

Population growth of northern anchovy and Pacific sardine using stage-specific matrix models

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ABSTRACT: We applied a stage-specific population matrix, the Lefkovich matrix, to the northern anchovy *Engraulis mordax* and the Pacific sardine *Sardinops sagax* to determine which vital rates in the life history have the most effect on population growth. Three vital rates considered are the daily stage-specific instantaneous mortality rate, stage duration and daily age-specific fecundity per female. The models incorporate variability in growth rates among individuals and link simpler stage-based and more complicated individual-based modeling approaches. The elasticity of population growth rate for anchovy (percentage change from a 1% change of a vital rate) was greatest for mortality in yolk-sac larvae, fecundity of 2 yr old fish (111 to 135 mm), and stage duration in late larvae (11 to 35 mm). For sardine, elasticity was greatest for mortality in life stages of egg and yolk-sac larvae, fecundity of 5 and 6 yr old fish (211 to 250 mm), and stage duration in the early larvae (5 to 10 mm). When stage duration was variable, elasticity was $\frac{1}{10}$ as large as when stage duration was constant, indicating that sensitivity of populations to changes in vital rates is reduced by variation in growth rates. Population growth rates for both species increased with variance in individual growth rates. Thus, a population with individuals that grow at varying rates is more likely to increase. Our models indicate that growth rates are important determinants of population growth and recruitment and it is likely that growth and mortality rates are linked. We suggest, therefore, that inexpensive estimates of larval growth rates could be used to help forecast future recruitment.

KEY WORDS: Population matrix projection model · Sensitivity · Stage-specific vital rates · Pelagic fish · Stage duration

INTRODUCTION

Recruitment of juveniles is the key factor controlling population abundance of short-lived fish such as anchovies and sardines. Recruitment prediction, a subject of considerable practical significance, requires detailed knowledge of the factors influencing survival in the first months of life. These fish inhabit diverse and variable regions of the coastal ocean, and the processes controlling their recruitment are complex. Thus, we may expect regional differences, nonlinear relationships, and stochastic variability of parameters in the underlying models. Once plausible models are identified, missing or imprecise parameter estimates often hinder recruitment prediction. Existing assessment procedures, e.g. the egg production method (Lasker 1985) and fishery catch-at-age models

(Megrey 1989, Methot 1989, Deriso 1993), provide estimates of spawning biomass and vital rates for some life stages (Smith 1985, Butler et al. 1993). There are an increasing number of estimates of larval fish mortality (Beyer 1989, Pepin 1991) from laboratory and field studies (reviewed by Houde & Zastrow 1993). The collection of vital rates for various life stages, although not contemporaneous, provides a basis for studying population changes (Crouse et al. 1987).

Determining the sensitivity of population growth to changes in vital rates of each life stage is a useful way to study the mechanisms underlying population growth and recruitment of marine fish (MacCall 1980). Smith (1985) advanced this idea using a life table approach, in which he determined the stage-specific vital rates which could cause a 5-fold change in recruitment of the northern anchovy *Engraulis mordax*. Smith et al. (1992) extended this work to the Pacific sardine

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Sardinops sagax using the Lefkovitch matrix, which is a generalization of the Leslie matrix (Lefkovitch 1965, Crouse et al. 1987, Caswell 1989). Smith et al. (1992) changed the value of each vital rate while holding others unchanged to achieve a 30% annual increase or decrease from a stationary population, a typical rate of population change during periods of sharp growth or decline. Barnes et al. (1992) demonstrated a 27% annual increase of Pacific sardine during 1983 to 1991 in the presence of a fishery. Butler et al. (1993) reviewed the literature, including recent estimates, and compared population growth for the minimum and maximum value for each parameter to identify critical life history stages for recruitment prediction.

In Smith et al. (1992) and Butler et al. (1993), the vital rates were first tuned to reach a stationary population ($\lambda = 1$ where $\lambda = N_t/N_{t-1}$ and N_t is the population size at time t). These 2 studies assumed that fish grew at the same rate, so that the time spent in each stage was constant. Recent modeling work has shown, however, that changes in the variance as well as mean growth may affect fish survivorship (Pepin 1989, DeAngelis et al. 1993, Rice et al. 1993). Thus, variation in individual growth rates within stages may be important. In this paper, we relaxed the assumption of fixed stage duration and allowed the duration to vary because fish grow at different rates. We used a general formula to compute the sensitivity for each stage-specific vital rate and used a measure of elasticity which makes it easier to compare the sensitivity of the population to vital rate changes. In addition, we approximated 95% confidence intervals of the population growth index through simulations and investigated the impact of variance of duration within stages on population growth.

MATERIALS AND METHODS

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

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

where n_t is a $q \times 1$ vector describing the stage distribution of population at time t , q is the number of stages, and t is measured in days.

A is the population projection matrix:

$$\begin{matrix} P_1 & F_2 & \cdot & & F_q \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ & & & & \\ 0 & 0 & 0 & G_{q-1} & P_q \end{matrix} \quad (1)$$

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 F_i is the fertility per fish per day; $i = 1, \dots, q$. For a stable population, the dominant eigenvalue of matrix **A**, λ , measures the population growth on the unit time basis. The corresponding eigenvector (**W**) is the stable stage distribution because

$$\begin{aligned} \mathbf{A}W &= \lambda W \\ \text{and} \quad \mathbf{A}n_t &= \lambda n_t = n_{t+1}. \end{aligned} \quad (2)$$

The natural logarithm of λ [$\ln(\lambda) = r$] is the intrinsic rate of population change.

In Eq. (1), each of the elements, P_i , G_i , and F_i , depends on the probability of growing into the next stage, γ_i (Appendix A). Various methods are available for estimating the growth probability which primarily depends on the duration within a stage (Caswell 1989). We assumed the duration (d_i) follows a negative binomial distribution with parameters γ_i (probability of successes) and k_i (number of successes), because this distribution is flexible and is widely used in modeling the duration distribution (Blythe et al. 1984, Caswell 1989). The 2 parameters, γ_i and k_i , of a negative binomial distribution are the growth probability and number of pseudostages within a stage. The pseudostages are imaginary stages which help to model the distribution of duration within stage. The duration is analogous to the number of trials taken to observe k_i successes. Estimates of mean duration and the coefficient of variation [$CV(d) = SD(d)/\text{mean}(d)$] are then used to estimate the 2 parameters (Table 1). For details of description of matrix **A** and procedures of modeling growth rates, see Appendix A.

For the anchovy, 9 life stages were defined: eggs, yolk-sac larvae, larvae <10 mm in length, and larvae to adults grouped by 25 mm length intervals. The interval size of 25 mm was an arbitrary choice. The CVs of duration were available for 6 stages. The CV for anchovy eggs (= 0.10) was computed from the incubation time of eggs in laboratory rearing experiments (Lo 1983). CVs for 5 stages from 5 to 110 mm were computed from back-calculated growth rates from daily increments in otoliths of 94 juvenile anchovies born in March 1980 (Butler 1989) (Table 1). No CVs were available for the yolk-sac larval stage and the 2 adult stages, so values from adjacent stages were used: the CV of the early larvae (5 to 10 mm) was applied to the yolk-sac stage, and the CV for the prerrecruits was also applied to the adult stages.

For the sardine, 13 life stages were defined in the same way as for the anchovy. CVs for 7 stage durations from 5 to 110 mm were computed from back-calculated length-age data for 46 sardines with birth dates

Table 1. *Engraulis mordax* and *Sardinops sagax*. Summary statistics for duration (days) in stages. Durations from early larvae to later stages for anchovies and sardines were back-calculated with assumed birth dates in March 1980 for anchovies, February and June 1984 for sardines. γ and k are parameter estimates for negative binomial distribution, computed from sample mean and SD. Lv: larvae; Jv: juvenile; Prerec: prerecruits; Adt: adult. Numbers in parentheses are estimates from the adjacent stage. The CV of duration for anchovy eggs was also used for sardine eggs

Length interval (mm):			5 to 10	11 to 35	36 to 60	61 to 85	86 to 110	111 to 135	136 to 160
Anchovy									
Life stage:	Eggs	Ys Lv	Early Lv	Late Lv	Early Jv	Late Jv	Prerec	Early Adt	Late Adt
N	69	—	92	94	94	94	45	0	0
Mean	2.69	—	18.23	40.81	65.74	93.13	158.10	—	—
SD	0.26	—	4.74	9.04	10.13	31.73	64.31	—	—
CV	0.095 (0.26)		0.26	0.22	0.15	0.34	0.41	(0.41)	0.41
γ	0.98	—	0.48	0.33	0.39	0.08	0.04	—	—
k	2.63	—	8.17	13.59	25.67	7.88	5.82	—	—
Sardine									
Life stage:	Eggs	Ys Lv	Early Lv	Late Lv	Early Jv	Jv I	Jv II	Jv III	Jv IV
N	—	—	42	46	46	45	38	25	2
Mean	—	—	16.13	59.13	29.07	31.29	53.03	71.46	90.11
SD	—	—	4.38	10.13	5.55	6.98	17.70	13.85	22.23
CV	(0.095) (0.27)		0.27	0.17	0.19	0.22	0.33	0.19	0.25
γ	—	—	0.45	0.37	0.49	0.39	0.14	0.27	0.15
k	—	—	7.41	21.62	14.10	12.24	7.68	19.40	13.89

in February and June 1984 (Table 1) (Butler 1989). The CVs of eggs, yolk-sac larvae, and 4 stages >160 mm were not available. CV for anchovy eggs was used for sardine eggs as anchovy and sardine egg development is similar (Zweifel & Lasker 1976). The CV of early larvae (5 to 10 mm) was applied to the yolk-sac larvae. The CV for the juveniles (136 to 160 mm) was also applied to the older stages.

Data analyses. In matrix **A** (Eq. 1), P_i and G_i are nonlinear functions of the daily instantaneous mortality rate (IMR, z_i) and duration (d_i), and the fertility (F_i) naturally also depends on daily age-specific fecundity (f_j) for age j (Appendix A). These vital rates (z_i , d_i , f_j) are the primary input parameters. Based on these available estimates for vital rates, one can derive each element in matrix **A** (Appendix A; Eqs. A1 to A6). Although the vital rates are the central focus of the sensitivity analyses in this study, we also included P_i , G_i , and F_i for comparative purposes because they are commonly used in other studies (Crouse et al. 1987, Caswell 1989).

Estimates of daily IMR (z), duration (d) for each stage, and the daily age-specific fecundity (f_j) of northern anchovies and Pacific sardines were obtained from the literature (Smith 1985, Lo 1986, Butler 1987, Butler et al. 1993) (Tables 2 to 5). The age-specific fecundity rates were later converted to length-specific fecundity rates (see Appendix A). For a detailed description of the stage-specific vital rates of anchovies and Pacific

sardines, see Butler et al. (1993). Butler selected z values for the early-juvenile stage of the anchovy and juvenile-1 stage of the sardine to achieve a stationary population ($\lambda = 1$). In contrast, we obtained regression estimates of z for both stages in anchovy and sardine from a Pareto function of z regressed on age (cumulated duration) (Lo 1986; Table 2). Vital rates z_i , d_i and f_j were applied to each pseudostage within Stage i , i.e. $P_{im} = P_{ik}$; $G_{im} = G_{ik}$ for $m \neq k$ where m and k refer to pseudostages within Stage i . This relationship is not true for fertility (F_i), so an average fertility over the pseudostages was computed within a stage.

Elasticity analyses. The change of the population growth, λ , due to the change of any one vital rate (x) within a stage can be measured by the sensitivity index (S_x):

$$\begin{aligned} S_x &= \frac{\partial \lambda}{\partial x} \\ &= \sum_i \sum_j \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \\ &= \sum_i \sum_j S_{ij} \frac{\partial a_{ij}}{\partial x} \end{aligned} \quad (3)$$

The sensitivity index (S_{ij}) for each element of matrix **A** (a_{ij}) was computed:

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_j w_j}{\sum (w_i v_i)}$$

Table 2. *Engraulis mordax*. Daily instantaneous mortality rate (IMR) and stage duration for anchovies. SD is computed from CV, which measures among-year variation. Lv: larvae; Jv: juvenile; Adt: adult

Stage	Name	IMR			Duration (days)			Length (mm)
		Estimates	CV	SD	Estimates ^a	CV	SD	
1	Egg	0.2310	0.36	0.0832	2.90	0.22	0.63	
2	Yolk-sac	0.3660	0.15	0.0560	3.60	0.17	0.62	H ^b -4
3	Early Lv	0.2860	0.05	0.0147	12.00	0.31	3.75	5-
4	Late Lv	0.0719	0.05	0.0038	45.00	0.20	9.00	11-
5	Early Jv	0.0107 ^c	0.05	0.0006	62.00	0.22	13.75	36-
6	Late Jv	0.0044	0.05	0.0002	80.00	0.24	19.50	61-
7	Prerecruit	0.0031	0.05	0.0001	287.00	0.38	108.00	86-
8	Early Adt	0.0021	0.18	0.0004	1000.00	0.13	125.00	111-
9	Late Adt	0.0021	0.18	0.0004	1250.00	0.10	125.00	136-160

^aValues of this column were derived from growth curves (Butler et al. 1993) and may differ from Table 1
^bHatching
^cRegression estimate from $\ln(z) = 0.47 - 1.0347 \ln(\text{age} + 1)$ based on data from Stages 1 to 7 where age is cumulative duration

where w_i is the i th element of the right eigenvector and v_j is the j th element of the left eigenvector ($\mathbf{A}W = \lambda W$, $V'\mathbf{A} = \lambda V'$) (Caswell 1989). For example, S_{12} is the sensitivity index for G_1 (Eq. 1). Formulas for the sensitivity index of vital rates are given in Appendix B.

When vital rates differ in magnitude, it is useful to examine the percentage change of population growth due to a 1% change of a vital rate. The elasticity (e_x) can be used to compute the daily population growth when vital rates change. The proportional sensitivity or elasticity, e_x , is defined:

$$e_x = \frac{\partial \lambda / \lambda}{\partial x / x} \quad (4)$$

For example, if e_x is -0.005, then the population decreases by 0.005% for a 1% increase of vital rate x . The elasticities are computed from an expanded matrix \mathbf{A} , the dimensions of which are $n \times n$, where $n = \sum k_i$ and k_i is the number of pseudostages within Stage i .

Table 3. *Engraulis mordax*. Batch fecundity/1000 by age for northern anchovy population in which 90% of females mature in the first year

Age (yr)	Fish weight (g)	Batches yr ⁻¹	Eggs batch ⁻¹	Eggs female ⁻¹ d ⁻¹ (f_j) Estimates	SD ^a
1	8.7	5.3	4.2378	61.5352	1.85
2	14.6	11.9	7.8604	256.2706	7.69
3	18.3	19.2	10.1322	532.9815	15.99
4	21.2	23.5	11.9128	766.9885	23.01
5	24.5	23.5	13.9390	897.4425	26.92
6	24.2	23.5	13.9390	897.4425	26.92
7	24.5	23.5	13.9390	897.4425	26.92

^aSD = estimates \times 0.03 (Hunter et al. 1985)

Variability of estimate of daily population growth rate λ . Once matrix \mathbf{A} is determined, λ can be computed by using mathematical packages (e.g. MATLAB) or by continuous multiplication of matrix \mathbf{A} with an arbitrary initial stage vector (n_0): $\mathbf{A}^t n_0 = n_t$; $\lambda = n_t / n_{t-1}$ for large t . We used the continuous multiplication procedure. The elements of matrix \mathbf{A} (a_{ij}) are functions of vital rates, which are estimated with errors, thus the estimate of λ is also subject to error.

Monte Carlo simulations were used to estimate the variance of $\hat{\lambda}$ and as % confidence interval (CI) of λ . In this simulation, IMR, d within each stage, and the daily f_j were drawn independently from normal distribution with means equal to best estimates (Butler et al. 1993; Tables 2 to 5). The SDs of vital rates of both species were estimated from range values reported in Butler et al. (1993) as $SD(x) = [\max(x) - \min(x)]/4$, except for the IMR of anchovy eggs and daily fecundity rates. The CV for anchovy eggs is 0.36 (Jacobson & Lo 1992); for fecundity of anchovy, 0.03 (Hunter et al. 1985). The CV for fecundity was also applied to the sardine (Tables 3 & 5).

In the simulation, vital rates were checked to be sure they were biologically reasonable (no negative values were allowed). For each set of simulated input parameters, Eqs. A1 to A6 (Appendix A) were used to compute elements in matrix \mathbf{A} . $\hat{\lambda}$ was calculated by continuous multiplication of matrix \mathbf{A} 3000 times. Mean and SD were obtained from 1000 simulations. The 95% CI for λ was also obtained.

Table 4. *Sardinops sagax*. Daily instantaneous mortality rates (IMR) and stage duration for Pacific sardines. SD is computed from CV which measures among-year variation. Lv: larvae; Jv: juvenile; Adt: adult

Stage	Name	IMR			Duration (days)			Length (mm)
		Estimates	CV	SD	Estimates ^a	CV	SD	
1	Egg	0.7200	0.63	0.4525	2.5	0.25	0.63	—
2	Yolk-sac	0.6690	0.22	0.1447	3.1	0.20	0.63	H ^b -4
3	Early Lv	0.2417	0.22	0.0520	11.0	0.36	4.00	5-
4	Late Lv	0.0964	0.21	0.0205	35.0	0.21	7.50	11-
5	Early Jv	0.0560	0.23	0.0130	25.0	0.23	5.75	36-
6	Jv I	0.0146 ^c	0.21	0.0031	50.0	0.25	12.50	61-
7	Jv II	0.0040	0.22	0.0009	110.0	0.15	16.50	86-
8	Jv III	0.0028	0.21	0.0006	146.0	0.14	20.00	111-
9	Jv IV	0.0022	0.23	0.0005	170.0	0.16	27.50	136-
10	Prerecruit	0.0011	0.20	0.0002	175.0	0.16	27.50	161-
11	Early Adt	0.0011	0.20	0.0002	381.0	0.25	95.00	186-
12	Adult	0.0011	0.36	0.0004	663.0	0.20	130.00	211-
13	Late Adt	0.0011	0.36	0.0004	2773.0	0.14	391.25	236-250

^aValues of this column were derived from growth curves (Butler et al. 1993) and may differ from Table 1

^bHatching

^cRegression estimate from $\ln(z) = 2.03 - 1.29 \ln(\text{age} + 1)$ based on data from Stages 1 to 10 where age is the cumulative duration

RESULTS

Northern anchovy

The projection matrix **A** with time step equal to 1 d was constructed (Table 6). Each entry of matrix **A** was used for all pseudostages within a stage. The dimensions of the expanded matrix **A** are 79 × 79. The dominant eigenvalue of the expanded matrix **A** is 1.00105. The intrinsic daily population growth rate is

$\ln(1.00105) = 0.00105$ (Table 7). A crude estimate of the annual population growth rate is 1.46 (1.00105^{365}).

The elasticity analysis indicated that a relative change in the IMR of yolk-sac anchovy larvae results in the largest percentage change in population growth. For fecundity, the population is most sensitive to the 1% change in daily fecundity rate of 2 yr old fish (111 to 135 mm; Stage 8). For the duration of stages, the population growth is mostly sensitive to a percentage change in late larvae (Stage 4; Fig. 1).

Elasticity estimates for 3 vital rates can be used to compute the percentage change of population growth for $x\%$ change of 1 particular vital rate. For example, if the IMR of yolk-sac larvae is reduced by 10%, i.e. from 0.37 to 0.33 (Table 2), then the daily population growth will be increased by 0.0052% ($e_x \times 10\%$; Table 7). If the duration of the late larval stage is increased by 10% from 45 to 49 d, the population would be decreased by 0.00212% daily. If the daily fecundity of 2 yr old females is increased by 5% from 256 to 269, the population would be increased by 0.00428% ($e_x \times 5\%$) daily.

From the 1000 simulation runs, we obtained the mean and SD for $\hat{\lambda}$ as 1.0016 and 0.0011. The 95% CI for λ is 0.9992 to 1.0054, and includes $\lambda = 1$. Thus, the null hypothesis of a stationary population is not rejected.

Table 5. *Sardinops sagax*. Batch fecundity/1000 by age for Pacific sardine population in which 50% of females mature at age 2

Age (yr)	Fish weight (g)	Batches yr ⁻¹	Eggs batch ⁻¹	Eggs female ⁻¹ d ⁻¹ (f_j) Estimates	SD ^a
1	52.7	0	0	0	0
2	93.0	6	24.459	402.066	12.06
3	123.0	12	32.349	1063.529	31.91
4	152.0	15	39.976	1642.849	49.29
5	170.0	19	44.710	2327.370	69.82
6	193.0	23	50.759	3198.512	95.96
7	202.0	28	53.126	4075.419	122.26
8	205.0	30	53.915	4431.370	132.94
9	205.0	35	53.915	5169.932	155.10
10	205.0	40	53.915	5908.493	177.25
11	205.0	40	53.915	5908.493	177.25
12	205.0	40	53.915	5908.493	177.25
13	205.0	40	53.915	5908.493	177.25

^aSD = estimates × 0.03 (Hunter et al. 1985)

Table 6. *Engraulis mordax*. The projection matrix (Eq. 1) of northern anchovy with variable duration and number of pseudostages within each stage. $\lambda = 1.00105$. k : number of pseudostages (Eq. A4). For stage definition, see Table 2

Stage	1	2	3	4	5	6	7	8	9
1	0.224×10^{-1}	0.0	0.0	0.0	0.0	0.0	0.928×10^1	0.978×10^2	0.351×10^3
2	0.771	0.136	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	0.0	0.558	0.336	0.0	0.0	0.0	0.0	0.0	0.0
4	0.0	0.0	0.415	0.638	0.0	0.0	0.0	0.0	0.0
5	0.0	0.0	0.0	0.293	0.576	0.0	0.0	0.0	0.0
6	0.0	0.0	0.0	0.0	0.413	0.898	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	0.0	0.972×10^{-1}	0.977	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0	0.202×10^{-1}	0.992	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.590×10^{-2}	0.993
k	3	3	7	14	26	8	6	6	6
Total number of pseudostages = 79									
The expanded projection matrix consists of the first 3 'pseudostages' with $P_i = 0.0224$ and $G_i = 0.771$ and the next 3 pseudostages with $P_i = 0.136$ and $G_i = 0.558$, etc. Fertilites for the last 3 stages are the averages of fertilities for the pseudostages within stages									

Pacific sardine

The projection matrix A with time steps equal to 1 d was constructed (Table 8). The dimensions of the expanded matrix A are 167×167 and the dominant eigenvalue is 1.00014. The intrinsic daily population growth rate is $\ln(1.00014) = 0.00014$ (Table 7). A crude estimate of the annual population growth rate would be 1.052 (1.00014³⁶⁵).

Table 7. *Engraulis mordax* and *Sardinops sagax*. Estimates of daily population growth rate (λ), standard errors in parentheses and the most elastic stages of anchovy and sardine for 2 models: fixed duration and variable duration within stage. IMR: instantaneous mortality rate; YL: yolk-sac larvae; EL: early larvae; LL: late larvae; CI: confidence interval

	Fixed duration within stage	Variable duration within stage
Anchovy		
λ		
Direct computation	1.000479	1.00105
Simulation		1.0016 (0.0011)
95 % CI		0.9992–1.0054
Elasticity (e_x)		
IMR	EL: -0.0048	YL: -0.00052
Duration	EL: -0.0048	LL: -0.000212
Fecundity	Age 2: 0.00043	Age 2: 0.000857
Sardine		
λ		
Direct computation	0.99983	1.00014
Simulation		1.0003 (0.0011)
95 % CI		0.9987–1.002
Elasticity (e_x)		
IMR	LL: -0.00160	Egg, YL: -0.0004
Duration	LL: -0.00161	EL: -0.00007
Fecundity	Age 5: 0.0008	Age 5: 0.0002

Similar to northern anchovies, the elasticity analysis for sardines indicated that the largest percentage change in population growth came from a relative change in the IMR of egg and yolk-sac sardine larvae, followed by larval stages (Table 7, Fig. 2). For f_j per female, population growth is most sensitive to the percent-age change in 5 yr old females (211 to 235 mm; Stage 12). For stage duration, the population growth is most sensitive to a relative change in early larvae (Stage 3).

A 10% increase of the daily IMR for the yolk-sac larvae from 0.67 to 0.74 (Table 4) would result in a decrease of 0.004% for the population. Likewise, with a 10% decrease of duration for the early larvae from 11 to 10 d, the population would be increased by 0.0007% daily. If the daily fecundity of 5 yr old females is increased by 20% from 2327 to 2792, the population would be increased by 0.004% daily (Table 7).

From the simulation, we obtained mean and SD of λ as 1.0003 and 0.0011. The 95% CI for λ is 0.9987 to 1.0028. From the 95% CI of λ , we cannot ascertain the direction of population growth of sardines.

Elasticity of entries of matrix A (P_i , G_i and F_j)

For both anchovies and sardines, the elasticity of population growth to the probability of survival and staying in the stage (P_i) increases with stages until the last stage. Population size apparently is more sensitive to P_i than to the probability of survival and growing into the next stage, G_i , and fertility, F_j (Figs. 3 & 4).

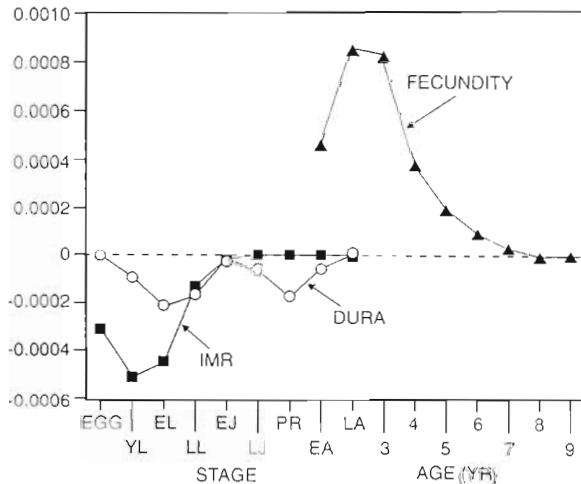


Fig. 1. *Engraulis mordax*. Elasticity of instantaneous mortality rate (IMR), duration (DURA) within each stage and daily age-specific fecundity for northern anchovy. YL: yolk-sac larvae; EL: early larvae (4 to 10 mm); LL: late larvae (11 to 35 mm); EJ: early juvenile (36 to 60 mm); LJ: late juvenile (61 to 85 mm); PR: prerecruits (86 to 110 mm); EA: early adult (111 to 135 mm); LA: late adult (136 to 160 mm)

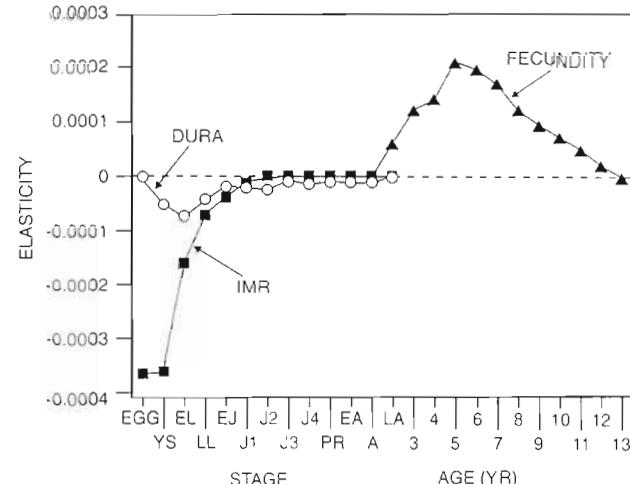


Fig. 2. *Sardinops sagax*. Elasticity of instantaneous mortality rate (IMR), duration (DURA) within each stage and daily age-specific fecundity for Pacific sardine. YL: yolk-sac larvae; EL: early larvae (5 to 10 mm); LL: late larvae (11 to 35 mm); EJ: early juvenile (36 to 60 mm); J1: juvenile (61 to 85 mm); J2: juvenile (86 to 110 mm); J3: juvenile (111 to 135 mm); J4: juvenile (136 to 160 mm); PR: prerecruits (161 to 185 mm); EA: early adult (186 to 210 mm); A: adult (211 to 235 mm); LA: late adult (236 to 250 mm)

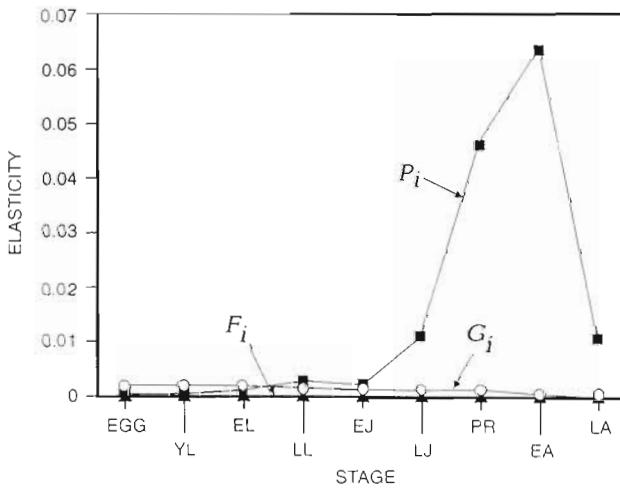


Fig. 3. *Engraulis mordax*. Elasticity of P_i , G_i and F_i , elements of matrix A (Eq. 1) within each stage for northern anchovy. YL: yolk-sac larvae; EL: early larvae (5 to 10 mm); LL: late larvae (11 to 35 mm); EJ: early juvenile (36 to 60 mm); LJ: late juvenile (61 to 85 mm); PR: prerecruits (86 to 110 mm); EA: early adult (111 to 135 mm); LA: late adult (136 to 160 mm)

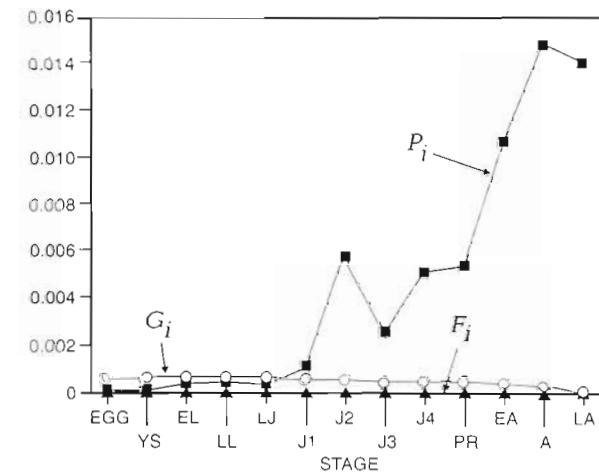


Fig. 4. *Sardinops sagax*. Elasticity of P_i , G_i and F_i , elements of matrix A (Eq. 1) within each stage for Pacific sardine. YL: yolk-sac larvae; EL: early larvae (5 to 10 mm); LL: late larvae (11 to 35 mm); EJ: early juvenile (36 to 60 mm); J1: juvenile (61 to 85 mm); J2: juvenile (86 to 110 mm); J3: juvenile (111 to 135 mm); J4: juvenile (136 to 160 mm); PR: prerecruits (161 to 185 mm); EA: early adult (186 to 210 mm); A: adult (211 to 235 mm); LA: late adult (236 to 250 mm)

Relationship between variations of stage duration and λ

In order to see how the variability of stage duration affects the rate of population growth, we considered 8 cases. In each case, all the initial CV values (Table 1) were multiplied by a constant, c , between 0 and 3.0.

For example, when $c = 0$, the duration within a stage does not vary. For $c = 2$, this set of CV is twice those CV values given in Table 1. We then computed $1/\lambda$ for each case. For both species, λ increases with the constant (Fig. 5). Thus, a population with variable growth among individuals is more likely to increase in the long run, if everything is equal. These results are consistent

Table 8. *Sardinops sagax*. The projection matrix (Eq. 1) of Pacific sardine with variable stage duration and number of pseudostages within each stage. $\lambda = 1.00014$, k : number of pseudostages (Eq. A4). For stage definitions, see Table 3

Stage	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.119×10^{-1}	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.149×10^3	0.341×10^3	0.120×10^4
2	0.475	0.944×10^{-1}	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	0.0	0.418	0.349	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	0.0	0.0	0.436	0.457	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	0.0	0.0	0.0	0.451	0.369	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6	0.0	0.0	0.0	0.0	0.577	0.678	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	0.0	0.307	0.919	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0	0.767×10^{-1}	0.838	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.159	0.912	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.858×10^{-1}	0.915	0.0	0.0	0.0
11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.837×10^{-1}	0.959	0.0	0.0	0.0
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.403×10^{-1}	0.975	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.235×10^{-1}	0.993	
k	2	3	6	17	15	16	8	23	15	15	15	16	16

Total number of pseudostages = 167

The expanded projection matrix consists of the first 2 'pseudostages' with $P_t = 0.0119$ and $G_t = 0.475$ and the next 3 pseudostages with $P_t = 0.0944$ and $G_t = 0.418$, etc.
Fertilities for the last 3 stages are the averages of fertilities for the pseudostages within stage

with the findings by Caswell (1989). Such a population does not readily react to the change of vital rates because of low elasticities (Table 7).

DISCUSSION

Our model incorporated the variation of somatic growth within stage (variable growth). We believe that this is more realistic than models assuming fixed stage duration (fixed growth). If the variances of somatic duration are unknown, fixed stage durations may have to be assumed although the results might be biased. For comparison purposes, we computed the population growth (λ) and elasticity of vital rates for both species using fixed growth (Appendices A & B). Our results for anchovies and sardines show that the λ from models with variable duration was always higher than the λ from models with fixed duration (Table 7). These results indicated that variation in growth rates of individuals enhanced the population growth, primarily due to size-dependent mortality (Tables 2 & 4). While the mathematical consequences of growth variability within each stage are clear, it will also be necessary to confirm the importance of these phenomena by field measurements. Pepin (1989) reported that mean and variance of growth rates of 1 cohort affect the survival rates of the population. Rice et al. (1993) found that high variation in larval growth leads to increased cohort survival after 60 d, when the predation is size-dependent.

Population growth in our models for anchovies and sardines with variable duration is more sensitive to the percentage change of IMR and fecundity than to the percentage change in stage duration. With fixed duration, population growth is equally sensitive to the percentage change of mortality (IMR) and growth (duration) and not so sensitive to fecundity (Table 7). Elasticity values for IMR and duration from fixed growth are nearly 10 times that from variable growth. This difference implies that when the variance in the growth rates of individuals increases, the sensitivity of the population to changes in those rates decreases. The most elastic stages for both IMR and duration may differ depending on models used, yet the most elastic stages are from eggs to late larvae. Butler (1989) found that population growth of sardines was correlated with mortality of larvae, which is consistent with this study.

The population growth is a function of mean and variance of stage-specific vital rates, as

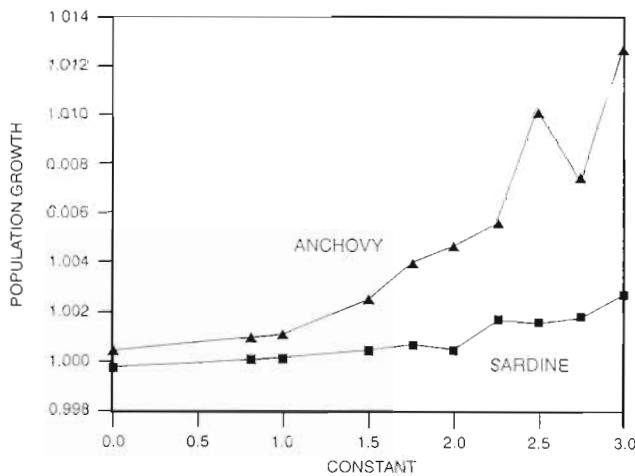


Fig. 5. *Engraulis mordax* and *Sardinops sagax*. Relationship between the population growth rate (λ) and the constant used to multiply the coefficient of variation (CV) of stage duration for northern anchovies and Pacific sardines (Table 1). For example, when constant = 0.5, the CV values for anchovies are 0.5 times the CV values of stage duration (Table 1): e.g. CV of stage duration is 0.0475 (= 0.5 \times 0.095) for anchovy eggs, 0.13 (= 0.5 \times 0.26) for yolk-sac larvae, 0.21 for prerecruits

demonstrated by the relationship between population growth and the constant used to multiply the CV of stage duration (Fig. 5). For northern anchovies and Pacific sardines, the most sensitive stages are early life stages whose vital rates have reasonable estimates. However, as for most fish populations, precise estimates of CVs for stage duration are not available. It would be useful to investigate the robustness and bias of population growth estimates from matrix models introduced by using crude estimates of both mean and CV of vital rates.

The most elastic stages for both species are similar: for the IMR, they are egg and yolk-sac larval stages, and for stage duration, they are early and late larval stages (Figs. 1 & 2). The correspondence may be due to biological similarities between anchovies and sardines, and, perhaps, a general pattern in short-lived pelagic fish. Alternatively, it may result from use of identical parameter values in our models for both species, e.g. CV of egg duration. Maximum elasticities were greater for anchovies than for sardines. Thus, our models project that anchovy populations would change size more quickly than sardine populations, in response to proportional changes in a vital rate (Table 7).

Results from our models indicate that growth rates of early life history stages are important determinants of recruitment and population growth. It may be possible, therefore, to provide fishery managers with useful indicators of future recruitment based on

larval growth rate data (Huppert et al. 1980). Pepin (1990) found that short-term variability in recruitment was associated with fluctuation in plankton abundance, indicating that growth rates may be an important factor in determining year-class strength. These fluctuations may be correlated with large-scale climatic forcing (Koslow et al. 1987). Predator and prey abundance are often correlated (Pepin 1990), suggesting that large year classes in pelagic fish may occur when increases in predator abundance lag behind prey abundance.

Mortality rates are another important determinant of population growth and recruitment success. In practice, growth rates are much easier and cheaper to estimate because they require smaller sample sizes than estimating mortality. Representative specimens have several weeks or months of growth history stored in their otoliths. In addition, growth rate (the inverse of stage duration) and stage mortality may covary because mortality is due largely to predation risks that depend on size. Linkages between growth and mortality rates could be evaluated empirically if sufficient growth and mortality rate data were available (Butler 1989).

In the future, our assumptions require closer scrutiny. We need to improve the precision and accuracy of estimates of parameter values. Also, field research is required to refine and determine the covariance of vital rates. For example, rapid growth in one stage may confer growth rate advantages in subsequent stages, hasten the onset of maturity and provide additional advantages for evading sources of mortality as indicated by DeAngelis et al. (1993) from their individual-based models. The covariance is also essential for analytical computation of variance of λ estimates. This material was not pursued in this paper because we lacked data on covariance (Houllier et al. 1989, Alvarez-Buylla & Slatkin 1991).

Our analyses demonstrate that matrix population models are useful tools for examining population changes which respond to changes of vital rates of certain life stages more readily than to others. Although we do not have contemporaneous sets of vital rates for anchovies and sardines, the results of our analyses provide insight into population changes in these 2 species and help define the future research directions on the vital rates of important life stages. These stages may have a direct impact on the success of recruitment.

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Appendix A. Description of matrix A

To construct matrix **A** (Eq. 1), we used the procedures based on Caswell (1989):

P_i and G_i. Both P_i and G_i are functions of the survival probability (p_i) and the growth probability (γ_i) on a daily basis:

$$\begin{aligned} P_i &= p_i (1 - \gamma_i) \\ \text{and } G_i &= p_i \gamma_i \end{aligned} \quad (\text{A1})$$

where p_i is computed as

$$p_i = e^{-z_i} \quad (\text{A2})$$

and z_i is the daily instantaneous mortality rate (IMR).

γ_i is computed as follows, assuming fixed or variable stage duration models.

Fixed duration: Duration (days, d_i) in each stage is the same for all individuals. Under the assumption of a stable age distribution $[1, p_i/\lambda, \dots, (p_i/\lambda)^{d_i-1}]$ within a stage, the growth probability was computed as the proportion of the oldest age group to all age groups:

$$\begin{aligned} \gamma_i &= \frac{(p_i/\lambda)^{d_i-1}}{1 + (p_i/\lambda) + \dots + (p_i/\lambda)^{d_i-1}} \\ \gamma_i &= \frac{(1 - p_i/\lambda)(p_i/\lambda)^{d_i-1}}{1 - (p_i/\lambda)^{d_i}} \end{aligned} \quad (\text{A3})$$

An iterative procedure was used with an initial guess for λ because γ_i depends on λ . The iteration stops when the difference of the last 2 λ s is less than 0.0001.

Variable duration: d_i within a stage was modelled by a negative binomial distribution with parameters γ_i and k_i :

$$\Pr(d_i = x) = \binom{\bar{x}-1}{k_i-1} \gamma_i^{k_i} (1 - \gamma_i)^{\bar{x}-k_i}$$

for $x = k_i, k_i + 1, k_i + 2, \dots$

where γ_i is the probability of growing into the next pseudostage (analogous to probability of success) and k_i is the number of pseudostages within Stage i (number of successes). In other words, a fish in Stage i is assumed to pass through each of k_i pseudostages with the growth probability γ_i . $\Pr(d_i = x)$ gives the probability that a fish in Stage i will pass through all k_i pseudostages and graduate to Stage $i + 1$ in x days. No assumption was imposed on the within-stage age distribution. For $\gamma_i = 1$, $\Pr(d_i = k_i) = 1$. Both γ_i and k_i were computed as functions of the mean and variance of duration, d_i , that follows a negative binomial distribution:

$$\gamma_i = \frac{1}{\text{CV}_i^2 \bar{d}_i + 1} \quad (\text{A4})$$

and

$$k_i = \frac{1}{\text{CV}_i^2 + (1/\bar{d}_i)}$$

where CV_i is the coefficient of variation of d_i . The quantity \bar{d}_i is the average duration for Stage i . When the $\text{CV} = 0$, then $\gamma_i = 1$ and $k_i = \bar{d}_i$, the duration for each stage is fixed as in fixed duration. When CV increases, k decreases and can be less than 1. We set 1 as the lower bound for k , as k is theoretically the number of pseudostages.

For the matrix model based on variable duration, the computation of λ is based on an expanded matrix **A**, which includes all the pseudostages with dimension equal to $\sum k_i$. In the case where $k_i = 1$, the dimension of the expanded matrix **A** is reduced to that of the original matrix **A**. In Eq. (A4), the mean values, \bar{d}_i , are listed in column 6 of Tables 2 & 4 and the CVs are listed in Table 1. Sensitivity analyses were conducted for each of the 2 models (see Appendix B).

F_i(fertility). We computed the daily fecundity per fish for Stage i (m_i) as

$$m_i = \left[\sum_j (f_j w_{ij}) \right] \times 0.5 / \sum_j (w_{ij}) \quad (\text{A5})$$

where f_j is the age-specific fecundity rate (the number of eggs per female of age j per unit time) (Tables 3 & 5). The weight, w_{ij} , is the proportion of fish that are of age j :

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

where t_{1j} is the beginning age and t_{2j} is the ending age for the fish of age group j .

Caswell (1989) provided the general procedure for computing the stage-specific fertility (F_i): fertility varies with egg mortality, adult mortality, growth probability, spawning time and the time of census. For anchovies and sardines, plankton surveys are usually conducted continuously throughout the day. If we take stage distribution at the peak spawning time as n_t (Eq. 2) and assume fish spawn only at the peak spawning time, the fertility at the sampling time will be surviving eggs (Butler et al. 1993). The F_i values computed in this paper may differ from Butler et al. (1993) because Butler et al. (1993) assumed only 1 survey within 1 time unit.

The peak spawning time is 22:00 h for anchovies and 20:00 h for sardines. In our case, the time unit is 1 d. If a tow was taken at 01:00 h, for anchovies $u = \frac{1}{24}$ and for sardines $u = \frac{5}{24}$. For a census taken at the elapsed time after spawning, u ($0 < u < 1$), the stage-specific fertility as a function of time (start of tow (u)):

$$\begin{aligned} E_i(u) &= m_i \bar{p}_i^u \\ &= m_i e^{-z_i u} \end{aligned}$$

We integrated the above equation to obtain an average fertility for Stage i (F_i):

$$\begin{aligned} F_i &= \int_0^1 E_i(u) du \\ &= \frac{m_i [1 - \exp(-z_i)]}{z_i} \end{aligned} \quad (\text{A6})$$

Appendix B. Sensitivity indices for vital rates

The basic formula for sensitivity indices for vital rates is

$$\frac{\partial \lambda}{\partial x} = \sum_i \sum_j \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}$$

The elasticity index can be obtained from Eq. (4). The quantity $\partial \lambda / \partial a_{ij}$ was given in Eq. (3). In the following sections, we derived formulas primarily for $\partial a_{ij} / \partial x$ where x are vital rates specifically for our matrix population models. The subscripts for stages are omitted for simplicity.

Fixed duration. Sensitivity to age-specific fecundity (f_j): From Eqs. (A5) & (A6), we have

$$\begin{aligned} \frac{\partial \lambda}{\partial f_j} &= \sum_i \sum_k \frac{\partial \lambda}{\partial a_{ik}} \frac{\partial a_{ik}}{\partial f_j} = \sum_k \frac{\partial \lambda}{\partial a_{1k}} \frac{\partial a_{1k}}{\partial f_j} \\ &= \sum_k \frac{\partial \lambda}{\partial F_k} \frac{\partial F_k}{\partial f_j} \end{aligned} \quad (\text{A7})$$

where

$$\begin{aligned} \frac{\partial F_k}{\partial f_j} &= \frac{\partial F_k}{\partial m_k} \frac{\partial m_k}{\partial f_j} \\ &= \frac{p_1 - 1}{\ln(p_1)} \frac{w_{kj}}{\sum_j w_{kj}} \end{aligned}$$

$$\text{and } \frac{\partial m_k}{\partial f_j} = \frac{w_{kj}}{\sum_j w_{kj}}$$

Indices i and k refer to stage, and index j refers to age.

Sensitivity to instantaneous mortality rate (z_i): $\partial \lambda / \partial z_i$:

$$\frac{\partial \lambda}{\partial z} = \frac{\partial \lambda}{\partial p} \frac{\partial p}{\partial z} = \frac{\partial \lambda}{\partial p} (-1)e^{-z} \quad (\text{A8})$$

where $\partial \lambda / \partial p$ is derived as follows:

$$\frac{\partial \lambda}{\partial p} = \frac{\partial \lambda}{\partial P} \frac{\partial P}{\partial p} + \frac{\partial \lambda}{\partial G} \frac{\partial G}{\partial p}$$

where

$$\frac{\partial P}{\partial p} = (1 - \gamma) - p \frac{\partial \gamma}{\partial p}$$

$$\frac{\partial G}{\partial p} = \gamma + \frac{\partial \gamma}{\partial p}$$

where $\partial \lambda / \partial p$ is computed from Eq. (A3):

$$\frac{\partial \gamma}{\partial p} = \frac{q^{d-1}}{[1 - q^d]^2} [(1 - q^d)(d - 1 - qd) + (1 - q)q^d d]$$

where $q = p/\lambda$.

Sensitivity to stage duration (d_i): $\partial \lambda / \partial d_i$:

$$\begin{aligned} \frac{\partial \lambda}{\partial d} &= \frac{\partial \lambda}{\partial G} \frac{\partial G}{\partial d} + \frac{\partial \lambda}{\partial P} \frac{\partial P}{\partial d} \\ &= \frac{\partial \lambda}{\partial a_{i+1,i}} \frac{\partial G}{\partial d} + \frac{\partial \lambda}{\partial a_{i,i}} \frac{\partial P}{\partial d} \end{aligned} \quad (\text{A9})$$

where

$$\begin{aligned} \frac{\partial G}{\partial d} &= \frac{\partial}{\partial d} p\gamma \\ &= p \frac{\partial \gamma}{\partial d} \end{aligned}$$

$$\begin{aligned} \frac{\partial P}{\partial d} &= \frac{\partial}{\partial d} p(1 - \gamma) \\ &= -p \frac{\partial \gamma}{\partial d} \end{aligned}$$

The quantity $\partial \gamma / \partial d$ is computed from Eq. (A3):

$$\begin{aligned} \frac{\partial \gamma}{\partial d} &= \frac{\partial}{\partial d} \frac{(1 - q)q^{d-1}}{(1 - q^d)} \\ &= q^{d-1} \frac{(q - 1)\ln(q)}{(1 - q^d)^2} \end{aligned}$$

where $q = p/\lambda$.

Variable duration: The sensitivities to both age-specific fecundity (f_j) and IMR (z_i) are computed the same way as in fixed duration. The sensitivity to the stage duration (d_i), Eq. (A9), still applies, except the quantity $\partial \lambda / \partial d$ needs to be computed from Eq. (A4):

$$\frac{\partial \gamma}{\partial d} = -\frac{CV^2}{(CV^2 \bar{d} + 1)^2}$$

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