

Effects of California El Niño 1982–1984 on the northern anchovy

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ABSTRACT

El Niño caused physical and biological changes in the northern anchovy habitat off southern California. Anomalous sea surface temperatures, surface currents, mixed layer depths, and plankton biomass levels began to appear in late 1982 and persisted into 1984. Growth of juvenile and adult anchovy slowed during El Niño, probably due to reduced availability of zooplankton prey. A decrease in size-at-age in early 1983, with a recovery in late 1984, can be explained by movements of the stock and the latitudinal cline in size-at-age. Spawning range expanded in 1983 due to shifts in sea surface temperature boundaries. Early larval mortality was unusually high in the yolk-sac stage. Fecundity per unit spawning biomass was low in 1983, due primarily to a high proportion of first-year spawners. Size-at-age was very low by spring 1984, but specific fecundity was surprisingly high. Although El Niño had a variety of significant effects on the northern anchovy, the stock seems to have recovered in 1985.

1. Introduction

The northern anchovy, *Engraulis mordax*, in the California Current and the anchoveta, *Engraulis ringens*, in the Peru Current, are ecological analogs: relatively small, short-lived, pelagic planktivores living in highly variable eastern boundary current systems (Parrish *et al.*, 1983). Sardine and anchovy stocks are notoriously variable and prone to collapse under fishing pressure exacerbated by environmental stress. Notable examples in the eastern Pacific have been the California sardine in the late 1940's (Murphy, 1966) and the Peruvian anchoveta in the early 1970's (Walsh *et al.*, 1980).

Three distinct subpopulations or stocks of northern anchovy have been differentiated along the west coast of North America (Vrooman *et al.*, 1981; see Fig. 1). The large central stock spawns in the Southern California Bight between Point Conception (34.5N) and Punta Baja (30N). Since 1980, spawning biomass of the central stock has been estimated by the egg production method (Parker, 1980) at the La Jolla

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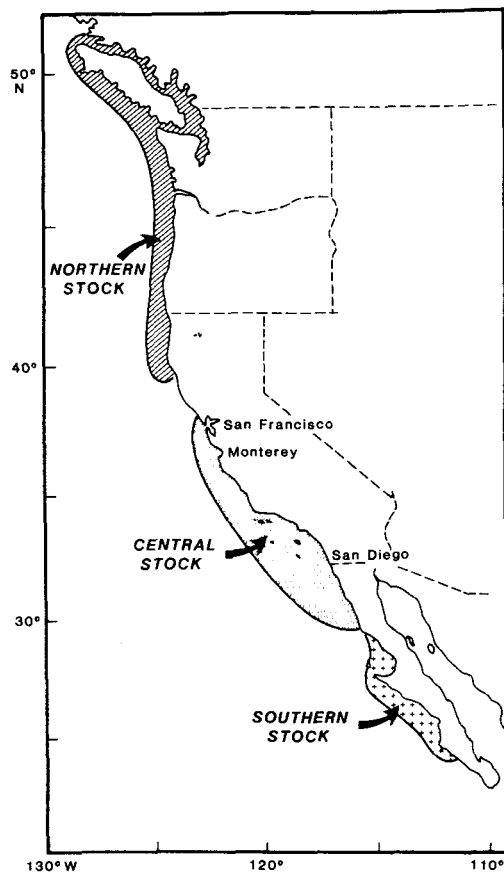


Figure 1. Northern anchovy stocks.

Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS).

The egg production method defines spawning biomass as the daily production of eggs divided by the daily specific fecundity of the adult population. Daily egg production is derived from an ichthyoplankton survey and egg development rates measured in the laboratory. Daily specific fecundity is derived from a trawl sample yielding estimates of average female weight, batch fecundity, sex ratio, and the proportion of females spawning each night. Trawls and egg tows are taken concurrently on a survey conducted during the seasonal peak of spawning activity, from February to April. Some spawning activity is observed year-round, but 73% of all spawnings occur in February to April (Parrish *et al.*, 1986). Larval growth and mortality can also be estimated from the ichthyoplankton samples. Juveniles and adults are sampled and aged two or three times a year by the California Department of

Table 1. Northern anchovy central stock population parameter estimates, 1980–1985. Spawning biomass and spawning female weight from Bindman (1985). Year class size from Methot (in prep.), 1985 value is a preliminary estimate subject to change.

	1980	1981	1982	1983	1984	1985
Spawning biomass, 10^3 metric tons (c.v.)	870 (.262)	635 (.216)	415 (.257)	652 (.211)	306 (.165)	458 (.188)
Spawning female weight, g	17.5	13.4	18.8	11.2	12.0	14.5
Mean age in February, yrs	1.80	1.80	2.46	1.29	1.76	1.46
Year class size, 10^9 fish	63	14	45	35	109	(39)

Fish and Game (DFG) Sea Survey program. Table 1 lists some results of NMFS and DFG surveys in 1980–1985.

Spawning biomass of the central stock has been declining since 1975 (Fig. 2). The 1984 biomass was the lowest since 1962, but the 1985 estimate may indicate a recovery. Catch increased until 1981, largely from intense Mexican fishing effort, but never reached a level sufficient to explain the decline in spawning biomass. The stock was dominated by 2 to 4-year-old fish until 1979, but 1 and 2-year-olds have dominated since the recruitment of a very large 1978 year class (Mais, 1981). A relatively large 1982 year class was recruited in 1983: the 1982 year class made up 75% of the stock in February 1983. Such a small and young stock is particularly vulnerable to environmental stresses because it may be unable to recover from successive year-class failures. Fecundity of the northern anchovy is strongly age-dependent (Parrish *et al.*, 1986).

An unusually strong and well-documented El Niño caused substantial changes in the eastern equatorial Pacific from mid-1982 to August 1983. Changes in the

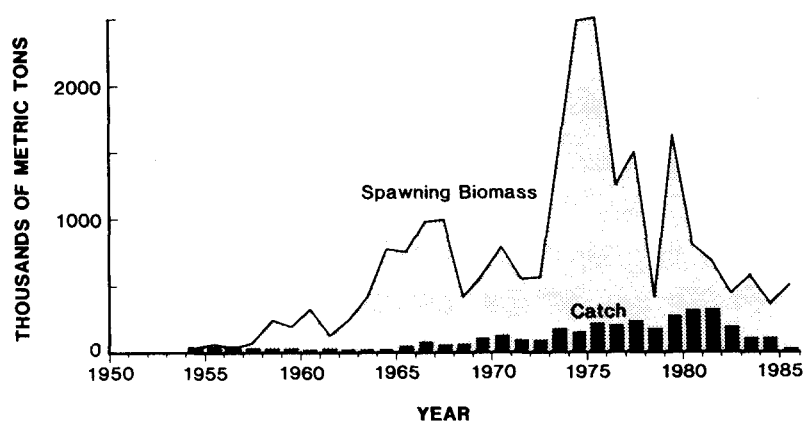


Figure 2. Spawning biomass of northern anchovy central stock and total U.S. and Mexican catch (MacCall and Methot, 1983).

California Current system were observed beginning in late 1982 (McGowan, 1983; Simpson, 1983; Fiedler, 1984a). Fiedler (1984b) provided a preliminary report of effects of the California El Niño on the northern anchovy central stock, based on data available by the end of 1983. This report is a more complete review of effects manifested in data from NMFS biomass surveys and DFG Sea Surveys and in the derived stock and spawning parameters estimated for management purposes. We compare the El Niño years of 1983 and 1984 with the 1980–1985 “anti-El Niño” years (1980–1982 and 1985). Much of the data reported here have appeared previously in internal reports, but we present original analyses and synthesis.

2. Methods

a. Environmental time series. Water temperature and sea level have been recorded since about 1920 at Scripps Pier in La Jolla, California (32.9N, 117.3W). The center of the central stock spawning range in 1980–1984 was ~60 km directly offshore of this coastal station. Monthly surface temperature anomalies were obtained from Smith (1985a). Monthly mean sea levels (J. Simpson, Scripps Institution of Oceanography, pers. comm.) were corrected for a secular rise of +0.21 cm/yr, but not for inverse barometric effects, before calculating monthly anomalies. Both series were then smoothed with a resistant nonparametric algorithm (Ryan *et al.*, 1981) to remove high-frequency spikes and isolate interannual variability.

We compared monthly Scripps Pier surface temperature anomalies to monthly sea surface temperature anomalies based on ship, buoy and satellite observations and published in the Oceanographic Monthly Summary (NOAA/National Weather Service). By simple linear regression over 48 months from 1981 through 1984, Scripps Pier temperature anomalies explain 59.1% of the variability of sea surface temperature anomalies in an area covering the center of the northern anchovy habitat in the Southern California Bight (31–34N within 150 km of the coast). Therefore, sea surface temperature variability in the anchovy habitat is adequately described by the Scripps Pier surface temperature record.

b. Egg production. Spawning biomass surveys for egg production estimates since 1980 have covered coastal waters to ~250 km offshore between San Francisco, California and Punta Baja, Baja California (Table 2). Planktonic eggs and small larvae were sampled at 7.5 km intervals with a 25 cm net (333 μ m mesh in 1980–1982 and 150 μ m mesh since 1983), towed vertically to the surface from a depth of 70 m in one minute (CALVET). Ichthyoplankton samples were collected with a 71 cm Bongo net of 505 μ m mesh, towed obliquely from a depth of 200 m (CALBOBL). This net effectively samples anchovy larvae <10 mm with measured corrections for size-dependent extrusion and avoidance during daylight (Lo, 1983). Adults were sampled with a 15 m midwater trawl with a 6 mm mesh liner in the cod end.

The egg production estimate of spawning biomass is equal to daily production of

Table 2. CalCOFI anchovy biomass surveys for egg production estimates.

Cruise	Dates	# CALVET Tows
8003	20 Mar–10 Apr 1980	537
8004	12 Apr–29 Apr 1980	424
8102	12 Feb–10 Mar 1981	690
8104	31 Mar–27 Apr 1981	444
8202	18 Jan–9 Mar 1982	993
8302	4 Feb–1 Apr 1983	850
8403	7 Feb–30 Mar 1984	944
8502	28 Jan–8 Mar 1985	909

eggs divided by specific fecundity. Daily egg production is estimated by extrapolating staged egg abundances back to the time of spawning, using temperature-dependent egg development rates measured in the laboratory. Specific fecundity, the daily production of eggs per unit biomass, is calculated as follows:

$$\text{Specific fecundity} = \frac{R S F}{W}$$

where

R = female fraction by weight,

S = spawning incidence, day^{-1} ,

F = batch fecundity, eggs,

W = spawning female weight, g.

R , S , F , and W are estimated from subsamples of the midwater trawl catches. Details and assumptions of the egg production method are covered in Lasker (1984).

c. Larval mortality. Survival curves for yolk-sac larvae (up to 4.0 mm) and first-feeding larvae (4.0–6.0 mm) were generated from CALVET staged larval counts. Shrinkage corrections were based on Theilacker (1980). Extrusion of larvae ≤ 4.0 mm through the 333 μm mesh used through 1982 was corrected according to Lo (1983). Avoidance of the CALVET net during daylight by 3.75–6.25 mm larvae was measured as night/day catch ratios in 0.5 mm size intervals and corrected by the following factors: 1.17, 1.34, 1.99, 2.52, and 2.92. Ages and durations of 0.5-mm stages were calculated from Gompertz growth equations for yolk-sac (Lo, 1983) and feeding larvae (Lo, NMFS/Southwest Fisheries Center, pers. comm.). Growth is temperature-dependent for yolk-sac larvae; growth of feeding larvae shows little temperature-dependence within seasons (Methot, 1981). Production of hatching eggs was calculated from estimates of production of spawned eggs and egg mortality from analyses of CALVET egg counts.

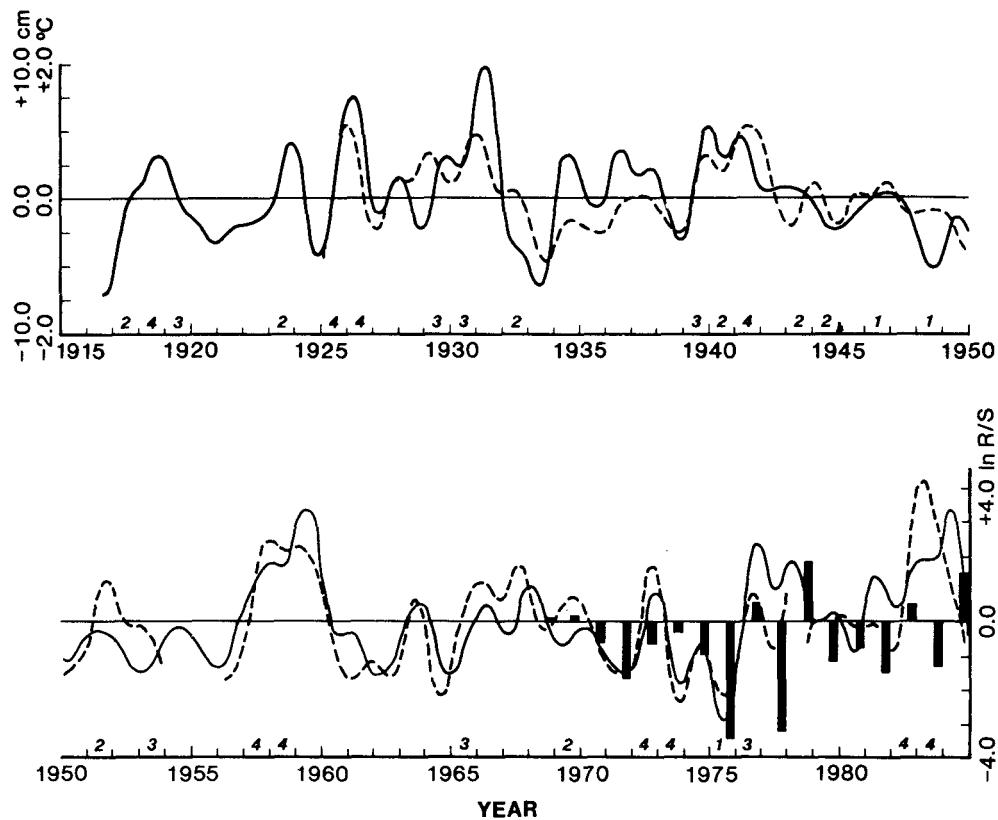


Figure 3. Smoothed monthly anomalies of surface temperature ($^{\circ}\text{C}$, solid line) and sea level (cm, dashed line) at Scripps Institution of Oceanography Pier in La Jolla, California (32.9°N , 117.3°W). Numbers are rankings of ENSO events (Rasmusson, 1984): 1 = weak, 2 = moderate, 3 = strong, 4 = very strong ($\ln R/S$ = recruitment index, see text).

d. Age-length. The California Department of Fish and Game regularly conducts an anchovy central stock biomass survey in February–March and a recruitment survey in September–October. Recruitment surveys are confined to nearshore waters within the 100 m isobath. Nighttime 15 m midwater trawl samples are taken to determine age and size composition. These data were kindly provided by Ken Mais, California Department of Fish and Game. Von Bertalanffy growth curves were fit to the mean sizes at age for each of the 1978 to 1984 year classes. By this model, growth rate decreases linearly with size and seasonal variations are ignored.

3. Results

a. Historical relationship to El Niño. Interannual variability of surface temperature and sea level in the Southern California Bight is dominated by large positive anomalies every few years, usually corresponding to ocean-wide El Niño/Southern Oscillation

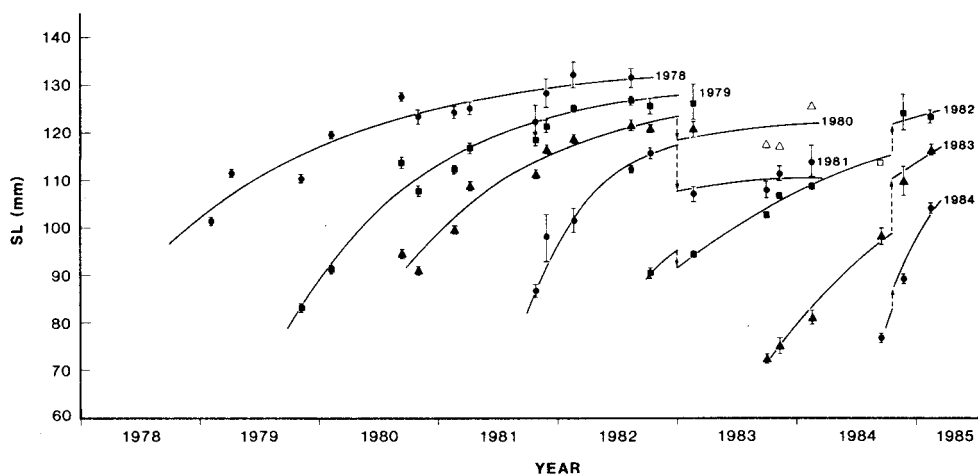


Figure 4. Growth of northern anchovy year classes from DFG age-length data. Von Bertalanffy growth curves are fit to mean lengths (± 2 s.e., except open symbols where s.e. > 5 mm).

(ENSO) events (Fig. 3). Smoothed monthly surface temperature and sea level anomalies since 1925 are highly correlated ($r = +0.71$, $P \ll .001$, sea level record lagged by 1 month). Thus, the temperature record itself provides a good index of El Niño in the Southern California Bight. A notable exception in recent years is the warm anomaly in 1981, which was not associated with a sea level anomaly or an ENSO event.

A northern anchovy recruitment index, equal to the number of recruits in year $t + 1$ divided by the number of spawners in year t , was calculated from data in MacCall and Methot (1983). Reliable recruitment estimates are not available for years prior to 1968. The recruitment index is not significantly correlated with yearly surface temperature anomaly ($r = +0.34$, $P > .05$). There is no simple relationship between recruitment and El Niño in the 17-year record containing three El Niño events and one non-ENSO warm event.

b. Juvenile and adult growth. Figure 4 illustrates growth curves fit to observed mean lengths for 1978–1984 year classes. There are obvious discontinuities between October 1982 and February 1983 and between September and November 1984. Therefore, growth curves were fit to the 1980 and 1981 year-class data before the first break, to the 1982 and 1983 year-class data between the breaks, and to the 1984 year-class data after the second break. Comparison of predicted lengths with the observations not used to fit the curves suggests that 1-, 2-, and 3-year-old fish (1982, 1981 and 1980 year classes) were 3, 10, and 5 mm shorter than expected, respectively, beginning in early 1983. Similarly, 1984, 1983 and 1982 year-class fish underwent sudden increases in length of 4, 11, and 6 mm between September and November 1984.

Table 3. Juvenile lengths and growth rates, on October 1 of birth year, from fitted growth curves in Figure 6. Estimates in parentheses are based on limited data.

	Year Class							
	1978	1979	1980	1981	1982	1983	1984	1985
Length, mm	96.5	78.8	91.7	81.8	89.6	71.2	78.8	(79.4)
Growth rate, mm/yr	91.2	124.5	116.0	261.3	79.4	78.1	(259.2)	—

Growth of 1982 and 1983 year-class fish during El Niño was 13–70% (mean = 47%) slower than growth of 1978–1981 year-class fish at the same age (Table 3). 1982 year-class fish had attained a mean length of only 109 mm as 2-year-olds, in March 1984, compared with 116–120 mm for the 1978 to 1980 year classes (Fig. 4). Juveniles in the 1983 and 1984 year classes were as much as 25 mm shorter than in 1978–1982.

Regional differences in historical mean growth rates and lengths-at-age were revealed by fitting von Bertalanffy growth curves to subsets of 1973–1982 DFG age-length data. Growth rates are higher north of the U.S.-Mexico border (29.8 mm/yr at 100 mm) than to the south (16.9 mm/yr at 100 mm). In these data, there was no difference in asymptotic length to the north and south of the border (133.4 and 134.4 mm, respectively).

During 1978–1982, 1- and 2-year-old fish were ~7 mm shorter south of the U.S.-Mexico border than to the north (Table 4). In February 1983, very few fish were sampled south of the border, but the length of “northern” 1-year-olds was about equal to the normal length of “southern” 1-year-olds. However, northern 2-year-olds were significantly shorter than the 1978–1982 mean for southern 2-year-olds.

c. Spawning range. Figure 5 illustrates 1980–1985 spawning ranges as indicated by distributions of eggs. The cold-water boundary corresponding approximately to the 14°C isotherm in 1980–1982 (Fiedler, 1983) had moved far to the north in 1983. No surface water <14°C was observed south of Pt. Conception after the first week of February 1983 (GOSSTCOMP sea surface temperature maps, National Environmental Satellite, Data, and Information Service). Anchovy eggs were found much

Table 4. Mean (s.e.) standard length at age (mm) of anchovy caught north and south of the U.S.-Mexico border on DFG winter anchovy acoustic surveys.

		Age, years			
		1	2	3	4
1978–1982	N	99.8 (.35)	119.2 (.25)	126.8 (.29)	134.2 (.72)
	S	93.1 (.63)	112.6 (.52)	122.4 (.66)	122.6 (2.02)
1983	N	94.3 (.31)	107.2 (.84)	120.5 (.86)	126.2 (1.93)
	S	94.9 (1.73)	106.5 (2.16)	—	—

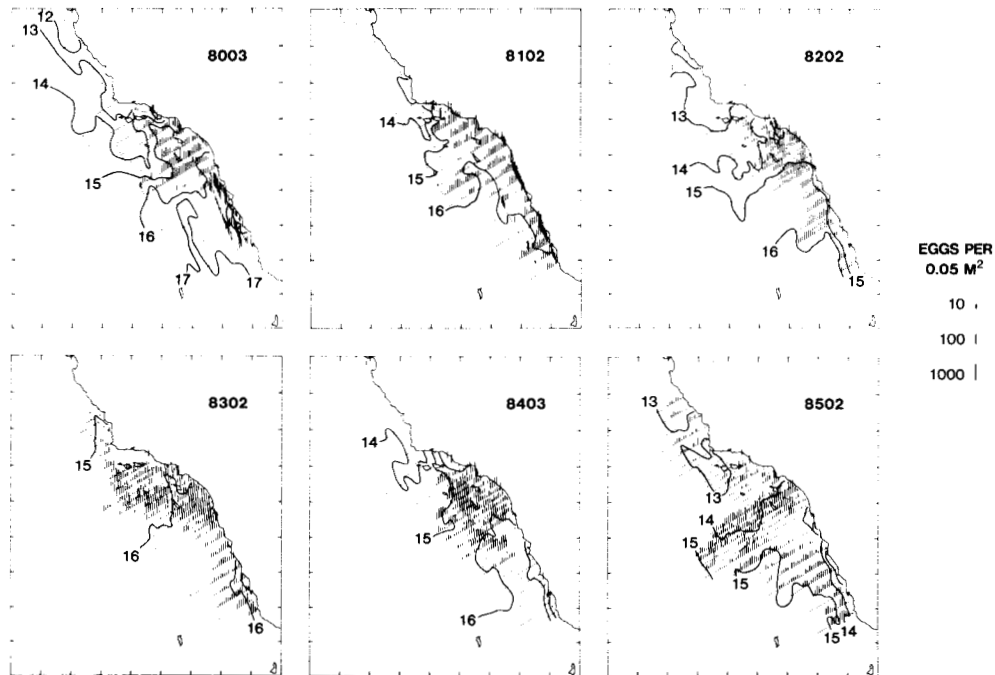


Figure 5. Surface isotherms ($^{\circ}\text{C}$) and egg distributions on anchovy biomass cruises (CalCOFI 8003-4, 8102, 8202, 8302, 8403, and 8502).

farther north and offshore than in 1980–1982: spawning range increased by 43%, as measured by the area containing 95% of the sampled eggs. In 1984, the cold-water boundary was again present south of Pt. Conception, but spawning continued relatively far offshore. Very few eggs were found in the area off northern Baja California south of Ensenada, but the presence of adults and larvae (Hewitt, 1985) indicates that spawning activity had ceased shortly before sampling. In 1985, scattered eggs were found in 13°C water to the north of Pt. Conception, while large numbers of eggs were found unusually far offshore to the south of the Channel Islands.

d. Larval survival. Figure 6 illustrates survival of anchovy yolk-sac and first-feeding larvae. In every year except 1983, mortality (slope of the survival curves) increases at 4 mm. In 1983, yolk-sac mortality was significantly higher than in other years, and was equal to mortality after feeding began. There were no significant differences in first-feeding mortality among these years (Table 8).

4. Discussion

a. El Niño and other clupeoid stocks. El Niño causes striking biological changes in the eastern equatorial Pacific off Peru and Ecuador. Onshore and poleward transport

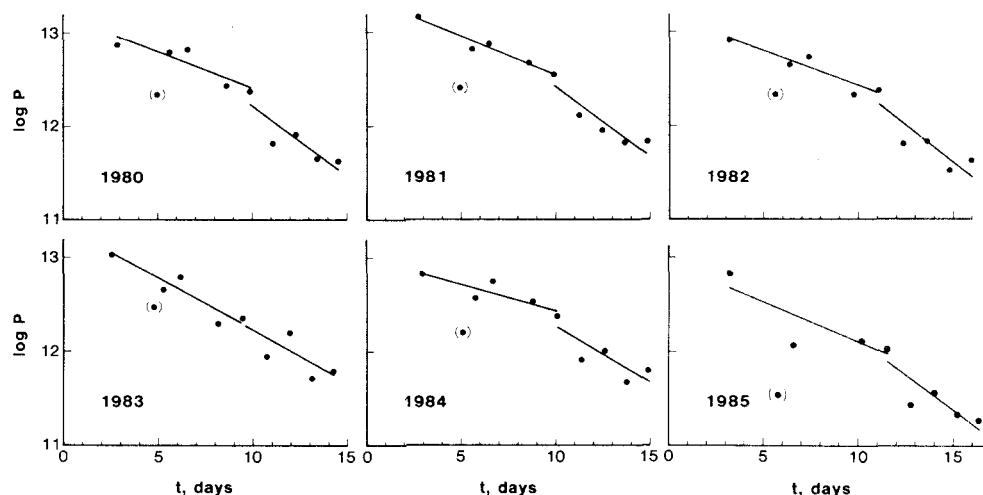


Figure 6. Survival of yolk-sac and first-feeding larvae from CALVET samples. P = daily production of larvae in 0.5-mm size intervals. First point is daily production of hatching eggs. Production of 2.0-mm larvae (in parentheses) was not used in curve-fitting.

of warm surface waters depresses the thermocline/nutricline, reducing the nutrient input from below which normally drives this very productive coastal upwelling ecosystem. Large drops in primary productivity and standing crops at all trophic levels are observed (Barber and Chavez, 1983).

The Peruvian anchoveta fishery was the world's largest for nearly a decade until three successive poor year classes in 1971–1973 decimated the stock. Larval mortality was unusually high in the El Niño years of 1967, 1972, and 1977. Walsh *et al.* (1980) attributed this to the poleward movement of adult spawners into a suboptimal habitat for first-feeding larvae, with low availability of appropriate food organisms and increased abundance of euphausiid predators. Tsukayama and Alvarez (1980) observed reduced size and more variable sexual maturity of adult anchovies in the warm-water years from 1964 to 1978. Santander (1980) observed that egg production was low in 1971–1973 and that spawners were concentrated very near the coast during the 1972–1973 El Niño. They remained extremely vulnerable to the fishing fleet even as the stock declined from low recruitment and overfishing. In this case, a natural environmental perturbation was compounded by overfishing.

The variability of many stocks of short-lived, pelagic, schooling fishes such as engraulids and clupeids has been related to El Niño (Shannon *et al.*, 1984). However, the effects of El Niño are not universally adverse. For example, the sardine (*Sardinops sagax*) actually increased during recent El Niño events, concurrent with the decline of the anchoveta stock (Santander, 1980; Pastor Feria, 1984).

b. California El Niño 1982–1984. El Niño 1982–1983 in the eastern equatorial Pacific has been extensively reported and documented (cf. Cane, 1983; Tropical

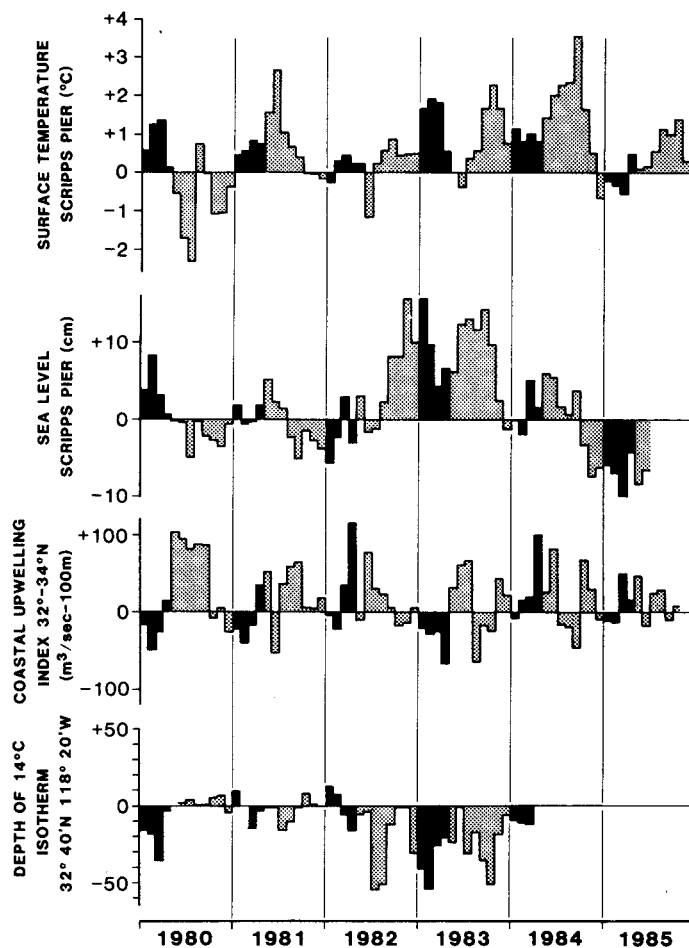


Figure 7. Monthly anomalies of surface temperature and sea level at Scripps Pier, coastal upwelling index in a 3×3 degree square at 33°N , 119°W (A. Bakun, NOAA/NMFS/Pacific Fisheries Environmental Group, pers. comm.), and depth of the 14°C isotherm at 32.7°N , 118.2°W (D. McLain, NOAA/NMFS/PFEG, pers. comm.). Peak anchovy spawning months, January–April, are solid black.

Ocean-Atmosphere Newsletters 16, 21, 24, and 28). As early as July 1982, anomalies in the structure of the water column off southern California signalled the extension of El Niño into the northeastern Pacific (Fig. 7). The 14°C isotherm is generally in the top of the seasonal thermocline in the Southern California Bight (Lynn *et al.*, 1982), and thus represents the mixed layer depth. A deepened mixed layer and elevated sea level were the first changes observed. Surface temperature changes were significant by January 1983. Large positive anomalies occurred in three successive periods: winter 1982–83, late summer 1983, and summer 1984. During peak anchovy spawning in 1983, surface temperature and sea level at La Jolla were 1.5°C and 9.1 cm above

normal. During 1984 spawning, the anomalous conditions had abated somewhat, but the largest surface temperature anomalies occurred later in summer 1984.

The positive sea level anomaly during winter 1982–1983 represents an unusually strong poleward countercurrent along the coast (Lynn, 1983). Offshore Ekman transport (coastal upwelling index) was low in early 1983. Changes in wind-driven flow in the California Current System were caused by large-scale atmospheric perturbations during winter 1982–1983: intensification and expansion of the Aleutian low and reduced strength of the North Pacific high (Simpson, 1984). Finally, the unusually deep 14° isotherm marks the depth of nitrate-depleted surface waters at this latitude (Cullen *et al.*, 1983). Therefore, two sources of exogenous nutrients in Southern California Bight surface waters—advection from the north and mixing from below the nutricline—were diminished during 1983. McGowan (1985) demonstrated that the nitracline, on a transect perpendicular to the coast, 100 km north of San Diego (CalCOFI line 90), was anomalously deep from March to December 1983, coinciding with the deep thermocline.

c. Biological effects of California El Niño 1982–1984. In May 1983, phytoplankton biomass in the Southern California Bight was relatively low (Table 5). Integrated chlorophyll was only 54% of the March–June historical mean (-1.79 standard deviation units, $p \sim .05$). Measured primary productivity was almost twice the rate of $500 \text{ mg C m}^{-2} \text{ day}^{-1}$ predicted from Smith and Eppley's (1982) regression analysis of productivity vs. daylength and Scripps Pier temperature anomaly, adjusted for incomplete coverage of the 16-station SCBS grid in 1983. However, the Scripps Pier temperature anomaly was only $+0.01^\circ\text{C}$ in May, compared with $+1.49^\circ\text{C}$ in January–April. Equatorward winds that cause coastal upwelling and offshore transport were stronger than normal in May, following four months of unusually low winds. The high productivity of this diminished phytoplankton stock probably reflects a short-term response to the temporary relaxation of warm-water conditions in late spring and early summer 1983 (see Fig. 7).

In March and April, the subsurface chlorophyll maximum layer was up to 70 m deeper than normal beyond ~ 50 km from the coast (McGowan, 1983). From July through December, the chlorophyll maximum was anomalously deep even near the coast. In late summer 1983, chlorophyll levels in the upper 50 m were as much as an order of magnitude lower than usual (McGowan, 1985). Reduced surface chlorophyll levels during El Niño (Fiedler, 1984a) can be explained in part by the deepened chlorophyll maximum layer. Kelp production off southern California was severely reduced by nutrient depletion during 1983 (Dayton and Tegner, 1984; Zimmerman and Robertson, 1985). Phytoplankton production may have been similarly affected.

Available data indicate that during peak spawning activity in 1983, El Niño affected the vertical distribution of phytoplankton more than absolute levels of productivity or biomass. Survival of first-feeding anchovy larvae is dependent on a critical density, size

Table 5. Areally-weighted means of integrated euphotic zone phytoplankton biomass, mg chl a m⁻², and primary productivity, mg C m⁻² day⁻¹, at four stations between San Diego and Los Angeles and up to 100 km offshore (stations 101, 202, 205, and 206, Southern California Bight Study, Food Chain Research Group, Scripps Institution of Oceanography). SCBS data from R. Eppley (SIO/FCRG, pers. comm.). CalCOFI data from University of California, Scripps Institution of Oceanography, Physical, Chemical and Biological Data Reports, SIO References 84-25 and 85-14.

Cruise	Dates	Chlorophyll	Productivity
SCBS-3	16-24 June 1975	30.1	1675
SCBS-7	2-9 June 1976	32.4	492
SCBS-16	7-12 May 1980	40.9	416
SCBS-18	5-12 May 1981	24.2	766
SCBS-22	16-25 May 1983	17.3	942
CalCOFI 8404	9-16 April 1984	33.9	—
CalCOFI 8505	1-8 May 1985	47.3	—

range, and species composition of food organisms. Optimal conditions are frequently found in subsurface layers of larger naked dinoflagellates in stratified waters of the Southern California Bight (Lasker, 1981). We do not know of any sampling that was adequate to detect phytoplankton community change in the Southern California Bight during El Niño. However, seasonal and spatial variations of species composition in earlier studies have been linked to environmental conditions characterized as “upwelling” and “nonupwelling.” Assemblages correlated with the two sets of conditions are generally dominated by diatoms and dinoflagellates, respectively.

Goodman *et al.* (1984) found a dinoflagellate assemblage correlated with high temperature, a deep chlorophyll maximum layer, and low silicate in the Southern California Bight. These environmental conditions are typical of late summer in most years, but prevailed for much of 1983. If phytoplankton community changes did occur in 1983, they would be expected to favor such a dinoflagellate assemblage. First-feeding larvae actually prefer certain types of dinoflagellates (Scura and Jerde, 1977), which would explain why we did not detect reduced survival of first-feeding larvae in spring 1983.

Smith and Eppley (1982) did not find a significant relationship between total anchovy biomass in the Southern California Bight and estimated annual primary production between 1951 and 1979, although a major decline in biomass, from 1957 to 1961, was associated with the unproductive 1957-1959 El Niño. They did find that zooplankton biomass in the Southern California Bight was positively correlated with estimated primary production. Bernal (1979) found that monthly macrozooplankton biomass off southern California was consistently below the 1949-1969 means from May 1957 through February 1960. At the extreme of this 34-month negative anomaly, in January 1959, zooplankton biomass was only 18% of the long-term monthly mean.

Zooplankton biomass in the Southern California Bight, from Bongo net samples on

Table 6. Median zooplankton biomasses, g/1000 m³, in CalCOFI region 7, Southern California Inshore, from CALBOBL tows. Large gelatinous organisms were removed from 6 samples in 8502, and only 4 samples in all other cruises combined. 8004 and 8104 medians (*) were significantly greater than the other 6 by Kruskal-Wallis one-way anova.

Cruise	Dates	N	Zooplankton biomass
8003	28 Mar-7 Apr 1980	44	186.4
8004	12 Apr-28 Apr 1980	29	833.8*
8102	12 Feb-7 Mar 1981	32	224.6
8104	31 Mar-19 Apr 1981	37	444.4*
8202	27 Jan-9 Mar 1982	31	305.8
8302	9 Feb-20 Mar 1983	32	98.4
8403	16 Feb-14 Mar 1984	32	219.8
8502	19 Feb-1 Mar 1985	25	138.0

early spring egg production cruises, was not significantly lower in 1983 than in 1980-1982 and 1984-1985 (Table 6). However, beginning in April 1983, zooplankton volumes along CalCOFI line 90 in the center of the Bight were significantly lower than 1949-1969 median values (McGowan, 1984, 1985). The greatest anomalies were found in July and August in the normal offshore maximum 100-200 km from the coast. Reduced availability of zooplankton prey may affect the growth of late larvae, juveniles, and adults.

d. Effects on growth. The age-length data indicate unusually slow growth of juvenile anchovies during summer 1983 and 1984. Butler (NMFS/Southwest Fisheries Center, pers. comm.) found that juvenile length, adjusted to an age of 210 days, was 71.9 mm in 1983 and 76.6 mm in 1984, compared with 83.0-83.5 in 1980-1982. This is equivalent to a weight deficit of 36% in 1983. The most problematic signals in the growth curves are the discontinuities in early spring 1983 and late summer 1984. A distributional shift of the central stock during El Niño, along with regional variability within the stock, may have contributed to the sudden changes in size-at-age. Many warm-water and tropical species appeared off California during El Niño, beyond the normal limits of their ranges (Lea, 1984). Parrish *et al.* (1985) analyzed age-length data from DFG trawls between 1966 and 1983. Mean length of two-year-olds increases from 104 mm in Sebastian Viscaïno Bay (central Baja California, 28N) to 120 mm in Santa Barbara Channel (34N). Within the Southern California Bight, mean length increases by 7-8 mm from shallow, nearshore waters to the offshore limits of the stock's range.

Given the latitudinal and onshore-offshore clines in length-at-age, trawls on NMFS biomass surveys suggest that smaller anchovies moved into the DFG survey area from the south during El Niño, while larger fish moved out of the area, to the north and west of Pt. Conception. February 1983 (and 1985) trawls caught anchovies up to the limit of sampling at Morro Bay (35.5N). In 1980-1982 and 1984, no anchovies were caught

between Pt. Conception (34N) and Monterey (36.5N). Spawning females caught north of Santa Barbara (34N) in 1983 had a mean weight of 12.9 g, which is greater than the unusually low overall mean of 11.2 g and close to the 1980–1985 anti-El Niño range of 13.4–18.8 g (Table 1). However, an influx of small southern fish cannot entirely explain the changes in length-at-age during El Niño: 2-year-olds in the Southern California Bight in 1983 were shorter than normal 2-year-olds south of the U.S.-Mexico border.

Adult northern anchovy in the Southern California Bight, including probable immigrants from the south, grew significantly slower than normal in 1983. Environmental conditions that may have limited growth in the Southern California Bight during El Niño, such as temperature and plankton biomass, were similar to normal conditions in coastal waters further south. The reduced growth rates of 1982 year-class fish as adults, and juvenile fish during summer 1983 and summer 1984, were most likely caused by El Niño's impact on the availability of appropriate zooplankton prey. We have seen no data on taxonomic changes in the zooplankton community during this El Niño event. Colebrook (1977) found that during the last major California El Niño of 1957–1959, the biomasses of all important taxonomic groups were reduced in 1958 and 1959, relative to 1956–1957.

e. Effects on spawning. Table 7 summarizes central stock spawning activity from 1980 to 1985. Spawning effort by a multiple spawner like the northern anchovy is the number of eggs produced per unit spawning biomass in one spawning season, or daily specific fecundity times the duration of the spawning season. Estimates of spawning season duration are not readily available, although birth-date analysis of 1983 year-class recruits show peak occurrence from February to April, similar to previous years (Methot, 1983; Butler and Methot, unpubl. data). Parrish *et al.* (1986) found that duration of peak spawning activity increases somewhat with age. We estimated the effect of age composition on spawning duration using their monthly mean age-specific spawning activities and the two extremes of age distribution observed during the 1980–1985 period: in 1982, 79% of spawning activity would be expected in February–April, while in 1983, 82% would occur during that peak spawning period. We assume there were no significant changes in duration of spawning from 1980 to 1985 and that specific fecundity, measured on a 4–8 week biomass survey, is a valid measure of relative spawning effort by the stock during peak spawning.

Specific fecundity was low in 1983 and high in 1984, compared with 1980–1985 anti-El Niño years (Table 7). Two important components of specific fecundity may determine changes: batch size (batch fecundity) per unit weight and frequency of production of batches (spawning incidence). The variation in specific fecundity during 1980–1985 is more closely related to variation in spawning incidence ($r^2 = 0.50$) than to variation in fecundity per unit weight ($r^2 = 0.00$).

Batch fecundity was lower in 1983–1984 than in 1980–1982 and 1985. Most of this

Table 7. Northern anchovy central stock spawning parameter estimates, 1980–1985, from Stauffer and Picquelle (1980, 1981), Picquelle and Hewitt (1983, 1984), Hewitt (1985), and Bindman (1985). Batch fecundities for a standard 14.95-g female from Hunter *et al.* (1984) and Lo (NOAA/NMFS/Southwest Fisheries Center, pers. comm.). Coefficients of variation in parentheses, except in 1983 when large-scale geographic variations were noted and the analysis was stratified to reduce the variance of the final estimates.

	1980	1981	1982	1983	1984	1985
Spawning female weight, g	17.50 (.055)	13.37 (.039)	18.83 (.019)	11.20	12.02 (.038)	14.49 (.022)
Female fraction	.475 (.120)	.501 (.063)	.472 (.047)	.549	.582 (.053)	.609 (.032)
Batch fecundity observed, at 14.95 g	7788 (.075)	8208 (.052)	10845 (.038)	5297	5485 (.057)	7343 (.046)
	6423 (.064)	9237 (.022)	9055 (.025)	7870 (.034)	7640 (.033)	8234 (.030)
Spawning incidence, day ⁻¹	.145 (.125)	.106 (.122)	.120 (.081)	.094	.160 (.132)	.120 (.129)
Specific fecundity, eggs/day-g	30.28 (.197)	33.03 (.152)	32.53 (.103)	24.35	42.43 (.132)	37.00 (.142)
Egg production, 10 ¹² eggs/day	26.34 (.101)	20.96 (.111)	13.51 (.237)	17.25	12.98 (.122)	16.95 (.156)

change seems to have been caused by reduced spawning female weight. Normalized batch fecundities for a standard size female were slightly low in 1983–1984, but the 1980 value was even lower. Spawning female weight in 1983 and 1984 was reduced due to younger age structure, reduced size-at-age and, perhaps, early sexual maturation. The 1983 stock was relatively young, but mean age was near normal in 1984 (Table 1). We have shown that the size-at-age of spawners was reduced in 1983 and 1984. A relatively large proportion of small fish were sexually mature in 1983 and 1984 (John Hunter, NMFS/Southwest Fisheries Center, pers. comm.). Although these fish were not aged, their size was typical of one-year-old fish.

Spawning incidence was relatively low in 1983 and high in 1984. Parrish *et al.* (1986) found that spawning incidence is strongly age-dependent. Although 1983 had the youngest mean age (Table 1) and lowest spawning incidence (Table 7), we note no correlation between mean age of spawners and spawning incidence in 1980–1985 ($r^2 = +0.07$). Regional variability and changes in stock composition caused by a northward

shift cannot explain the low spawning incidence in 1983. Picquelle and Hewitt (1984) found greater specific fecundity in the south than in the north. Reduced spawning incidence and specific fecundity in 1983 was caused by the unusually young age structure of the stock, compounded by small size-at-age.

The high spawning incidence and specific fecundity in 1984 are surprising, because growth of the 1984 spawners had been slow during 1983. Spawning effort during the peak spawning season is supported by fat stores accumulated in early summer of the preceding year (Hunter and Leong, 1981). It seems unlikely that fat storage could be normal while somatic growth, especially of the recruiting 1983 year class, was reduced. The presence of anchovy larvae and spent females, but no eggs, at the southern end of the spawning range in the latter half of March suggests that the spawning season was abbreviated in 1984. Perhaps the high spawning effort could not be sustained due to low fat stores. The high spawning incidence may be a compensatory response to the low spawning biomass in 1984, but the mechanism for such a response is unknown.

Variation in the stock's total egg production was not related to the specific fecundity of the spawners. Total egg production was not reduced in 1983, despite the low specific fecundity, because recruitment of the moderately strong 1982 year class had increased spawning biomass. Total egg production decreased in 1984 when the exceptionally high spawning effort was not sufficient to compensate for the low spawning biomass.

f. Effects on larval mortality. We observed a consistent increase in larval mortality at the size when yolk-sac absorption and initiation of feeding activity are expected to occur, except in 1983 when mortality of yolk-sac larvae was unusually high. Nighttime avoidance of the CALVET net is conceivable and would contribute to the apparent increased mortality of active, first-feeding larvae. Lo (1986) analyzed larval survival to 20 days in 1.0-mm size intervals from CALBOBL sample counts. She used a survival model with a mortality rate that decreases with age after hatching ($B = \text{mortality} \cdot \text{age}$, Table 8). The high mortality coefficient for larvae up to 20 days old in 1983 probably reflects the high yolk-sac mortality detected in the present analysis of CALVET samples. We could not describe CALVET sample counts in 0.5-mm size intervals with such a model, perhaps because the CALVET net is a less efficient sampler of large larvae and CALBOBL counts require large corrections for extrusion of small larvae (Lo, 1983).

The most important cause of mortality of yolk-sac larvae is predation (Blaxter and Hunter, 1982). Starvation cannot occur unless an inadequate yolk supply in poor quality eggs is exhausted before development has proceeded far enough to allow feeding activity. In this case, larval production at some size <4 mm would apparently increase as yolk was exhausted and growth slowed, but would subsequently drop as these larvae succumbed to starvation or predation. We observed no such pattern in the 1983 larval abundance data. Increased predation is the most reasonable explanation for the abnormally high yolk-sac mortality in 1983. Cannibalism may have been one

Table 8. Daily production of eggs and 8-mm larvae (10^{12} /day), and intervening egg and larval mortalities (day^{-1} , standard error in parentheses), 1980–1985. 2-8mm larval mortality coefficients (= mortality \cdot age, dimensionless) and larval production from Lo (1985 and pers. comm.).

	1980	1981	1982	1983	1984	1985
Egg production	26.34	20.96	13.51	17.25	12.98	16.95
Egg mortality	.39 (.10)	.13 (.16)	.17 (.26)	.23 (.29)	.23 (.09)	.29 (.17)
Yolk-sac mortality	.077 (.011)	.082 (.005)	.074 (.008)	.110 (.013)	.055 (.010)	.084 (.014)
First-feeding mortality	.150 (.024)	.147 (.018)	.159 (.025)	.112 (.025)	.120 (.022)	.151 (.025)
2-8mm larvae mortality	1.22 (.031)	1.53 (.032)	1.81 (.036)	2.05 (.110)	1.47 (.153)	2.13 (.103)
8mm larvae production	0.22	0.19	0.20	0.13	0.26	0.13

cause of high predation mortality, but the adult population was small compared to historical levels and there is a great variety of other potential larval predators in the Southern California Bight.

Yolk-sac anchovy larvae are vulnerable to capture by calanoid copepods and euphausiids in the laboratory (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974). No data are available on changes in the abundance of these predators during El Niño 1982–1984, but Colebrook (1977) found that the biomass of these taxonomic groups was reduced during the 1957–1959 El Niño in the California Current.

One exotic and voracious predator did appear off southern California during 1983 and 1984—the pelagic phase of the red crab, *Pleuroncodes planipes*. Large numbers of these organisms were occasionally caught in midwater trawls and CALBOBL tows (Smith, 1985b) and stranded on southern California beaches. *Pleuroncodes* can feed as a visual predator, or in a filtering mode by swimming to the surface, spreading the thoracic limbs, and sinking slowly while grazing larger phytoplankton and microzooplankton (Longhurst *et al.*, 1967). Weakly mobile yolk-sac larvae would be particularly vulnerable to this feeding mechanism. Although we have no direct evidence that *Pleuroncodes* was an important larval anchovy predator in the Southern California Bight during 1983, extremely high predation rates on eggs and yolk-sac larvae have been observed in the laboratory (10–40 liters filtered per day, Gail Theilacker, NMFS/Southwest Fisheries Center, pers. comm.).

Production of 8-mm larvae, the net result of spawning and survival of eggs and early larvae, was relatively low in 1983 and 1985 (Table 8). Anomalous offshore transport by a displaced offshore eddy may have affected apparent larval survival in 1985 (Fiedler, in prep.). Central stock larval production and mortality estimates by Hewitt (1982) indicate that production of larvae at 14 days after hatching (~8 mm) ranged between 0.16 and 0.25×10^{12} /day from 1962 to 1979, with two exceptions: 1963 (0.45)

and 1978 (0.11). In spite of low larval production, the 1978 year class was the largest observed since reliable estimates began in 1968. This illustrates an important caveat for fisheries recruitment studies limited by the paradigm that survival of early life history stages is the sole determinant of year-class strength. Despite variability in survival and growth of eggs and early larvae, survival of late larval and juvenile stages may ultimately determine the successful recruitment of a particular year class in some stocks.

5. Summary and conclusions

Data from a variety of sources show that the temperature and structure of the surface layer, surface currents, and upwelling intensity in the anchovy habitat off southern California were altered during El Niño 1982–1984. Total phytoplankton biomass was slightly reduced in spring 1983, but availability of food organisms in surface waters may have been further reduced by the extreme deepening of the chlorophyll maximum layer. Macrozooplankton biomass was significantly less than normal for most of 1983.

Distribution of the anchovy stock apparently shifted to the north in 1983, along with sea surface temperature boundaries. Spawning range expanded. Specific fecundity was low in 1983 due to an unusually high proportion of young females in the spawning stock. Yolk-sac mortality was abnormally high in spring 1983, most likely caused by predation. Growth of juveniles and adults was significantly slowed during 1983, probably due to reduced availability of zooplankton prey. Spawning effort in 1984 was high, so that reproductive output was normal in spite of the reduced size and abundance of spawning females.

Low recruitment in 1983 was caused by a combination of factors: low specific fecundity, high mortality of yolk-sac larvae, and possibly high predation pressure on juveniles due to an influx of scombrid predators from the south (Bernard *et al.*, 1985). By February 1985, length-at-age and stock size had returned to pre-El Niño levels, due to strong recruitment of the 1984 year class. The northern anchovy population has undergone large fluctuations in the past and yet continues to persist. We expect that the anchovy will continue to experience and respond to the low-frequency environmental perturbations characteristic of eastern boundary current systems.

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