

MODELING DETERMINISTIC EFFECTS OF AGE STRUCTURE, DENSITY DEPENDENCE, ENVIRONMENTAL FORCING, AND FISHING ON THE POPULATION DYNAMICS OF *SARDINOPS SAGAX CAERULEUS* IN THE GULF OF CALIFORNIA

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ABSTRACT

We used an age-structured deterministic model to investigate how population dynamics of Pacific sardine, *Sardinops sagax caeruleus*, in the Gulf of California are affected by age structure, density-dependent recruitment, environmental forcing, and fishing. Density-dependent recruitment had a very strong effect; it stabilized the population dynamics and caused mesoscale (4–5 year) cycles in abundance. A sinusoidal function was used to vary survival rates with constant period of 60 years and various amplitudes. This representation of environmental forcing caused long-term cycles in the abundance of sardine, similar to the pattern observed in real stocks. A linearly increasing fishing schedule over a period of 25 years on a stock with environmental forcing caused strong reductions in abundance that extended for up to 20 years, and mesoscale oscillations for up to 40 years after the harvest period. The negative impact was longer if harvest started when survival rates were at their maxima, but biomass decreased most when harvest started at the descending node of survival rates. A stability analysis indicated that the sardine stock in the Gulf of California is unstable; however, when age structure is included in the simulations the stock is very resilient and can recover from low levels of biomass. This theoretical result was probably due partly to the absence of stochastic effects in our model.

INTRODUCTION

Variability in abundance is a pervasive aspect of all natural biological populations. Abundance changes over time due to stochastic and deterministic factors; here we focus on the latter. Much of our current knowledge about deterministic effects on population variation comes from theoretical work because most data sets are short and because deterministic effects are obscured by stochastic environmental effects and measurement error. Theoretical studies indicate that in the absence of sto-

chasticity, factors such as age structure, density dependence, and environmental forcing can cause populations to fluctuate with different frequencies (May 1973; Caswell 1989; Botsford 1986).

Some populations experience quasi-periodic oscillations in annual survival rates due to environmental effects on recruitment. Examples may include Pacific sardine in the Gulf of California and off the Pacific coast of North America. Variation in sardine abundance coincides with the mesoscale frequency (5 to 10 years) of El Niño events (Huato-Soberanis and Lluch-Belda 1987), and low-frequency oscillations (50 to 60 years) observed in many clupeoid fish species throughout the world (Lluch-Belda et al. 1989).

As a result of their close relation to the physical environment, short life span, and variable recruitment, small pelagic fish populations (e.g., sardines and anchovies)—the most important group of fish species in the world in terms of volume captured—have complex dynamics (Sharp and Csirke 1983), and their management is particularly difficult. Furthermore, the fact that small pelagic fish populations experienced oscillations of several orders of magnitude long before fisheries existed (Baumgartner et al. 1992) prompts one to ask if fisheries management can affect the dynamics of these important stocks.

PACIFIC SARDINE IN THE GULF OF CALIFORNIA

The Gulf of California (henceforth referred to as the gulf) has many features in common with major upwelling systems. Bathymetric characteristics, strong tidal mixing, and seasonal upwelling result in high productivity and abundance of commercially important marine fish species (Álvarez-Borrego and Lara-Lara 1991). The gulf's most important fishery resources by volume and economic value are small pelagic fish and shrimp. Three species of small pelagic fish are represented in the gulf in a guild similar to those of the California and Humboldt Current systems: Pacific sardine (*Sardinops sagax caeruleus*), northern anchovy (*Engraulis mordax*), and Pacific mackerel (*Scomber japonicus*). A difference is the presence in

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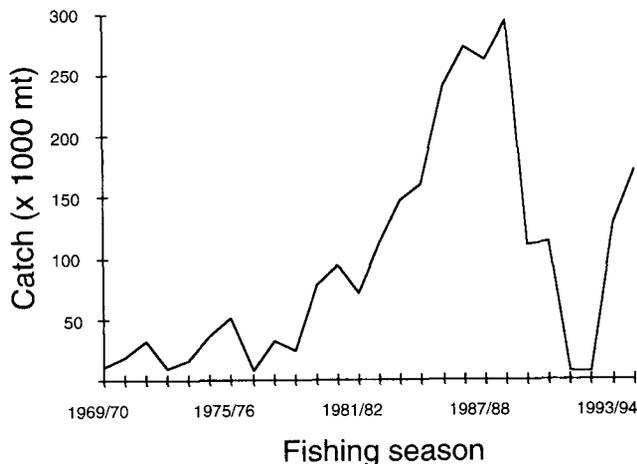


Figure 1. Pacific sardine catch in the Gulf of California, Mexico. Sardine fishing seasons start in mid-October and end the following year. Because of changes in the fishery and in management regulations, the number of months during which fishing occurred changed from 7 to 11 in 1977, to 12 in 1982, and then to 10 in 1989.

the gulf of more tropical species such as thread herring (*Opisthonema* spp.) and round herring (*Etrumeus teres*; Cisneros et al. 1990).

The Pacific sardine in the gulf is the main component of the Mexican fishery for pelagic fish, with maximum annual recorded landings of 292,000 metric tons (MT). Pacific sardine were first harvested in the gulf during the late 1960s after the collapse of the sardine fishery off the west coast of California and Baja California (Lluch-Belda et al. 1986). Sardine landings increased steadily over two decades, peaked in 1988–89, and then declined rapidly to a minimum of about 7,000 MT in the 1991–92 fishing season (figure 1).

Decreased sardine abundance in the gulf before 1991–92 may have been due to excessive fishing during a period of adverse environmental conditions. A shift in the age structure of the stock and catch to younger ages, and excessive harvest rates during the decline indicated overexploitation of the stock (Cisneros-Mata et al. 1990). The appearance in 1985 of northern anchovy in the commercial catch (Hammann and Cisneros-Mata 1989) suggested that anchovy may have been replacing sardine. The species replacement hypothesis can probably now be discarded because recent data indicate that the species have coexisted in the gulf (Holmgren-Urba and Baumgartner 1993), and because both sardine and anchovy presently seem to be increasing in abundance. The potential effect of harvest on the gulf's sardine stock has yet to be clarified, although it has been repeated ad nauseam how excessive fishing in combination with natural phenomena caused the collapse of the Pacific sardine in California and the anchoveta in Peru.

In a study based on virtual population analysis (VPA; Gulland 1965, cited in Pope 1972) it was proposed that

both fishing and sardine stock biomass increased in parallel in the gulf during the last two decades (Cisneros-Mata et al. 1995). This hypothesis makes the implicit assumption that fishing started when the sardine stock was at a low point in a long-term cycle of abundance. Analysis of scale deposition in anaerobic sediments indicates that the cycle of sardine abundance in the gulf apparently is not coupled to that of the same species in the California Current (Holmgren-Urba and Baumgartner 1993). The hypothesis that sardine abundance cycles in the gulf is supported by the recent recovery in catches (figure 1) and abundance (unpubl. data).

In this work we analyze how (1) age structure, (2) density dependence, (3) periodically oscillating survival rates, and (4) fishing affect the dynamics of Pacific sardine in the Gulf of California, Mexico. We developed a deterministic age-structured model with density-dependent recruitment for the Pacific sardine stock of the Gulf of California and performed numerical simulations under various conditions. We included sinusoidal variation in survival rates to represent low-frequency environmental forcing. We then analyzed the effects of harvest beginning at different points in the underlying cycle for survival rates to understand how fishing pressure affects a population of small pelagic fish experiencing low-frequency oscillations. Our objective is to understand the importance of deterministic mechanisms in the dynamics of exploited small pelagic populations. Our eventual goal is to develop appropriate management schemes. We address stochastic environmental effects, which are also important, in another paper.

MATERIALS AND METHODS

We consider a time-discrete model for a population with more than one age class. The first age class comprises the juveniles (recruits); the remaining classes comprise the adults. For such a population the total number of individuals in a given year (N_t) is composed of the number of recruits in that year (R_t) plus survivors from the previous year (S_t):

$$N_t = R_t + S_t \quad (1)$$

Assuming constant annual survival rates for recruits and adults, this year's number of adults (S_t) is given by the number of recruits from the previous year that survived to the present year ($p_1 R_{t-1}$), plus adults of last year that survived to the present year ($p_2 S_{t-1}$):

$$S_t = p_1 R_{t-1} + p_2 S_{t-1} \quad (2)$$

where p_1 and p_2 are the net annual natural survival rates of recruits and adults, respectively. Combining equations 1 and 2 we have:

$$N_t = R_t + p_1 R_{t-1} + p_2 S_{t-1} \quad (3)$$

Equation 3 is a discrete time model for population growth; if recruitment is constant, then population size will merely depend on survival rates, the size of annual recruitment, and the adult stock size in the previous year; that is, $N_t = R(1 + p_1) + p_2 S_{t-1}$. If recruitment is not constant, one can include a function in equation 3 to model variation in annual recruitment. We took this approach and included a Shepherd (1982) stock-recruitment function in equation 3. Cisneros-Mata et al. (1995) found that Shepherd's model fit data for sardine in the gulf.

Shepherd's model yields a curve with a dome that is more or less pronounced, depending on the strength of the density dependence:

$$R_t = \frac{aS_{t-1}}{1+(S_{t-1}/b)^c} \quad (4)$$

where R_t is recruitment size in year t , S_{t-1} is parental stock size in the previous year, and a , b , and c are parameters that shape the curve. Here, a is maximum per capita recruitment; b is the parental stock size above which density dependence dominates density-independent factors; and c measures the strength of the density dependence. Inclusion of equation 4 in equation 2 yields the following nonlinear, second order, discrete model for the annual adult stock size as a function of past stock sizes and survival rates:

$$S_t = p_1 \frac{aS_{t-2}}{1+(S_{t-2}/b)^c} + p_2 S_{t-1} \quad (5)$$

To determine the stability properties of model 5, we used a standard technique (e.g., Edelstein-Keshet 1988) that consists of a perturbation to the linearized system at an equilibrium point. If the perturbation grows with time, the system is unstable, and vice versa. Briefly, model 5 was transformed into a system of two equations, and the Jacobian was evaluated at steady states to find conditions for stability. (For details, see Appendix.) From this analysis, we found model 5 to be stable over the range of parameters satisfying

$$2 > 1 - p_1 ab^c \left[\frac{b^c + (\dot{S})^c (1-c)}{(b^c + (\dot{S})^c)^2} \right] > p_2, \quad (6)$$

where p_1 , a , b , and c are the same as described above, and \dot{S} is the equilibrium adult stock size.

We included age structure in our model population of sardine by combining equation 5 with a 7 year-class Leslie matrix; that is, annual recruitment was computed with Shepherd's model and a constant survival rate for the 6 age classes comprising the parental stock.

Parameter values of the Shepherd stock-recruitment relationship for the sardine of the Gulf of California were

(from Cisneros-Mata et al. 1995): $a = 2.697$ recruits per adult; $b = 1.471 \times 10^{10}$ adults; and $c = 6.499$, with standard errors of 0.3, 1.13×10^9 , and 2.23, respectively.

In all simulations, initial numbers in the population were set arbitrarily as 100×10^6 recruit sardines, and biomass trends were computed over a period of 400 years. Numbers (N_t) were converted to biomass with: $W_t = N_t W_\infty [1 - e^{-K(t-t_0)}]^\beta$, where W_t is weight at age t ; W_∞ (g) = αL_∞^β is maximum weight, and $L_\infty = 204$ mm (standard length); $K = 0.86y^{-1}$; and $t_0 = -0.014y$ (Cisneros-Mata et al. 1995) are parameters of the von Bertalanffy individual growth function. The standard errors of L_∞ , K , and t_0 are 3.14, 0.07, and 0.04. The parameters of the length-weight relationship, $\alpha = 4.21 \times 10^{-6}$ (SE = 1.01×10^{-6}) and $\beta = 3.28$ (SE = 0.03) were computed with samples of sardine taken from the commercial landings during the 1994-95 fishing season.

Mean adult annual survival rates (p_2) for the unfished Pacific sardine stock in the gulf were computed as: e^{-M} , where yearly instantaneous natural mortality rate $M = e^{1.46 - 1.01 \ln t_{max}}$ (Hoenig 1983) and $t_{max} = 7y$ (Wong 1973) is longevity of sardine. For recruits the survival rate (p_1) was arbitrarily increased by 5% because there is evidence that in clupeids and other fish species survival decreases with age (Hoenig 1983). We used the resulting values, $p_1 = 0.57$ and $p_2 = 0.55$, as baseline survival rates in our analyses.

We investigated the effect of density-dependent recruitment on stability of the sardine population by computing annual biomass trajectories using different values of parameter c of the stock-recruitment relationship. The values chosen for c were one-half and double the baseline value (which we call $c_0 = 6.499$), both within a 95% confidence interval of c_0 .

Periodic environmental forcing was simulated by introduction of a sine function of mean annual juvenile and adult natural survival rates. The equation was: $X_t = X_0 + d \sin(2\pi \frac{1}{T} t)$, where X_t = survival rate at time t ; X_0 = original survival rate (p_1 or p_2); d = amplitude; and T = period of oscillations. We chose a period of 60 years for all trials because we were interested in using a frequency similar to that observed in pelagic stocks (Lluch-Belda et al. 1989; Baumgartner et al. 1992). We conducted a series of trials with three different wave amplitudes d (0.2, 0.3, and 0.4) and observed the effects on dynamics of model sardine population. The values tested for d were chosen to avoid survival rates above one, and zero or less.

To investigate how fishing affects a population of Pacific sardine already experiencing cyclic oscillations in survival due to environmental forcing, we introduced an additional mortality factor affecting survival rates of adults and juveniles. For adults, we used a linearly increasing instantaneous fishing mortality (F) schedule over a 25-

year period, ranging from $F = 0.08$ in year 1 to $F = 2$ in year 25, and $F = 0$ in all other years. For juveniles, we arbitrarily used the same schedule but multiplied by $1/3$, based on the idea that juveniles are usually under less fishing pressure than adults. Both the time span and the final fishing mortality were chosen to emulate the fishing schedule experienced by Pacific sardine in the gulf. Computations using length-based cohort analysis (Jones 1981) yielded an F of 1.4 for the mid-1980s (Cisneros-Mata et al. 1990).

The resulting linearly increasing annual fishing mortality coefficients F 's were converted to annual survival rates as: $S_F = e^{-F}$; total survival after natural and fishing mortality occurred was computed as $S_T = X_t * S_F$. We simulated fishing during 25 years starting at four points in the baseline cycle of survival rates: increasing, peak, decreasing, and trough. For these trials we arbitrarily fixed the amplitude of oscillations of survival rates to the intermediate value ($d = 0.3$) tested in the previous section.

RESULTS

The stability condition of the system (equation A5 in the Appendix) was not met: $2 > 2.62 > 0.55$; thus we concluded that, for the particular set of parameter values used, our model for Pacific sardine in the Gulf of California is intrinsically unstable. The condition for stability was met when we changed the value of parameter c to $0.5c_0$, but not to $2c_0$, and the null equilibrium (a collapse of the stock) is also stable (Appendix), which makes biological sense. However, adding age structure stabilized the sardine population, as demonstrated in the simulations.

Density-dependent recruitment had a strong effect in the dynamics of the model sardine population. Time series plots of biomass of adults at time t vs. biomass of recruits at time $t+1$ changed from a smooth parabola for $c = 0.5c_0$, to orbital shapes at high population values for c_0 and $2c_0$ (figure 2). Mean size of the stock decreased with increasing density dependence. The trajectories of total biomass with the baseline (c_0) density-dependence value showed a two-point limit cycle with a period of 5 years. The oscillations disappeared when the strength of density dependence was decreased to $c = 0.5c_0$, and increasing c to $1.5c_0$ produced oscillations of the same amplitude as those with c_0 but decreased the period to 4 years (figure 2).

For the three amplitudes tested for the sinusoidal function of survival rates, total sardine biomass over time showed periodic oscillations of mesoscale frequency superimposed on the 60-year period caused by oscillating survival rates (figure 3). Increasing d reduced the frequency of oscillations at low population sizes and increased the amplitude at high population sizes; the largest

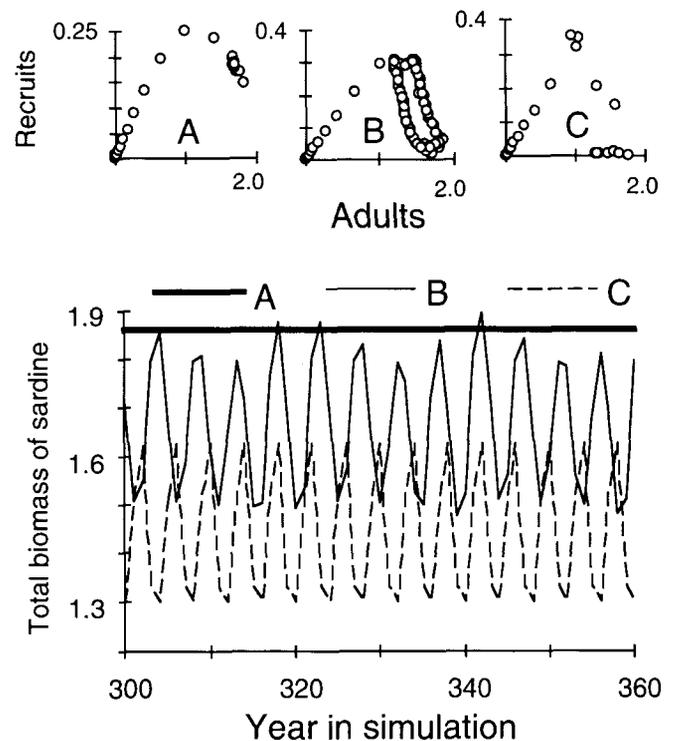


Figure 2. Effects of density-dependent recruitment on the dynamic behavior of a model Pacific sardine population. Baseline indicates the default value $c_0 = 6.499$ (from Cisneros-Mata et al. 1995), which is a measure of the strength of density dependence in Shepherd's (1982) stock-recruitment function. *Top panel*, stock-recruitment trajectories for the three scenarios: $0.5c_0$ (A), baseline (B), and $2c_0$ (C). *Bottom panel*, trajectories of total biomass computed with the same three values of c . All figures are in millions of metric tons.

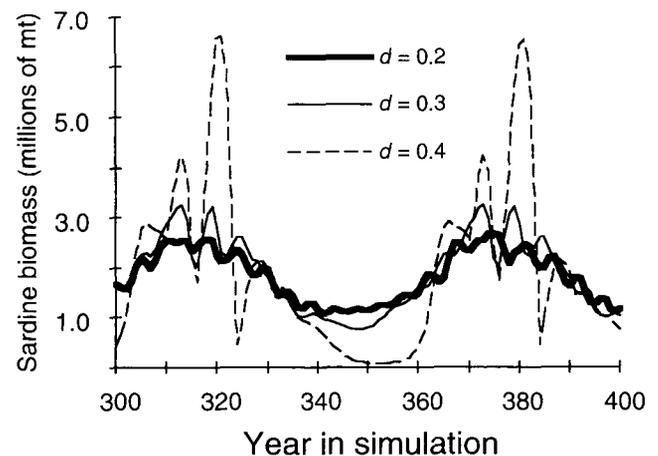


Figure 3. Effects of environmental forcing with different amplitudes and constant period (60 years) on juvenile and adult survival rates in the Pacific sardine population model. Parameter d measures the relative amplitude of the sinusoidal trajectories of annual survival rates.

value of d almost caused the stock to collapse (figure 3). The trough/peak values of juvenile survival for the three values of d used were: $0.37/0.77$ for $d = 0.2$; $0.27/0.87$ for $d = 0.3$; and $0.17/0.97$ for $d = 0.4$. The values for adult survival were: $0.35/0.75$; $0.25/0.85$; and $0.15/0.95$. Thus virtual extinction when $d = 0.4$ was

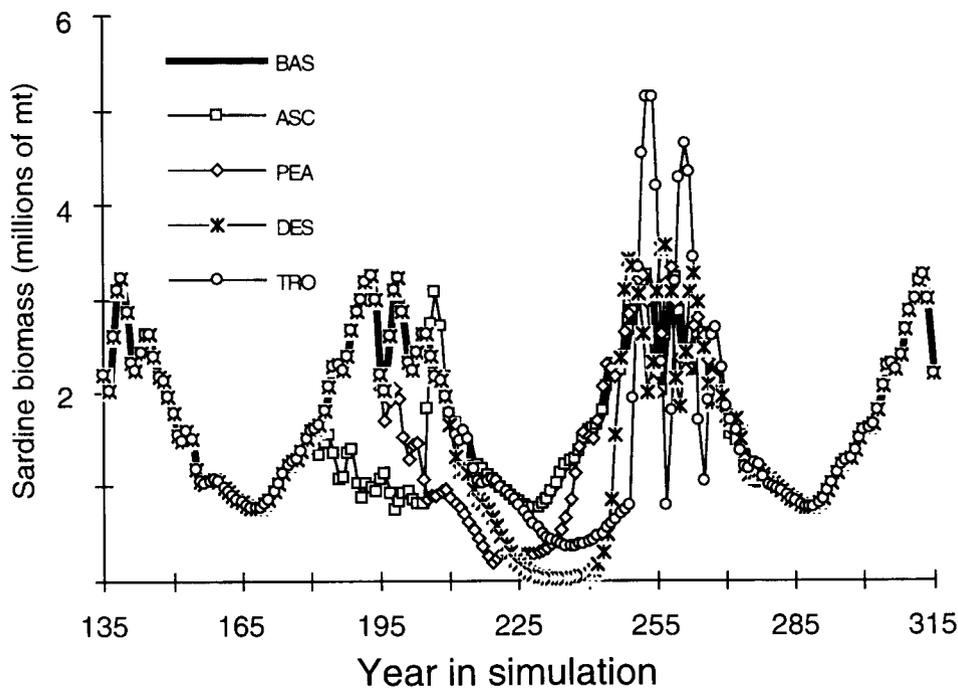


Figure 4. Simulated effect of 25 years of increased fishing pressure starting at four different points of a 60-year cyclic Pacific sardine population. The amplitude of oscillations is $d = 0.3$. BAS indicates an unfished population; ASC corresponds to initial harvest at the ascending node of the cycle, PEA at the peak, DES at the descending node, and TRO at the trough.

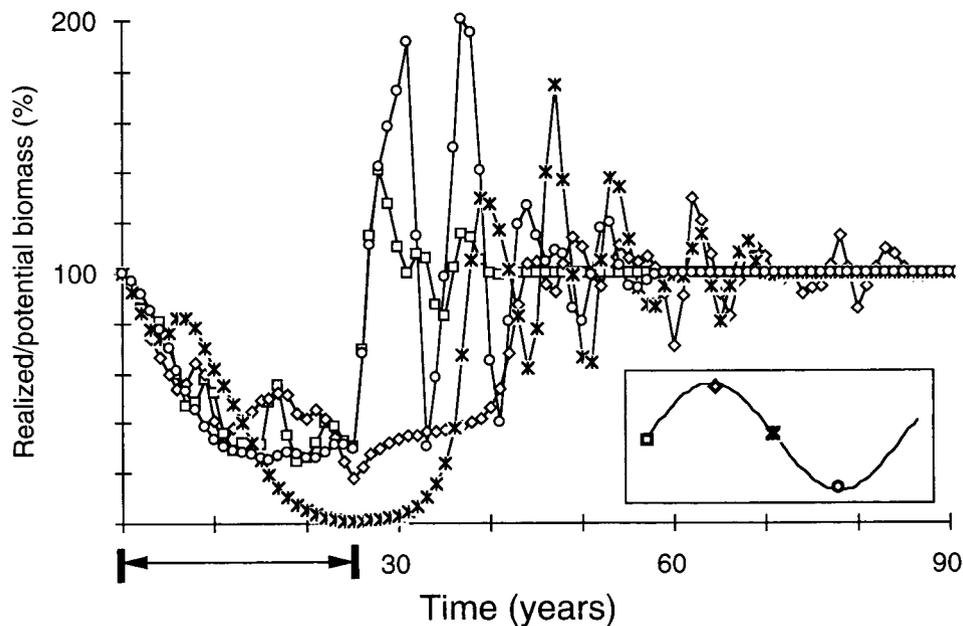


Figure 5. Simulated ratios of realized/potential biomass of a 60-year cyclic Pacific sardine population under 25 years of increasing fishing pressure starting at four different points in the sinusoidal cycle of survival rates. The *double-headed arrow* indicates the period of fishing (F). The insert represents the cycle of survival rates causing the oscillations of sardine biomass, and shows the beginning of fishing in the four scenarios.

due to the dynamic behavior of the population, and not to null survival rates due to forcing.

For the four starting points at the 60-year cycle of sinusoidal survivorships, fishing severely decreased population size (figure 4). For a clearer representation, we

computed the ratio of realized to potential sardine biomass and scaled all four cases to the same starting point of fishing (figure 5). The stock was significantly affected both during the fishing period and after it had ended. When fishing began at the descending node of the

regime, sardine biomass was quite low during the last decade of fishing. The overall effect in terms of time it took to recover after harvest was worst when fishing started at the peak of the regime, and the widest oscillations were caused when fishing started at the trough (figure 5). Oscillations in the ratio of realized/potential biomass continued long after fishing had ceased. Values other than 100% result from baseline and realized trajectories being out of phase, thus oscillations indicate changes in the dynamic behavior of the model population due to fishing pressure.

DISCUSSION

Our analysis indicates that for the underlying assumptions and range of parameter values used, age structure, environmental forcing, and density dependence can strongly affect the long-term dynamic behavior of the sardine population in the gulf. Density-dependent recruitment effects produced cycles of mesoscale frequency. Fishing had a strong impact; it reduced potential biomass and altered the oscillations imparted by a forcing environment.

Oscillations of mesoscale frequency in the biomass of sardine were driven by density-dependent recruitment, as shown in figure 2. The existence of density dependence in small pelagic fishes has been questioned, probably because of difficulty in finding convincingly supportive empirical data (e.g., Armstrong et al. 1989; Koslow 1992). For the Pacific sardine in the California Current, Jacobson and MacCall (1995) found a relation between spawning biomass and number of recruits, suggesting compensatory mortality of juveniles. Recruitment success in these species has been related to ambient indicators such as plankton biomass or annual sea temperature (Ware 1991; Jacobson and MacCall 1995). Cannibalism has also been hypothesized as an important density-dependent factor affecting recruitment in small pelagic fish (Sharp 1987). Smith et al. (1989) concluded that for sardine and anchovy off Peru, cannibalism of adult fish on their eggs could cause low-frequency changes in biomass.

For the Pacific sardine in the gulf no mechanism has been identified to explain the overcompensatory relation found between adults and recruits. Recent studies showed the presence of Pacific sardine eggs in stomachs of adults of the same species (López-Martínez, Centro de Investigaciones Biológicas del Noroeste, Guaymas, Son., pers. comm.), thus suggesting cannibalism. A probable mechanism that results in increased cannibalism in the gulf is the intrusion of anomalous warm-water masses that shorten the spawning season and compress adult distribution northward (Hammann 1991). Strong sardine recruitment has been shown to occur after cool, anti-El Niño years present in the gulf with mesoscale frequency

(Huato-Soberanis and Lluch-Belda 1987). These concepts seem to complement each other: expansion of spawning habitat for sardine during cool years results in low cannibalism, increased probability of survival, and good recruitment; the opposite occurs during warm years.

Adding age structure to our sardine model had a stabilizing effect on the population trajectories. This is in agreement with results by Botsford and Wickham (1978) who showed that removing older individuals could destabilize the stock of a model crab population. Before reaching stable age distribution and geometric growth, populations modeled with a Leslie matrix with no density dependence will oscillate with a period equal to the mean generation time (Caswell 1989). For sardine in the gulf, mean generation time—defined as the average age of mature females in a population at stable age distribution (Stearns 1992)—is 3 years as compared to the 4- and 5-year cycles caused by density dependence. Our results show that regulatory mechanisms will override oscillations due to age structure, even when the population increases from a very low level. Nevertheless, it seems likely that the combined effect of a lagged response of total biomass due to age structure (Caswell 1989) and density dependence caused the oscillations after the fishing period.

Environmental forcing on survival rates strongly affected the dynamic behavior of sardine in our model population. No conclusion can be drawn regarding the amplitude and period of oscillations because the values chosen here as baselines were completely arbitrary. Judging by the recovery that the sardine stock is experiencing, it would seem that environmental forcing in the gulf, if it exists, probably has a period of less than 60 years.

Although nonmechanistic, the approach we used here was intended to explore the consequences of cyclic variation of survival rates. Regardless of its nature, an environmental regime will ultimately affect survival rates and probably the fecundity of sardine and other species. Existence of cyclic environmental forcing seems likely, given the low-frequency oscillatory behavior of Pacific sardine in and outside the Gulf of California. Lluch-Belda and collaborators (1991a, b, 1992) provided evidence of a direct relation between sea-surface temperature and abundance and distribution range of Pacific sardine in the California and Humboldt Currents. Smith (1995) discussed the potential effects that warming in the California Current might have on the population growth of Pacific sardine over the past decade. For example, decreased incubation period and maturation time due to high temperature might result in lower mortality and higher biomass.

Our results indicate that harvest strongly affects the sardine stock experiencing environmental forcing. It took up to 20 years after fishing had ended for the stock to

recover its baseline biomass level, and up to 40 years for oscillations to subside. Because the scale of recovery is probably similar to the time span of most real fisheries, these results point out the importance of adequate management to prevent economic, if not biological, collapse. Our results also suggest the resilience of the sardine stock in the gulf, because it was able to recover from near collapse after the harvest period. However, random environmental and demographic effects, in addition to density-independent effects, could drive the real population to extinction.

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APPENDIX

To determine its stability properties, model 5 was first reexpressed as a system of two first-order equations:

$$S_t = f(S_{t-1}, Y_{t-1}) = p_1 \frac{aY_{t-1}}{1 + (Y_{t-1}/b)^c} + p_2 S_{t-1} \quad (\text{A1a})$$

$$Y_t = g(S_{t-1}, Y_{t-1}) = S_{t-1} \quad (\text{A1b})$$

A steady state (or equilibrium) occurs when, for suitable values \dot{S} and \dot{Y} , we have $S_t = \dot{S} = S_{t-1}$ and $Y_t = \dot{Y} = Y_{t-1}$. Thus, \dot{S} and \dot{Y} must satisfy:

$$\dot{S} = f(\dot{S}, \dot{Y}) = p_1 \frac{a\dot{Y}}{1 + (\dot{Y}/b)^c} + p_2 \dot{S} \quad (\text{A2a})$$

$$\dot{Y} = g(\dot{S}, \dot{Y}) = \dot{S} \quad (\text{A2b})$$

Note that the null equilibrium ($\dot{S} = 0$ and $\dot{Y} = 0$) is stable. Equation A2a implies that

$$\dot{S} = \frac{p_1 a \dot{Y}}{(1 - p_2) \left[1 + (\dot{Y}/b)^c \right]} \quad (\text{A3a})$$

and

$$\dot{Y} = \dot{S} \quad (\text{A3b})$$

When values of S_t and Y_t are close to a steady state (\dot{S}, \dot{Y}) , equation A1 can be approximated as a linear system. Expressed in matrix form, this system is:

$$\begin{bmatrix} s_t \\ y_t \end{bmatrix} = \begin{bmatrix} \partial f / \partial s & \partial f / \partial y \\ \partial g / \partial s & \partial g / \partial y \end{bmatrix}_{\dot{S}, \dot{Y}} \begin{bmatrix} s_{t-1} \\ y_{t-1} \end{bmatrix}, \quad (\text{A4})$$

where f and g are given by equations A1a and A1b, respectively. s_t and y_t represent small perturbations $S_t - \dot{S}$ and $Y_t - \dot{Y}$ from the equilibrium points \dot{S} and \dot{Y} . The matrix of partial derivatives in equation A4 is known as the Jacobian (J), and the condition for stability of the system is (Edelstein-Keshet 1988):

$$2 > 1 + \text{Det}(J) > |\text{Tr}(J)|, \quad (\text{A5})$$

where $\text{Det}(J)$ is the determinant and $\text{Tr}(J)$ the trace of J . In the particular case of equation A4

$$\begin{aligned} \partial f / \partial s &= p_2, \quad \partial f / \partial y = p_1 a \left[\frac{b^{2c} + b^c Y^c (1-c)}{(b^c + Y^c)^2} \right], \\ \partial g / \partial s &= 1, \quad \text{and} \quad \partial g / \partial y = 0 \end{aligned}$$

Therefore

$$J = \begin{bmatrix} p_2 & p_1 a \left[\frac{b^{2c} + b^c Y^c (1-c)}{(b^c + Y^c)^2} \right] \\ 1 & 0 \end{bmatrix}_{\dot{S}, \dot{Y}} \quad (\text{A6})$$

Finally—for given values of the parameters a , b , c , p_1 , and p_2 —the equilibrium population size is found by solving system equation A3:

$$\dot{S} = b \left(\frac{ap_1}{1-p_2} - 1 \right)^{1/c} \quad (\text{A7})$$