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

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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.

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%·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%·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 \( \mathbf{A} \) describes the transition of a population from time \( t \) to time \( t+1 \) in terms of vital rates of each life stage:

\[
\mathbf{A} \mathbf{n}_t = \mathbf{n}_{t+1}
\]

where \( \mathbf{n}_t \) is a vector describing the population at each stage at time \( t \), and \( \mathbf{A} \) is the transition matrix:

\[
\begin{pmatrix}
p_1 & m_2 & \cdots & m_q \\
G_1 & p_2 & 0 & 0 \\
0 & G_2 & p_3 & 0 \\
& & \ddots & \ddots \\
0 & 0 & 0 & G_{q-1} & p_q
\end{pmatrix}
\]

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 \( (\gamma_i) \) (Caswell 1989):

\[
p_i = e^{-z_i}
\]

and

\[
P_i = p_i(1 - \gamma_i)
\]

and

\[
G_i = p_i \gamma_i
\]

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

where \( z_i \) is the daily instantaneous mortality rate (IMR) and \( d_i \) is the duration (d) within the \( i \)th stage. The derivation of \( p_i, G_i, \) and \( \gamma_i \) follow Crouse et al. (1987) and Caswell (1989).

The maternity parameter \( m_i \) is computed as:

\[
m_i = \frac{\sum f_i w_i}{\sum w_i}
\]

where \( f_i \) (the age-specific fecundity rate) is the number of eggs per fish of age \( j \) per unit time, and \( w_i \) is the proportion of fish that are of age \( j \):}

\[
w_i = \exp(-a_j) - \exp(-a_i)
\]

where \( t_1 \) is the beginning and \( t_2 \) 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 \( Q_i = e^{-z_i} \), where \( z \) is the daily instantaneous mortality rate and \( t \) is the time from peak spawning to the time of census.

The dominant eigenvalue \( \lambda \) 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%·d⁻¹. The results are given in annual growth of the population, which is equal to \( \lambda^{365} \), since the duration of stages was measured in days. We estimated \( \lambda \) from the dominant eigenvalue of the matrix \( \mathbf{A} \) using MathCAD.

We measured the importance of natural variability in mortality, duration, and fecundity parameters at each stage by calculating \( \lambda \) for a series of values for each parameter. Initial conditions were a stationary population, and we examined changes of \( \lambda \) 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).

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): 

\[ M_{w} = (1.92 \cdot y^{-1}) \cdot w^{0.28}, \]

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 1: Fecundity Schedule of Northern Anchovy

<table>
<thead>
<tr>
<th>Year</th>
<th>Wt (g)</th>
<th>Spawns per year</th>
<th>Batch (eggs)</th>
<th>L(s)</th>
<th>z = .76</th>
<th>LsMx</th>
<th>Daily</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8.7</td>
<td>5.3</td>
<td>4237.8</td>
<td>22460.3</td>
<td>1000</td>
<td>11230170</td>
<td>30747</td>
</tr>
<tr>
<td>2</td>
<td>14.6</td>
<td>11.9</td>
<td>7860.4</td>
<td>93538.8</td>
<td>468</td>
<td>21888070</td>
<td>59926</td>
</tr>
<tr>
<td>3</td>
<td>18.3</td>
<td>19.2</td>
<td>10132.2</td>
<td>194538.2</td>
<td>216</td>
<td>21010130</td>
<td>57523</td>
</tr>
<tr>
<td>4</td>
<td>21.2</td>
<td>23.5</td>
<td>11912.8</td>
<td>279590.8</td>
<td>102</td>
<td>14277491</td>
<td>39090</td>
</tr>
<tr>
<td>5</td>
<td>24.5</td>
<td>23.5</td>
<td>13939.0</td>
<td>327566.5</td>
<td>48</td>
<td>7861596</td>
<td>21524</td>
</tr>
<tr>
<td>6</td>
<td>24.5</td>
<td>23.5</td>
<td>13939.0</td>
<td>327566.5</td>
<td>22</td>
<td>3603232</td>
<td>9865</td>
</tr>
<tr>
<td>7</td>
<td>24.5</td>
<td>23.5</td>
<td>13939.0</td>
<td>327566.5</td>
<td>10</td>
<td>1637833</td>
<td>4848</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Stage</th>
<th>Size (mm)</th>
<th>Daily natural mortality</th>
<th>Duration (days)</th>
<th>Daily fecundity/female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>0.12&quot;</td>
<td>0.231&quot;</td>
<td>0.45&quot;</td>
<td></td>
</tr>
<tr>
<td>Yolk-sac larvae</td>
<td>0.19&quot;</td>
<td>0.366&quot;</td>
<td>0.59&quot;</td>
<td></td>
</tr>
<tr>
<td>Early larvae</td>
<td>0.187&quot;</td>
<td>0.286&quot;</td>
<td>0.345&quot;</td>
<td></td>
</tr>
<tr>
<td>Late larvae</td>
<td>0.0747&quot;</td>
<td>0.0719&quot;</td>
<td>0.087&quot;</td>
<td></td>
</tr>
<tr>
<td>Early juvenile</td>
<td>0.0009&quot;</td>
<td>0.0141&quot;</td>
<td>0.017&quot;</td>
<td></td>
</tr>
<tr>
<td>Late juvenile</td>
<td>0.0029&quot;</td>
<td>0.0044&quot;</td>
<td>0.0053&quot;</td>
<td></td>
</tr>
<tr>
<td>Prerecruit</td>
<td>0.0029&quot;</td>
<td>0.0184&quot;</td>
<td>0.0034&quot;</td>
<td></td>
</tr>
<tr>
<td>Early adult</td>
<td>0.0011&quot;</td>
<td>0.0021&quot;</td>
<td>0.0036&quot;</td>
<td></td>
</tr>
<tr>
<td>Late adult</td>
<td>0.0011&quot;</td>
<td>0.0021&quot;</td>
<td>0.0036&quot;</td>
<td></td>
</tr>
</tbody>
</table>

**Assuming that 90% of females mature at age 1 and that the batch fecundity is given by the formula:**

\[ \text{Batch} = -1104 + 614 \times \text{wt} \] (Hunter et al. 1985).

*Butler 1987, Waldron et al. 1989
*Fiedler et al. 1986
*Hunter et al. 1985
*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).

### Table 3

**Fecundity Schedule of Pacific Sardine**

<table>
<thead>
<tr>
<th>Age (g)</th>
<th>Spawns</th>
<th>Batch</th>
<th>M(x)</th>
<th>Daily</th>
<th>L(x)</th>
<th>Survivors to day 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>52.7</td>
<td>0</td>
<td>13860</td>
<td>0</td>
<td>1000</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>93</td>
<td>6</td>
<td>24459</td>
<td>146754</td>
<td>402</td>
<td>670</td>
</tr>
<tr>
<td>3</td>
<td>123</td>
<td>12</td>
<td>32349</td>
<td>388188</td>
<td>1063</td>
<td>449</td>
</tr>
<tr>
<td>4</td>
<td>152</td>
<td>15</td>
<td>39976</td>
<td>599640</td>
<td>1642</td>
<td>301</td>
</tr>
<tr>
<td>5</td>
<td>170</td>
<td>19</td>
<td>44710</td>
<td>849490</td>
<td>2326</td>
<td>202</td>
</tr>
<tr>
<td>6</td>
<td>193</td>
<td>23</td>
<td>50759</td>
<td>1167457</td>
<td>3196</td>
<td>135</td>
</tr>
<tr>
<td>7</td>
<td>202</td>
<td>28</td>
<td>53126</td>
<td>1487528</td>
<td>4073</td>
<td>91</td>
</tr>
<tr>
<td>8</td>
<td>205</td>
<td>30</td>
<td>53915</td>
<td>1617450</td>
<td>4428</td>
<td>61</td>
</tr>
<tr>
<td>9</td>
<td>205</td>
<td>35</td>
<td>53915</td>
<td>1887025</td>
<td>5166</td>
<td>41</td>
</tr>
<tr>
<td>10</td>
<td>205</td>
<td>40</td>
<td>53915</td>
<td>2156600</td>
<td>5904</td>
<td>27</td>
</tr>
<tr>
<td>11</td>
<td>205</td>
<td>40</td>
<td>53915</td>
<td>2156600</td>
<td>5904</td>
<td>18</td>
</tr>
<tr>
<td>12</td>
<td>205</td>
<td>40</td>
<td>53915</td>
<td>2156600</td>
<td>5904</td>
<td>12</td>
</tr>
<tr>
<td>13</td>
<td>205</td>
<td>40</td>
<td>53915</td>
<td>2156600</td>
<td>5904</td>
<td>8</td>
</tr>
</tbody>
</table>

Female eggs per female to first census

<table>
<thead>
<tr>
<th>Stage</th>
<th>Female eggs</th>
<th>Survivors to first census</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prerecruit</td>
<td>134</td>
<td>80.5</td>
</tr>
<tr>
<td>Juveniles</td>
<td>647.6</td>
<td>388.9</td>
</tr>
<tr>
<td>Small adults</td>
<td>1576.3</td>
<td>946.6</td>
</tr>
<tr>
<td>Large adults</td>
<td>2811.5</td>
<td>1688.3</td>
</tr>
</tbody>
</table>

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

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 4

**Stage-Specific Life-History Parameters of the Pacific Sardine**

<table>
<thead>
<tr>
<th>Stage</th>
<th>Size (mm)</th>
<th>Daily natural mortality</th>
<th>Duration (days)</th>
<th>Daily fecundity/female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>0.31±</td>
<td>0.72±</td>
<td>2.12±</td>
<td>0± 0± 0±</td>
</tr>
<tr>
<td>Yolk-sac larvae</td>
<td>0.394±</td>
<td>0.6698±</td>
<td>0.971±</td>
<td>1.4± 2.5±</td>
</tr>
<tr>
<td>Early larvae</td>
<td>0.1423±</td>
<td>0.2417±</td>
<td>0.3502±</td>
<td>5± 11±</td>
</tr>
<tr>
<td>Late larvae</td>
<td>0.057±</td>
<td>0.0964±</td>
<td>0.139±</td>
<td>20± 35±</td>
</tr>
<tr>
<td>Early juvenile</td>
<td>0.029±</td>
<td>0.056±</td>
<td>0.081±</td>
<td>17± 25±</td>
</tr>
<tr>
<td>Juvenile I</td>
<td>0.109 ±</td>
<td>0.123±</td>
<td>0.0023±</td>
<td>80± 110±</td>
</tr>
<tr>
<td>Juvenile II</td>
<td>0.110 ±</td>
<td>0.022±</td>
<td>0.004±</td>
<td>105± 146±</td>
</tr>
<tr>
<td>Juvenile III</td>
<td>0.001±</td>
<td>0.002±</td>
<td>0.004±</td>
<td>110± 170±</td>
</tr>
<tr>
<td>Juvenile IV</td>
<td>0.001±</td>
<td>0.002±</td>
<td>0.004±</td>
<td>160± 185±</td>
</tr>
</tbody>
</table>

*Smith 1973
*Smith et al. 1989
*Lasker 1964
*Butler 1991
*Butler and Rojas de Mendiola 1985
*Castillo et al. 1985
*Butler 1987
*Peterson and Wroblewski 1984
*Kimura and Sakagawa 1972
*By analogy to northern anchovy
*MacGregor 1957, Clark 1934, Le Clus 1989
*Murphy 1966, MacCall 1979
*Walford and Mosher 1943, Phillips 1948
*Used to tune model to lambda = 1.0

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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%·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>
<thead>
<tr>
<th>Stage</th>
<th>Natural mortality</th>
<th>Duration</th>
<th>Fecundity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>Min. 0.66 Max. 1.30</td>
<td>Min. 0.85 Max. 1.02</td>
<td>0.03 0.05</td>
</tr>
<tr>
<td>Yolk-sac larvae</td>
<td>1.65</td>
<td>0.60</td>
<td>1.93</td>
</tr>
<tr>
<td>Early larvae</td>
<td>2.78</td>
<td>0.64</td>
<td>2.67</td>
</tr>
<tr>
<td>Late larvae</td>
<td>2.57</td>
<td>0.65</td>
<td>1.78</td>
</tr>
<tr>
<td>Early juvenile</td>
<td>1.90</td>
<td>0.88</td>
<td>1.20</td>
</tr>
<tr>
<td>Late juvenile</td>
<td>1.09</td>
<td>0.95</td>
<td>1.07</td>
</tr>
<tr>
<td>Prerecruit</td>
<td>1.35</td>
<td>0.84</td>
<td>0.98</td>
</tr>
<tr>
<td>Early adult</td>
<td>1.06</td>
<td>0.95</td>
<td>1.06</td>
</tr>
<tr>
<td>Late adult</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

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

**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 ~2%·y⁻¹, whereas the slowest growth rate of the early larval stage results in a population decrease of 28%·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%·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%·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.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Natural mortality</th>
<th>Duration</th>
<th>Fecundity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>Min. 0.66 Max. 1.30</td>
<td>Min. 0.85 Max. 1.02</td>
<td>0.03 0.05</td>
</tr>
<tr>
<td>Yolk-sac</td>
<td>1.65</td>
<td>0.60</td>
<td>1.93</td>
</tr>
<tr>
<td>Early</td>
<td>2.78</td>
<td>0.64</td>
<td>2.67</td>
</tr>
<tr>
<td>Late</td>
<td>2.57</td>
<td>0.65</td>
<td>1.78</td>
</tr>
<tr>
<td>Early juvenile</td>
<td>1.90</td>
<td>0.88</td>
<td>1.20</td>
</tr>
<tr>
<td>Late juvenile</td>
<td>1.09</td>
<td>0.95</td>
<td>1.07</td>
</tr>
<tr>
<td>Prerecruit</td>
<td>1.35</td>
<td>0.84</td>
<td>0.98</td>
</tr>
<tr>
<td>Early adult</td>
<td>1.06</td>
<td>0.95</td>
<td>1.06</td>
</tr>
<tr>
<td>Late adult</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

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%·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 ~2%·y⁻¹, whereas the slowest growth rate of the early larval stage results in a population decrease of 28%·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%·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%·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 day. 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, Engraulis 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%·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 for 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%·y⁻¹. The addition of fishing mortality results in a 44%·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.

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LITERATURE CITED


