

# LIMNOLOGY AND OCEANOGRAPHY

January 1982

Volume 27

Number 1

*Limnol. Oceanogr.*, 27(1), 1982, 1-17

## Primary production and the anchovy population in the Southern California Bight: Comparison of time series<sup>1</sup>

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### *Abstract*

Two new time series for the Southern California Bight are presented: anchovy biomass, 1951-1979, and primary production, estimated for the years 1920-1979 from 15 cruises conducted between 1974 and 1979. Annual and longer term averages show little relationship to each other except that values for both were low in the climatically warm water years 1957-1958. The primary production time series is similar to two existing time series: CalCOFI zooplankton in the bight and microplankton in Santa Monica Bay, 1951-1966. Thus estimated primary production does reflect the carrying capacity of these waters for lower trophic level consumers.

Seasonal averages of anchovy larvae are highest in the winter and spring quarters when primary production is increasing. Interannual variation was pronounced in both seasonal average primary production and seasonal average abundance of anchovy larvae. About 50% of the variation in number of anchovy larvae was explained by variation in primary production in the same quarter and zooplankton standing stock three quarters earlier. In 1966, the year of maximum anchovy abundance, the energy expended in anchovy egg production was equivalent to about 1.8% of primary production. The anchovy ration was about 18% of primary production. The ratio of zooplankton biomass to primary production was highest in years when anchovy biomass was greatest.

The eastern margins of the oceans are regions of high productivity (Cushing 1969) and the California Current is one of the major sites of long term study of eastern boundary current and upwelling systems. Gulland (1971) stated that the ultimate controls of fish abundance were primary productivity and ecological efficiency. Murphy (1966) described the oceanic conditions which lead to high abundance of plankton and planktivorous

fishes and Lasker (1970) provided a lengthy time series of the caloric requirements of a single major fish population—the Pacific sardine. The coincidence and alternation of massive populations of planktivorous fishes in the eastern boundary current regions remain one of the major questions in marine ecology.

We here examine functional relationships between primary production and anchovy population using two lengthy time series: estimated Southern California Bight primary production (1920-1979) and estimated biomass of that portion of the central subpopulation of the

<sup>1</sup> Supported by U.S. DOE contract DE-AM03-76SF00010.

northern anchovy, *Engraulis mordax* (Girard), which inhabits the Southern California Bight region (1951–1979), and we compare these new time series with zooplankton abundance previously reported for the region. To what extent does primary production set limits on anchovy production? What other environmental and biological features may ultimately control the population size of the anchovy?

Time series have many uses and provide a valuable component in the study of marine ecosystems. At the descriptive level they can exist as records of species succession over time or as trends in environmental conditions. They can establish the magnitude of variability on temporal (e.g. Robinson 1970) or spatial scales (Blackburn 1973; Larrance 1971) of interest. They are useful in developing inferences on the regulation of populations through environmental change or overfishing, as in developing methods of predicting fish recruitment from the environmental conditions during larval drift (Cushing 1975, p. 236). In principle, time series of populations at different trophic levels can be used to examine material and energy flow in food webs and the variability and range of values of transfer efficiencies. It remains to be seen whether we can recognize from time series of changes in populations such things as interactions between species independent of changes due to climate-related environmental change or fishing intensity, since the latter are strong signals in the records.

The apparent spawning biomass of the central stock of the northern anchovy increased for about 15 years, reaching in 1966 a standing stock 30 times that in 1952. Radovich and MacCall (1979) fit the logistic equation to this increase; the two parameters of interest from their analysis are the maximum rate of population increase and the maximum carrying capacity of the environment. For the central stock, their estimates of the parameters are 0.3 million tonnes per year increase at an intermediate spawning biomass of 2 million tonnes and a maxi-

mum carrying capacity of ca. 4 million tonnes. A large fraction of the population is likely to be made up of nonspawners, thus the impact of the anchovy on its environment may be considerable and greater than estimated by the spawning biomass. Reproduction of the central stock of anchovy failed in 1974 and 1975, and the spawning biomass fell by 1976 to about 1 million tonnes. It began a small recovery to about 1.8 million tonnes in 1979 (Stauffer: SW Fish. Center Admin. Rep. LJ-79-22).

The anchovy is omnivorous, filtering and biting zooplankton and filtering phytoplankton. Loukashkin (1970) found far more zooplankton than phytoplankton in the stomachs he examined and concluded that large copepods and euphausiids were the most important food items. O'Connell (1972) analyzed the feeding behavior of captive anchovy schools and concluded that biting was their most efficient method of feeding but that biting the larger zooplankters could be usefully augmented by filtering small zooplankters and phytoplankton. Available studies suggest strongly that the anchovy is omnivorous and feeds on carnivores, other omnivores, herbivores, and directly on phytoplankton.

The northern anchovy is a schooling fish, thus its impact is not applied evenly throughout the habitat (Smith 1970; Hewitt and Smith 1979; Koslow 1980). The 4-million-tonne central stock (Fig. 1) may be distributed among 100 school groups, 9 km in diameter (Fiedler 1977) with 15 schools per square kilometer within the groups (Smith 1977). Analysis of pictures from free-fall cameras (Graves 1977) indicated that anchovy form schools at densities up to  $366 \cdot \text{m}^{-3}$ ; the average concentration estimated from purse seine sets was  $15 \text{ kg} \cdot \text{m}^{-2}$  (Hewitt et al. 1976) (range,  $0.1\text{--}125 \text{ kg} \cdot \text{m}^{-2}$ ).

Fish have been considered in studies of production and nutrient cycles. Ryther et al. (1971) stated that an average annual rate of primary production of the order of  $1,000 \text{ g C} \cdot \text{m}^{-2}$  is needed to satisfy Peruvian anchoveta (*Engraulis ringens*) production. Whitley and Packard (1971) found

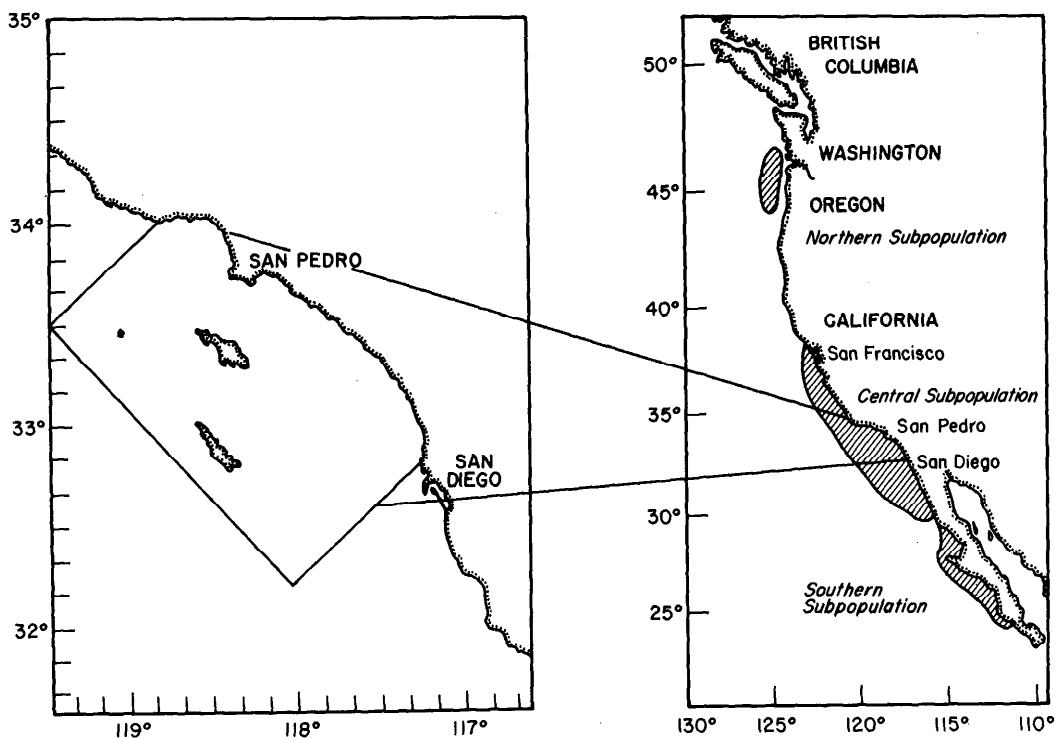


Fig. 1. Left—survey boundary for primary production measurements in Southern California Bight. Right—subpopulation distributions of northern anchovy, *Engraulis mordax*.

a local enrichment of 40% of ammonium-N in a surface water sample taken in a Peruvian anchoveta school. Dugdale (1976) emphasized the role of the Peruvian anchoveta in recycling nitrogen. Menhaden schools can modify oxygen and ammonium levels in shallow coastal water (Oviatt et al. 1972).

We thank E. Stewart for many calculations, especially those related to the pier temperature anomalies, R. Lasker and J. Hunter for editing and discussions on fish population energetics, and G. Stauffer for checking the anchovy population model. We also thank W. Thomas for editing and review. D. Gruber collected the anchovy larval data on cruises of the Food Chain Research Group. S. Tont provided discussions and introduced us to use of the pier temperature anomaly time series. We are indebted to many people for the long Scripps pier temperature and CalCOFI zooplankton and anchovy time series.

### Methods

**Anchovy biomass**—The best description of the methods used to take the plankton net tows and estimate anchovy larval abundance is given by Kramer et al. (1972). Estimation of anchovy spawning biomass is described by Smith (1972). We derived an additional method for use here, estimation of *total* anchovy biomass from anchovy *spawning* biomass. Estimates of mortality of the central subpopulation and fecundity and proportionate maturity (MacCall 1974; Hunter and Goldberg 1980) were used to construct a stationary population. Juvenile biomass, as a proportion of total biomass, was estimated as 40% for spring, when the population biomass was at a minimum and as 68% for fall, when it was at a maximum.

**Primary production**—Measurements were made at 15 stations in the Southern California Bight on 15 cruises from September 1974 to July 1979. Station loca-

tions are shown elsewhere (Eppley et al. 1978). At each station water samples were taken with PVC Niskin bottles at six depths in the euphotic zone. Samples of 200-ml volume were inoculated with  $^{14}\text{C}$  ( $4 \mu\text{Ci}$ ), incubated on deck for 24 h using neutral density screens to simulate irradiance at the sampling depths, and then filtered with Whatman GF/C glass-fiber filters. The radioactivity of the filters was measured by scintillation counting. Further details are given by Eppley et al. (1979a). Data were calculated as production in  $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  integrated over the depth of the euphotic zone.

To assess total primary production over the area of the bight, we weighted the value at each station ( $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) by an area of arbitrary dimensions: 85 km in the longshore direction, this being the distance between transect lines, and the geometric mean distance between stations along the transect lines. Thus the area represented by a station increased offshore because of the quasi-logarithmic distance between stations on the transect lines. The total area represented is about 30,000  $\text{km}^2$ . The total production of this area was calculated as the sum of the production at each station times the area represented. Average production over the area can be expressed as the total production/total area to give  $\text{t C}\cdot\text{km}^{-2}\cdot\text{d}^{-1}$  ( $=\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) for each cruise.

The temperature anomaly for a given calendar date is the difference between the temperature measured on that day and the 54-year mean temperature (1920–1974) for that date. In practice this 54-year mean temperature was interpolated from mean monthly values. Daylength was interpolated for 33°N latitude from the Smithsonian Meteorological Tables.

*Zooplankton*—In addition to the two time series estimated for this paper—primary production 1920–1979 and anchovy spawning biomass 1951–1979—we used three previously published time series: zooplankton displacement volume (Longhurst et al. 1972); the displacement volume time series of microplankton in Santa Monica Bay (Haydock 1973); and the record of fish scale deposition rate

(Soutar and Isaacs 1974) and the biomass estimates derived from them (Smith 1978). The methods used to determine plankton volume in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) are given by Ahlstrom and Thraillkill (1963) as is the derivation of  $\text{g}\cdot\text{m}^{-2}$  from  $\text{cm}^3$  displacement vol  $\cdot 1,000 \text{ m}^{-3}$ .

## Results

*Primary production*—Measured primary production ranged from 0.091 to 1.410  $\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  during the 1974–1979 cruises. Primary production was greater nearshore than offshore, especially at stations 301–303 (Eppley et al. 1978). The maximum primary production of cruise 3 coincided with the maximum negative anomaly of Scripps pier temperatures ( $-2.03^\circ\text{C}$ ) for the week of the cruise (Fig. 2). The minimum primary production of cruise 9 coincided with the maximum positive anomaly ( $2.13^\circ\text{C}$ ). The maximum daylength for the 15-cruise series was 14.3 h and the minimum 10.1, near the total range for 33°N latitude.

For the 15-cruise series, 59% of the variation in primary production was explained by variation in Scripps pier temperature anomaly and daylength. The equation for this relationship is

$$P = \exp(-3.78 - 0.372T + 0.227D) \quad (1)$$

where  $P$  is primary production ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ),  $T$  is pier temperature anomaly ( $^\circ\text{C}$ ) average over the 6–8 days of each cruise, and  $D$  is daylength (h) for that period.

Values of measured primary production, estimated primary production, Scripps pier temperature anomalies, and daylength are given in Table 1 with the multiple correlation coefficients, the standard error of the coefficients, the  $t$ -test of significance of the coefficients, and the ANOVA of the regression. The statistical evaluation is based on the assumption of independence of values; serial correlation can be expected to diminish the significance levels of the coefficients moderately, but the time series is too short to examine these effects.

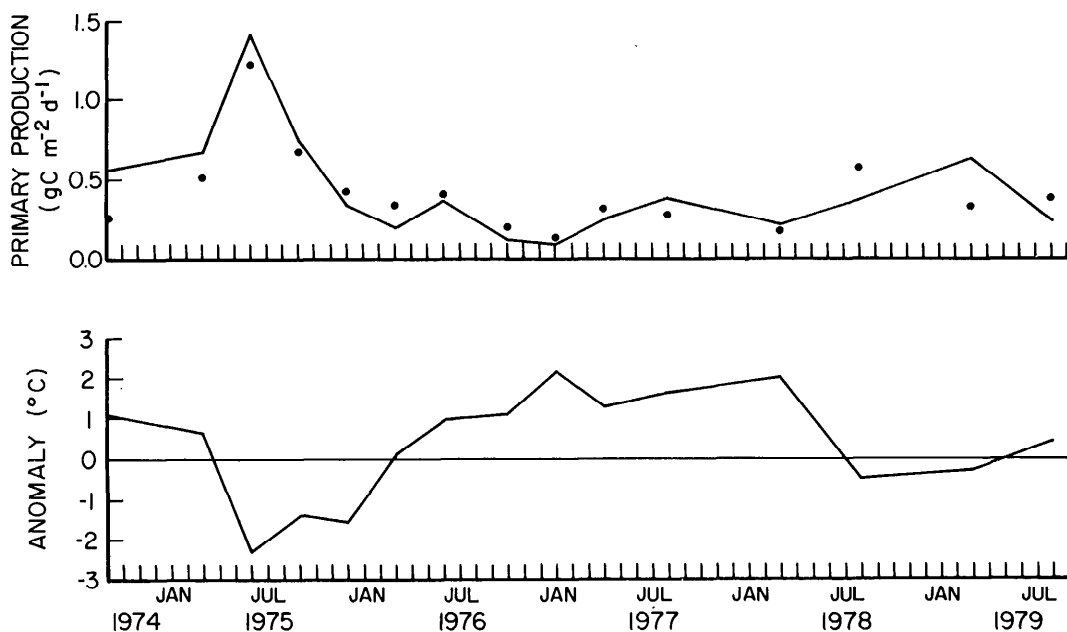


Fig. 2. Upper—time series of measured (●) and predicted (—) primary production in Southern California Bight, 1974–1979. Lower—temperature anomaly at Scripps pier during cruises.

Nonlinearity of primary production with daylength is pronounced at all temperatures. For example, in cruise 3 the average production per hour of daylength was  $0.099 \text{ g C} \cdot \text{m}^{-2}$  for June, and in cruise 5 the average production per hour of daylength in December was  $0.033$ . Overall, in warmer periods, the production per hour of daylength was  $0.026 \text{ g C} \cdot \text{m}^{-2}$  in summer and  $0.009$  in winter. Thus daylength and the other seasonal variables it represents in Eq. 1 may account for a factor of about three in daily primary production rate at  $33^{\circ}\text{N}$  latitude.

The apparent response to the temperature anomaly is also highly nonlinear. The 15-fold variation in the temperature anomaly is associated with a factor of five in primary production. Temperature anomalies  $>1.2^{\circ}\text{C}$  below the seasonally adjusted average were always associated with high productivity in this series. Temperature anomalies  $>1.5^{\circ}\text{C}$  above the seasonally adjusted average were associated with lower primary production.

*Estimated primary production*—We used Eq. 1 with the Scripps pier temper-

ature time series (actually the temperature anomaly) and daylength averaged for each quarter to calculate quarterly estimates and annual averages of primary production to 1920 (Table 2)—a time well before primary production could be estimated at sea. The entire time series of annual average primary production and the maximum and minimum seasonal averages are plotted in Fig. 3. The mean quarterly primary production ranged from  $0.226$  to  $0.603 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ; the corresponding coefficients of variation from 25 to 31% (Table 2). The average of the annual averages is  $0.392 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  (SD of the annual average  $0.078$ , C.V. 20%).

*Zooplankton standing stock*—The regional average of preserved zooplankton displacement volume is listed by season and year in Table 3. These values differ from those previously reported (Longhurst et al. 1972) because they are arranged in quarters centered on March, June, September, and December to correspond with the primary production time series. The months of the CalCOFI survey sampled with the highest fidelity

Table 1. Average primary production ( $\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ) measurements in Southern California Bight during 15 cruises, September 1974–August 1979. Anomaly in temperature (PTA) measured at Scripps pier, averaged over the days of each cruise, is given along with mean daylength during each cruise. These parameters are used in Eq. 1 to calculate production.

	Cruise	Production	PTA (°C)	Daylength (h)	Production from Eq. 1
13–20 Sep 74	1	0.568	1.11	12.1	0.237
26 Feb–6 Mar 75	2	0.681	-1.38	11.5	0.507
16–25 Jun 75	3	1.41	-2.22	14.3	1.221
6–17 Sep 75	4	0.744	-1.40	12.5	0.664
2–10 Dec 75	5	0.336	-1.58	10.1	0.407
13–23 Mar 76	6	0.199	0.10	12.0	0.340
2–9 Jun 76	7	0.364	0.90	14.2	0.399
20–27 Oct 76	8	0.117	1.07	11.2	0.194
28 Jan–4 Feb 77	9	0.091	2.15	10.6	0.113
25 Apr–2 May 77	10	0.248	1.29	13.3	0.310
3–10 Aug 77	11	0.374	1.63	13.4	0.262
13–18 Mar 78	12	0.207	2.00	11.9	0.169
15–23 Aug 78	13	0.360	-0.48	13.1	0.577
3–8 Mar 79	14	0.638	-0.30	11.4	0.320
23–28 Aug 79	15	0.244	0.41	13.0	0.368

$$\text{Eq. } P = \exp(-3.78 - 0.372T + 0.227D)$$

Parameters	Coeff.	SD coeff.	Student's <i>t</i>
Intercept	-3.78		
PTA	-0.372	0.087	-4.23
Daylength	0.227	0.097	2.33
$r^2 = 0.65$			

Due to	df	ANOVA		
		SS	MS	F
Residual	12	0.56	0.05	
Regression	2	1.03	0.52	11.08
Total	14	1.59		0.002

in each season are January, April, July, and October (Eber 1977).

The seasonal cycle of average zooplankton standing stock is in phase with that of estimated primary production (Fig. 4), but has a greater range of values. This difference may only reflect the smoothing effect of the primary production equation. The mean zooplankton volumes ranged from 9.86 to 34.87  $\text{g} \cdot \text{m}^{-2}$ , C.V. from 42 to 73% (Table 3).

*Microplankton standing crop*—The Santa Monica Bay microplankton data are reported here (Table 4) primarily to point out the close relation between the weights of this mixture of net phytoplankton, detritus, and small zooplankton retained by a 0.076-mm mesh and the weight of zooplankton retained by the

CalCOFI 0.55-mm silk mesh. The coefficients of variation of the annual averages are nearly identical even though the microplankton was sampled in the upper 15 m of Santa Monica Bay and the plankton displacement volume was sampled over the entire Southern California Bight from the upper 140 m of the water column. In Table 4 are listed the annual averages of primary production, microplankton, zooplankton, and northern anchovy larvae. The annual average microplankton and annual average zooplankton vary in a nonlinear way with the estimated primary production (Fig. 5). The coefficients of annual variation (Table 4) are lowest in primary production, more than twice as high in microplankton and zooplankton and more than four times as high for anchovy larvae.

Table 2. Quarterly and average annual primary production ( $g\ C\ m^{-2}\cdot d^{-1}$ ) from Southern California Bight as estimated from primary production measurements, 1974–1979, Scripps pier temperature anomalies, and daylengths.

	Mar	Jun	Sep	Dec	Avg
1920	0.366	0.587	0.411	0.305	0.417
1921	0.451	0.489	0.471	0.229	0.410
1922	0.503	0.536	0.396	0.242	0.419
1923	0.337	0.537	0.244	0.162	0.320
1924	0.270	0.529	0.587	0.345	0.433
1925	0.367	0.449	0.398	0.144	0.340
1926	0.129	0.318	0.407	0.186	0.260
1927	0.370	0.633	0.383	0.160	0.387
1928	0.315	0.540	0.503	0.244	0.401
1929	0.460	0.424	0.276	0.165	0.331
1930	0.250	0.559	0.315	0.132	0.314
1931	0.142	0.227	0.219	0.254	0.211
1932	0.383	0.616	0.556	0.278	0.458
1933	0.485	0.922	0.673	0.299	0.595
1934	0.230	0.367	0.334	0.178	0.277
1935	0.409	0.488	0.407	0.251	0.389
1936	0.334	0.384	0.239	0.178	0.284
1937	0.412	0.424	0.332	0.168	0.334
1938	0.329	0.692	0.368	0.272	0.415
1939	0.501	0.533	0.291	0.100	0.356
1940	0.238	0.576	0.352	0.157	0.331
1941	0.168	0.526	0.384	0.164	0.311
1942	0.352	0.536	0.351	0.200	0.360
1943	0.293	0.685	0.335	0.186	0.375
1944	0.347	0.796	0.454	0.215	0.453
1945	0.489	0.617	0.285	0.299	0.423
1946	0.397	0.421	0.346	0.264	0.357
1947	0.314	0.490	0.357	0.268	0.357
1948	0.463	0.781	0.473	0.340	0.514
1949	0.515	0.837	0.352	0.294	0.500
1950	0.399	0.681	0.450	0.235	0.441
1951	0.356	0.553	0.490	0.215	0.404
1952	0.403	0.774	0.456	0.251	0.471
1953	0.458	0.710	0.481	0.244	0.473
1954	0.359	0.502	0.413	0.229	0.376
1955	0.457	0.656	0.315	0.317	0.436
1956	0.482	0.685	0.362	0.204	0.433
1957	0.315	0.456	0.336	0.130	0.309
1958	0.193	0.587	0.278	0.115	0.293
1959	0.193	0.304	0.233	0.154	0.221
1960	0.334	0.656	0.456	0.216	0.416
1961	0.304	0.680	0.479	0.301	0.441
1962	0.407	0.911	0.429	0.230	0.494
1963	0.338	0.652	0.323	0.159	0.368
1964	0.339	0.920	0.356	0.352	0.492
1965	0.348	0.890	0.392	0.194	0.456
1966	0.339	0.527	0.324	0.218	0.352
1967	0.357	0.773	0.252	0.195	0.394
1968	0.357	0.595	0.377	0.230	0.365
1969	0.377	0.704	0.445	0.207	0.433
1970	0.326	0.719	0.394	0.253	0.423
1971	0.537	0.595	0.332	0.418	0.471
1972	0.409	0.484	0.338	0.168	0.350
1973	0.309	0.677	0.525	0.326	0.459
1974	0.439	0.634	0.326	0.300	0.425
1975	0.530	0.893	0.671	0.342	0.609
1976	0.389	0.493	0.338	0.095	0.329

Table 2. Continued.

	Mar	Jun	Sep	Dec	Avg
1977	0.290	0.678	0.362	0.126	0.364
1978	0.199	0.612	0.304	0.229	0.336
1979	0.346	0.657	0.293	0.222	0.380
Mean	0.357	0.603	0.384	0.226	0.392
SD	0.097	0.155	0.097	0.070	0.078
C.V. %	27	26	25	31	20

*Northern anchovy spawning biomass*—The time series of abundance of anchovy larvae are listed in Table 4 (annual values) and Table 5 (quarterly values). These values are a subset of those reported for the California Current (Smith 1972; Stauffer and Parker: SW Fish. Center Admin. Rep. LJ-78-9; Stauffer: SW Fish. Center Admin. Rep. LJ-79-22). They were assessed every third year after 1966.

The seasonal abundance of anchovy larvae is out of phase with primary production and zooplankton volume. Anchovy larvae show a seasonal maximum in January–March, while primary production and zooplankton biomass maxima are centered on June (*see quarterly mean values*: Tables 2, 3, 5). This phase difference has been noted before for anchovy

Table 3. Zooplankton standing stock ( $g\cdot m^{-2}$ ).

	Mar	Jun	Sep	Dec	Avg
1951	15.22	21.16	7.00	8.52	12.98
1952	12.63	20.40	17.50	10.50	15.26
1953	16.59	66.51	31.05	6.54	30.18
1954	10.96	32.12	9.13	7.61	14.95
1955	11.26	24.51	13.09	13.39	15.56
1956	17.35	42.31	22.83	22.69	26.29
1957	16.59	14.16	5.63	4.57	10.24
1958	7.00	11.26	2.44	2.28	5.75
1959	5.02	8.52	7.30	5.78	6.66
1960	13.09	20.09	9.74	3.65	11.64
1961	14.61	44.60	6.85	9.89	18.99
1962	26.03	100.76	24.20	8.07	39.76
1963	21.46	71.99	7.31	15.68	29.11
1964	28.77	37.14	42.01	15.37	30.82
1965	10.05	20.09	17.50	7.46	13.77
1966	14.00	22.22	20.55	15.81	18.15
Mean	15.04	34.87	15.26	9.86	18.76
SD	6.28	25.40	10.80	5.44	9.71
C.V. %	42	73	71	55	52

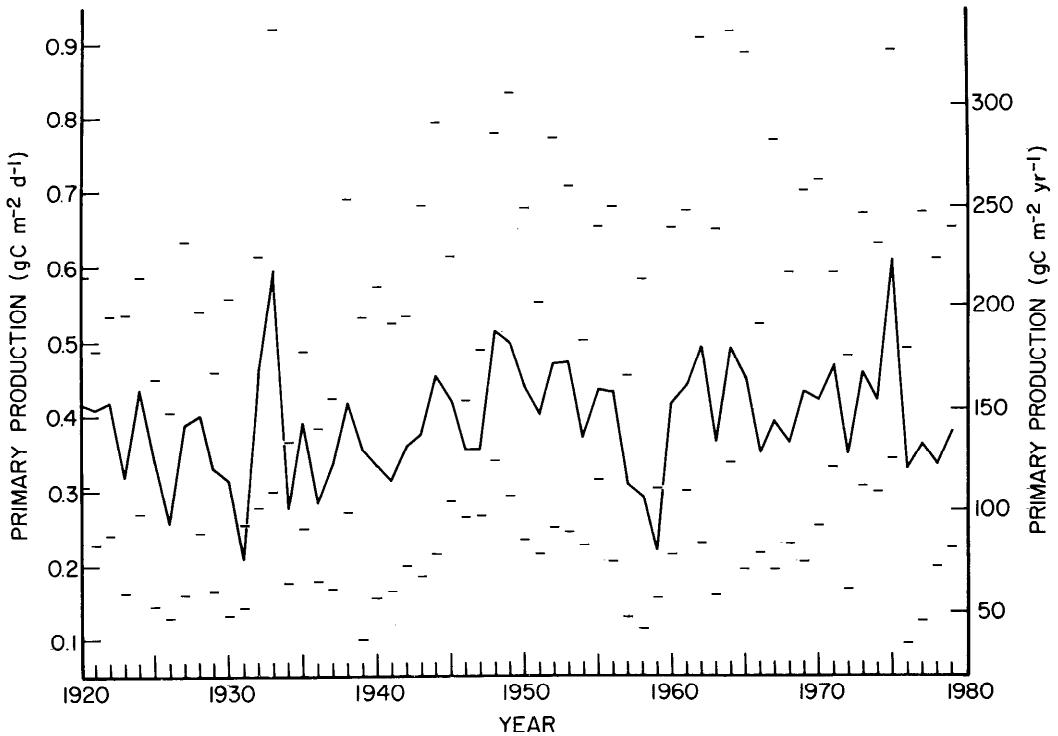


Fig. 3. Estimated annual primary production in Southern California Bight, 1920–1979. Dashes indicate maximum and minimum seasonal production rates for each year. Data from Table 2 indicate that maximum seasonal production is in June quarter in 93% of the years and that minimum seasonal production is in December quarter 85% of the years.

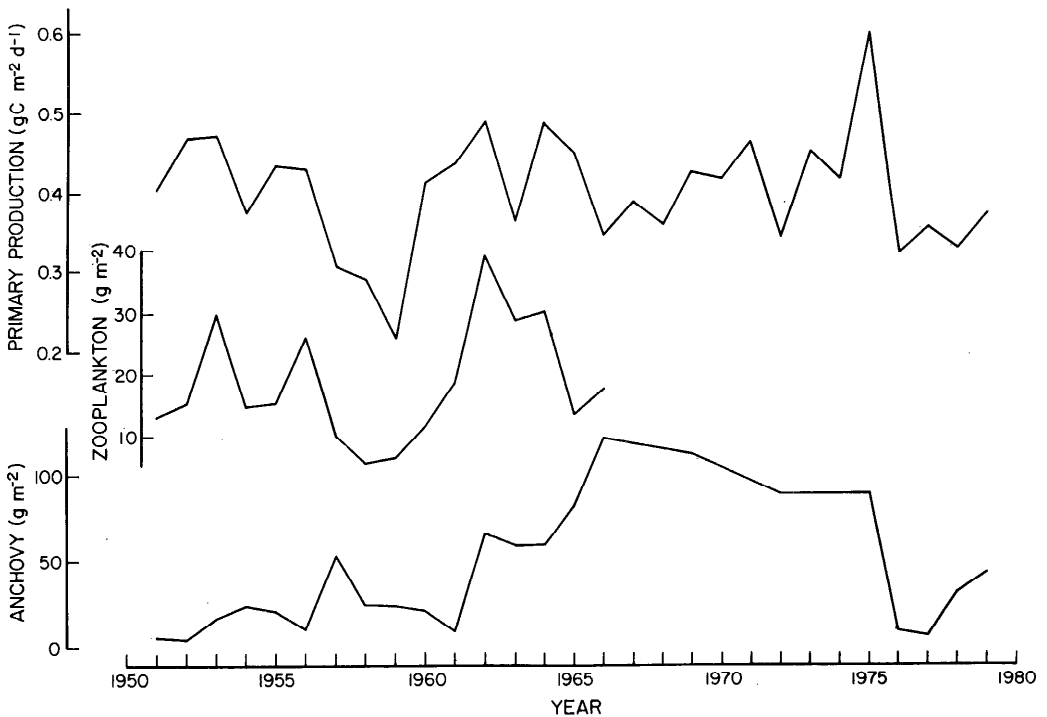




Table 4. Annual average primary production ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ), microplankton and zooplankton standing stock ( $\text{g}\cdot\text{m}^{-2}$ ), and anchovy larvae ( $\text{No.}\cdot\text{m}^{-2}$ ).

	Primary productivity	Micro-plankton*	Zooplankton	Larval northern anchovy
1951	0.404	29	13	5.1
1952	0.471	35	15	3.9
1953	0.473	78	30	14.6
1954	0.376	39	15	21.9
1955	0.436	37	16	18.8
1956	0.433	78	26	9.2
1957	0.309	31	10	48.7
1958	0.293	18	6	22.8
1959	0.221	18	7	21.4
1960	0.416	28	12	19.7
1961	0.441	43	19	9.0
1962	0.494	98	40	59.0
1963	0.368	67	29	53.7
1964	0.492	76	31	55.7
1965	0.456	39	14	(77.4)†
1966	0.352	41	18	116.1
Mean	0.402	47.2	18.8	34.8
SD	0.078	24.2	9.7	31.1
C.V. %	19	51	52	89

\* Santa Monica Bay, upper 15 m only.

† Estimated from samples in winter, spring, and summer quarters only.

eggs and plankton volume (Smith and Lasker 1978). The mean abundance of anchovy larvae in winter (January, February, and March) is  $74.2\cdot\text{m}^{-2}$  (SD 74.9, C.V. 101%) for the 19-year series. The mean abundance in spring is  $66.0\cdot\text{m}^{-2}$  (SD 63.7, C.V. 97%). The mean autumn abundance is  $7.7\cdot\text{m}^{-2}$  (SD 10.6, C.V. 138%). The mean of annual seasonal averages is  $43.9\cdot\text{m}^{-2}$  (SD 36.1, C.V. 82%). Most of the coefficient of variation is due to the extreme trend in abundance. The means comparable to the primary production and zooplankton standing stock seasons are "March" 71.5, "June" 50.1, "September" 14.8, and "December" 29.9 larvae $\cdot\text{m}^{-2}$ .

*An apparent relationship of anchovy larvae to zooplankton abundance and phytoplankton production*—Although the annual values in Fig. 4 suggest no dependence of anchovy larvae on plankton,

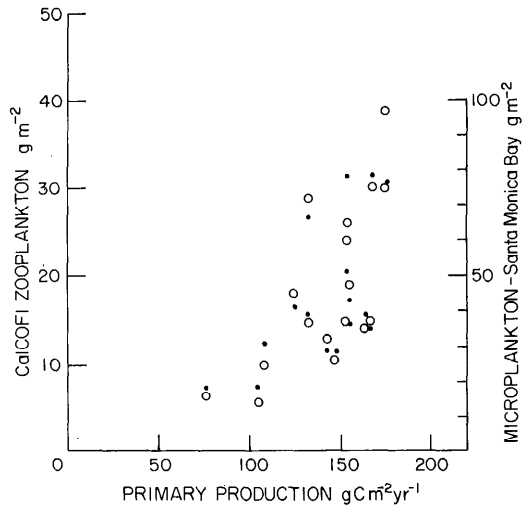


Fig. 5. Comparison of zooplankton concentrations in Southern California Bight with estimated primary production in the bight. Zooplankton data are from two series. ○—From bight portion of CalCOFI station grid which covers California Current region. ●—Data from Santa Monica Bay collected by personnel of the City of Los Angeles Hyperion Waste Treatment facility. Values are annual averages of monthly (CalCOFI) or weekly (Hyperion) net collections. Mesh of CalCOFI nets was 0.505 mm, that of Hyperion net was finer (about 0.076 mm). For comparing these values on the same scale one can use an exponential curve of the form  $z = a \exp(bp)$  where  $a$  is intercept,  $b$  is slope,  $z$  is zooplankton average annual concentration in  $\text{g}\cdot\text{m}^{-2}$ , and  $P$  is primary production in  $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ . For Southern California Bight zooplankton with the CalCOFI net, constant  $a$  is 1.97 and  $b$  is 0.014. For Santa Monica Bay microplankton,  $a$  is 6.25 and  $b$  is 0.013.

statistical exploration of the quarterly values has led us to postulate a relationship between the abundance of anchovy larvae and the zooplankton standing stock and primary production in the study area. The 59 quarterly production values (Table 2), zooplankton standing stocks (Table 3), and the northern anchovy larvae from 1951–1965 (Table 5) are all positively intercorrelated to a moderate degree. In addition to the direct correlation, the zooplankton-anchovy larvae cross-correlation was maximum at a lag of three

←

Fig. 4. Estimated annual primary production, annual mean CalCOFI zooplankton concentrations, and anchovy total biomass in Southern California Bight.

Table 5. Time series of abundance of northern anchovy larvae (No.  $\cdot$  m<sup>-2</sup>) in Southern California Bight study area.

	Feb	May	Aug	Nov	Avg
1951	2.5	9.6	1.9	6.4	5.1
1952	1.7	5.6	5.5	2.8	3.9
1953	9.1	4.1	10.9	34.2	14.6
1954	64.0	12.7	9.5	1.3	21.9
1955	30.9	19.3	23.5	1.3	18.8
1956	4.9	19.5	10.1	2.1	9.2
1957	104.9	77.5	10.3	2.0	48.7
1958	36.1	48.1	6.3	0.5	22.8
1959	31.7	52.3	0.9	0.7	21.4
1960	41.3	32.7	4.4	0.4	19.7
1961	1.5	26.2	7.9	0.3	9.0
1962	51.2	154.4	28.4	2.0	59.0
1963	150.3	60.9	1.1	2.3	53.7
1964	87.5	117.7	4.6	12.8	55.7
1965	136.3	116.7	43.6	22.1	98.9 (77.4)
1966	167.0	221.4	53.9	12.2	116.1
1969	259.3	83.6	42.7	—	99.5
1972	36.6	175.4	55.7	27.4	89.2 (70.0)
1975	193.9	16.8	28.9	—	66.8
N	19	19	19	17	19
Mean	74.2	66.0	18.4	7.7	43.9
SD	74.9	63.7	18.4	10.6	36.1
C.V. %	101	97	100	138	82

quarters for the anchovy. The multiple correlation parameters of the abundance of anchovy larvae as determined by the zooplankton standing stock three quarters previously and the primary production of the same quarter are summarized in Table 6. The relationship explains only 46% of the abundance of larvae, but the *t*-ratio is highly significant for both zooplankton and primary production. The ANOVA of the regression *F*-test is also highly significant. These relationships would suggest that the intensity of spawning activity of the adult anchovy in part depends on zooplankton abundance three quarters earlier and in part on the productivity of the area in the same season. This might be expected if the fish accreted fat (Smith and Lasker 1978) in the preceding year which enhanced subsequent reproduction.

*Adult and juvenile anchovy biomass*—The estimated spawning biomass of anchovy is derived from the "larval index" (Smith 1972; Smith and Burris: SW Fish.

Table 6. Prediction of quarterly anchovy larvae in Southern California Bight area from zooplankton standing stock and phytoplankton production.

	Anchovy larvae (A)	Lagged zooplankton (Z)	Primary production (P)	
Anchovy larvae (A)			0.41	
Lagged zooplankton (Z)		0.54	-0.04	
Regression Eq.: $A = 298 + 12.58Z + 904P$				
Parameters	Coeff.	SD coeff.	Student's <i>t</i>	
Intercept	-298	104	-2.88	
Z	12.58	2.24	5.61	
P	904	206	4.39	
$r^2 = 46.0\%$ adjusted for df				
Due to	df	ANOVA SS	MS	F
Residual	53	4,786,028	90,302	
Regression	2	4,404,895	2,202,448	24.39
Total	55	9,190,923		

Center Admin. Rep. LJ-78-24; Stauffer and Parker: SW Fish. Center Admin. Rep. LJ-78-9), which is used for management of the U.S.-based fishery. The time series of estimated spawning biomass (Table 7) illustrates the nature of the annual variability of biomass density of the Southern California Bight portion of the subpopulation habitat. The local density in  $g \cdot m^{-2}$  increased 12-fold in the 5 years 1952-1957, decreased 5-fold in the 4 years 1957-1961, and increased 12-fold in the 5 years 1961-1966. The maximum annual increase was 6-fold in 1961-1962 and the maximum annual decrease was 8-fold in 1975-1976. The total range of values was 28-fold. Since the study area does not contain the entire population, these changes may involve both reproduction and migration. Sampling error, particularly at higher population densities, is of course appreciable, and both bias and imprecision may be contributing to extreme values. In Fig. 6 the Southern California Bight time series is plotted with the time series of the entire central subpopulation. The population increases of 1957 and 1962, for example, were not

Table 7. Anchovy juvenile and adult biomass and Southern California Bight biomass density.

Year*	Spawning biomass estimated			Total biomass assumed		Autumn biomass assumed	
	g	$\text{g}\cdot\text{m}^{-2}$	% of central subpop.	g	$\text{g}\cdot\text{m}^{-2}$	g	$\text{g}\cdot\text{m}^{-2}$
1951	$5.4 \times 10^{10}$	1.80	34	$9.1 \times 10^{10}$	3.03	$1.7 \times 10^{11}$	5.67
1952	4.2	1.40	30	7.1	2.37	1.3	4.33
1953	$1.6 \times 10^{11}$	5.33	35	$2.7 \times 10^{11}$	9.00	5.0	16.67
1954	2.3	7.67	33	3.9	13.00	7.2	24.00
1955	2.0	6.67	26	3.4	11.33	6.2	20.67
1956	$9.8 \times 10^{10}$	3.27	22	1.6	5.33	3.0	10.00
1957	$5.2 \times 10^{11}$	17.33	47	8.7	29.00	$1.6 \times 10^{12}$	53.33
1958	2.4	8.00	19	4.0	13.33	$7.5 \times 10^{11}$	25.00
1959	2.3	7.67	16	3.9	13.00	7.2	24.00
1960	2.1	7.00	15	3.5	11.67	6.5	21.67
1961	1.0	3.33	9	1.7	5.67	3.0	10.00
1962	6.3	21.00	23	$1.1 \times 10^{12}$	36.67	$2.0 \times 10^{12}$	66.67
1963	5.7	19.00	15	1.0	33.33	1.8	60.00
1964	5.9	19.67	23	1.0	33.33	1.8	60.00
1965	7.9	26.33	19	1.3	43.33	2.5	83.33
1966	$1.2 \times 10^{12}$	40.00	38	2.0	66.67	3.7	123.33
1969	$1.1 \times 10^{12}$	36.67	41	1.8	60.00	3.4	113.33
1972	$7.1 \times 10^{11}$	23.67	28	1.2	40.00	2.2	73.33
1975	$7.1 \times 10^{11}$	23.67	22	1.2	40.00	2.2	73.33
1976	$8.9 \times 10^{10}$	2.97	—	$1.5 \times 10^{11}$	5.00	$2.8 \times 10^{11}$	9.33
1977	$6.2 \times 10^{10}$	2.07	—	1.0	3.33	1.9	6.33
1978	$3.0 \times 10^{11}$	10.00	25	5.0	16.67	9.4	31.33
1979	$4.0 \times 10^{11}$	13.33	25	6.7	22.23	$1.3 \times 10^{12}$	43.33
N		23			23		23
Mean		13.38			22.49		41.69
SD		11.18			18.64		34.67

\* No data for 1967, 1968, 1970, 1971, 1973, or 1974.

confined to the study area but in fact extended offshore more than 370 km (Smith 1972; fig. 11; Kramer and Ahlstrom 1968).

Comparison of the annual time series of phytoplankton production, zooplankton standing stock, and the assumed annual maximum biomass of anchovy (Fig. 4) shows coincidental local minima of almost 3 years' extent in the late 1950s during a North Pacific equivalent of the Peruvian "El Niño." Concurrent increases in total anchovy population (Fig. 6) suggest, however, that this decrease in anchovy was essentially a local or coastal phenomenon confined to the Southern California Bight.

*Energetics*—After 1957, the total subpopulation of northern anchovy increased in the succeeding years but the Southern California Bight portion of the population decreased (Fig. 6). In 1966, the local portion of the population

reached a maximum in the time series. The years 1957 and 1966 are interesting ones for examining the energy requirements of anchovy in relation to zooplankton and primary production, as these years were anchovy biomass maxima in the bight. We will examine anchovy egg production as one aspect of limiting energetics. Respiration and growth cannot be usefully estimated because the distribution of swimming speed and of age composition is not known, but if we use the reproductive rate calculated for the current population (Hunter and Goldberg 1980; Hunter pers. comm.), the rate of egg production can be estimated. The spawning biomass in 1957 was  $17.33 \text{ g}\cdot\text{m}^{-2}$  or  $8.67 \text{ g}\cdot\text{m}^{-2}$  of females. Egg production is now estimated at  $389 \cdot \text{g}^{-1}$  of female per batch for 20 batches (Hunter pers. comm.). The calorific value of a  $3.01 \times 10^{-5} \cdot \text{g}^{-1}$  anchovy egg is  $1.64 \times$

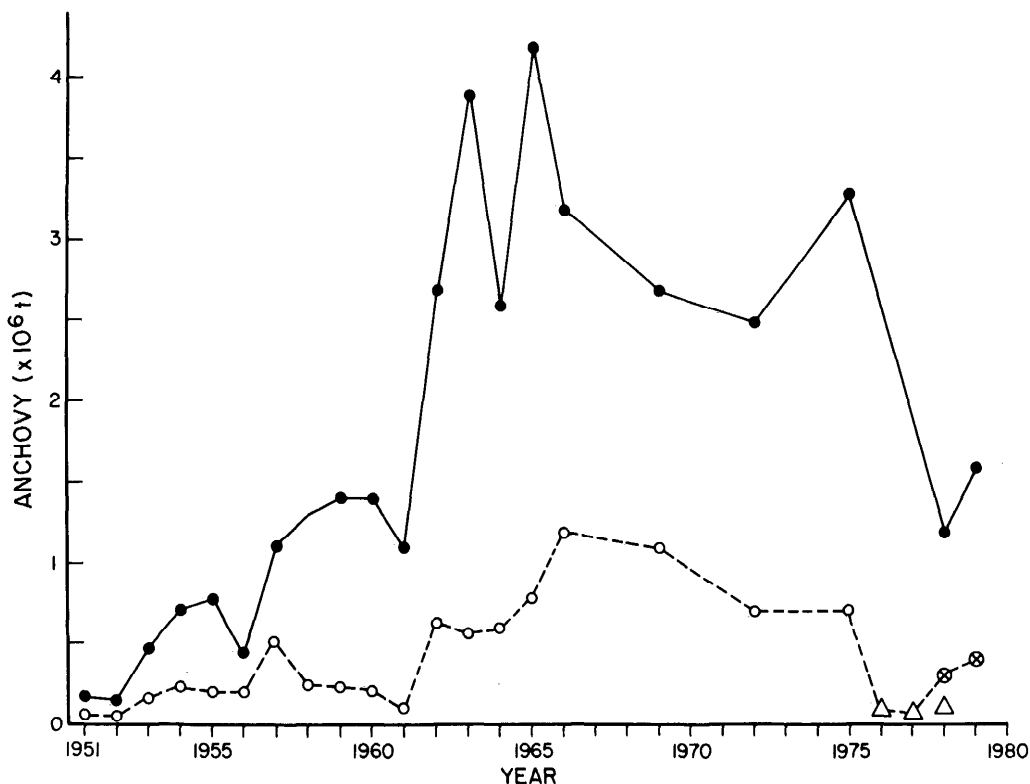


Fig. 6. Estimated spawning biomass of central subpopulation of northern anchovy (Stauffer: SW Fish. Center Admin. Rep. LJ-79-22, ●) and that segment spawning in Southern California Bight study areas (Smith and Burris: SW Fish. Center Admin. Rep. LJ-78-24, ○). The 1976–1978 figures (△) were obtained by ratio of Southern California Bight studies anchovy larvae to those of CalCOFI winter cruises of 1975. The 1978–1979 figures (⊗) were obtained by a fixed ratio (0.25) of central subpopulation. No estimates of central subpopulation spawning biomass are available for 1967–1968, 1970–1971, 1973–1974, and 1976–1977.

$10^{-4}$  kcal (Hunter pers. comm.). Egg production is then  $11 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ . In 1957 primary production was  $113 \text{ g C} \cdot \text{m}^{-2}$ . If the calorific value is  $11.4 \text{ kcal} \cdot \text{g}^{-1} \text{ C}$  (Platt and Irwin 1973), then the reproduction investment in eggs of anchovy was about 0.9% of the annual primary production. (In the ensuing 4 years, the spawning biomass decreased by a factor of five.)

In 1966 the values were: Phytoplankton production =  $1,466 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , maximum anchovy biomass =  $173 \text{ kcal} \cdot \text{m}^{-2}$ , anchovy spawning biomass =  $56 \text{ kcal} \cdot \text{m}^{-2}$ , and egg production =  $26 \text{ kcal} \cdot \text{m}^{-2}$ . The egg production in 1966 was then apparently 1.8% of the local phytoplankton production. If anchovy reproduction is about 10% of ration (Hunter

and Leong pers. comm.) then that ration was about 18% of primary production in 1966.

*Long term population changes*—Soutar and Isaacs (1974) used fish-scale deposition rates as recorded in the varved sediments of the Santa Barbara Basin to estimate relative anchovy abundance for the period 1785–1970 in 5-year intervals. Recent estimates of absolute population biomass were used (Smith 1978) to assign values to the anchovy and other populations detected by scale deposition. No significant correlations with primary production were found for the anchovy biomass, the total *epipelagic* biomass which includes Pacific sardine (*Sardinops sagax caerulea*), the Pacific mackerel

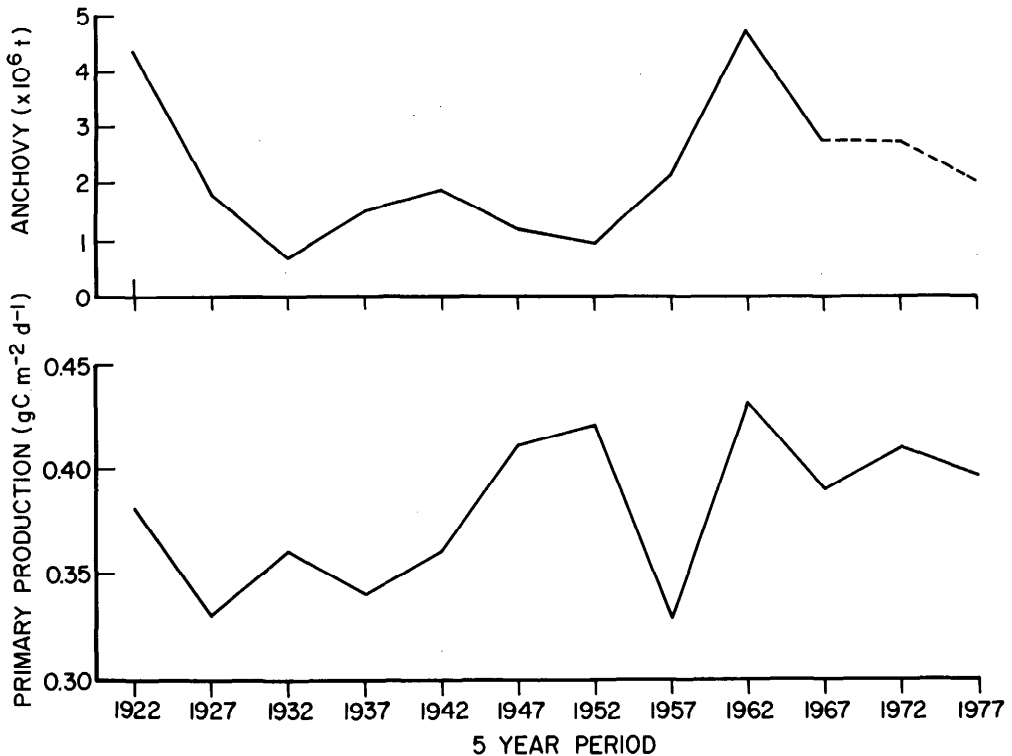


Fig. 7. Five-year mean values for anchovy biomass and estimated primary production, 1920–1979.

(*Scomber japonicus*), and the Pacific saury (*Cololabis saira*), or the total pelagic biomass which includes also the Pacific hake (or whiting, *Merluccius productus*). The maximum correlation coefficient was only 0.3 for the northern anchovy (Fig. 7).

#### Discussion

*The primary production time series*—The temperature anomaly–daylength model includes two variables that control phytoplankton production: the rate of nutrient input and the seasonal change in photosynthesis. Departures from historical mean temperatures (the temperature anomalies) were correlated with phytoplankton standing stock as reflected by particulate organic nitrogen concentrations ( $\text{mg PON} \cdot \text{m}^{-2}$ ) and with the depth of the nitrate concentration gradient (Eppley et al. 1978). It was later shown that the depth of the nitrate concentration

gradient is related to the rate of nitrate uptake by phytoplankton in the euphotic zone and to the rate of primary production (Eppley et al. 1979a). The position of the nitracline evidently reflects the rate of nitrate input to the euphotic zone. Seasonal changes in photosynthetic rate per weight of chlorophyll, i.e. the productivity index, were also apparent (Eppley et al. 1977). Daylength is an appropriate variable to represent the suite of environmental factors that alter photosynthetic rate with season (such as irradiance and temperature), and it is independent of the temperature anomaly.

The temperature anomaly becomes coherent at different locations within the bight for periods longer than about 4–5 days (List and Koh 1976). The average anomaly over the 6–8-day cruise periods, as used here, is considered representative of events taking place throughout the bight. These events include coastal up-

welling, advection associated, for example, with current flows, and interannual differences in ocean climate.

The station grid (Eppley et al. 1978) or any other fixed station pattern, cannot be expected to provide synoptic data. Nor can the Scripps pier temperature be expected to reflect all events that influence the depths of the nitrate concentration gradient throughout the bight. That primary production (based on the Scripps pier temperature anomalies) was correlated with microplankton in Santa Monica Bay suggests, however, that the estimated primary production may be representative over 150 km along the coast. Satellite images of both temperature (R. Lasker pers. comm.) and chlorophyll (R. C. Smith pers. comm.) show different values in the Southern California Bight from those in the California Current regime some 150–200 km offshore. The images also suggest that the station pattern is representative within the bight, except for the Santa Barbara Basin in the extreme northwest portion well north of the station grid. These observations and the correlations between primary production and zooplankton suggest that we have made progress toward assessing the carrying capacity of the region for herbivores.

The estimating algorithm also promises to be useful with respect to contemporary events in the bight. For example, we are using it as a first-line "verification" of production estimated from chlorophyll data derived from the satellite images. In this role it serves as a first-order estimate when no cruise measurements are available, i.e. on all but infrequent occasions.

We anticipate that this simple approach to estimating primary production may prove useful in other subtropical and tropical areas. Tont (1976) found that diatom outbursts occurred historically off the Scripps pier during short period fluctuations in the pier temperature anomaly. Diatoms were associated with cold anomalies, i.e. upwelling. Three major blooms account, on average, for 85% of the annual diatom biomass at the pier. Herbrand and Voituriez (1979) found an even

stronger correlation between primary production and the depth of the nitracline in parts of the eastern tropical Atlantic than we found here. Nevertheless it is not clear why the Scripps pier temperature anomaly is so well correlated with the depth of the nitracline in the bight, as the surface waters are stratified except during strong upwelling events and the nitracline lies at a mean depth of 16 m on the shelf and deeper offshore. Further, the nitracline shows vertical displacements in response to the semidiurnal internal tides of as much as 15 m over 24 h (Eppley et al. unpubl.). Although it would not be surprising if other variables and other time scales (Tont 1976) ultimately prove more useful in estimating production than the temperature anomaly, it is surprising to us that the pier temperature anomaly and daylength account for as much of the variability in production as they do. For cruises 2–13, for example, the  $r^2$  for the correlation between measured and predicted production is  $>0.8$ .

Two new time series pertinent to plankton and fisheries have been prepared from CalCOFI hydrographic data (about 1950–present). Chelton (1980) has developed a "California El Niño" index of low frequency changes in steric height (from hydrography) observations in the California Current region. Bernal (1980) developed a time series index of anomalies in the strength of California Current flow based on the southward extension of its low salinity core. Both indices are correlated with zooplankton concentrations in the California Current, as is estimated primary production.

*Time scales*—On the geologic time scale it is clear that the seasonal upwelling and equatorward transport of the eastern boundary currents foster and maintain major populations of pelagic schooling fishes in several areas of the world (Cushing 1969). It is also quite clear from our study that increasing daylength in the bight each spring stimulates primary production, secondary production, and the production of spawn in the dominant fish population. With the exception of the sustained decrease of primary pro-

duction in the warm water years of 1958–1959, and the coincident decrease in the anchovy biomass in the bight (Figs. 4, 6, 7), there is little evidence for annual or 5-year-time-scale control of anchovy abundance by primary production.

*Nutrient regeneration*—The concepts of new vs. regenerated primary production have not yet entered into the discussion of transfer efficiency in the literature. New production was defined by Dugdale and Goering (1967) as that resulting from allochthonous nutrient entering the euphotic zone. In local waters this is primarily nitrate from subeuphotic waters (Eppley et al. 1979a). Elsewhere river water, rain, or nitrogen fixation might be important nutrient sources for new production. Regenerated production results from nutrient recycling within the euphotic zone. In Southern California Bight waters new production averaged about 35% and regenerated production 65% of total production. New production can be viewed as that fraction of primary production available for export from the euphotic zone, i.e. the amount that can be removed without a decline in phytoplankton production, as long as the nutrient input rate remains unchanged. Most of the export is the sinking flux of particulate organic matter, such as in fecal pellets. The fish catch accounts for only a small fraction of global new production (Eppley and Petersen 1979).

Both zooplankton and anchovies are important in nutrient recycling in the bight (McCarthy and Whitley 1972). The anchovy is a schooling fish and this behavior must contribute to patchiness of regenerated nutrients such as ammonium. Oviatt et al. (1972) found elevated ammonium concentrations behind menhaden schools in the coastal Atlantic. Our rough calculations suggest that the average ambient ammonium concentration of  $0.35 \mu\text{M}$  (Eppley et al. 1979b) should be approximately doubled behind an anchovy school. If we assume an anchovy concentration of  $15 \times 10^3 \text{ g wet wt} \cdot \text{m}^{-2}$  within a school (Hewitt et al. 1976) and 0.28 dry wt:wet wt we get a school biomass  $4.2 \times 10^3 \text{ g dry wt} \cdot \text{m}^{-2}$ . If the ammonium excretion rate is  $0.1 \times 10^{-3} \text{ mol N} \cdot (\text{g dry}$

wt) $^{-1} \cdot \text{d}^{-1}$  (for other rates see McCarthy and Whitley 1972), the daily nitrogen excretion is  $0.4 \text{ mol N} \cdot \text{m}^{-2}$ . Further, if the thickness of the school is 10 m and the school occupies a water mass for 10 min, the ammonium input will be  $0.3 \times 10^{-3} \text{ mol N} \cdot \text{m}^{-3}$  in 10 min. For comparison, the mean ammonium assimilation rate by phytoplankton in the bight is about  $0.13 \times 10^{-3} \text{ mol N} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ , which could be supplied by a fish school in 5 min. McCarthy and Kamykowski (1972) found elevated levels of urea-N in La Jolla Bay for several weeks associated with a high incidence of blue sharks, another example of the importance of fish in pelagic nutrient recycling.

*Concentration of schooling fish*—The anchovy schooling behavior may be significant in providing nutrients for phytoplankton in two different ways, as it imposes both spatial and temporal variability in nutrient distribution. The temporal variability in nutrient input rate could influence relative phytoplankton species success, as demonstrated in cultures by Turpin and Harrison (1980). The spatial variability is characterized by brief but intense local episodes of grazing and nutrient excretion. Conversely, the long intervals between these episodes promotes local recovery of prey in an environment enriched by the excreted nutrients.

In the absence of predation on the phytoplankton and the nutrient recycling associated with it, new production would be equivalent to total production, as in an axenic algal culture. Nutrient recycling increases total production by 2-fold, on an average, in the Southern California Bight (Eppley et al. 1979a). The closest approach to a total absence of epipelagic fish in the bight was during the hiatus after the decline of the sardine and before the rise of the anchovy in the late 1950s (Smith 1978). Such biological interaction as nutrient regeneration by fish would not be evident in the estimated annual primary production because the latter is calculated from the physical variables. However, the zooplankton and microplankton time series might reflect the role of fish in nutrient recycling. Clearly fish predation is not a major regulator of

zooplankton stocks since primary production and zooplankton are correlated (Fig. 5). However, ratios of zooplankton biomass to estimated primary production might be revealing with respect to nutrient recycling via fish. Average ratios (from Table 4) are 0.035 for 1951–1960 when anchovy biomass was low and 0.050 for 1961–1966 when it was higher, suggesting that there was a larger zooplankton biomass per unit primary production when anchovies were abundant than when they were less abundant. In other words if a constant ratio exists between zooplankton and primary production, production may be underestimated because of failure to include nutrient regeneration by fish in the estimating algorithm.

*Transfer efficiencies*—The anchovy egg production in the bight was apparently as much as 1.8% of primary production in 1966, the year of maximum anchovy biomass. We have also estimated that anchovy food consumption was about 18% of the primary production in 1966. These values suggest rather high anchovy predation on zooplankton in 1966, but no crash of the zooplankton biomass is apparent in Fig. 4. Steele and Frost (1977) suggested that fish predation might be very dependent on the size of individual zooplankton. Koslow (1980) showed that the predation of anchovy schools on zooplankton off southern California was size-dependent, with larger animals taken in preference to small, depending somewhat on the size distribution of zooplankton encountered by the school. The CalCOFI zooplankton collections have not yet been analyzed from the standpoint of differentiating different size groups or taxa in the plankton. Cushing (1975) reviewed information on the transfer efficiency of the herbivore trophic level; values of about 0.2 are common, which are supported by our calculations of about 0.18.

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Submitted: 17 December 1980

Accepted: 2 June 1981