

THE RISE AND FALL OF THE PACIFIC SARDINE, *SARDINOPS SAGAX CAERULEUS* GIRARD, IN THE GULF OF CALIFORNIA, MEXICO

MIGUEL A. CISNEROS-MATA,
MANUEL O. NEVÁREZ-MARTÍNEZ
Instituto Nacional de la Pesca
Centro Regional de Investigaciones Pesqueras (INP-CRIP)
Guaymas, Sonora, 85400
México

M. GREGORY HAMMANN*
Centro de Investigación Científica y de
Educación Superior de Ensenada (CICESE)
Apartado Postal 2732
Km. 107 Carr. Tijuana-Ensenada
Ensenada, Baja California, 22800
México

*Address all correspondence to M. Gregory Hammann, CICESE, P.O. Box 434844, San Ysidro, CA 92143. Fax (011+526) 174-51-54.

ABSTRACT

The Pacific sardine has been the most important species in the wetfish fishery in the Gulf of California, Mexico, for the past 20 years. In recent years, the sardine population has rapidly declined while the population of the northern anchovy, a newcomer to the gulf, has been increasing. The history of the sardine fishery, and population trends from 1969 to 1990 were examined with virtual population analysis (VPA) based on length frequencies converted to age. Schaefer's model was used to characterize catch and effort data from Guaymas, Sonora (Mexico). A time series of population biomass estimates was constructed from the results of the VPA and weight-at-age data. These results are discussed in light of the relative roles that fishing pressure and competition with the increasing population of northern anchovy may play in the observed changes of the sardine population.

INTRODUCTION

High interannual variability in populations of small pelagic fish (e.g., anchovy and sardines) is common (Csirke 1988). Beverton (1983) classified these species of fishes as highly unpredictable, vulnerable to exploitation, and difficult to manage. Classic examples can be found in the collapse of the Peruvian anchoveta (*Engraulis ringens*) in the early 1970s (Pauly et al. 1987); the collapse of the Pacific sardine (*Sardinops sagax caeruleus*) during the 1950s and the subsequent increase of northern anchovy (*Engraulis mordax*) in the California Current; and the collapse of the Japanese sardine (*Sardinops melanosticta*) population during the 1940s and its recovery during the 1970s (Kondo 1980).

With the discovery of sardine and anchovy scales preserved in anaerobic sediments off Santa Barbara, California (Soutar and Isaacs 1969; Baumgartner et al. 1992), it was possible to construct a long time series of fish abundance, from which it was evident that large interannual fluctuations in the population levels of both species occurred well before the fisheries began. Environmental factors such as food availability and competition (Lasker and MacCall 1983), predation (Butler 1991), and abiotic fac-

tors such as circulation patterns (Parrish et al. 1983) and temperature received increased emphasis in the study of the causes of population variability of these pelagic fishes, whereas a dominant role of the fisheries was questioned.

Nevertheless, fisheries exploitation cannot be discounted as a contributor to the collapses of pelagic fisheries around the world. Excess removal by fishing may provide available niche space for food competitors (MacCall 1986), and the fisheries may increase the amplitude of natural variations and drive a population to extremely low levels from which it may not recover (Lluch-Belda et al. 1989).

In this paper we analyze the early increase and later decline in the population and fishery of the Pacific sardine in the Gulf of California, Mexico, and we discuss the possible relationship to the recent arrival and population increase of the northern anchovy. Our objectives are to (1) show two decades of sardine population growth followed by the current decline, (2) demonstrate a density-dependent relationship between the adult sardine and offspring, and (3) propose an ecological mechanism to explain the sardine/anchovy relationship in the Gulf of California.

HISTORY OF THE FISHERIES

The sardine fishery in Mexico began during the fall of the sardine fishery in California, USA, during the 1940s. At that time, the fishery was between Ensenada and Cedros Island, but during the 1950s, fishing extended southward into Magdalena Bay (figure 1). During the late 1960s Pacific landings of sardine decreased, and fishmeal plants and canneries were installed in Guaymas in the Gulf of California, where the sardine resource was abundant. Since that time, Guaymas has been the major port for the sardine fisheries in Mexico (Lluch-Belda, et al. 1986; Cisneros-Mata et al. 1987).

Annual wetfish landings and Pacific sardine catch per unit of effort (CPUE) show four periods in the Gulf of California: (1) exploration and establishment, 1969/70–1975/76; (2) development and growth, 1976/77–1981/82; (3) expansion and stabilization, 1982/83–1988/89; and (4) decline, 1989/90–present (figure 2, table 1).

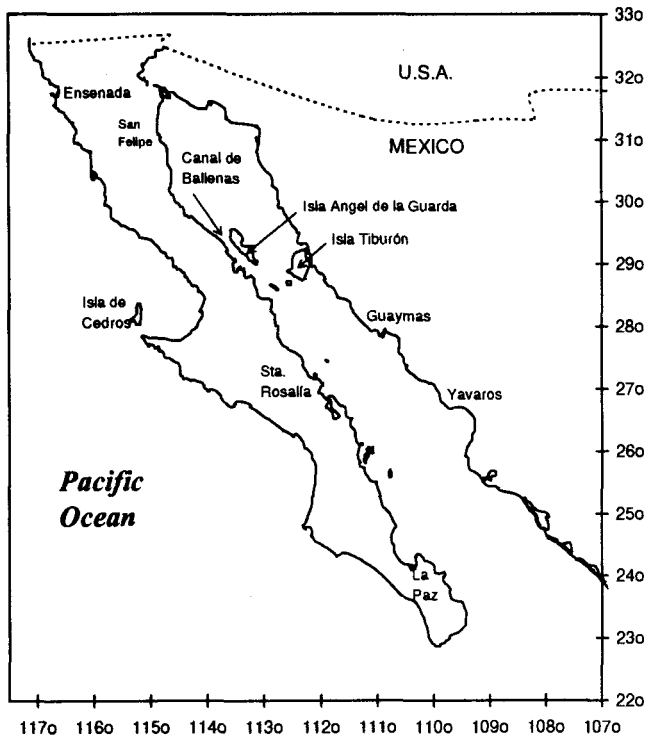


Figure 1. Map of Gulf of California, showing the principal ports for the sardine fishery.

Several important events occurred during these four periods. First, in 1970, the Pacific sardine fishery in Ensenada was closed and the vessels were moved to Guaymas. These boats were small (40–60 MT) and fished only from October to May (“winter fishing”). During the second period, in 1977, larger boats began to enter the fleet at Guaymas; first twenty-eight 120 MT ships were commissioned from Peru by the Mexican government after the fall of the Peruvian anchovy fishery. In 1979/80 the first landings during the June–September period were reported. During the early 1980s, as the newly installed processing plants increased the demand for sardine, the fishery expanded southward, and Yavaros, Sonora, began developing into an important sardine port (Estrada-Garcia et al. 1986; Cisneros-Mata et al. 1987). During this period, fishing effort was mostly characterized by short, one-day trips.

During the third period, in 1982/83, a regime of “summer fishing” was established, and the larger vessels began to operate farther from their home port of Guaymas, especially in the fertile “Canal de las Ballenas” (between the large islands and the western coast of the gulf) and in the area north of Tiburón Island. Pacific sardine CPUE increased directly with fishing power and with the increased experience of the fishermen. The fleet began using modern technology to locate schools, combining spotter planes with video sonars installed on the vessels. Trips during this period often lasted three days.

TABLE 1
 Total Pacific Sardine and Northern Anchovy Catches; Standard Effort; and C/f for Pacific Sardine in the Gulf of California, 1969–1992

Fishing season	Std. effort (# trips)	Total catch (MT)	Pacific sardine catch (MT)	Anchovy catch (MT)	C/f sardine (MT/trip)
69/70	597.20	15,992	11,287	0	18.90
70/71	988.28	23,194	19,558	0	19.79
71/72	1,358.48	37,163	32,617	0	24.01
72/73	380.96	38,605	9,924	0	26.05
73/74	750.46	31,239	16,180	0	21.56
74/75	1,271.18	55,350	36,648	0	28.83
75/76	1,878.45	63,094	51,263	0	27.29
76/77	372.97	38,352	8,802	0	23.60
77/78	1,111.87	58,691	32,600	0	29.32
78/79	731.42	54,447	24,627	0	33.67
79/80	1,587.84	112,637	77,566	0	48.85
80/81	2,133.20	126,121	93,989	0	44.06
81/82	1,270.91	137,813	71,425	0	56.20
82/83	1,583.50	226,304	111,526	0	70.43
83/84	1,838.65	189,518	146,467	0	79.66
84/85	2,280.80	197,803	169,076	0	74.13
85/86	3,160.04	287,357	240,226	2,081	76.02
86/87	3,534.41	304,872	272,574	39	77.12
87/88	3,370.69	284,934	261,363	777	77.54
88/89	3,776.26	321,799	294,095	7,706	77.88
89/90	1,629.98	212,857	109,942	18,493	67.45
90/91	1,532.86	235,060	113,631	12,768	74.13
91/92	—	105,431	6,431	5,168	—

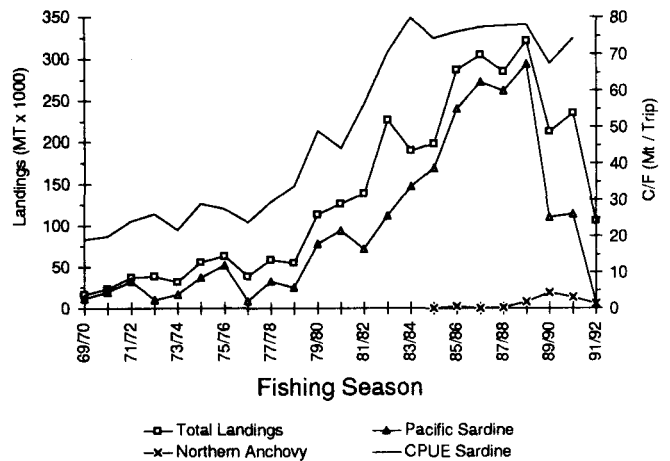


Figure 2. Total for small pelagics, Pacific sardine, and northern anchovy landings in metric tons (Guaymas and Yavaros combined), and total catch per unit of effort for Pacific sardine (metric tons/trip) in the Gulf of California, 1969–92.

In 1985, juvenile northern anchovy were discovered near Guaymas in the Gulf of California, and in 1986 they first appeared in commercial sardine landings (Cisneros-Mata et al. 1987; Hammann and Cisneros-Mata 1989). The Pacific sardine CPUE began to level off in 1984/85, and landings fell drastically after the 1988/89 fishing season.

In the following sections we analyze the time series (Instituto Nacional de la Pesca) of landings and fishing effort (number of trips) from the commercial sardine

fleet of Guaymas, Sonora, Gulf of California, Mexico, from 1969 to 1990.

METHODS AND MATERIALS

Port sampling at Guaymas (Sonora, Mexico) has been carried out routinely since the 1972/73 sardine fishing season in the Gulf of California. From 1972 to 1983, 60 kg samples were collected from 2–4 vessels daily (depending on landings), and monthly length-frequency distributions were determined. Starting in 1984, a minimum sample size of 10 kg was determined for port sampling of length frequencies, and 2–5 vessels were sampled daily. The length-frequency distribution and weight-length relationship of the monthly samples were used to determine size composition and total numbers of the monthly landings reported in metric tons at the fisheries office. The monthly size compositions were combined to determine total numbers caught per size class per fishing season.

The Schaefer (1954) model (yield = $af - bf^2$) was employed to describe the relation between the catch and effort data during fishing seasons from 1969/70 to 1989/90 for the fleet operating in Guaymas. Effort data were not available from Yavaros. The number of trips was defined as the unit effort. The total yearly standard effort (f), in number of trips for each vessel size, was standardized to the fishing power of the most traditional vessel size (10–60 MT) by dividing the total yearly catch of each vessel size n by the CPUE of the standard vessel (Ricker 1975). The CPUE was calculated for Pacific sardine from total yearly catch and effort (number of trips) of each of eight size categories of vessels operating in the sardine fisheries in the gulf: net tonnages of (1) 10–60 MT, (2) 61–100 MT, (3) 101–120 MT, (4) 121–140 MT, (5) 141–160 MT, (6) 181–200 MT, (7) 201–220 MT, and (8) >221 MT. Thus the overall CPUE was calculated for each year in the time series as follows:

$$CPUE_{total} = \frac{CATCH_{total}}{\sum_1^8 \left(\frac{CATCH_n}{CPUE_{(10-60t)}} \right)}$$

To estimate the annual number of organisms at age from the age structure observed in the commercial landings at Guaymas, the program ELEFAN III (VPA I; Gayanilo et al. 1989) was used to carry out a virtual population analysis (VPA; Jones 1984). Length-frequency distribution was transformed to age distribution with von Bertalanffy individual growth parameters and an age-length key. This procedure is used when age data are lacking over the entire time series (Clark 1991), with the assumption that growth parameters are constant over time, which is probably not the case. With the results

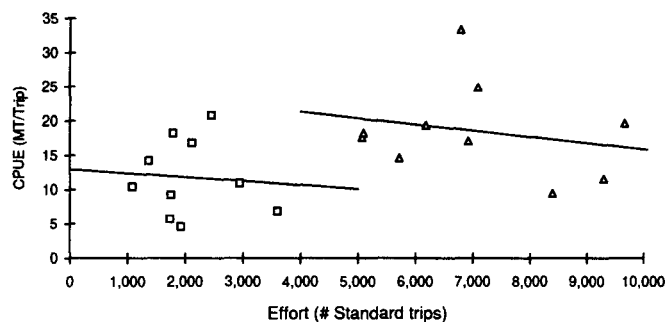


Figure 3. Relation between the catch per unit of effort and standard effort (trips) for the Pacific sardine fishery at Guaymas, Gulf of California, during two ten-year periods: 1969–79 and 1980–90 (solid line = Schaefer model).

from VPA, the Shepherd (1982) recruitment stock (P)–(R) function $R = \gamma P / (1 + (P/k)^g)$ was fit using the Marquardt nonlinear algorithm in the program FISH-PARM (Prager 1989).

During the 1988/89 and 1989/90 fishing seasons, age was determined from otoliths of 1283 Pacific sardines randomly sampled from 10 kg port samples. Data from both fishing seasons were combined to better represent the population, and the resulting individual growth parameters and the age-length key were used to transform length to age frequency over the entire time series. We recognize that we did not consider possible changes in growth rate over time, but otoliths were not collected in the early years of the fishery, so age was not routinely determined.

RESULTS

The relation between CPUE and standard effort shows a positive slope with increasing fishing effort, which in this case represents increased efficiency with acquired experience and new technology (sonar, spotter planes). Lines adjusted (Schaefer's model) for two ten-year periods (1969/79 and 1980/90), however, show decreasing trends, different only in the level of effort and CPUE (figure 3). Table 2 shows the calculated parameters and statistics for the lines describing the Schaefer model for the entire data set, and for each of the two ten-year periods.

The von Bertalanffy growth parameters describing the 1988/89–1989/90 fishery seasons are: $L_{\infty} = 203.7$

TABLE 2
 Schaefer Model $Y = af + bf^2$ Parameters; Standard Deviations Are in Parentheses

Period	a	b
1969–90	10.8289 (6.6227)	0.00097 (0.00054)
1969–79	12.9567 (5.8705)	–0.000565 (0.0026)
1980–91	24.9174 (7.0474)	–0.00089 (0.00144)

TABLE 3
Age-Length Key in Percent for Pacific Sardine in the Gulf of California, Determined from Otoliths
Sampled during the 1988/89 and 1989/90 Fishing Seasons

Size class SL mm	Age group							Total	N
	0	1	2	3	4	5	6		
<120	100.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	15
121-130	76.29	23.71	0.00	0.00	0.00	0.00	0.00	100.00	10
131-140	61.45	38.16	0.39	0.00	0.00	0.00	0.00	100.00	54
141-150	25.16	67.60	7.24	0.00	0.00	0.00	0.00	100.00	162
151-160	1.88	52.96	27.97	17.19	0.00	0.00	0.00	100.00	203
161-170	0.00	19.50	60.99	19.51	0.00	0.00	0.00	100.00	264
171-180	0.00	4.93	49.42	45.65	0.00	0.00	0.00	100.00	281
181-190	0.00	0.00	14.15	41.90	40.89	3.06	0.00	100.00	159
191-200	0.00	0.00	2.48	14.67	44.24	31.11	7.50	100.00	75
201-210	0.00	0.00	0.28	1.89	31.31	49.58	16.94	100.00	38
211-220	0.00	0.00	0.00	1.11	23.18	21.34	54.37	100.00	22
								Total	1283

mm SL, $K = 0.8577 y^{-1}$, $t_0 = -0.01394 y$ ($r^2 = 0.99$, $N = 1283$); we used an age-length key to convert length to age (table 3). The extrapolated number at age of Pacific sardines landed per fishing season between 1972/73 and 1989/90 is given in appendix table A.

Using VPA, we determined the number of sardines per year class (appendix table B). The resulting time series shows that the number of spawners increased slowly until 1986, and later decreased; the number of recruits increased from 1975 to 1985 and then fell sharply during the following three years (figure 4). The tendencies for poor recruitment and, in particular, two rapid decreases in recruitment rate during 1977-79 and 1983-85 can be clearly observed in figure 5 and table 4 as decreases in the ratio between the parent stock (age classes 1-6) and the following year's recruitment (class 0).

The stock-recruitment relationship for Pacific sardine is best fit by a parabola ($r^2 = 0.77$, $N = 13$; figure 6). The slope at the origin ($y = 2.697$) represents the maximum expected rate of adult recruitment that occurs when adult density and density-dependent mortality rates are low. The maximum P at the inflection point ($k = 1.471 \times 10^{10}$) is the limit above which density-dependent effects dominate over density-independent effects; below this point in figure 6, the population's vul-

TABLE 4
VPA Estimates of Recruits (Age Class 0), Spawners
(Age Classes 1-6), and the Recruit/Parent Ratio

Fishing season	Recruits	Spawners	R/S
72/73	3,712,574,464	Incomplete	n/a
73/74	1,943,336,448	Incomplete	n/a
74/75	1,335,047,680	2,010,681,427	1.46
75/76	2,935,448,576	1,201,404,588	4.49
76/77	5,389,423,616	1,583,896,484	4.47
77/78	7,077,535,232	3,109,534,029	2.94
78/79	9,151,337,472	4,252,955,992	1.38
79/80	5,874,631,168	5,668,992,507	1.51
80/81	8,562,187,264	4,605,747,499	2.16
81/82	9,955,485,696	5,389,356,656	2.69
82/83	14,500,033,280	6,144,694,987	3.60
83/84	22,115,801,600	9,020,887,807	3.17
84/85	28,562,339,840	12,541,800,346	1.88
85/86	23,633,075,200	18,087,533,010	0.66
86/87	11,851,628,800	17,630,978,732	0.56
87/88	9,961,348,096	11,487,350,637	n/a
88/89	Incomplete	8,594,568,598	n/a
89/90	Incomplete	Incomplete	n/a

nerability and thus the probability of a population crash increases. The compensation factor ($g = 6.499$) measures the force of density-dependence; values greater than 1.0 indicate strong overcompensation (Shepherd 1982). This

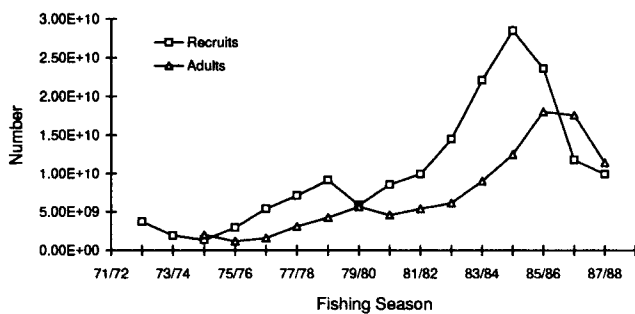


Figure 4. Numbers of recruits and adults for the Pacific sardine in the Gulf of California as determined by VPA on data from the fishery at Guaymas, Gulf of California.

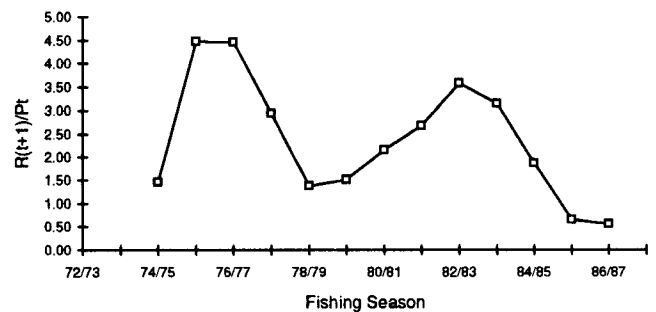


Figure 5. Recruitment rate for Pacific sardine in the Gulf of California R_{t+1}/P_t .

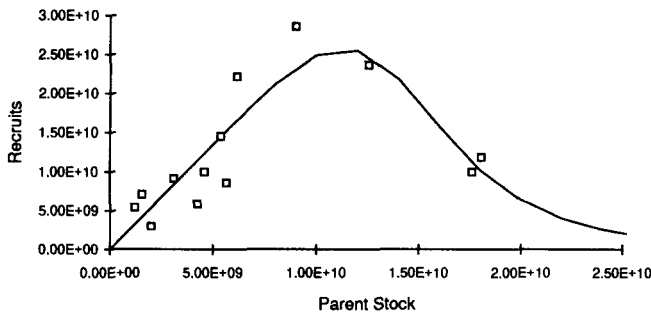


Figure 6. Shepherd stock-recruitment relationship for Pacific sardine fishery at Guaymas, Gulf of California. Numbers of recruits and parents were determined from VPA.

is the first evidence suggesting stock overcompensation for Pacific sardine in the Gulf of California as a population-stabilizing mechanism: the net rate of recruitment increases when population size is low, and decreases when it is high (Tyler and Gallucci 1980; Shepherd 1982).

We used results of VPA, in combination with weight-at-age data (the length-weight relationship was used to transform length-based von Bertalanffy parameters to weight-based parameters) to construct a time series of total and spawning biomass, which we compared to total Pacific sardine landings in the Gulf of California (figure 7). Maximum spawning biomass (1.159 million MT) occurred in the 1986/87 fishing season. In figure 8, the proportion of spawning biomass extracted by the fishery can be observed; in all but the earliest years, the rate of exploitation was above 20 percent of the spawning biomass.

DISCUSSION

In marine pelagic fish populations, the mechanisms of density-dependent regulation are reflected in the parent/progeny relation (Clark 1991), which can facilitate fishery management. But when catch-and-effort data from the commercial fleet are used, a warning of an imminent decline in population may come too late for effective regulatory actions to be initiated (Hampton and Majkowski 1986). An increasingly efficient fleet increases landings, even when recruitment is poor. A comparison of the time series of number of recruits and adults (figure 4) to that of landings and CPUE (figure 2) suggests that this may have been the case for the Pacific sardine fisheries in the Gulf of California. Maximum landings were reached in 1988/89, and CPUE did not fall off until 1990/91, even though several years earlier, in 1985/86, recruitment began to decrease.

The cyclic behavior in recruitment rate ($R_{(t+1)}/P_t$) as shown in figure 5 demonstrates a large inter-annual variability and declining trend in early survival (egg[parent] to recruit); in 1976 and 1983, survival to recruitment reached a maximum and then dropped

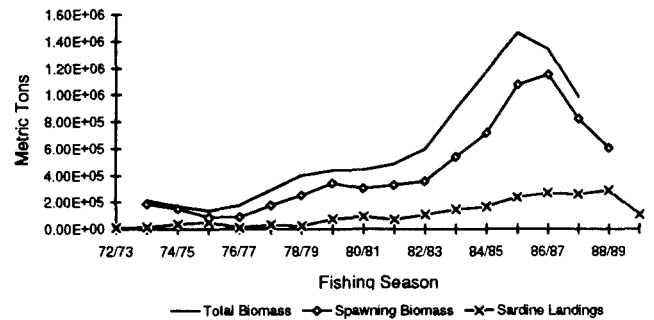


Figure 7. Total and spawning biomass of the Pacific sardine in the Gulf of California as determined by VPA and weight-at-age calculations. Pacific sardine landings are included for comparison.

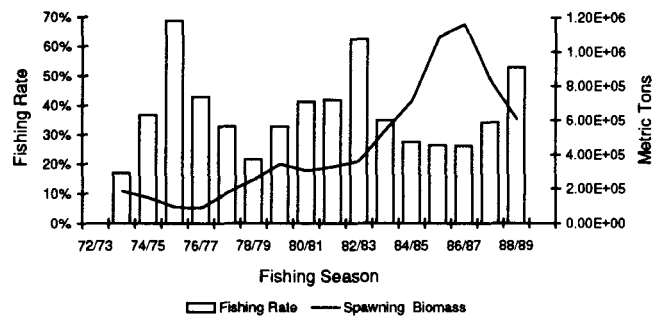


Figure 8. Fishing rate for the Pacific sardine in the Gulf of California expressed as the percentage of the Pacific sardine spawning biomass landed by the fisheries.

abruptly during the following three years. The decrease in recruitment rate in 1977/79 and 1984/86 (figure 5) could be due to environmental factors (these periods follow El Niño events); to interspecific relationships (e.g., competition for food, predation on eggs and larvae) with adult northern anchovy, which began to increase in the gulf in 1985 (Hammann and Cisneros-Mata 1989); or to a combination of both.

The El Niño events of 1976/77 and 1983/84, and the warming observed in 1989/90 may also have affected recruitment of Pacific sardine in the gulf. It has been argued that the invasion of warm waters during El Niño changed the geographic distribution of sardine captures (Lluch-Belda et al. 1986) and spawning (Hammann et al. 1988) in the gulf. Hammann et al. (1988) and Hammann (1991) suggested that density-dependent mortality of sardine eggs and larvae may occur when the warm-water intrusion of an El Niño event reduces habitat. Nevertheless, recruitment appeared to improve during such conditions. Hammann et al. (1991) described the increased availability and CPUE of sardine during warm summer conditions, which are enhanced during an El Niño event. During the warm periods of 1976/77, 1983/84, and 1989/90, over 50 percent of the spawning biomass was taken by the fishery (figure 8), and it is likely that the following poor recruitment results from

the reduction of the spawning biomass during the previous year. This high overfishing of spawning stock was previously evidenced from length-based cohort analysis (Jones 1984; Cisneros-Mata et al. 1990).

The suggested overcompensation in the sardine population may be due to cannibalism or lack of food sufficient for adult maturity and growth (Harris 1975; Shepherd 1982). It is possible that competition between sardine and anchovy adults could have decreased the relative availability of food for sardine under the described population conditions (sardine decreasing, anchovy increasing). Studying the abundance of scales deposited and preserved in anoxic sediments off Santa Barbara in the California Current ecosystem, Lasker and MacCall (1983) proposed competition between these two species as a mechanism to explain the decline in the sardine population. On the other hand, Butler (1987) found little evidence for competition between these two species, and suggested predation on sardine eggs and larvae by northern anchovy adults as a plausible explanation.

The causes of interannual variability in recruitment of small pelagic fish species are still not understood. A combination of factors such as changes in the environment, intra- and interspecific relationships, and fishing may be responsible for the observed variability. Lluch-Belda et al. (1989) proposed that long-term environmental variations may give rise to "regimes" of anchovy or sardine. Nevertheless, a long-term change in the dominant population is the net result of many yearly changes in recruitment success. Cury and Roy (1989) described an "optimal environmental window" when all biotic and abiotic environmental conditions would permit successful recruitment. Cury (1988) combined population ecology and evolutionary biology to explain recruitment variability. According to Cury's hypothesis, when the population biomass is low, rapid changes can occur in the genome because of genetic drift (genetic revolution); the result would be organisms better adapted to compete advantageously with the dominant existing population and thereby increase their population.

Although the Pacific sardine is widely distributed in the Gulf of California (Cisneros-Mata et al. 1990, 1991) and does not restrict its spawning to the coastal areas (Nevárez-Martínez 1990; Hammann 1991), overfishing must also be considered to have played an important role, given the high rates of exploitation during environmental conditions such as El Niño, as shown in this paper.

ACKNOWLEDGMENTS

The authors would like to express their appreciation to R. Rosenblatt, J. R. Hunter, P. E. Smith, O. Sosa, L. Calderon, and three anonymous reviewers for their valuable comments on drafts of this manuscript. Partial funding for MGH was provided by CONACYT grants

D112-904325 and T9201-1110. MACM was partially supported by CONACYT and the Center for Ecological Health Research (CEHR) at UC Davis.

LITERATURE CITED

- Baumgartner, T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. Calif. Coop. Oceanic Fish. Invest. Rep. 33:24-40.
- Beverton, R. J. H. 1983. Science and decision-making in fisheries regulations. FAO Fish. Rep. 291(3):919-936.
- Butler, J. L. 1987. Comparison of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph.D. thesis, UC San Diego, Scripps Institution of Oceanography, La Jolla, Calif. 242 pp.
- . 1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax caeruleus*, larvae in the California Current. Can. J. Fish. Aquat. Sci. 48: 1713-1723.
- Cisneros-Mata, M. A., J. P. Santos-Molina, J. A. De Anda-Martínez, A. Sánchez-Palafox, and J. Estrada-García. 1987. Pesquería de sardina en el noroeste de México (1985/86). Secretaría de Pesca, Instituto Nacional de la Pesca (Centro Regional de Investigación Pesquera, Calle 20 No. 605 Sur, Guaymas, Sonora, México. In Spanish.) 79 pp.
- Cisneros-Mata, M. A., J. A. De Anda-Martínez, J. Estrada-García, and F. Páez-Barrera. 1990. Evaluación de las pesquerías de sardina y crinuda del Golfo de California. Inv. Mar. CICIMAR. (Centro Regional de Investigación Pesquera, Calle 20 No. 605 Sur, Guaymas, Sonora, México. In Spanish.) 5(1):19-26.
- Cisneros-Mata, M. A., M. O. Nevárez-Martínez, G. Montemayor-López, J. P. Santos-Molina, and R. Morales-Azqueitia. 1991. Pesquería de sardina en el Golfo de California. 1988/89-1989/90. Secretaría de Pesca, Instituto Nacional de la Pesca (Centro Regional de Investigación Pesquera, Calle 20 No. 605 Sur, Guaymas, Sonora, México. In Spanish.) 80 pp.
- Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734-750.
- Csirke, J. 1988. Small shoaling pelagic fish stocks. In Fish population dynamics, 2nd ed., J. A. Gulland, ed. John Wiley and Sons, Ltd. pp. 271-302.
- Cury, P. 1988. Pressions sélectives et nouveautés évolutives: une hypothèse pour comprendre certains aspects des fluctuations a long terme des poissons pélagiques cotiers. Can. J. Fish. Aquat. Sci. 45:1099-1107. (In French)
- Cury, P., and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46:670-680.
- Estrada-García, J. J., M. A. Cisneros-Mata, F. Páez-Barrera, and J. P. Santos-Molina. 1986. Informe de la temporada de pesca 1984/85 del recurso sardina del Golfo de California. Secretaría de Pesca, Instituto Nacional de la Pesca (Centro Regional de Investigación Pesquera, Calle 20 No. 605 Sur, Guaymas, Sonora, México. In Spanish.) 160 pp.
- Gayanilo, F. C., Jr., M. Soriano, and D. Pauly. 1989. A draft guide to the complete ELEFAN. ICLARM Software 2, 70 pp.
- Hammann, M. G. 1991. Spawning habitat and egg and larval transport, and their importance to recruitment of Pacific sardine, *Sardinops sagax caeruleus*, in the Gulf of California. In Long-term variability of pelagic fish populations and their environment, T. Kawasaki, S. Tanaka, Y. Toba, and A. Taniguchi, eds. Proc. Inter. Symp., Sendai, Japan, 14-18 Nov. 1989. Pergamon Press. pp. 271-278.
- Hammann, M. G., and M. A. Cisneros-Mata. 1989. Range extension and commercial capture of the northern anchovy, *Engraulis mordax* GIRARD, in the Gulf of California, México. Calif. Fish Game 75(1):49-53.
- Hammann, M. G., T. Baumgartner, and A. Badan-Dangon. 1988. Coupling of the Pacific sardine (*Sardinops sagax caeruleus*) life cycle with the Gulf of California pelagic environment. Calif. Coop. Oceanic Fish. Invest. Rep. 29:102-109.
- Hammann, M. G., M. O. Nevárez-Martínez, and J. A. Rosales-Casián. 1991. Pacific sardine and northern anchovy in the Gulf of California, Mexico: current results of SARP Mexico. Inter. Counc. Explor. Sea, C.M. 1991/H:20 Session V. Pelagic Fish Committee.
- Hampton, J., and J. Majkowski. 1986. Scientists fear SBT problems worsening. Austr. Fish. 45(12):6-9.

- Harris, J. G. K. 1975. The effect of density-dependent mortality in the shape of the stock and recruitment curve. *J. Cons. Int. Explor. Mer* 36(2):144-149.
- Jones, R. 1984. Assessing the effects of exploitation pattern using length composition data (with notes on VPA and cohort analysis). *FAO Fish. Tech. Pap.* 256, 118 pp.
- Kondo, K. 1980. The recovery of the Japanese sardine: the biological basis of stock-size fluctuations. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 177:332-354.
- Lasker, R., and A. MacCall. 1983. New ideas on the fluctuations of the clupeoid stocks off California. *In* CNC/SCOR Proc. JOA. 1982. General symposia, Ottawa, pp. 110-120.
- Lluch-Belda, D., F. J. Magallon, and R. A. Schwartzlose. 1986. Large fluctuations in the sardine fishery in the Gulf of California: possible causes. *Calif. Coop. Oceanic Fish. Invest. Rep.* 27:136-140.
- Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* 8:195-205.
- MacCall, A. D. 1986. Changes in the biomass of the California Current ecosystem. *In* Variability and management of large ecosystems, K. Sherman and L. M. Alexander, eds. pp. 33-54.
- Nevárez-Martínez, M. O. 1990. Producción de huevos de la sardina monterrey (*Sardinops sagax caeruleus*) en el Golfo de California: una evaluación y crítica. MS CICESE. Ensenada, B.C., México. 144 pp. (In Spanish)
- Parrish, R. H., A. Bakun, D. M. Husby, and C. S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983. G. D. Sharp and J. Csirke, eds. F.A.O. Fish Rep. 291(3):731-777.
- Pauly, D., M. L. Palomares, and F. C. Gayanilo. 1987. VPA estimates of the monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta 1953-1981. *In* The Peruvian anchoveta and its upwelling ecosystem: three decades of change, D. Pauly and I. Tsukayama, eds. ICLARM Studies and Reviews 15:142-166.
- Prager, M. H. 1989. FISHPARM. Nonlinear parameter estimation for fisheries. Version 3.0S. Dep. Oceanogr. Norfolk, Va. 23529-0276, Old Dominion Univ.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382 pp.
- Schaefer, M. B. 1954. Some aspects of the dynamics of populations, important for the management of the commercial fisheries. *Bull. Inter-American Trop. Tuna Comm.* 1(2), 56 pp.
- Shepherd, J. G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *J. Cons. Int. Explor. Mer* 40(1):67-75.
- Soutar, A., and J. D. Isaacs. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 13:63-70.
- Tyler, A. V., and V. F. Gallucci. 1980. Dynamics of fishes stocks. *In* Fisheries management, R. T. Lackey and L. A. Nielsen, eds. John Wiley and Sons, Ltd., pp. 111-147.

APPENDIX

TABLE A
Extrapolated Number at Age Landed for Pacific Sardine during the 1972/73–1989/90 Fishing Seasons

Fishing season	Age group						
	0	1	2	3	4	5	6
72/73	3,133,383	13,425,410	45,666,913	39,228,900	13,235,721	2,764,819	498,679
73/74	16,741,262	72,393,799	88,166,998	44,233,550	1,794,785	317,963	53,240
74/75	47,035,026	161,535,666	157,014,290	105,218,551	20,193,833	2,903,489	400,540
75/76	15,605,009	74,117,268	162,452,972	155,165,309	64,999,901	15,155,542	3,229,809
76/77	5,262,777	21,350,104	26,533,098	23,792,531	9,831,777	2,034,705	367,870
77/78	115,800,868	294,008,455	113,581,970	50,590,617	891,605	96,609	8,063
78/79	94,983,542	343,535,473	196,070,961	109,401,235	2,111,679	161,790	1,015
79/80	154,597,944	505,440,690	355,245,351	155,613,460	1,430,664	107,064	0
80/81	164,534,047	429,892,897	416,906,517	239,909,972	23,272,732	3,154,846	403,816
81/82	157,486,142	750,038,860	540,628,391	308,403,207	9,230,516	1,611,066	1,377,457
82/83	371,061,856	506,761,675	173,801,735	98,428,643	13,253,265	2,124,768	311,353
83/84	609,260,149	1,617,097,260	798,927,693	417,018,826	2,812,890	448,017	72,767
84/85	507,456,510	950,187,947	456,370,461	205,426,795	2,051,467	206,131	14,194
85/86	848,822,010	1,488,370,539	604,561,334	291,579,325	7,537,525	691,550	34,393
86/87	279,070,465	1,293,491,642	1,416,569,958	760,870,718	48,427,842	8,935,977	1,575,422
87/88	62,056,812	417,784,958	1,121,192,041	711,980,420	91,344,428	13,835,597	1,916,147
88/89	347,345,255	1,022,465,830	1,000,269,366	689,021,662	138,145,412	29,368,112	5,902,236
89/90	15,744,474	213,400,502	442,274,047	286,199,637	60,387,835	22,587,039	9,343,703

TABLE B
Virtual Population Analysis Estimates of Population Number at Age for Pacific Sardine during the 1972/73–1989/90 Fishing Seasons

Fishing season	Age group						
	0	1	2	3	4	5	6
72/73	3,712,574,464	1,828,364,416	554,549,696	131,834,272	21,167,092	—	—
73/74	1,943,336,448	1,682,751,232	866,306,176	221,926,896	34,953,600	1,763,075	—
74/75	1,335,047,680	870,927,104	716,326,080	335,851,360	72,291,528	14,690,023	595,332
75/76	2,935,448,576	575,088,128	291,269,760	224,440,736	85,838,456	19,966,972	4,800,536
76/77	5,389,423,616	1,321,900,800	212,964,784	34,095,716	11,985,341	2,403,069	546,774
77/78	7,077,535,232	2,442,326,528	585,899,840	79,448,232	1,728,014	119,430	11,985
78/79	9,151,337,472	3,135,966,464	917,703,424	192,859,248	6,184,875	240,472	1,509
79/80	5,874,631,168	4,090,689,280	1,264,491,904	290,707,232	21,627,746	1,476,345	0
80/81	8,562,187,264	2,682,035,712	1,528,759,168	348,017,472	37,453,108	8,881,838	600,201
81/82	9,955,485,696	3,949,766,656	987,031,424	428,444,320	18,876,978	3,189,933	2,047,345
82/83	14,500,033,280	4,615,188,480	1,377,709,568	130,532,976	17,896,864	2,904,328	462,771
83/84	22,115,801,600	6,626,971,520	1,851,060,735	537,761,664	4,378,843	606,890	108,155
84/85	28,562,339,840	10,078,614,400	2,081,420,000	367,508,992	13,872,996	362,861	21,097
85/86	23,633,075,200	13,203,678,720	4,145,572,480	686,666,960	46,353,188	5,217,757	43,905
86/87	11,851,628,800	10,637,752,320	5,270,338,560	1,564,715,840	139,168,690	16,988,524	2,014,798
87/88	9,961,348,096	5,432,792,320	4,184,076,160	1,572,530,020	260,840,720	34,652,868	2,458,549
88/89	—	4,682,058,752	2,297,138,720	1,250,579,600	292,648,420	64,594,770	7,548,336
89/90	—	—	1,547,267,072	450,866,520	163,179,200	51,179,030	11,949,601