larval stage (early summer) and age 3 (defined here as recruitment). Data were obtained mainly from the California Departments of Fish and Game (CDFG) and Water Resources and the California Interagency Ecological Program (IEP) databases (Table 1)[2]. These data included various indices and estimates of abundance and egg production, from which mortality or survival indices or estimates were calculated. Density dependence was indicated by either positive relationships between mortality rate and abundance or by saturating relationships between early and later life stages indicating a carrying capacity.

Methods

Environmental variables used in analyses included freshwater flow variables and abundance of mysid shrimp. Freshwater flow into the estuary is estimated by the California Department of Water Resources. A related variable is the mean position of the 2-psu (practical salinity units) near-bottom isohaline expressed as kilometres from the mouth of the estuary (X_2; Jassby et al. 1995). X_2 is a useful integrator of flow conditions over a time scale of weeks,

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

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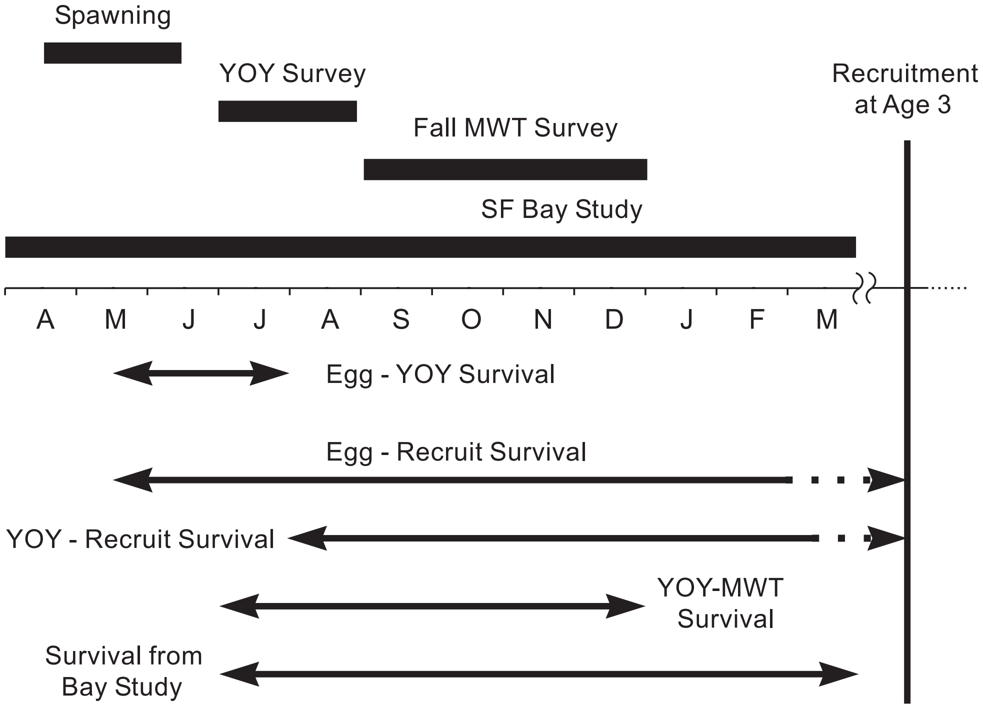
Fig. 1. Schematic diagram showing the months covered by each sampling program (bars above time scale) and over which survival was examined in this study (arrows).



provides a geographic context, and is more closely linked to habitat conditions for estuarine species than is freshwater flow (Jassby et al. 1995; Kimmerer and Orsi 1996; Kimmerer et al. 1998). X_2 was determined for 1968–1992 by interpolation between fixed salinity monitoring stations and for other years by a lagged regression with the log of freshwater flow (Jassby et al. 1995). X_2 was averaged over April–June for most analyses, that being the time of greatest vulnerability to flow conditions; in analyses of survival during summer–fall, the averaging period was June–December. Abundances of mysid shrimp, *Neomysis mercedis* and *Acanthomysis* spp. (Orsi and Mecum 1996), were obtained from the IEP zooplankton monitoring study as an indicator of food availability to young striped bass (Heubach et al. 1963; Stevens 1966). Values used were annual means based on samples taken once or twice monthly during April–November at a salinity range of 0.5–6 psu.

Data on striped bass (Table 1) comprised estimates of adult abundance and egg production and population abundance estimates or indices of young striped bass (Fig. 1). These data were used to calculate estimates or indices of mortality or survival (Table 1).

Adult abundance

CDFG tagged adult striped bass during their spring spawning migrations and resampled the population during a census of angler catches and subsequent spring tagging (Stevens et al. 1985). We used age- and sex-stratified numbers of fish tagged and tagged and untagged recaptures. The Petersen estimate of abundance was determined using the method of Bailey (1951) for ages 3–7 and 8 and over. Age-3 females are not fully vulnerable to capture, so their abundance was estimated from that of males assuming a 1:1 sex ratio. Recruitment was calculated as abundance at age 3, multiplied by the proportion of wild-reared fish determined by recovery of tags applied at the hatchery.

Potential egg production

Raw fecundity (eggs per fecund female) was obtained from Knudsen and Urquhart (1988) for eight years during 1978–1988. Significant differences among years had no time trend, so we pooled the fecundity data for all years and calculated fecundity as the prediction of a generalized linear model with age as the independent variable using a linear link function and a variance function proportional to the mean (Venables and Ripley 1997):

$$\text{Fecundity} = (0.21 \pm 0.01)\text{age} - (0.57 \pm 0.06)$$

with fecundity in millions of eggs per female. Potential egg production was calculated as age-specific abundance times fecundity, corrected for the proportion of females migrating to the spawning grounds and the proportion that were mature. The migration correction was calculated as the sex ratio (female to male) for ages 4 and 5 in data from the tagginng surveys, 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). Annual potential egg production estimates were highly correlated ($r = 0.96$, $N = 26$) with those used by Stevens et al. (1985) based on fewer years of fecundity data.

Young striped bass abundance

The summer YOY index of abundance assesses the population at 38 mm mean length (Chadwick 1964; Turner and Chadwick 1972). This index is based on two to five surveys conducted during 1959–1995 (except 1966) at approximately 2-week intervals starting in June. The YOY index was calculated by CDFG according to Turner and Chadwick (1972). It was considered invalid in 1983, when the striped bass population was seaward of the sampled area, and in 1995, when mean size of the captured fish never reached 38 mm.

The fall midwater trawl (MWT) index is based on surveys taken during 1967–1995 (except 1974 and 1979) monthly from September to December at 57–113 (median 88) stations. Ten-minute oblique tows from near the bottom to the surface were taken with a 3.7-m^2 midwater trawl with a variable mesh body (20.3–2.5 cm) and a

1.3-cm stretch mesh codend. The MWT abundance index was calculated by CDFG as described in Moyle et al. (1992).

We estimated population abundance for each of the YOY and MWT surveys to estimate mortality rates. We assumed a nominal towing speed of 0.8 $m\cdot s^{-1}$ and 100% net efficiency for a sample volume of 720 m^3 for the YOY survey and a sample volume of 7000 m^3, the median value based on flowmeter readings taken since 1985, for the MWT data. Total population size for YOY data was computed by summing the catch per unit volume at each station times a volume weighting factor for each station, while for MWT data, we summed abundance estimates by each of 17 regions used in calculating the index of abundance.

We also used data from the San Francisco Bay study (Armor and Herrgesell 1985). Surveys have been taken monthly starting in 1980, except in winter months since 1989. At each of 35–52 stations throughout the estuary, one 5-min tow each was taken with an otter trawl with a 4.9-m headrope, 2.5-cm stretch mesh body, and a 1.3-cm stretch mesh codend, and a 12-min oblique tow was taken with a midwater trawl as described above. We used abundance data (per area or volume, respectively) from both trawls at stations in the northern estuary. Estimates of population abundance were calculated from the San Francisco Bay study separately for otter and midwater trawls, as described for fall midwater trawls above.

Mortality and survival

Two mortality estimates were calculated for adult striped bass (Table 1). One was the slope of the natural log of the Petersen abundance estimate versus age, not including age 8+ fish. The other was obtained from CDFG's tagging program as –ln(survival), where survival was calculated using Ricker's (1975) eq. 5.1 (Stevens et al. 1985). The Petersen mortality estimate is by age-class, so each age-class included is equally weighted. The tagging estimate is by year, and each tagged fish is given equal weight so the younger, more abundant age-classes are better represented.

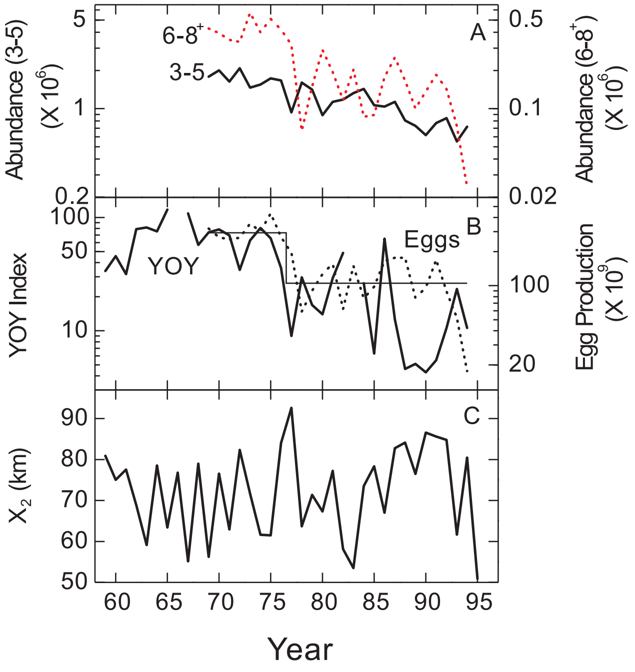
Survival calculations included an egg–YOY survival index, the ratio of the YOY index to potential egg production. An egg–recruit survival estimate was calculated as the ratio of the 3-year-old Petersen estimate of abundance to potential egg production 3 years earlier. YOY–recruit survival was examined using plots of the YOY index versus recruitment. Apparent mortality rate for the combined summer YOY and fall MWT surveys (Table 1, row 13) was calculated as the mean rate of decline of log abundance for each year with YOY and MWT data except 1976 and 1983 (incompletely sampled). The log abundance data for each year were first fit to a quadratic function in time. Residuals from this fit had no apparent time trend within years, suggesting that this was a suitable model. Apparent mortality rate was calculated for each year as the negative slope of the fitted curve between 1 July and 1 November. Apparent mortality from the San Francisco Bay study was estimated as the slope of the linear regression of log population size versus day for each survey from July to April.

In determining apparent mortality rates, we assumed that interannual variation in catchability did not bias our results, but there was a potential for bias due to incomplete sampling in tidal freshwater by the San Francisco Bay study. We repeated the analysis of apparent mortality by correcting the San Francisco Bay study data for the monthly proportion of the population in the YOY and MWT surveys in regions landward of the San Francisco Bay study sampling stations. The analysis of apparent mortality was then repeated using these corrected values and the results compared with the uncorrected values for the same time periods.

Density dependence

Evidence of density dependence was developed in three ways. First, we fit a Beverton–Holt curve to recruitment versus the YOY index. We also examined the residuals from this curve for evidence that carrying capacity had declined. A similar analysis was performed using the MWT index in place of the YOY index above. Second, we examined the influence of young striped bass abundance on egg–recruit survival. Because egg–YOY survival was known to be related to X_2, we included both X_2 and the YOY index as independent variables in a multiple regression. Third, we used regression of apparent mortality rates on mean log abundance for each of the three sets of data on young striped bass abundance. A positive relationship, indicating high mortality when fish are abundant, was taken as evidence of density dependence. Using mean log abundance as the independent variable eliminates the potential bias inherent in relationships between two variables from the same data source (cf. Myers and Cadigan 1993).

Fig. 2. Time course of abundance indices of several life stages of striped bass and environmental data. (A) Adult abundance estimates at ages 3–5 (solid line) and 6 and older (dashed line); (B) summer townet index of YOY (thick solid line), potential egg production (broken line), and fit of a step function in 1976–1977 (thin solid line); (C) mean X_2 from April to June.

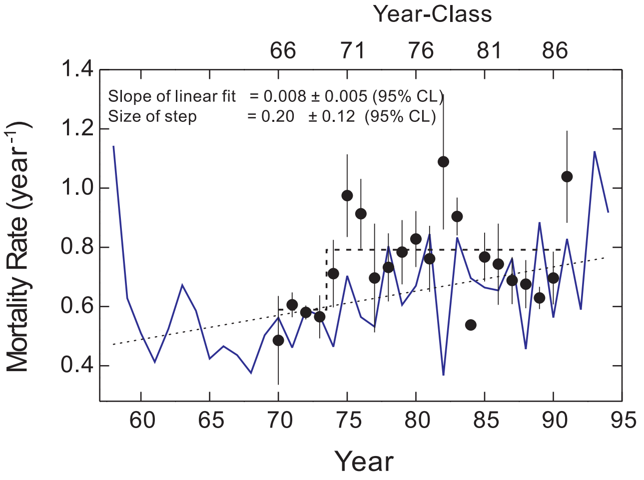


Data analyses used the S-Plus statistical language (Venables and Ripley 1997). We emphasized graphical techniques for exploring raw data before fitting models and for checking that assumptions of statistical models were met. Regressions were by ordinary least squares if the data met assumptions of normality and homoscedasticity. If not, we used either a generalized linear model (GLM) or a robust, iteratively reweighted least squares procedure ("rlm"; Venables and Ripley 1997). 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 some cases where there was evidence of a step change in time, we used tree regression to identify the timing of the step (Venables and Ripley 1997) and then fit the step to the data by regression or GLM, accepting the step model only if the residuals contained no autocorrelation.

Results

Adult abundance, potential egg production, and the YOY

Fig. 3. Tagging estimates of mortality by year (solid line) and Petersen estimates by year-class (symbols with 95% CLs). 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. The dotted line was fit to the tagging data using robust regression (p = 0.001, 35 df), and the dashed line is a step function fit to the Petersen estimates for year-class 1970–1971.



index all declined during the period covered by the data (Figs. 2A and 2B). Patterns of decline of younger (ages 3–5) and older (ages 6–8 and older) adults were different: younger adults declined continually, while older adults declined in several episodes, particularly 1976–1978 and 1994–1995. These patterns were consistent among age-classes within each of these age groups. The sharp decline in older, more fecund adults around 1977 (Fig. 2A) produced a sharp decline in potential egg production (Fig. 2B). A regression of potential egg production on a step change between 1976 and 1977 gave a downward step from 2.9 × 10^{11} to 1.0 × 10^{11} eggs that explained 78% of the variance (p < 0.0001, 24 df), and the residuals had no time trend or autocorrelation. The sharp decline in egg production propagated into the YOY index in the same year (Fig. 2B). The influence of flow conditions indexed as X_2 (Fig. 2C) on YOY can be seen in data from droughts in 1977, 1985, and 1987–1991 and in data from high-flow years such as 1982 and 1986.

Tagging and Petersen estimates of adult mortality differed in pattern, but both increased over time (Fig. 3). The linear trend in the tagging estimate of mortality was significant, even including the high mortality calculated in 1959. The Petersen estimate of mortality did not have a significant linear trend (p > 0.2, 20 df) but fit a step function with a shift occurring in year-class 1970–1971 as determined by tree regression (robust linear regression on step function, p = 0.009, r^2 = 0.29, 20 df).

The log of the survival index from egg to YOY was strongly related to X_2 (robust regression slope = –0.028 ± 0.012, 95% CL, p = 0.0001, r^2 = 0.47, 23 df). Neither the egg–YOY survival index nor the residual from the regression had a significant time trend (linear regression, p > 0.1), nor were they related to the geometric mean of egg abundance and the YOY index (linear regression and by inspection of plots, p > 0.1). These results suggest that there was little or no density-dependent mortality between the egg and the summer YOY index.

Fig. 4. Egg–recruit survival. (A) The log of survival versus that predicted from the model including X_2 and the YOY index (Table 2), with the 1:1 line; (B) X_2 versus the YOY index, with the size of the circles representing relative magnitude of egg–recruit survival and contour lines of survival determined by the model.

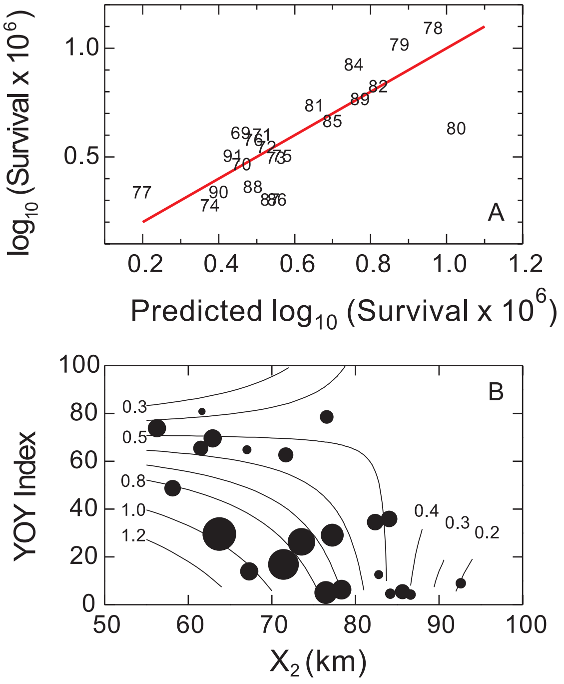


Table 2. Regression statistics: log of egg–recruit survival versus X_2, YOY index, and the interaction.

Independent variable	Parameter	SE	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 × YOY index	0.00055	0.00013	0.0002	

Egg–recruit survival was not simply related to environmental variables. A significant relationship was obtained between $\log_{10}$ egg–recruit survival and X_2 averaged over April–June, the YOY index, and the interaction between X_2 and the YOY index (Fig. 4A; Table 2). Fitted values from this model projected on the plot of X_2 versus the YOY index (Fig. 4B) illustrate that, at low values of the YOY index, egg–recruit survival increases with decreasing X_2, while at low values of X_2, egg–recruit survival is negatively influenced by increasing YOY index.

The Beverton–Holt curve appeared to be a reasonable description of the relationships between recruitment at age 3 and both the YOY and MWT indices, albeit with considerable residual variation (Fig. 5A; Table 3). Most of the data points were on the saturated portion of the curve, for which further increases in the YOY or MWT index do not result in proportional increases in recruitment. This part of the curve represents carrying capacity, and deviations of the points above and below this part of the curve may represent interannual differences in carrying capacity. The residuals

Table 3. Regression statistics for Beverton–Holt curves fit to relationship between abundance at age 3 and either the YOY index or the MWT index.

Parameter	YOY	MWT
b (maximum or carrying capacity)	0.98±0.24	0.96±0.27
a (initial slope)	0.12±0.10	0.0011±0.0010
df	22	21
p	0.001	0.016
Time trend of weighted residuals	–0.28±0.008	–0.026±0.007
Correlation of weighted residuals versus mysid abundance	0.01	0.46 (p = 0.03)

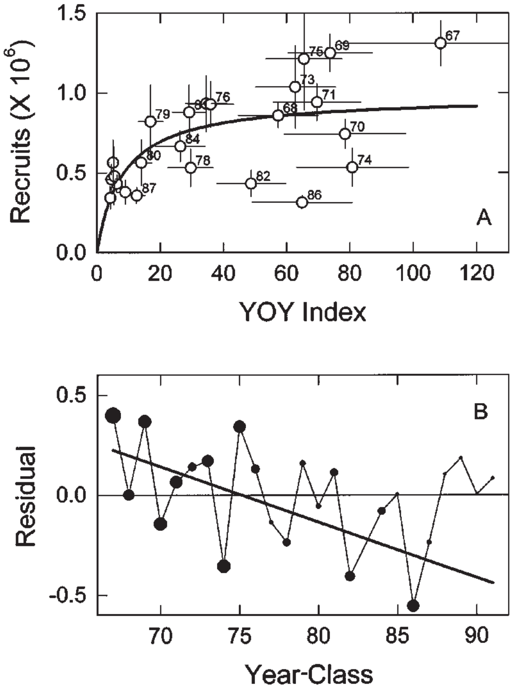
Note: Parameters are given with 95% CIs.

from both curves had downward time trends that were significant when the points were weighted by the value of the respective young striped bass index (Fig. 5B; Table 3). 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 the YOY or MWT index above the half-saturation value of the curve in Fig. 5A. The residuals from the Beverton–Holt relationships for both YOY and MWT were uncorrelated with X_2 or export flow during April–June of the first year ($p > 0.3$). The residuals from the Beverton–Holt relationship for YOY versus recruits were uncorrelated with summer–fall abundance of mysid shrimp ($p > 0.8$), but residuals for the MWT relationship, weighted by the value of the MWT index to emphasize effects on carrying capacity, were correlated with mysid abundance (Table 3).

The log of abundance in the combined YOY and MWT surveys decreased rapidly in the first few months and then more slowly through fall and early winter (Fig. 6). Similar plots of the San Francisco Bay study MWT 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 (Fig. 6) is absent from the San Francisco Bay study data because the townet more efficiently captures the smaller fish, whose initial mortality rates are very high, than do the nets used in the San Francisco Bay study.

Apparent mortality rates for juvenile fish from the three sets of data (combined summer–fall surveys and the San Francisco Bay study otter trawl and MWT surveys) were positively related to the mean log of abundance for each set of data (Fig. 7); slopes of all three regressions were significantly different from zero ($p < 0.01$). The results for the San Francisco Bay study corrected for incomplete coverage of the population were also statistically significant, although they differed in numerical values from those shown. Apparent mortality rates were unrelated to export flows ($p > 0.1$) but were related to X_2 with negative slopes (i.e., higher X_2 (low flow) was associated with lower apparent mortality).

Fig. 5. (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 are standard errors. (B) Time course of residual from Fig. 5A. The straight line is fitted by linear regression weighted by the YOY index (see text).



Discussion

We interpret our analyses of striped bass in the San Francisco Estuary as follows: year-to-year variability in early survival is affected by flow conditions, so abundance in the summer YOY stage is largely a function of egg production (which has declined) and flow or X_2 (which has no trend). However, this variability is damped by density-dependent survival from the YOY index to recruitment. Under low YOY abundance, recruitment is on the ascending limb of the Beverton–Holt curve and therefore is directly related to YOY abundance. However, when the YOY index exceeds about 20, variation in abundance of age-3 to age-5 adults is unrelated to YOY abundance (Figs. 2 and 5). Thus, the period of density-dependent survival produces a bottleneck that moderates environmental influences occurring during the first 3–4 months of life.

Several lines of evidence indicate density-dependent survival between the first summer and recruitment at age 3: the negative relationship between egg–recruit survival and the YOY index, the saturating YOY–recruit and MWT–recruit relationships, and the correlation of apparent mortality rates with mean $\log_{10}$ abundance in the combined summer–fall data and the San Francisco Bay study MWT and otter trawl data.

All three of the apparent mortality rates of young fish were negatively related to X_2. This is the opposite sign from that expected if mortality during that period was affected by flow conditions, as it is in the egg–YOY period. Presumably, this is an indirect effect: abundance of young striped bass in summer varied negatively with X_2 (because survival from egg to YOY varied negatively with X_2) and positively with apparent mortality rate (Fig. 5), resulting in a negative relationship between apparent mortality rate and X_2.

Evidence of density dependence is often difficult to detect, presumably because of the overwhelming influence of

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Fig. 6. Combined abundance data from the summer townet survey and fall MWT survey (log scale) plotted against survey dates expressed as calendar month. Each line presents the data from a single year. Dotted lines and open circles identify points not used to determine rates of decline. The thick line is a quadratic function fit to all the remaining data.

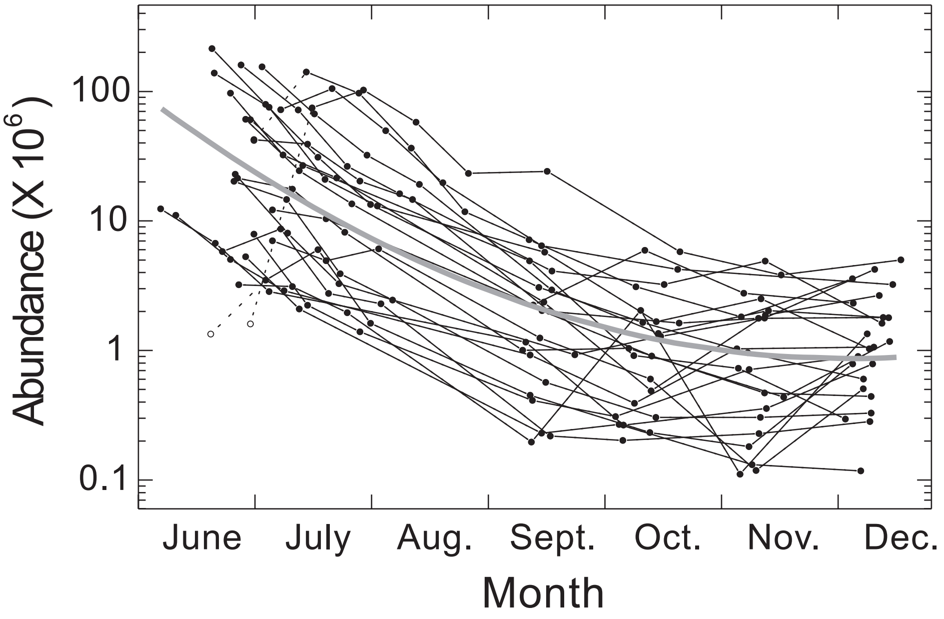
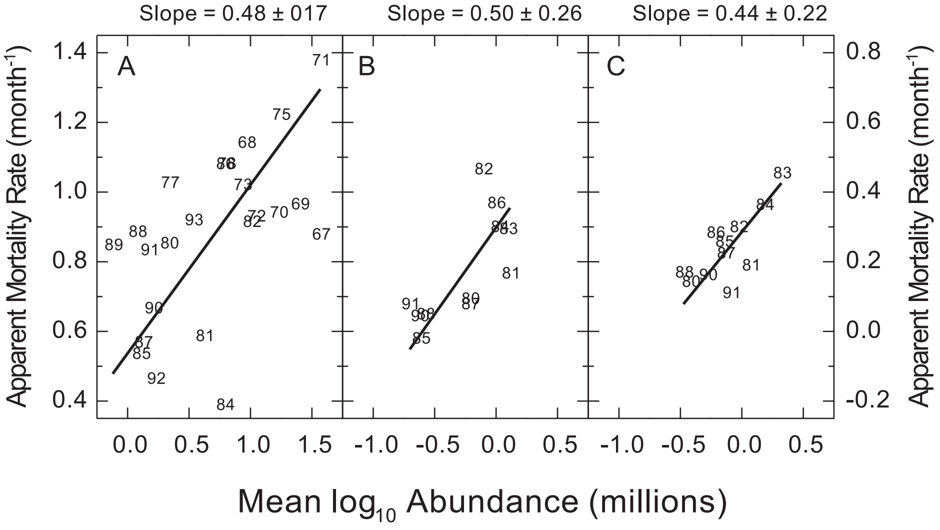


Fig. 7. Apparent mortality rate plotted against mean log population size for (A) combined summer and fall surveys (left axis), (B) the San Francisco Bay study MWT (right axis), and (C) the San Francisco Bay study otter trawl (right axis). Numbers are years, and lines give geometric mean regression slopes, shown at the top with 95% CLs.



environmental factors that cause density-independent variation in survival (Houde 1989; Shepherd and Cushing 1990). Saturating stock–recruit curves have been shown for a number of marine fish populations (Myers et al. 1995). Myers and Cadigan (1993) showed density dependence in several demersal fish stocks by comparing juvenile abundance with mortality, as done here. The life stage in which density dependence occurs, and therefore the likely mechanisms, are most often identified where space is a limiting factor. For example, spawning of salmonids in streambeds can reach a saturation point when the most favorable habitat is occupied first (Neilson and Banford 1983). Fish of coral reefs and rocky outcrops can experience density-dependent survival either during or shortly after settlement into spatially limited habitats (e.g., Ralston and Howard 1995).

Density-dependent mortality of striped bass has not been reported in other estuaries (Ulanowicz and Polgar 1980; Logan 1985; Rutherford et al. 1997), although recent increases in abundance in the Chesapeake may make density dependence easier to detect. However, juvenile abundance in the Hudson River Estuary was relatively invariant over a wide range of larval abundance (Pace et al. 1993, their fig. 6), suggesting density dependence between larval and YOY stages, earlier in the life cycle than observed in this study.

The mechanism(s) for density dependent survival of striped bass in the San Francisco Estuary can only be guessed at. Reasonable candidates generally include food limitation, cannibalism, response of predators, and density-dependent migration. The density-dependent feedbacks apparently occur after the YOY index is determined but before recruitment at age 3 years. Food limitation seems the most likely candidate, and the decline in carrying capacity roughly parallels the decline in food resources over the last two decades (Kimmerer and Orsi 1996; Orsi and Mecum 1996). Direct links between food abundance and carrying capacity were significant but weak (Table 3).

Predation, particularly cannibalism, is an alternative explanation for the density dependence. The abundance of adult striped bass has declined in parallel with that of younger fish, which should result in negative correlations between apparent mortality rate of young striped bass and abundance of older fish. However, the spatial distribution of adult striped bass (White 1986) in summer and fall is mainly to seaward of that of the younger fish (Turner and Chadwick 1972; W.J. Kimmerer, unpublished data). Furthermore, if cannibalism by the declining adult population were the cause of the density dependence, carrying capacity should have increased, not decreased. For cannibalism to have caused the observed pattern would require an additional condition: as the population decreased, either alternative prey decreased or availability of habitat for young striped bass declined. We have not tested for decreases in alternative prey of adult striped bass. The spatial extent of the juvenile striped bass population does not appear to have changed as the population declined (W.J. Kimmerer, unpublished data), so vulnerability to predators should not have increased, nor is it likely that changes in density-dependent migration are implicated in the declining carrying capacity.

Although it is difficult to identify specifically the mechanisms responsible for density-dependent feedbacks, we suggest that a decline in carrying capacity of the system has indeed occurred and has acted over time to reduce the potential for production of strong striped bass year-classes. This change apparently cannot be identified with a single cause but probably is a consequence of multiple factors (see Cowan et al. 1993). We are exploring this hypothesis further in a companion modeling study (K.A. Rose et al., unpublished).

How does the density-dependent mortality figure in the decline in striped bass abundance? The decline probably has several causes, but it is possible to weigh their importance by considering the life stages influenced by each potential cause of decline. We consider three segments of the life cycle: egg production to summer YOY, summer YOY to recruit, and recruit to adult over age 5, i.e., highly fecund adults. Substantial trends in survival during any of these life stages could indicate a mechanism for population decline.

For the time period over which we have complete data (1968–1994), time trends were not detected in either survival from egg to YOY or in X_2, the most important environmental predictor of early survival. For the YOY–recruit phase of the life cycle, we have presented evidence that mortality is density dependent and that carrying capacity has declined (Fig. 5B). In the adult phase, there is evidence that mortality has increased (Fig. 3). In addition, on at least two occasions (1977–1978 and 1992–1994), there was a downward spike in abundance of all age-classes over 5 years, followed in 1978 by a partial recovery (Fig. 2). The combined effect of increasing adult mortality and episodic drops in abundance of older adults is that the proportion of these larger, more fecund striped bass in the population has declined, resulting in a sharp drop in egg production (Fig. 2B). These episodic step changes may result from the difference in migratory patterns with age. Older striped bass migrate to sea more than younger ones (Secor and Piccoli 1996), and the ocean fishery takes larger striped bass than the fisheries in the bay (White 1986). In addition, catches of large striped bass in the ocean fishery were unusually high in 1977 (White 1986), the year preceding the biggest decline in fish older than 5 years (Fig. 2). Furthermore, 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 (W.A. Bennett, Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, U.S.A., personal communication).

Thus, the decline in striped bass population in the San Francisco Estuary appears to have resulted from a combination of two factors: the decline in carrying capacity resulting in lower recruitment and the decline in older adults due to higher mortality and episodic drops in abundance possibly due to climate. In this population the YOY index appears to be less predictive of recruitment than has been reported for other striped bass populations (Polgar 1981; Goodyear 1985; Rutherford et al. 1997).

Previous management of the striped bass stock of the San Francisco Estuary has focused on the YOY index and on environmental influences on survival from the egg to YOY. The existence of density dependence and decreasing carrying capacity after the YOY index is set, evidence of higher adult mortality and possible climate effects, and the lack of time trend in early survival or its predictors suggest that management and research efforts should be broadened to consider the juvenile and adult segments of the life cycle.

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