THE EFFECT OF NATURAL VARIABILITY OF LIFE-HISTORY PARAMETERS ON ANCHOVY AND SARDINE POPULATION GROWTH

JOHN L. BUTLER, PAUL E. SMITH, AND N. CHYAN-HUEI LO

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) populations were modeled with a stage-based matrix to examine how natural variation of life-history parameters affects per capita growth. In the model northern anchovy (*Engraulis mordax*) population, the greatest change in growth results from natural variation in the duration of, and the instantaneous mortality rate of, the early and late larval stages. In the model Pacific sardine (*Sardinops sagax*) population, the greatest change in growth results from natural variation in the duration of, and the instantaneous mortality rate of, the late larval stage. Temperature determines the duration of both egg and yolk-sac larval stages and the rate at which prerecruit sardine and anchovy mature. We believe that changes in the duration of both egg stages and yolk-sac larval stages may have greater effects on population growth than changes in any single stage.

RESUMEN

Se modelaron las poblaciones de anchoveta nortẽna (*Engraulis mordax*) y de sardina Monterrey (*Sardinops sagax*). Usando matrices basadas en estadios de vida, se examinó como la variación natural de los parámetros de las fases vitales afecta el crecimiento per capita. En las poblaciones modelo de anchoveta, el mayor cambio en crecimiento fué resultado de la variación natural de la duración y de la tasa instantánea de mortalidad de los estadios tempranos y tardíos de las larvas. En la población modelo de sardina, el cambio mayor en crecimiento fué resultado de la variación natural de la duración y tasa instantánea de mortalidad de los estadios larvales tardíos. La temperatura determina la duración de los estadios huevo y saco vitelino, así como la tasa a la cual las sardinas y anchovetas pre-reclutas maduran. Creemos que cambios en la duración de estadios huevo y de saco-vitelino podrían tener efectos mayores en el crecimiento poblacional que cambios en cualquiera de los estadios individuales.

INTRODUCTION

The Pacific sardine population (*Sardinops sagax*) in the northeast Pacific Ocean has greatly fluctuated during this century. Biomass peaked in 1932 at about 3,600,000 MT (Murphy 1966) and then fell to about 6,000 MT in 1975 (Barnes et al. 1992); it remained low for the rest of the decade. Recently the sardine has begun to recover off California and northern Baja California. Since the early 1980s the population has grown steadily at about $50\% \cdot y^{-1}$ (Smith et al. 1992) to reach a biomass of about 340,000 MT in 1991 (Barnes et al. 1992).

The northern anchovy (*Engraulis mordax*) population off California and Mexico has also undergone large changes. Stock size was low in the 1950s and 1960s, grew rapidly in the early 1970s, and reached a maximum biomass of about 1,700,000 MT in 1974 (Lo and Methot 1989). In the early 1970s, the northern anchovy's population growth rate was also about $50\% \cdot y^{-1}$.

Scale-deposition rates in anaerobic sediments indicate that both populations have undergone similar wide fluctuations before and since the development of modern fisheries (Soutar and Isaacs 1974; Smith and Moser 1988). Sardines appear to fluctuate more rapidly than anchovy, although Lasker and MacCall (1983) pointed out that calibrating scale-deposition rate to population size may exaggerate changes in total abundance of the species. Nevertheless the scale data indicate that large population fluctuations are common among these clupeoid stocks in the absence of fisheries, and that these fluctuations must be due to changes in the physical and biotic environment.

Global climate change will significantly affect the physical environment of marine ecosystems. Potential effects include changes in sea-surface temperature and in the intensity of upwelling (Bakun 1990). These physical changes will affect the distribution and dynamics of fish stocks. The stage-based matrix described here provides a means to test hypotheses concerning how environmental change will affect fish populations.

A number of important life-history parameters of marine fish are directly affected by changes in temperature. Temperature and food densities affect

growth at all stages. Instantaneous mortality of eggs and larvae are also a function of temperature (Houde 1989), and the size and age of first reproduction varies with temperature (Methot 1986). Because all of these parameters are linked by temperature, it is possible that some of the effects of global climate change can be investigated by means of stage-based population models and existing knowledge.

Previous attempts to model anchovy or sardine populations using stage-based models have been hampered by (1) a lack of theoretical framework (Smith 1985) or (2) an incomplete understanding of the range of variation for important life-history parameters (Smith 1985; Smith et al. 1992). Our objective in this paper is to model anchovy and sardine populations by using a stage-based matrix (Lefkovitch 1965) as a theoretical framework and to examine how natural variation of stage-specific vital rates affects population growth rates.

Vital rates for each stage of the model were obtained from the literature. For some stages the vital rate is unknown; in such cases we obtained a vital rate from literature on other populations of sardines and anchovy, or estimated by the methods described below. We have thus compiled the most comprehensive estimates of life-history parameters to date. We also examined the effect of fishing mortality on the two populations.

METHODS

The matrix (**A**) describes the transition of a population from time t to time $t+1$ in terms of vital rates of each life stage:

$$\mathbf{A}n_t = n_{t+1} \tag{1}$$

where n_t is a vector describing the population at each stage at time t, and **A** is the transition matrix:

$$\mathbf{A} = \begin{matrix} P_1 & m_2 & . & . & . & m_q \\ G_1 & P_2 & 0 & . & 0 & 0 \\ 0 & G_2 & P_3 & 0 & . & 0 \\ . & . & . & . & . & . \\ 0 & 0 & 0 & . & G_{q-1} & P_q \end{matrix} \tag{2}$$

where P_i is the probability of surviving and staying in stage i, G_i is the probability of surviving and growing into the next stage, and m_i is the maternity per fish per unit time (d); $i = 1, \ldots q$.

Both P_i and G_i are functions of the survival probability (p_i) and the growth probability (γ_i) (Caswell 1989):

$$p_i = e^{-z_i} \tag{3}$$

and $$P_i = p_i(1 - \gamma_i) \tag{4}$$

and $$G_i = p_i \gamma_i \tag{5}$$

where $$\gamma_i = [(1 - p_i)p_i^{d_i-1}]/[1 - p_i^{d_i}] \tag{6}$$

where z_i is the daily instantaneous mortality rate (IMR) and d_i is the duration (d) within the ith stage. The derivation of P_i, G_i, and γ_i follow Crouse et al. (1987) and Caswell (1989).

The maternity parameter m_i is computed as:

$$m_i = (\sum_j [f_j w_{ij}])/\sum_j [w_{ij}] \tag{7}$$

where f_j (the age-specific fecundity rate) is the number of eggs per fish of age j per unit time, and w_{ij} is the proportion of fish that are of age j:

$$w_{ij} = \exp(-z_i t_{1j}) - \exp(-z_i t_{2j}) \tag{8}$$

where t_{1j} is the beginning and t_{2j} is the ending age for the fish of age group j. Briefly, total annual production of eggs was estimated for each size class and apportioned on an average daily basis.

Anchovy spawn each day from sunset to midnight, with the peak at 2200 (Lo 1983). Sardine spawn between 2000 and 0400, with the peak near midnight (Smith 1973). In the model, the fecundity estimates of sardine were assumed to be knife-edged at 0000 h, and the fecundity estimates of anchovy were corrected for mortality from spawning (2200) to census at the end of day one (2400) by: $F_i = Q_i m_i$, where Q_i is the probability of surviving from spawning to the first census and $Q_i = e^{-zt}$, where z is the daily instantaneous mortality rate and t is the time from peak spawning to the time of census.

The dominant eigenvalue λ of the matrix represents the population growth rate. If $\lambda = 1.0$, the population is stationary, and if $\lambda = 1.5$, the population is growing at $50\% \cdot d^{-1}$. The results are given in annual growth of the population, which is equal to λ^{365}, since the duration of stages was measured in days. We estimated λ from the dominant eigenvalue of the matrix **A** using MathCAD.

We measured the importance of natural variability in mortality, duration, and fecundity parameters at each stage by calculating λ for a series of values for each parameter. Initial conditions were a stationary population, and we examined changes of λ with known deviations of each stage-specific vital rate.

Anchovy Vital Rates

The northern anchovy is a multiple spawner (Hunter and Goldberg 1980). Annual fecundity is

the number of eggs released per spawning (batch fecundity) times the number of spawnings in a season. The variation in batch fecundity and the variation of spawning rate with age are well known (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Parrish et al. 1986; Alheit, in press), but little is known of the interannual variation in number of spawnings per year. The spawning rate for northern anchovy varies interannually from once every 6.25 days to once every 10.6 days (Bindman 1985). At that rate the average female would spawn 5 to 10 times during the March–April spawning season. Some spawning occurs all year long, and Parrish et al. (1986) found evidence that the number of spawnings per year increases with age. The fecundity used in the model was a daily rate that apportioned spawning equally over the year (table 1). In reality, spawning is seasonal, but modeling the seasonality of spawning is beyond the scope of this paper. The daily fecundity was divided by two to estimate the number of female eggs.

The anchovy population was modeled on the basis of nine stages, as defined by Smith (1985). We derived minimum, maximum, and best estimates of daily instantaneous mortality rates and duration of each stage from literature values (table 2). The durations of the egg and yolk-sac stages are derived from incubation experiments at different temperatures (Lo 1983). Mean duration was based on the development rate at 16°C, which is about the average temperature for anchovy eggs. Mortality rates of egg, yolk-sac, and larval stages were estimated from field studies (Stauffer and Picquelle 1981; Bindman 1985). Durations of the larval and juvenile stages are from field studies of growth rates derived from daily increments in the otoliths (Methot and Kramer 1979; Butler 1987, 1989).

TABLE 1
Fecundity Schedule of Northern Anchovy

Year	Wt (g)	Spawns per year	Batch (eggs)	M(x)	L(x) z = .76	LxMx	Daily
0	0.0	0.0					
1	8.7	5.3	4237.8	22460.3	1000	11230170	30747
2	14.6	11.9	7860.4	93538.8	468	21888070	59926
3	18.3	19.2	10132.2	194538.2	216	21010130	57523
4	21.2	23.5	11912.8	279950.8	102	14277491	39090
5	24.5	23.5	13939.0	327566.5	48	7861596	21524
6	24.5	23.5	13939.0	327566.5	22	3603232	9865
7	24.5	23.5	13939.0	327566.5	10	1637833	4484

	Female eggs per female per day mean	90% maturity at year one*
Juveniles	11.7	10.5
Small adults	199.2	199.2
Large adults	448.4	448.4

*Assuming that 90% of females mature at age 1 and that the batch fecundity is given by the formula: Batch = −1104 + 614*wt (Hunter et al. 1985).

Mortality rates of the late larval and early juvenile stages are unknown. We estimated these rates from the relationship of mortality rate to body size (Peterson and Wroblewski 1984) and adjusted them to achieve a stationary population. The relationship between dry weight and mortality rate is given by Peterson and Wroblewski (1984): $M_{(w)} = (1.92 \cdot y^{-1})w^{-0.25}$, and the relation between length and dry weight for northern anchovy is dry weight = $0.000488*SL^{3.73}$, where SL is measured in cm (Butler 1987). For a 72.5-mm juvenile $M = 2.04$, and the daily rate is $z = 2.83/365.25 = 0.00557$. This value was adjusted to a "best" value of 0.0044 to obtain a lambda of 1.0. We chose the late juvenile stage for this adjustment because at present little is known about natural mortality in this stage.

TABLE 2
Stage-Specific Life-History Parameters of Northern Anchovy

Stage	Size (mm) Min.	Max.	Daily natural mortality Min.	Best	Max.	Duration (days) Min.	Best	Max.	Daily fecundity/female Min.	Best	Max.
Egg			0.12[a]	0.231[a]	0.45[b]	1.4[c]	2.9[c]	3.9[c]	0	0	0
Yolk-sac larvae	hatch	4	0.19[d]	0.366[d]	0.59[d]	1.4[c]	3.6[c]	3.9[c]	0	0	0
Early larvae	4	10	0.187[d]	0.286[d]	0.345[d]	8[e]	12[e]	23[e]	0	0	0
Late larvae	10	35	0.0470[f]	0.0719[f]	0.087[f]	35[g]	45[g]	71[g]	0	0	0
Early juvenile	35	60	0.0009[f]	0.0141[f*]	0.017[f]	45[g]	62[g]	100[g]	0	0	0
Late juvenile	60	85	0.0029[f]	0.0044[f]	0.0053[f]	60[g]	80[g]	138[g]	0	0	0
Prerecruit	85	110	0.0020[f]	0.0031[f]	0.0037[f]	200[h]	287[h]	632[h]	0	10.[i]	19.4
Early adult	110	135	0.0011[j]	0.0021[j]	0.0036[j]	750[h]	1000[h]	1250[h]	143.8	199.2[i]	230.7
Late adult	135	160	0.0011[j]	0.0021[j]	0.0036[j]	1000[h]	1250[h]	1500[h]	284.2	448.2[i]	529.0

[a]Bindman 1985
[b]Stauffer and Picquelle 1981
[c]Lo 1986
[d]Peterman et al. 1988
[e]Methot and Kramer 1979
[f]Peterson and Wroblewski 1984

[g]Butler 1987, Waldron et al. 1989
[h]Fiedler et al. 1986
[i]Hunter et al. 1985
[j]Methot 1989
*Used to tune model to lambda = 1.0

Adult natural mortality rates are assumed to be constant with age and were derived from the stock synthesis model (Methot 1989). We also examined the effect of an annual fishing mortality rate of 0.6 on all adult stages. We derived adult growth rates from fisheries data (Fiedler et al. 1986).

Sardine Vital Rates

Pacific sardine is also a multiple spawner. Batch fecundity estimates were based on MacGregor (1957) and Clark (1934). Little is known about the number of spawnings per year. Off Chile, the Pacific sardine (*S. sagax musica*) spawns every 7 days (Oliva et al. 1989), a rate similar to that of the northern anchovy. The South African pilchard, *Sardinops ocellatus*, spawns every 2–5 days, and older fish may spawn up to 80 times per year (Le Clus 1989). Fecundities in the life table (table 3) were estimated from batch fecundity times a total of 40 spawnings per year for the oldest age classes (the maximum rate is 80 spawnings per year, and the minimum is 24; table 4). We divided the daily fecundity by two to account for the number of female eggs.

We modeled the sardine population with thirteen stages as defined by Smith et al. (1992). The minimum, maximum, and mean daily instantaneous mortality rates and duration of each stage are derived from the literature (table 4). The durations of the egg and yolk-sac stages are derived from incubation experiments at different temperatures (Lasker 1964). Mean duration was derived from the development rate at 16°C, which is about the average temperature for sardine eggs (15.6°C; Butler 1987).

We estimated mortality rates of yolk–sac and larval stages from the field (Butler 1991). The best estimates of egg mortality rates are from unpublished data (N. C. H. Lo). Durations of the larval and juvenile stages are from field studies of growth rates calculated from daily increments in the otoliths (Butler and Rojas de Mendiola 1985; Castillo et al. 1985; Butler 1987). The mortality rates of the late larvae through stage III juveniles are unknown. We estimated these rates from the general relation-

TABLE 3
Fecundity Schedule of Pacific Sardine

Age	Wt (g)	Spawns	Batch	M(x)	Daily	L(x)	Survivors to day 1
1	52.7	0	13860	0	0	1000	0
2	93	6	24459	146754	402	670	201
3	123	12	32349	388188	1063	449	238774
4	152	15	39976	599640	1642	301	247239
5	170	19	44710	849490	2326	202	234783
6	193	23	50759	1167457	3196	135	216288
7	202	28	53126	1487528	4073	91	184730
8	205	30	53915	1617450	4428	61	134644
9	205	35	53915	1887025	5166	41	105297
10	205	40	53915	2156600	5904	27	80666
11	205	40	53915	2156600	5904	18	54072
12	205	40	53915	2156600	5904	12	36245
13	205	40	53915	2156600	5904	8	24296

	Female eggs per female per day	Survivors to first census
Prerecruit	134	80.5
Juveniles	647.6	388.9
Small adults	1576.3	946.6
Large adults	2811.5	1688.3

Batch fecundity = 263 eggs per gram (MacGregor 1957).

TABLE 4
Stage-Specific Life-History Parameters of the Pacific Sardine

Stage	Size (mm) Min.	Max.	Daily natural mortality Min.	Best	Max.	Duration (days) Min.	Best	Max.	Daily fecundity/female Min.	Best	Max.
Egg			0.31[a]	0.72	2.12[b]	1.4[c]	2.5[c]	3.9[c]	0	0	0
Yolk–sac larvae	hatch	4	0.394[d]	0.6698[d]	0.971[d]	1.4[c]	3.1[c]	3.9[c]	0	0	0
Early larvae	4	10	0.1423[d]	0.2417[d]	0.3502[d]	5[e]	11[e]	21[f]	0	0	0
Late larvae	10	35	0.057[d]	0.0964[d]	0.139[d]	20[g]	35[g]	50[g]	0	0	0
Early juvenile	35	60	0.029[d]	0.056[d]	0.081[d]	17[g]	25[g]	40[g]	0	0	0
Juvenile I	60	85	0.0116[h]	0.0197[h,*]	0.0285[h]	30[g]	50[g]	80[g]	0	0	0
Juvenile II	85	110	0.0023[h]	0.0040[h]	0.0058[h]	80[g]	110[g]	146[g]	0	0	0
Juvenile III	110	135	0.0016[h]	0.0028[h]	0.0040[h]	105	146[g,i]	185	0	0	0
Juvenile IV	135	160	0.0012[i]	0.0022[i]	0.0032[i]	110	170[i]	220	0	0	0
Prerecruit	160	185	0.0006[l]	0.0011[l]	0.0015[l]	110	175[i]	220	0	80[k]	161[k]
Early adult	185	210	0.0006[l]	0.0011[l]	0.0015[l]	190[m]	381[m]	570[m]	286[k]	389[k]	489[k]
Adult	210	235	0.0006[l]	0.0011[l]	0.0022[l]	400[m]	663[m]	920[m]	730[k]	946[k]	1114[k]
Late adult	235	260	0.0006[l]	0.0011[l]	0.0022[l]	1908[m]	2773[m]	3473[m]	1064[k]	1688[k]	3123[k]

[a]Smith 1973
[b]Smith et al. 1989
[c]Lasker 1964
[d]Butler 1991
[e]Butler and Rojas de Mendiola 1985
[f]Castillo et al. 1985
[g]Butler 1987

[h]Peterson and Wroblewski 1984
[i]Kimura and Sakagawa 1972
[j]By analogy to northern anchovy
[k]MacGregor 1957, Clark 1934, Le Clus 1989
[l]Murphy 1966, MacCall 1979
[m]Walford and Mosher 1943, Phillips 1948
*Used to tune model to lambda = 1.0

ship of mortality rate to body size (Peterson and Wroblewski 1984). The relationship between dry weight and length is given by: dry weight = $0.0122*SL^3.35$, where standard length is measured in cm (Butler 1987). The predicted mortality rate was 0.0053 for stage I juveniles, and we adjusted this value to 0.0197 to achieve a theoretically stationary population. The mortality rates of stage IV juveniles and prerecruits are assumed to be the same as the mortality rates for northern anchovy of the same body size. Adult growth rates were derived from otolith readings (Phillips 1948); adult mortality rates were derived from the cohort analysis (Murphy 1966; MacCall 1979). Natural mortality was set at $0.4\% \cdot y^{-1}$. We also examined the effect of annual fishing mortality rates of 0.25 and 0.6.

RESULTS

Anchovy

Natural variations in individual stage-specific mortality or duration (table 5) result in changes of population growth from equilibrium to an annual increase or decrease of about threefold. The most influential stage appears to be the early larval. Natural variation in instantaneous mortality rates or duration of this stage lead to the largest changes in the population growth rate. The fastest growth rate of the early larvae results in a 278% increase in the population, whereas the slowest growth rate results in a 74% decrease (table 5). The least sensitive is the late adult stage: at that point, variations in growth and mortality have minimal effect on population growth. The sensitivity of the model to natural variations in fecundity may be an underestimate. The values in the literature are largely taken from biomass estimate studies, and none of these studies has encompassed a major environmental perturbation.

TABLE 5

Eigenvalue (λ^{365}) of Lefkovitch Matrix after Change in the Stage-Specific Life-History Parameters of Northern Anchovy

	Natural mortality		Duration		Fecundity	
Stage	Min.	Max.	Min.	Max.	Min.	Max.
Egg	1.27	0.66	1.30	0.85		
Yolk-sac larvae	1.65	0.60	1.93	0.93		
Early larvae	2.78	0.64	2.67	0.26		
Late larvae	2.57	0.65	1.78	0.37		
Early juvenile	1.90	0.88	1.20	0.71		
Late juvenile	1.09	0.95	1.07	0.85		
Prerecruit	1.35	0.84	0.98	0.79	0.95	1.02
Early adult	1.06	0.95	1.06	0.97	0.86	1.12
Late adult	1.00	1.00	1.00	1.00	0.97	1.16

TABLE 6

Eigenvalue (λ^{365}) of Lefkovitch Matrix after Change in the Stage-Specific Life-History Parameters of Pacific Sardine

	Natural mortality		Duration		Fecundity	
Stage	Min.	Max.	Min.	Max.	Min.	Max.
Egg	1.29	0.68	1.21	0.84		
Yolk-sac larvae	1.23	0.85	1.34	0.90		
Early larvae	1.31	0.82	1.47	0.72		
Late larvae	1.43	0.79	1.47	0.79		
Early juvenile	1.17	0.89	1.11	0.89		
Juvenile I	1.15	0.95	1.09	0.89		
Juvenile II	1.04	0.96	1.03	0.97		
Juvenile III	1.04	0.96	1.03	0.98		
Juvenile IV	1.04	0.97	1.03	0.98		
Prerecruit	1.02	0.98	1.01	0.99	0.98	1.00
Early adult	1.04	0.97	1.03	0.98	1.00	1.00
Adult	1.05	0.91	1.01	0.99	1.00	1.01
Late adult	1.05	0.86	0.99	1.00	1.00	1.11

There is some evidence that reproduction is drastically reduced during major El Niño events. Under such conditions the population declines rapidly.

We tested the effect of fishing on the anchovy population by using values of natural mortality of 0.76 and fishing mortality of 0.6 for both adult stages. Under these conditions the anchovy population declined at a rate of $5\% \cdot y^{-1}$.

Sardine

The population growth rate of the Pacific sardine appears to be most sensitive to changes in egg and larval stages (table 6). Reported values for egg mortality vary widely in the literature (Smith 1973; Smith et al. 1989). Extremely high values of egg mortality — 88% in the first day — were reported for the Pacific sardine off Peru (Smith et al. 1989). At this rate the model indicates that the population declines at the rate of 32% per year. The fastest growth of the early and late larval stages results in population growth rates of $43\% \cdot y^{-1}$, whereas the slowest growth rate of the early larval stage results in a population decrease of $28\% \cdot y^{-1}$ (table 6). The population is least sensitive to changes in the vital rates of the older stages, prerecruit through late adult.

Fishing affects the mortality rate of all adult sardine stages. If fishing mortality is 0.25, then the population declines at a rate of $18\% \cdot y^{-1}$. During the decline of the sardine fishery, fishing mortality was as high as 0.8 (Murphy 1966). At this level, the population declines at $50\% \cdot y^{-1}$. High fishing mortality reduces the abundance of the oldest age classes, which have the highest reproductive potential because of their larger size and greater number of spawnings.

DISCUSSION

For the northern anchovy, natural variation in the duration of, and the instantaneous mortality rate of the early and late larval stage has the greatest effect on population growth (table 5). These results are similar to those of Smith (1985), who used a stage-based model to examine the role of vital rates in the dynamics of anchovy recruitment. Smith concluded that changes in the late larval stage have the greatest potential to affect survival and recruitment. Our results indicate that the anchovy population is also sensitive to changes in the early larval stage (table 5). The difference between our model and Smith's (1985) is largely due to the low mortality rate (0.16) that Smith used for this stage. The higher mean mortality rate (0.29) in our model leads to greater sensitivity, since faster or slower growth rates have a greater cumulative effect. High abundance of the early larval stage is a prerequisite to strong recruitment, but high larval abundance does not necessarily indicate strong year classes (Peterman et al. 1988).

In this model, we have also tried to examine the role of changes in fecundity. The variation in batch fecundity and spawning rate with age are well known, but little is known of interannual variability in the number of spawns per year. Estimated spawning rates for northern anchovy have varied from once every 6.25 days to once every 11 days. However, the Japanese anchovy, *Engraulis japonica*, spawns once every 1.4 days, and the Cape anchovy, *Engraulis capensis*, spawns as seldom as once every 16 days. Clearly, the number of spawns can vary significantly.

The sensitivity of the anchovy population matrix to changes in the vital rates of both early and late larvae is due to the dynamics of these stages. Natural mortality is high (Peterman et al. 1988), and the duration is long relative to egg stages. Changes in either value produce large effects. The observed natural variation in mortality rate of the early stage is quite large. Smith (1985) also identified the late larval stage of anchovy as important to recruitment variation. Variation in the duration of this stage is largely due to changes in temperature rather than difference in food densities (Methot and Kramer 1979; Owen et al. 1989).

Most life-table parameters do not change independently. The development rate of northern anchovy eggs and yolk-sac larvae is temperature-dependent (Zweifel and Lasker 1976, Lo 1986), as are larval growth rates (Methot and Kramer 1979). At about 22°C the egg, yolk-sac, and early larval stages would be brief. If all these stages are at their lower limits, the model population more than doubles each year. The population model can be stabilized if reproduction is restricted to the prerecruit stage (85–110 mm), with fecundity reduced to only 7 eggs per female per day. In other words, these life-history parameters are then similar to those of a small tropical anchovy, *Encrasicolina purpurea* (Clarke 1989; Somerton, in press).

From 1922 to 1942, temperatures at Scripps Pier averaged 17.1°C; from 1943 to 1974, temperatures averaged 16.6°C, excluding El Niño years 1957–59. The duration of both incubation and the yolk-sac stage are a function of temperature (Lasker 1964; Zweifel and Lasker 1976). Given these relationships, the Lefkovitch model, adjusted to stability at colder temperatures (11°C), predicts that the northern anchovy population would grow at an annual rate of 7% during warmer years (22°C), and that the sardine population would grow at $4\% \cdot y^{-1}$. Thus, temperature effects on the early stages alone cannot explain the difference in abundance of the two species from 1922 to 1942 and from 1943 to 1973. Temperature's effect on spawning rates in both species is unknown, as are its effects on the age of maturation and on the growth rate of juveniles.

The sardine population appears to be less sensitive to changes in vital rates than the anchovy population by an order of magnitude. Changing the duration of the early larval stage changes growth rates by $+40\%$ or $-27\% \cdot y^{-1}$. The addition of fishing mortality results in a $44\% \cdot y^{-1}$ decline in the population. Clark and Marr (1955) debated whether the environment or fishing caused the decline of the sardine population. Our results indicate that either the environment or fishing can produce these changes.

Some discussion of the assumptions of this model is warranted. The stage-specific model assumes that the population reaches a stable age distribution. In reality, stage-specific life-history parameters vary from year to year, and the population probably never achieves a stable age distribution. The fecundity estimates are averaged over all seasons and assumed to be constant on a daily basis. In reality, fecundity has a seasonal component, and most fecundity estimates are made during the peak season. It is also important to note that these fecundity estimates have been made during the course of biomass estimates and that few, if any, long-term studies exist. There is some indication that fecundity may be near zero during extreme environmental conditions (Csirke 1980; Ware and Tsukayama 1981).

The model also does not treat density-dependent effects. Growth rates predicted by the model are not sustained indefinitely in nature. Density-dependent effects on the population could be modeled by

changing fecundity, mortality, or duration with population size. The model's sensitivity to changes in the larval stages suggests that cannibalism may be an important density-dependent feedback mechanism. Density-dependent influences are usually weak compared to density-independent factors, but MacCall (1981), Alheit (1987), Valdés et al. (1987), and Valdés Szeinfeld (1991) have indicated that cannibalism is an important density-dependent effect in clupeoid fishes. Cannibalism on eggs may, in fact, be largely density-independent (Smith et al. 1989), whereas cannibalism on larvae from different schools, because of the population's sensitivity to larval mortality rates, may be density-dependent.

CONCLUSIONS

Natural variation in stage-specific vital rates can account for the large changes in population size observed in nature. The Lefkovitch model predicts changes in population growth that are as great as those indicated by the time series of these populations. Both populations are more sensitive to variation in the parameters of larval stages than to adult parameters. However, more research is needed on interannual variation of adult reproductive parameters, since these variations may have greater impact than indicated in the present model.

The sensitivity of the models to larval duration and mortality rate does not, however, indicate that these stages can be used to predict recruitment. Variance of postmetamorphic stages is sufficient to mask the relation between larval abundance and subsequent recruitment. These results are in accordance with those of Bradford (1992).

Many of these vital rates covary. Durations of both the egg and yolk-sac stages are temperature-dependent, and the maturation and spawning rates also vary with temperature. Changes in the ambient temperature could significantly change the life history of these species.

ACKNOWLEDGMENTS

LITERATURE CITED

Alheit, J. 1987. Egg cannibalism versus egg predation: their significance in anchovy. *In* The Benguela and comparable ecosystems, A. I. L. Payne, J. A. Gulland, and K. H. Brink, eds. Afr. J. Mar. Sci. 5: 467–470.

———. In press. Application of daily egg production method to clupeoid fishes. *In* Advances in the early life history of fishes, Pt. 2. Ichthyoplankton methods for estimating fish biomass, J. R. Hunter, N. C.-H. Lo, and L. A. Fuiman, eds. Natural History Museum of Los Angeles County Science Series.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247:198–201.

Barnes, J. T., L. D. Jacobson, A. D. MacCall, and P. Wolf. 1992. Recent population trends and abundance of the Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 33:60–75.

Bindman, A. G. 1985. The 1985 spawning biomass of the northern anchovy. NMFS-SWFC Admin. Rep. No. LJ-85-21, 21 pp.

Bradford, M. J. 1992. Precision of recruitment predictions from early life stages of marine fishes. Fish. Bull. U. S. 90:439–453.

Butler, J. L. 1987. Comparison of the early life history parameters of Pacific sardine and northern anchovy with implications of species interactions. Ph. D. thesis, Univ. Calif., San Diego, 242 pp.

———. 1989. Growth during the larval and juvenile stages of the northern anchovy, *Engraulis mordax*, in the California Current during 1980–84. Fish. Bull. U. S. 87:645–652.

———. 1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax caerulea*, larvae in the California Current. Can. J. Fish.. Aquat. Sci. 48:1713–1723.

Butler, J. L., and B. Rojas de Mendiola. 1985. Growth of larval sardines off Peru. Calif. Coop. Oceanic Fish. Invest. Rep. 26:113–118.

Castillo, G., E. Aguilera, G. Herrera, P. A. Bernal, J. L. Butler, J. Chong, H. Gonzalez, C. Oyarzun, and C. Veloso. 1985. Larval growth rates of the Pacific sardine, *Sardinops sagax*, off central Chile, determined by daily ring counts in otoliths. Biol. Pesquera, Chile 14:3–10.

Caswell, H. 1989. Matrix population models: construction, analysis and interpretation. Sunderland, Mass.: Sinauer Assoc., Inc., 328 pp.

Clark, F. N. 1934. Maturity of the California sardine (*Sardinops caerulea*), determined by ova diameter measurements. Calif. Dep. Fish. Game Fish Bull. 42:5–49.

Clark, F. N., and J. C. Marr. 1955. Part II: Population dynamics of the Pacific sardine. Calif. Coop. Oceanic Fish. Inv. Prog. Rep. 1 July 1953–31 March 55.

Clarke, T. A. 1989. Seasonal differences in spawning, egg size, and early development time of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull. U. S. 87:593–600.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 177:307–313.

Fiedler, P. C., R. D. Methot, and R. P. Hewitt. 1986. Effects of California El Niño 1982–1984 on the northern anchovy. J. Mar. Res. 44: 317–338.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. U. S. 87:471–495.

Hunter, J. R., and S. R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull. U. S. 77: 641–652.

Hunter, J. R., and B. J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. U. S. Dept. Commer., NOAA tech. Memo., NOAA-TM-NMFS-SWFC-36, 99 pp.

Kimura, M., and G. T. Sakagawa. 1972. Observations on scale patterns and growth of the Pacific sardine reared in the laboratory. Fish. Bull. U. S. 70:1043–1052.

Lasker, R. 1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964:399–405.

Lasker, R., and A. MacCall. 1983. New ideas on the fluctuations of the clupeoid stocks off California. *In* Symposium of Joint Oceanography Assembly 1982, Ottawa, Canada.

Le Clus, F. 1989. Size-specific seasonal trends in spawning of pilchard, *Sardinops ocellatus*, in the northern Benguela system, 1973/74. Afr. J. Mar. Sci. 8:21–31.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1–18.

Lo, N. C. H. 1983. Re-estimation of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. U. S. Dept. Comm., NOAA tech. Memo., NOAA-TM-NMFS-SWFC-31, 33 pp.

———. 1986. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, Engraulis mordax, eggs and larvae. Fish. Bull. U. S. 84:395–407.

Lo, N. C. H., and R. D. Methot. 1989. Spawning biomass of the northern anchovy in 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:18–31.

MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20: 72–82.

———. 1981. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as Engraulis. In Report and supporting documentation of the workshop on the effects of environmental variation on the survival of larval pelagic fishes, G. D. Sharp, ed. Lima, 1980, I. O. C. Workshop Rep. 28, UNESCO, Paris, pp. 201–220.

MacGregor, J. S. 1957. Fecundity of the Pacific sardine (Sardinops caerulea). Fish. Bull. U. S. 57:427–449.

Methot, R. D. 1986. Synthetic estimates of historical abundance and mortality for northern anchovy, Engraulis mordax. NOAA-NMFS-SWFC Admin. Rep. LJ-86-29:1–85.

———. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. Amer. Fish. Soc. Symp. 6:66–82.

Methot, R. D., Jr., and D. Kramer. 1979. Growth of northern anchovy, Engraulis mordax, larvae in the sea. Fish. Bull. U. S. 77:413–423.

Murphy, G. I. 1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc. Cal. Acad. Sci. 34:1–34.

Oliva, J., J. Barandos, and M. Tirado. 1989. Determinación de la fecundidad y frequencia del desove de la sardina (Sardinops sagax), 1986. Comisión Permanente del Pacífico Sur (CPPS), Rev. Pacífico Sur (Número Especial) 341–348.

Owen, R. W., N. H. Lo, J. L. Butler, G. Theilacker, A. Alvariño, J. Hakeson, and J. R. Hunter. 1989. Growth and survival of northern anchovy, Engraulis mordax, larvae in contrasting sites. Fish. Bull. U. S. 87:673–688.

Parrish, R. H., D. L. Mallicoate, and R. A. Klingbeil. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, Engraulis mordax. Fish. Bull. U. S. 84:503–517.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (Engraulis mordax). Can. J. Fish. Aquat. Sci. 45:8–16.

Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41:1117–1120.

Phillips, J. B. 1948. Growth of the sardine (Sardinops caerulea), 1941–1942 through 1946–1947. Calif. Fish Game, Fish. Bull. 71:1–33.

Smith, P. E. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Réun. Cons. Int. Exp. Mer 164:282–292.

———. 1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42:69–82.

Smith, P. E., and H. G. Moser. 1988. CalCOFI time series: an overview of fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 29:66–80.

Smith, P. E., H. Santander, and J. Alheit. 1989. Comparison of the mortality and dispersal of sardine (Sardinops sagax sagax) and anchovy (Engraulis ringens) eggs off Peru. Fish. Bull. U. S. 87:497–508.

Smith, P. E., N. C.-H. Lo, and J. L. Butler. 1992. Life-stage duration and survival parameters as related to interdecadal population variability in Pacific sardine. Calif. Coop. Oceanic Fish. Invest. Rep. 33:41–49.

Somerton, D. C. In press. Stock assessment of nehu Enchrasicholina purpurea using the egg production method. Proc. Early Life Hist. Symp.

Soutar, A., and J. D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. 72(2):257–273.

Stauffer, G. D., and S. J. Picquelle. 1981. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. NMFS Admin. Rep. No. LJ-80-09, 22 pp.

Valdés, E. S., P. A. Shelton, M. J. Armstrong, and J. G. Field. 1987. Cannibalism in South African anchovy: egg mortality and egg consumption rates. In The Benguela and comparable ecosystems, A. I. L. Payne, J. A. Gulland, and K. H. Brink, eds. Afr. J. Mar. Sci. 5:613–622.

Valdés Szeinfeld, E. S. 1991. Cannibalism and intraguild predation in clupeoids. Mar. Ecol. Prog. Ser. 79:17–26.

Waldron, M., M. J. Armstrong, and R. M. Prosch. 1989. Aspects of the variability in growth of juvenile anchovy Engraulis capensis in the southern Benguela system. S. Afr. J. Mar. Sci. 8:9–19.

Walford, L. A., and K. Mosher. 1943. Studies on the Pacific pilchard or sardine 3. Determination of age of adults by scales and effect of environment on first year's growth as it bears on age determination. Fish. Wild. Serv. Spec. Sci. Rep. 21.

Ware, D. M., and I. Tsukayama. 1981. A possible recruitment model for the Peruvian anchovy. Bol. Inst. Mar Perú Callao. Vol. Extr.

Zweifel, J. R., and R. Lasker. 1976. Prehatch and posthatch growth of fishes — a general model. Fish. Bull. U. S. 74:609–621.