LIFE-STAGE DURATION AND SURVIVAL PARAMETERS AS RELATED TO INTERDECADAL POPULATION VARIABILITY IN PACIFIC SARDINE

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ABSTRACT

Surveys in the Southern California Bight have shown rapid increases in the spawning rate of Pacific sardine over the past decade. We found simple deterministic population models to be useful for examining the rates of change observed in the sardine population. We first describe the "best guess" parameters of an equilibrium sardine population with the Leslie matrix model. From this we determine that small changes in annual mortality rate of the 0-group impose high rates of change in the population. We then erect a Lefkovitch matrix model, which uses life stages rather than ages, to emphasize the parameters of the early life stages. From this study, we can specify the range of growth rates and the changes in survival rates for each developmental stage, as well as the adult parameters required to evaluate the observed rates of change.

Changes in egg production rates imply important changes in the sardine population. Therefore, examination of these rates of change can offer insight into the frequency and precision of population assessment and recruitment prediction required for effective management of fisheries on sardines and other stocks.

RESUMEN

Reconocimientos en la Cuenca del Sur de California han revelado que en la década pasada la tasa de desove de la sardina del Pacífico mostró un incremento pronunciado. Encontramos que modelos poblacionales deterministas simples son útiles para investigar las tasas de cambio observadas en poblaciones de sardinas. Describimos primero los parámetros que juzgamos mas atinados de una población de sardina en equilibrio con un modelo de matrices de Leslie; determinamos que pequeños cambios en la tasa de mortalidad anual del grupo de edad cero producen altas tasas de cambio en la población. Continuamos con la elaboración de un modelo de matrices de Lefkovitch, que al considerar fases vitales en vez de edades, hace hincapié en los parámetros de los estadios vitales tempranos. A partir de este estudio, podemos especificar el rango de las tasas de crecimiento, los cambios en las tasas de sobrevivencia para cada fase de desarrollo y los parámetros de los estadios adultos requeridos para evaluar las tasas de cambio observadas.

Cambios en las tasas de producción de huevos llevan consigo cambios importantes en la población de sardinas. Consecuentemente la investigación de tales tasas podría ayudar a discernir la frecuencia y precisión de la evaluación de la población, así como la predicción del reclutamiento, elementos requeridos para un manejo efectivo de las pesquerías de sardinas y otros stocks.

INTRODUCTION

The current recovery of Pacific sardine was predicted by Murphy (1967) based on a deterministic population model, and by Lenarz (1971), who used a stochastic model and incorporated autocorrelation of recruitment success. Records of the Pacific sardine fishery begin in the late 1800s (Schaefer et al. 1951), with small catches being used for bait in the rockfish fishery, and for canning. During World War I the fishery grew continuously at a rate of about 14% per year, doubling every five years. Brief deviations from the growth of the fishery were largely attributed to economic factors (Schaefer et al. 1951). The catch was chiefly landed in California, but fisheries extended northward to British Columbia.

The growth rate of the fishery slowed after the mid 1930s, and a succession of collapses began in 1945–47. California landings fell below the 1916 values in the 1961–62 season (Ahlstrom and Radovich 1970), where they have remained through 1991. California legislation in 1967 and 1973 prohibited the landing of sardines for any purpose and prevented the sale of incidental catches. The 1973 legislation stipulated that a 1,000-ton fishery could start as soon as the spawning biomass exceeded 20,000 tons; thus a small fishery began in 1986 and continues to grow (Wolf et al. 1987).

There has been relatively little directed research on the Pacific sardine population off California since

the decline of the 1960s; most of the research was reviewed by Ahlstrom and Radovich (1970). Smith (1972) updated and revised Ahlstrom's (1966) egg and larval time series. MacCall (1979) updated and revised Murphy's (1966) population data. Soutar and Isaacs (1974) augmented the record of sardine and other fish scales in the anaerobic varved sediments off California and added a record from Baja California (Soutar 1967; Soutar and Isaacs 1969). Lasker (1970) estimated the use of zooplankton energy by the historical sardine population.

The recovery of the sardine population was first detected in 1979, through surveys by the Ichthyoplankton Coastal and Harbor Studies in waters shallower than 40 meters off Santa Monica Bay, Palos Verdes, and Seal Beach in southern California. These bimonthly field studies were sponsored by the Southern California Edison Co. and NOAA Sea Grant and were staffed by the Los Angeles County Museum and the Institute for Marine and Coastal Studies of the University of Southern California (Brewer et al. 1980; Brewer and Smith 1982; Lavenberg et al. 1987). Wolf and Smith (1985, 1986) estimated the spawning biomass from the spawning area in 1985.

Sardine and anchovy fisheries constitute a relatively large fraction of the fluctuations in global catch (Murphy 1977; Smith 1985; Lluch et al. 1989). Although variations in recruitment are large for sardine and anchovy stocks, the major changes appear to be long term. Thus the "overfishing problem" is complicated by the "recruitment problem" and the "regime problem."

In the near future we plan to issue a series of matrix models for schooling coastal pelagic fishes. This paper concerns the relationship between population parameters and observed rates of change in the sardine population. We also plan to produce papers on the sensitivity of sardine and anchovy population size to changes in parameters based on Smith (1985) and Smith, Lo, and Butler (1991). In addition, we plan to compare the errors of estimation of the abundance of life stages with interannual changes in population size.

In this paper we use the recent remarkable increases in Pacific sardine egg abundance off southern California to pose questions about the causes of the increase. Is the current increase due to migration of sardine stocks from other habitats to the southern California area? How does the increase of spawning off southern California compare to the increase off Japan? Is the increase due merely to the fishing moratorium? Has the increase resulted from the decline in natural predators? Have other population param-

eters changed? Can normal fluctuations in recruitment rates be detected in time to improve fisheries management? Can critical changes in the recruitment rate be predicted from observations of the physical and biological environment of the sardine?

It is the purpose of this paper to explore some characteristics of Pacific sardine with respect to the observed changes in population size. We have prepared similar estimates for the northern anchovy (Smith 1985; Smith et al. 1991). First we postulate values for stage survival, growth, and reproduction parameters. We then determine which features of the population are most likely to control the sardine's reproductive success. Lastly, we describe the related features of the biological and physical environment. Although there are serious reservations surrounding the use of the simple Leslie (1945) and Lefkovitch (1965) matrix models for projecting population (Caswell 1989; Seber 1973), tractable methods have been developed for evaluating and extending these models (DeRoos et al. 1992). For this stage of our research, we chose the simplicity and flexibility of the Leslie (Vaughn and Saila 1976) and Lefkovitch (Crouse et al. 1987) matrix models.

METHODS

Abundance estimates for sardine eggs arise from quantitative techniques that were established in 1938 (Sette and Ahlstrom 1948) and that have not changed with respect to sardine eggs since then. Sardine population parameters have been selected from Butler (1987). Where values are missing for sardine, we used analogous parameters for the same stage of anchovy (Smith 1985; Lo 1986; Lo et al. 1989; Smith et al. 1991).

The egg time series, from representative surveys selected from 1957 to 1991, is shown in table 1, which lists the number of sardine eggs of all ages per 10 square meters of sea surface between CalCOFI line 76 (at times called 77 or 76.7) and line 94 (usually called 93 or 93.3). Data from all tows taken from January to June at CalCOFI stations 26 to 70 were used. Surveys were conducted from two to five times in the six-month period. The maximum number of stations was 293 in 1975; the minimum number was 77 in 1990 and 1991. The data reported in table 1 represent two series of egg abundances on the decadal scale with relatively even rates of decline (1957–69) or increase (1975–91).

Scale-deposition rates from the fossil record in the Santa Barbara Basin (Soutar and Isaacs 1974; Smith 1978; Smith and Moser 1988) are shown in table 2. A Velleman nonparametric, robust, resistant smoother (Velleman 1980; Velleman and Hoagland 1981; Min-

TABLE 1
Time Series of Sardine Eggs off Southern California

Year	Eggs per 10 m² sea surface
1957	22.65
1958	69.02
1959	143.85
1960	95.36
1961	12.85
1962	1.35
1963	11.29
1964	0.61
1965	3.66
1966	1.54
1969	0.27
1972	0
1975	2.43
1978	0.38
1981	0.87
1984	3.47
1985	9.27
1986	3.25
1987	16.14
1988	34.20
1989	53.34
1990	67.29
1991	137.11

TABLE 2
Smoothed Time Series of the Soutar-Isaacs[a] Sardine-Scale Series from the Santa Barbara Basin

Central year	Scale deposition	Smoothed[b] rates	Series
1812	2.44	2.44	R1
1817	2.58	2.58	R1
1822	3.72	2.87	R1
1827	1.29	3.18	R1
1832	5.15	3.42	R1
1837	3.11	3.81	R1
1842	3.74	4.51	R1
1847	7.72	5.64	R1
1852	5.11	6.70	R1
1857	15.19	7.07	R1
1862	8.47	5.96	F1
1867	0.62	3.10	F1
1872	0.25	0.71	F1
1877	0.00	0.08	F1
1882	1.00	0.98	R2
1887	1.49	3.30	R2
1892	8.72	5.24	R2
1897	12.08	5.71	R2
1902	4.61	5.50	F2
1907	1.99	5.18	F2
1912	2.99	4.93	F2
1917	5.85	4.72	F2
1922	6.85	4.61	F2
1927	3.99	4.27	F2
1932	1.99	3.22	F3
1937	3.11	1.88	F3
1942	0.50	0.84	F3
1947	0.37	0.29	F3
1952	0.00	0.08	F3
1957	0.00	0.02	F4
1962	0.32	0.00	F4
1967	0.00	0.00	F4

[a]Soutar and Isaacs 1974
[b]Velleman (1980) nonparametric resistant smoother

itab 1989) was used to define secular (long-term) trends and changes in trend. This smoother replaces each value by the median of the values immediately before and after it. Medians of 2, 3, 4, and 5 consecutive values were used in this smoother. Following each median smoother, a weighted running average of each value and the values immediately preceding and following is assembled, with the point value being given twice the weight of the adjacent values. Special methods are used to smooth the ends of the data sequence.

Secular change rates for all time periods were estimated by Marquardt algorithm nonlinear least squares fitted to an exponential function (Saila et al. 1988). We used the same procedure to extract secular rates of change from graphics published by Murphy (1967) and Lenarz (1971). The absence of the actual values in the latter cases should not be an impediment, since the data were based on theory and simulation in both cases.

We used a Leslie matrix of 13 year classes (Leslie 1945; Vaughn and Saila 1976) to estimate the survival rate during the first year of sardine life from the age-fecundity relation (table 3) and the adult survival rates from Butler (1987: table 2). We set the adult annual survival rate at a constant 0.67 (instantaneous mortality rate of 0.4 yr^{-1}) (table 4).

The Lefkovitch matrix also included 13 life stages (Crouse et al. 1987; Smith et al. 1991). Rather than using individual year classes as in the Leslie matrix, we assembled the adult year classes into only 3 stages: early adult, adult, and late adult. The fecundity of the adult stages is derived from the biomass-weighted fecundity of the year classes encompassed by the stages. Daily instantaneous mortality rates and durations (days) of stages are given in table 5. Each rate shown is varied individually while the other rates are held constant. We divided the early

TABLE 3
Sardine Fecundity Schedule

Age	Weight(g)	Eggs/g/batch	Batches/yr[a]	Eggs/female/year
1	52.7	0	0	0
2	93	257	4	95604
3	123	257	8	252888
4	152	257	12	468768
5	170	257	15	655350
6	183	257	17	799527
7	193	257	19	942419
8	202	257	20	1038280
9	205	257	20	1053700
10	205	257	21	1106385
11	205	257	21	1106385
12	205	257	22	1159070
13	205	257	23	1211755

[a]Butler 1987 (postulated by analogy to anchovy) and Smith et al. 1991.

TABLE 4
Projection Matrices of Leslie (1945) and Lefkovitch (1965)

Leslie Age-Based Matrix

f_0	f_1	f_2	f_3	•	•	•	f_n
p_0	0	0	0	•	•	•	0
0	p_1	0	0	•	•	•	0
0	0	p_2	0	•	•	•	0
0	0	0	p_3	•	•	•	0
•	•	•	•	•	•	•	0
•	•	•	•	•	•	•	0
•	•	•	•	•	•	•	0
0	0	0	0	0	0	p_{n-1}	0

Lefkovitch Size- or Stage-Based Matrix

p_0	f_1	f_2	f_3	•	•	•	f_n
g_0	p_1	0	0	•	•	•	0
0	g_1	p_2	0	•	•	•	0
0	0	g_2	p_3	•	•	•	0
0	0	0	g_3	•	•	•	0
•	•	•	•	•	•	•	0
•	•	•	•	•	•	•	0
•	•	•	•	•	•	p_{n-1}	0
0	0	0	0	0	0	g_{n-1}	p_n

f is the fecundity per fish per unit of time by age for Leslie matrix and for stage in the Lefkovitch matrix.

p is the probability of survival to the next age for Leslie matrix, and the probability of survival in the stage for the Lefkovitch matrix.

g is the probability of survival and growth into the next stage.

life history of the sardine into the following stages: egg, yolk-sac larva, first-feeding larva, late larva, early juvenile, juvenile I, juvenile II, juvenile III, juvenile IV, and pre-recruit. After we established best estimates for the parameters, we changed the least-known estimates—juvenile I and II—by trial

TABLE 5
Postulated Parameters of the Sardine Life Cycle

Stage name	Duration (days)	Instantaneous mortality rate (daily)	Eggs per fish per day
Egg	3	0.3	0
Yolk-sac larva	4	0.3	0
Early larva	11	0.14	0
Late larva	42	0.0556	0
Early juvenile	25	0.0365	0
Juvenile I	100	0.0239	0
Juvenile II	142	0.0140	0
Juvenile III	170	0.0025	0
Juvenile IV	170	0.0021	0
Pre-recruit	175	0.0021	0
Early adult	381	0.00178	169.72
Adult	663	0.00178	462.31
Late adult	2773	0.00178	1258.91

and error to achieve a neutral population growth rate ($\lambda = 1$).

Considering the range of rates of secular change in table 6, we established alternative population growth rates of $\lambda = 0.7$ and $\lambda = 1.3$. We then changed each population parameter, such as individual growth rate or mortality rate, until the population growth rate matched the $\lambda = 0.7$ or $\lambda = 1.3$ value or until the parameter went to zero or an unreasonable value. We manipulated the early life stages, keeping the natural mortality constant at 0.4 yr^{-1} and the fishing mortality at 0.25 yr^{-1}. In this form we would not expect great differences in re-

TABLE 6
Examples of Secular Changes in Sardine Population Size

Category	Time span (years)	r[a]	λ[b]	References
Theoretical				
Murphy	0–24	0.184	1.202	Murphy 1967
Lenarz	0–16	0.168	1.183	Lenarz 1971
Santa Barbara Basin scales				
Table 2 R1	1810–1860	0.027	1.028	
Table 2 F1	1860–1880	−0.103	0.902	
Table 2 R2	1880–1900	0.088	1.092	
Table 2 F2	1900–1930	−0.009	0.991	
Table 2 F3	1930–1955	−0.099	0.906	
Table 2 F4	1955–1970	−0.335	0.715	
Southern California				
Eggs	1975–1991	0.523	1.687	This paper
Eggs	1957–1969	−0.193	0.824	This paper
Recruits	1932–1964	−0.071	0.931	Murphy 1966 & MacCall 1979
Spawners	1932–1965	−0.108	0.898	Murphy 1966 & MacCall 1979
Benguela Current				
Spawners	1966–1982	−0.245	0.783	Crawford et al. 1983
Humboldt Current				
Spawners	1974–1981	0.126	1.134	Serra 1983
Kuroshio				
Eggs	1970–1978	0.488	1.514	Watanabe 1983

[a]r = annual intrinsic exponential rate of population change.
[b]λ = annual rate of sardine population growth (e^r).

sults from the Lefkovitch stage-and-size-specific matrix and the Leslie age-specific matrix.

RESULTS

The extreme rates of change indicated by all methods of estimating biomass, scale-deposition rates, standing crop of eggs, and virtual population incorporate not only the real rates of change of the population but also errors in the estimation of population levels and changes in age composition. Since many forms of error are multiplicative, the asymmetry in table 6 — i.e., high rates of increase exceed rates of decrease — could either be a characteristic of sardines and anchovies or merely an expression of the errors of estimation. Although we report the maximum and minimum rates of increase as results, we have narrowed the range of subsequent tests of population parameters to explore only the range λ = 0.7 to λ = 1.3. The lower λ is somewhat more interesting for fishery management.

The fastest rate of secular increase occurred in the standing crop of eggs. By 1991 there was an average standing crop of 137 sardine eggs per ten square meters. In 1975 the mean concentration of eggs in the same area was fewer than 3 per ten square meters. The average growth rate since 1975 is an instantaneous rate of 0.523 yr^{-1} (SE 0.038). The equivalent λ is 1.687. Even with errors in estimation of values and estimation of slope we would expect this result to be above a λ of 1.3, meaning that the spawning rate was expanding at more than 30% per year. The effects of changed reproductive parameters on estimated biomass are explored below.

The fastest rates of secular decline examined for this paper were in the scale-deposition rate from 1955 to 1970 (table 6), in Namibian sardine (*Sardinops ocellata*) spawners (Crawford et al. 1983), and in Pacific sardine spawners from 1932 to 1964 and recruits in 1965 off southern California (Murphy 1966; MacCall 1979). The California declines approached 20% to 30% per year, and were accompanied by many adults and some juveniles being taken by an active fishery.

Leslie Matrix

The fastest rates of increase cannot be obtained in theory from changing from a fishing instantaneous mortality of 0.25 yr^{-1} to a moratorium (0 yr^{-1}). The fastest population increase expected from a moratorium on fishing is about 20% per year (table 7A). The highest secular rate of increase from the prefishery scale-deposition rates was about 10% per year from 1880 to 1900 (table 6).

TABLE 7

Sardine Life-History Parameters Representing No Population Change, 30% Annual Decline, and 30% Annual Growth

	$\lambda = 1$	$\lambda = 0.7$	$\lambda = 1.3$
A. Leslie matrix (13)			
Fishing mortality	0.25	0.72	<0.0[a]
O-group survival S(1, 0)	6.51E-06	9.90E-07	1.84E-05
O-group mortality Z(yr^{-1})	11.94	13.83	10.91
O-group mortality Z(d^{-1})	0.033	0.038	0.030
Fecundity (batches yr^{-1})	23	3.50	65
Batch fecundity (eggs gm^{-1})	257	39	725
B. Lefkovitch matrix (13)			
Egg (spawn to hatch)			
IMR (d^{-1})	0.3	0.887	0.0003
Duration (d)	3	8.875	0.01
Yolk-sac larva (hatch–4 mm)			
IMR (d^{-1})	0.3	0.7401	0.0752
Duration (d)	4	9.875	1.0089
Early larva (4–10 mm)			
IMR (d^{-1})	0.14	0.2999	0.0582
Duration (d)	11	23.59	4.593
Late larva (10–35 mm)			
IMR (d^{-1})	0.0556	0.0974	0.0341
Duration (d)	42	73.7	25.87
Early juvenile (35–60 mm)			
IMR (d^{-1})	0.0365	0.10665	0.00032
Duration (d)	25	73.52	0.69
Juvenile I (60–85 mm)			
IMR (d^{-1})	0.0239	0.04137	0.014815
Duration (d)	100	173.85	62.56
Juvenile II (85–110 mm)			
IMR (d^{-1})	.0140	0.02623	.00755
Duration (d)	142	268.4	78.51
Juvenile III (110–135 mm)			
IMR (d^{-1})	.002495	.012427	—[b]
Duration (d)	170	996	—
Juvenile IV (135–160 mm)			
IMR (d^{-1})	.0021	0.01201	—
Duration (d)	170	1203	—
Pre-recruit (160–185 mm)			
IMR (d^{-1})	.0021	0.011715	—
Duration (d)	175	1206.5	—
Early adult (185–210 mm)			
IMR (d^{-1})	.0018	0.0064	<0[c]
Duration (d)	381	>3653	<1
Fecundity (d^{-1})	169.6882	—	1108.9
Adult			
IMR (d^{-1})	.0018	0.0066	<0[d]
Duration (d)	663	>3653	<1
Fecundity (d^{-1})	462.2455	—	2145.7
Late adult			
IMR (d^{-1})	.0018	>0.0274	<0[e]
Duration (d)	2773	>3653	<1
Fecundity (d^{-1})	1238.6	—	6595.5

[a]When fishing mortality is 0 (moratorium) λ = 1.214.
[b]When no value is mathematically possible the symbol — is used.
[c]When fishing mortality is 0, λ = 1.0625.
[d]When fishing mortality is 0, λ = 1.0725.
[e]When fishing mortality is 0, λ = 1.0513.

Variation in O-group mortality rate can effect either a 30% increase or decrease in λ. A decline of this magnitude would result from the first-year survivorship of 9.90 × 10^{-7} from each egg spawned, or 1 survivor for each 2.8 million eggs spawned. In the absence of fishing, a 30% increase would be

expected from a survivorship of 1.84×10^{-5}, or 1 survivor per 53,000 eggs. Population stability is achieved with a survivorship of 6.51×10^{-6} to the age of one year, or 1 survivor per 307,000 eggs. The instantaneous mortality rate for increase, stability, decrease is 10.91, 11.94, or 13.83 on an annual basis, or 0.030, 0.033, or 0.038 on a daily basis.

Neither of the fecundity rates in table 7 could, with values now perceived as reasonable, cause the rates of increase and decline tested. Of the two fecundity rates, batches of egg spawned per year has somewhat more impact than number of eggs per batch. To achieve the declines observed, the eggs per gram of female would have to drop to 39 from 257 or increase to 725 as a secular change. Fecundities approximating this range have been observed for single females. The number of egg batches per year would have to decline to 3.5 or increase to 65 to cause these extreme changes in sardine population growth rate. There might be only 3.5 spawnings per year if the fishery had removed all of the older spawners, but we are refraining from examining multiple effects in the Leslie model until the parameters are given stochastic ranges and the matrix becomes probabilistic rather than deterministic.

Lefkovitch Matrix

The instantaneous mortality rates, which yield a 30% decline (table 7B), look reasonable for the egg, yolk-sac, and early larva stages. The static rate is a daily exponential instantaneous rate -0.3, -0.3, and -0.14 for the first three stages, and the 30% decline equivalents are -0.887 for eggs, -0.7401 for yolk-sac larvae, and -0.2999 for early larvae. Rate changes of this magnitude for individual stages are probably measurable at sea with existing techniques. Field estimates of instantaneous mortality rates for late larvae through pre-recruits would require equipment that has not yet been designed, and sampling intensity far greater than that now accomplished. With current approaches, the changes in mortality rate in table 7 would probably be undetectable. Similarly, if smaller-parameter changes were distributed among stages, rather than isolated by stage as they are in this simulation, the changes might not be detectable from current field sampling practices.

An effective change in duration of the earlier stages would require protracted periods of extremely warm or cold water to explain secular changes in population growth rates. Temperature's effect on age or size of sardines at first maturity (by analogy to anchovy; Methot 1989) could be an important influence on population growth rate. De-

creasing population caused by slow growth of late larvae, juveniles, and pre-recruits would be easily detectable by otolith daily growth analysis. Secular increases caused by rapid growth would require sustained growth rates of .5 mm per day or more in the late larvae and 1 mm per day or more in juveniles and pre-recruits to be effective (tables 5 and 7B). The more subtle the effect to be measured, the more expense would be incurred; thus sampling costs and required precision would have to be examined from an economic standpoint. Lenarz (1971) showed that recruitment predictions (and assessments) would not have to be very precise to improve the quality of management for sustained economic yield.

DISCUSSION

The primary finding of this study is that a year-class (Leslie 1945) parameterization of critical population growth rates is not likely to reveal important changes in reproductive success of sardines. Although a stage-based (Lefkovitch 1965) approach requires much ancillary information, some of the earlier stages could provide useful limits on projections of recruitment as well as the usual stock assessment. Another finding is that the rate of increase in the standing crop of eggs cannot be explained by the fishing moratorium alone. We do not have enough information to decide which other factors may have contributed to the current regional increase of sardine eggs; the sustained increase for nearly two decades is as high as any sustained increase measured for sardine stocks, and higher than most.

Is the current increase due to migration of sardine stocks from other habitats to the southern California area?

With present data, we cannot rule out migration of other elements of the sardine species into this area. If the present stock is from a diminished "northern" stock, it probably arose from the remnants ("founders") of a breeding population of less than 2,000 tons. If the present stock arises from a similarly small group migrating into the area, that population too would arise from "founders," and the distinction may be detected genetically. If there is a constant interchange with other populations, the growth in spawning rates may merely represent added migration rates from a larger stock.

How does the increase of spawning off southern California compare to the increase off Japan?

The rate of increase of eggs per unit area is remarkably close to that off the Pacific coast of Japan; any difference could well be negligible.

Is the increase due merely to the fishing moratorium?

The rate of increase in egg abundance, if due entirely to adult biomass and not to increased spawning rates, is too rapid to be explained by the moratorium alone.

Has the increase been caused by a decline in natural predators?

The rate of increase of the sardine population may have been augmented by the decline of anchovy and mackerel in the same area. These species can prey on early stages of sardines. Bird and mammal biomass, and presumably the consumption of juveniles and adults, have increased, however.

Have other population parameters changed?

Warming would tend to decrease mortality of eggs and yolk-sac larvae, in the absence of other effects, by shortening the most vulnerable stages. Warming may accelerate sardine maturation, as it is thought to do for anchovy (Methot 1989). Not enough is known to speculate about how the other stages might be affected by the interactions among temperature-specific growth rate, the lower plankton volumes associated with warm water, and the introduction of exotic tropical predators associated with warming.

Can normal fluctuations in recruitment rates be detected in time to improve fisheries management?

From examining the life table of sardine, one would expect that the possibility of extremely large recruitment successes could be detected in advance, but not assured, by high egg production and high survival of eggs, yolk-sac larvae, and early larvae. The same has been found likely for anchovy (Smith 1985) and hake (Hollowed, this volume). For sardine, this information would be available nearly two years before recruitment to the fishery. Thus it is more likely to be useful than similar information for anchovy, which recruits at an earlier age. The advance warning would be somewhat longer for hake.

The late larvae and juvenile stages of anchovy, sardine, and hake are not well enough known to yield useful information on abundance, and quantitative sampling of these stages is not now practical. Information on growth rates would be very useful for all stages, since there is an interaction between size and mortality. If *growth and survival* rates were known for sardine eggs and larvae, and *only growth* rates were known for late larvae or early juveniles, then recruitment could probably be categorized as "near," "below," or "above" replacement, from existing sea-survey techniques.

Another feature of sardine recruitment is that on the scale of a few years and a few decades, the recruitment in a given year or decade is likely to be similar in sign to the immediately preceding year or decade (Murphy 1966; Lenarz 1971; Smith and Moser 1988); this should yield particularly useful information for stock management following documented recruitment failures even at higher stock sizes.

Can critical changes in the recruitment rate be predicted from observations of the sardine's physical and biological environment?

It does not seem likely that the necessary lists of age structure, fecundity rates, mortality rates, and growth rates at all seasons of the year will be known to sufficient accuracy (Lo 1986). Also, the biological and physical influences of environment have not been sufficiently well related to these population rates to be predicted by simple environmental indices: this is why environmental indices fail to meet the test of time (Lasker and MacCall 1983). For example, offshore transport of sardine larvae at the height of upwelling might be counteracted to some degree by increased food supply for the juveniles. We do not know which areas of the ocean are occupied by juvenile sardines (and juveniles of most of other species); therefore the physical and biological characterization of their immediate environment is not currently possible. Existing knowledge does not warrant consideration of single factors in the life table, let alone interaction among these factors. Current knowledge on the status of other pelagic fish stocks could help interpret the recruitment success of a sardine population (Butler 1991).

CONCLUSION

It should not be inferred from our emphasis on decadal-scale change that we believe that shorter-scale changes in recruitment are unimportant: it may well be that for fisheries management the interannual scale of recruitment is more important than the longer scale. Unfortunately, matrix methods and even life tables are less appropriate at the shorter time scales.

In general, we have found that the rapid apparent growth rate of the stocks of Pacific sardine off southern California is not likely to have resulted from the fishery moratorium alone: other parameters of survival and reproduction are probably acting in concert with the lowered fishing mortality rate if the population conforms to the models used in this study. It is possible that information on egg production and survival in the earliest life stages, together with growth rates of the later life stages before

recruitment could contribute to better fishery management.

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