NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SPAWNING IN SAN FRANCISCO BAY, CALIFORNIA, 1978-79, RELATIVE TO HYDROGRAPHY AND ZOOPLANKTON PREY OF ADULTS AND LARVAE

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ABSTRACT

Eggs and larvae of *Engraulis mordax* were sampled by nets monthly for one year. Either eggs or larvae were caught every month. Both were most abundant when water temperature was high. Mean egg abundance did not differ among stations but larvae were more abundant within the San Francisco Bay at high and low salinity than near the ocean entrance to the Bay. Larvae longer than 15 mm were collected over the shoals in spring and autumn but were in the channel during winter. Zooplankton and microzooplankton were abundant relative to mean California Current densities. Adult spawning biomass in the Bay was 767 tons in July 1978, based on egg abundance and fecundity parameters of oceanic animals. San Francisco Bay was a good spawning area for northern anchovy because food for adults and larvae was abundant and because advective losses of larvae would have been lower in the Bay than in coastal waters at the same latitude.

The northern anchovy, *Engraulis mordax*, is the most abundant fish in San Francisco Bay (Aplin 1967), but little is known about the seasonal duration or areal extent of northern anchovy spawning there (Eldridge 1977; Sitts and Knight 1979; Wang 1981). In the California Current, spawning is thought to be related to abundance of food for adults (Brewer 1978) or to seasonal patterns of abundance of food for larvae (Lasker 1978). Dense patches of appropriate food for larvae are believed to be necessary for survival of larvae (Lasker 1975; Scura and Jerde 1977). Zooplankton are generally more abundant in estuaries than in coastal and oceanic waters. Therefore, San Francisco Bay, the largest estuary on the west coast of North America, could be a favorable habitat for spawning northern anchovy and their developing larvae.

The northern anchovy could affect plankton dynamics in the San Francisco Bay (the Bay) by preying on zooplankton and by excreting concentrated nutrients for phytoplankton. It is the target of a seasonal bait fishery (Smith and Kato 1979), and it is an important forage fish for many other species (Recksiek and Frey 1978). Quantitative estimates of the adult stock size and numbers of eggs and larvae are needed to understand the ecology of this anchovy in the Bay.

This paper reports the results of a 1-yr survey of the northern anchovy eggs and larvae, zooplankton, and microzooplankton in San Francisco Bay. Distribution and abundance of eggs and larvae were related to water temperature, salinity, turbidity, stratification, abundances of potential adult prey, and potential larvae prey. The suitability of the Bay for spawning and development of larvae was assessed. An estimate of spawning stock abundance within the Bay was calculated from egg abundance, and the impact of this biomass of anchovies on the zooplankton was estimated.

MATERIALS AND METHODS

Study Site

San Francisco Bay consists of three major parts (Fig. 1): 1) Central Bay opens to the Pacific Ocean through the Golden Gate at lat. 37°49'N, long. 112°29'W; 2) North Bay receives the drainage from the Sacramento and San Joaquin Rivers and includes Suisun, San Pablo, and Richardson Bays; 3) South Bay is the largest single embayment, extending some 27 nmi from Coyote Creek in the south to the Oakland-San Francisco Bay Bridge in the north. The following description of San Francisco Bay was taken from Conomos and Peterson (1977). Mean depth is 6 m at mean lower low water, or 2 m if the large expanses of mudflats are included. There is a 10 m deep dredged ship channel in the northern part. Tides are mixed semidiurnal ranging from 1.7 m at the Golden Gate to 2.7 m at the south-

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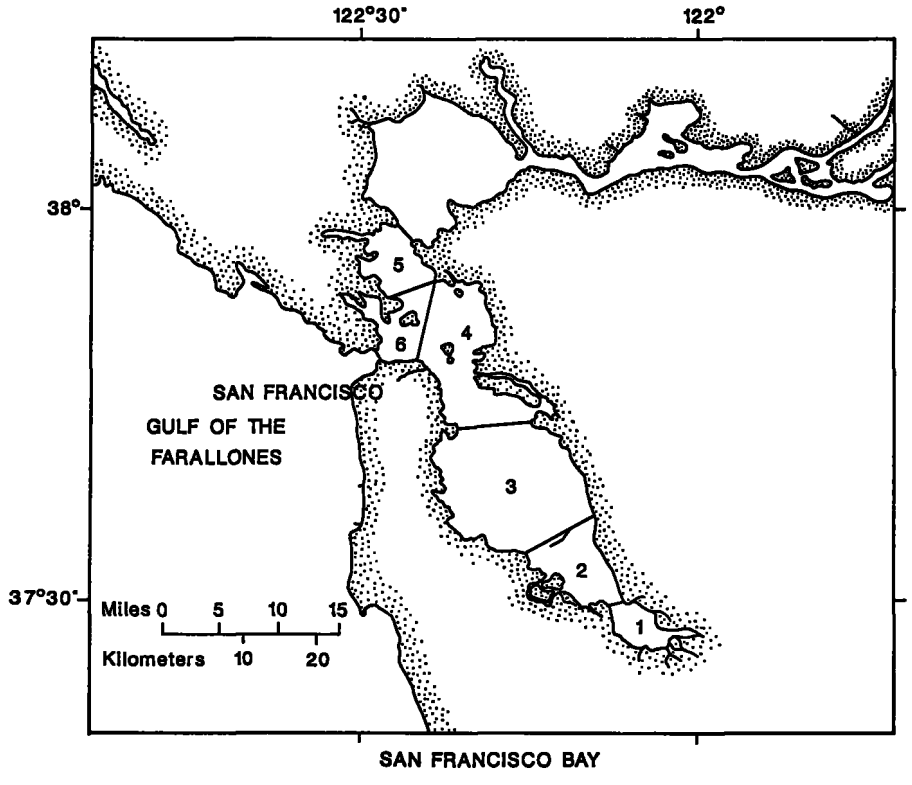

FIGURE 1.—Locations of stations and the areas represented by each station sampled monthly May 1978-April 1979.

ern end of South Bay. The tidal prism is 27% of the Bay volume. Maximum tidal currents occur in the channels and may be 225 cm/s (4.5 kn) at the Golden Gate. More than 90% of the freshwater entering San Francisco Bay enters North Bay from the Sacramento and San Joaquin Rivers. Less than 10% enters South Bay from small tributary streams and sewage. Because of the difference in freshwater inflow the northern and southern reaches are very different types of estuary. North Bay is partially-to-well-mixed with true two-layer estuarine circulation. South Bay, dependent for water exchange on tidal circulation and occasional incursions of freshwater from the north during wet winters, resembles a coastal lagoon.

The heterogeneous nature of San Francisco Bay requires that stations be representative of the diverse areas of the Bay. The stations (Fig. 1) were located in the channel adjacent to the shoals in the South Bay in 5-6 m of water (stations 1 and 2); just north of San Bruno Shoal in 3 m of water (station 3); east of Treasure Island over a dredge borrow pit in 10 m of water (station 4); in midchannel just south of the Richmond-San Rafael Bridge in 10-13 m of water (station 5); and north of Lime Point just inside the Golden Gate Bridge in 25-35 m of water (Station 6). These sites were near those of a previous trawl study (Aplin 1967) and they represented locations from South Bay, Central Bay, the outflow from North Bay, and the Pacific Ocean entrance to the Bay.

All South Bay stations were sampled in one day, all Central Bay stations were sampled on another day, usually the day following the South Bay sampling. This schedule and the pattern of tidal flow in the Bay (Tidal Current Chart, San Francisco Bay 1973) enabled all stations to be sampled before noon at approximately slack tide, low water. This schedule controlled for the effects of time of day, tide, and currents which can affect catches of ichthyoplankton (Eldridge 1977). Additional samples were taken in October 1978 and April 1979 at station 3 and over the shoals adjacent to this station.

Duplicate oblique ichthyoplankton tows and duplicate surface microzooplankton tows were made monthly at six stations for one year, May 1978-April

1979. Ichthyoplankton and zooplankton samples were collected from a 5 m Boston Whaler with a 1 m diameter, cylinder-cone net of 0.308 mm mesh nylon with a 0.200 mm mesh cod end. The net was attached to a sled which kept the lower rim of the net 10 cm above the bottom and which had a tow-bridle that did not obstruct the mouth of the net. A frame attached to the transom permitted the sled to be launched and retrieved over the stern while underway. The sled was lowered to the bottom while underway at 1-2 kn, towed at the bottom for 1 min, and then retrieved at a constant rate and constant wire angle. Tow time, excluding that spent lowering the net to the bottom, was approximately 6 min. The gear was effective because it often caught anchovies and herring longer than 30 mm, a size not usually captured in towed gear (Clarke 1983) or in a plankton purse seine (Murphy and Clutter 1972).

A calibrated flowmeter suspended off-center in the mouth of the net measured the amount of water filtered during the tow. Volumes calculated from the flowmeter readings were similar to a hypothetical volume calculated from net mouth area and tow distance: approximately 300 m^3/tow.

Microzooplankton was collected with a 0.5 m diameter net with 0.080 mm mesh, which was towed just submerged at the surface for 2 min during the ichthyoplankton tow. Because the flowmeter in this net frequently malfunctioned, hypothetical volumes calculated from mouth diameter and tow length (approximately 25 m^3/tow) were used to standardize catches of microzooplankton. The net probably did not filter as much water as calculated so microzooplankton were underestimated. All samples were preserved with 2% formaldehyde in seawater buffered with sodium borate.

Water turbidity was measured with a Secchi disk (Tyler 1968). Water samples for salinity and temperature measurements were taken with a Van Dorn water sampler from 1 m below the surface and from 1 m above the bottom. The temperature was measured to 0.1°C with a laboratory thermometer, and salinity was measured to 0.5‰ with a temperature-compensated refractometer.

Laboratory Procedures

Northern anchovy eggs were easily recognized and distinguished from other regional pelagic fish eggs by their oval shape and their size, approximately 0.75 mm × 1.25 mm. Eggs were not assigned to stages, but some of the embryos were developed enough to be identified as those of northern anchovies. Northern anchovy eggs were counted under a dissecting microscope; at the same time, fish larvae were picked from the samples. The northern anchovy can be separated from other similar looking larvae by its myomere count (43-47), its gut length, and its median fin positions (Miller and Lea 1972; McGowan and Berry 1984).

All northern anchovy larvae <10 mm long were measured to the nearest 0.1 mm using an ocular micrometer. Longer larvae were measured to 1 mm using vernier calipers or a plastic ruler graduated in millimeters. The distance from the tip of the snout to the tip of the notochord was measured in preflexion larvae, standard length in larger specimens.

Zooplankton were subsampled from a 500 mL pharmaceutical beaker by stirring and taking an aliquot with a 1 mL or 2 mL Stempel pipet. Zooplankton were identified to major taxonomic group under the dissecting microscope using standard references such as Smith (1977). All holoplanktonic, meroplanktonic, and nektonic invertebrates were considered to be zooplankton if they were suitably sized prey for adult anchovies. Isopods were included; adult shrimp and gelatinous invertebrates were not. Plankton was allowed to settle in water in a graduated cylinder to estimate zooplankton volume.

Microzooplankton were subsampled from a stirred beaker with a pipet. A settling chamber and inverted compound microscope with movable stage were used to count microzooplankton (0.050-0.200 mm diameter) at 100× magnification. Dinoflagellates known to be eaten by anchovy larvae were counted as microzooplankton.

Precision Estimates

The precision of the microzooplankton counts was estimated by the method of Lund et al. (1958). If the counts are treated as a Poisson variable then the 95% confidence limits for a single count are

$$\text{Upper limit} = X + 2.42 + 1.96(X + 1.5)^{1/2}$$
$$\text{Lower limit} = X + 1.42 - 1.96(X + 0.5)^{1/2}.$$

The limits are approximately ±20% if 100 organisms are counted. Confidence intervals for microzooplankton counts in this study range from ±50% at the lowest count (5) to ±9% at the highest count (659).

The precision of the zooplankton subsampling estimates was evaluated by taking triplicate subsamples, with replacement, from 10 randomly selected samples. The mean coefficient of variation (standard deviation divided by the mean) of the triplicates was 0.29.

The precision of the duplicate tows was evaluated by comparing numbers of eggs, larvae, and zooplankton settled volumes from the May, June, and July tows. No statistical difference was detected between first and second tows (2-tailed $P = 0.407$, Wilcoxon Matched Pairs test, Hull and Nie 1981: 228). The mean coefficient of variation for these paired tows was 0.22. Because there were no statistical differences between these duplicates, only one of each pair of the remaining samples was sorted.

Data Analysis

Eggs, larvae, zooplankton, microzooplankton, and plankton volume per 1,000 m^3 were calculated based on flowmeter readings. Temperature and salinity stratification variables were created by taking the difference between surface and bottom values. Salinity stratification represented the intensity of estuarine circulation or freshwater runoff; temperature stratification represented water column stability and revealed atmospheric temperature extremes.

Distributions of the variables were examined for skewness, kurtosis, and unreasonable range limits indicative of keypunch errors. Normality of the original variables and of $\log(X + 1)$ transformations was tested (Kolmogorov-Smirnov test; Hull and Nie 1981:224). Variances of the transformed variables were not heteroscedastic. Biological and environmental variables were plotted against month, station, and each other to look for spatial patterns, seasonal trends, and nonliner relationships (especially nonmonotonicity) between pairs of variables.

Analysis of variance (ANOVA) was used to assess the effects of month of the year and station location on numbers of eggs and numbers of larvae. Stepwise multiple linear regression was used to examine which of the other variables could account statistically for the variability in numbers of eggs and larvae. Logarithmic transformations of standardized numbers of eggs, larvae, zooplankton, and microzooplankton were used in the regressions and in the ANOVA's.

Ichthyoplankton abundance is often expressed as numbers of ichthyoplankton under an area of sea surface by multiplying density per cubic meter times water depth (Smith and Richardson 1977). In deep water tows are made below the depth range of most eggs and larvae, so the tow depth is used as the effective water depth. Standardizing a unit of sea surface area allows comparisons of total numbers of eggs and larvae in the water column from areas with different water depths. Abundance standardized to area of sea surface was used to estimate total egg production. However, larvae that were relatively uncommon in deep water could be as abundant as more concentrated larvae in shallow water, but exposed to different concentrations of predators and prey; therefore, densities of larvae and plankton were used to examine relationships between ichthyoplankton, other plankton, and environmental variables.

The method used to estimate spawning stock biomass was a direct estimate because it incorporated batch fecundity from histological data (Hunter and Goldberg 1980) and daily egg production estimates from ichthyoplankton surveys (Parker 1980). Parker's equation for the direct estimate of biomass from egg abundance is

$$S = P(ab'c)^{-1}d$$

where S = spawning biomass in tons
P = egg production in eggs/day
a = 3.96×10^8 egg/ton
b' = 0.159 the observed daily spawning fraction
c = 0.550 the proportional biomass of females
d = 1.080 a correction for potential misclassification of daily spawning fraction.

Parker (1980) estimated the coefficient of variation of the estimate of spawning stock to be 0.614. Most of this statistical error was due to error in the estimate of egg production. Daily egg production was estimated in my study by dividing the egg abundance by the number of days needed to hatch at the ambient temperature (interpolated from Zweifel and Lasker 1976, fig. 7).

Numbers per square meter of Bay surface were calculated by multiplying density per cubic meter times water depth at the station. The areas represented by the stations were estimated from the chart of the Bay in Conomos and Peterson (1977). Total numbers of eggs and larvae were calculated from estimates per square meter times the area represented by the sample.

RESULTS

Eggs and Larvae

Either eggs, larvae, or both were present every month of the year. Eggs were present every month except December and January. Only one egg was

collected in February and very few were collected in November. Larvae were present every month and at every station each month with four exceptions: during June, no larvae were collected at station 1, the southernmost station; during July and August no larvae were collected at station 6, the Golden Gate Bridge station; during March no larvae were collected at station 3 in South Bay. Eggs were present on each of the occasions when larvae were absent from the samples.

Egg density varied from 0 to 55,000 per 1,000 m^3 (mean = 3,000). The greatest number of eggs in a single sample was 14,640 at station 2 in July. Occurrence of eggs was seasonal: they were abundant in summer and absent in winter (Fig. 2).

Larvae varied from 0 to 4,400 per 1,000 m^3 (mean = 259). The greatest number of larvae in a single sample was 1,420 in September at station 2. Larval abundance was also seasonal with peak density in late summer and fall (Fig. 2).

Two-way ANOVA of log-transformed standardized densities of eggs and larvae were performed with month and station as fixed factors in separate analyses. The interaction mean square (not significant) was used as the denominator in the F-tests because there was just one observation per cell of the design (Montgomery 1976:156). Densities of eggs differed significantly among months ($P < 0.001$, Table 1) but not among stations ($P = 0.104$). Densities of larvae were significantly different among months ($P = 0.010$) and among stations ($P = 0.014$) (Table 2).

Seasonal patterns of abundance of eggs and larvae were unmistakeable, but differences among stations were not as clear so three hypotheses were tested: 1) stations 1, 2, and 3, South Bay stations, differed from stations 4, 5, and 6; 2) stations 4 and 6, Golden Gate and Central Bay stations, differed from stations 1, 2, 3, and 5, South Bay stations plus the station at the outflow of San Pablo Bay; 3) stations 3, 4, and 6, the stations most influenced by ocean water, differed from stations 1, 2, and 5, the Bay stations. These hypotheses were tested using linear contrasts (Nie et al. 1975:425), a procedure that compared the geometric means of the groups of stations.

None of the three contrasts was significant for eggs but all three were significant ($P < 0.05$) for larvae. The difference between the mean of stations 4 and 6 and the mean of stations 1, 2, 3, and 5 was highly significant ($P = 0.001$).

Further comparisons of mean densities of larvae were done using Duncan's Multiple Range test. This a posteriori procedure identified groups of means which did not differ significantly from each other at a specified level (Nie et al. 1975:427). The rank order of the stations in increasing mean density of larvae was 4, 6, 1, 3, 5, 2. Three groupings were produced by the Duncan procedure at the 0.05 level. The mean of stations 4 and 6 was smaller than the mean of the other four. The mean of stations 5 and 2 was greater than that of the other four. Station 4 was significantly lower and station 2 significantly higher than the mean of the other four stations.

A summary of the analyses of variance follows. Eggs and larvae were seasonal in abundance, eggs more strongly than larvae. Numbers of eggs, which would be subject to passive drift and dispersal, were not significantly different among locations in the Bay. Larvae did differ in abundance among the six stations. Based on a priori and a posteriori tests, station 4 and station 6, the stations most influenced by oceanic water, had low densities of larvae while the other stations within the Bay had high mean densities of larvae. This pattern was true for station 5, near the Richmond-San Rafael Bridge, as well as for stations 1, 2, and 3 in the South Bay. Among the within-bay stations, station 1, the southernmost, ranked lowest in both egg density and larval density although it was not statistically different from the other inner stations—2, 3, and 5.

The stations also differed in the proportion of eggs to larvae. While the ratio of eggs to larvae was generally greater than 10:1, at station 3 the ratio of the mean number of eggs to mean number of larvae was <10:1 (Fig. 3). The proportions were statistically different among stations (Chi-square $P <$

TABLE 1.—Analysis of variance of northern anchovy eggs: month by station.

Source of variation	Sum of squares	df	Mean square	F	Significance
Residual	42.23	54	0.78		
Constant	286.22	1	286.22	366.02	0.000
Month	128.93	11	11.72	14.99	0.000
Station	7.56	5	1.51	1.93	0.104
Month × station	0.48	1	0.48	0.61	0.437

TABLE 2.—Analysis of variance of northern anchovy larvae: month by station.

Source of variation	Sum of squares	df	Mean square	F	Significance
Residual	25.77	54	0.48		
Constant	220.65	1	220.65	462.43	0.000
Month	13.72	11	1.25	2.61	0.010
Station	7.59	5	1.52	3.18	0.014
Month × station	1.16	1	1.16	2.43	0.125

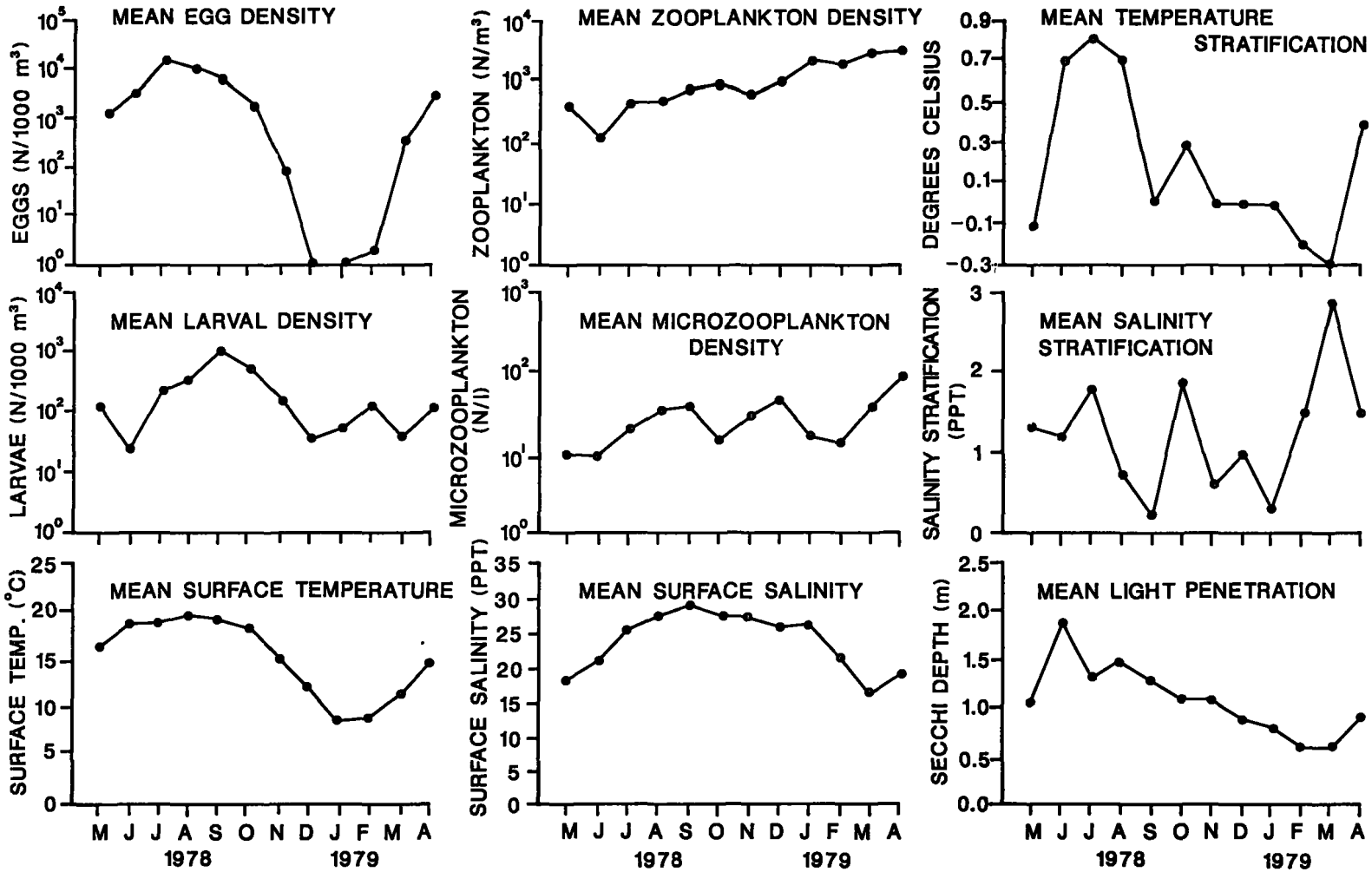

FIGURE 2.—Monthly abundance of northern anchovy eggs, larvae, microzooplankton, zooplankton, and monthly values of surface water temperature, surface salinity, temperature stratification, salinity stratification, and light penetration.

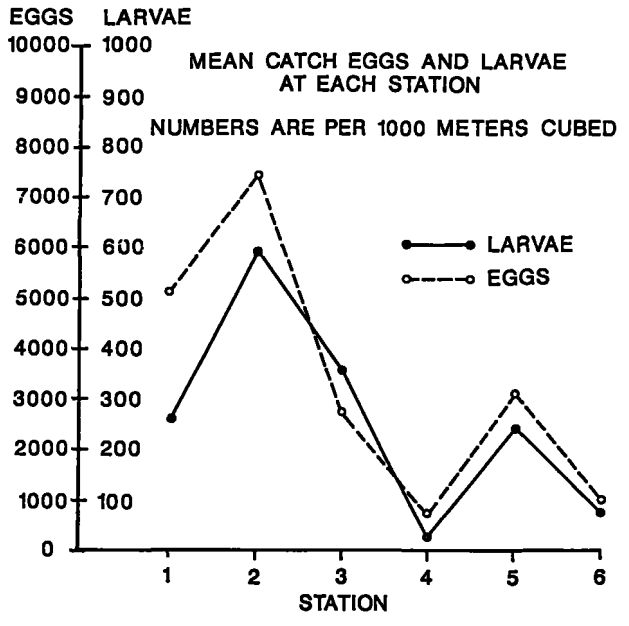

FIGURE 3.—Relative abundances of northern anchovy eggs and larvae at each station showing the difference between station 3 and the other stations.

0.01 with 5 degrees of freedom). Station 3 deviated most from the expected ratio. Station 1 also differed by having relatively fewer larvae than expected.

Zooplankton

Zooplankton catch varied from 13.6-9,560 individuals/m^3. Mean catch was 1,170/m^3. No seasonal pattern was apparent (Fig. 2). There was a gradual increase in zooplankton abundance over the course of the study. This linear trend was significant ($P < 0.01$). Copepods, especially *Acartia* spp., dominated the catches (Table 3). Brachyuran (crab) zooeae and cirrepedian (barnacle) nauplii and cyprids were occasionally abundant. Potential predators on northern anchovy larvae, such as chaetognaths and pontellid copepods, were often present but in relatively low numbers. Counts of zooplankton for each sample are reported in McGowan (unpublished M.A. Thesis, San Francisco State University, San Francisco, CA).

Zooplankton catch was significantly correlated with all variables except surface salinity and salinity stratification. Negative correlations were observed with egg density, surface temperature, temperature stratification, and Secchi depth. Positive correlations were found with larvae and microzooplankton.

TABLE 3.—Zooplankton: relative density, May 1978-April 1979.

Taxon	mean ±1 SE		$n \cdot m^{-3}$	%
Copepoda				
Acartia	1,120	±	192	96.05
harpacticoida	4.67	±	1.55	0.40
other	3.48	±	0.75	0.30
shrimp zoeae	3.82	±	1.28	0.33
crab zoeae	12.27	±	4.27	1.04
mysids	1.31	±	1.16	0.10
amphipods	0.39	±	0.16	0.03
pelecypods	1.10	±	0.35	0.09
chaetognaths	0.59	±	0.23	0.05
polychaetes	1.26	±	0.50	0.11
isopods	0.23	±	0.12	0.02
barnacle nauplii	9.18	±	2.04	0.78
barnacle cyprids	6.18	±	1.49	0.52
gastropods	0.74	±	0.37	0.06
cumaceans	0.08	±	0.05	0.01
cladocerans	0.81	±	0.31	0.07

Microzooplankton

Microzooplankton catch at the surface (0.080 mm mesh net) varied from 1 to 300 per liter (mean = 28.8). No clear seasonal trend was apparent (Fig. 2). Copepod nauplii were the most abundant microzooplankton followed by tintinnids and rotifers (Table 4). Dinoflagellates such as *Ceratium* and *Peridinium* were occasionally more abundant than copepod nauplii. The spiny, armored *Ceratium* species were not included in the density estimates because northern anchovy larvae prefer unarmored forms (Scura and Jerde 1977). Microzooplankton density was negatively correlated with Secchi disk depth ($r = -0.34$, $P = 0.004$) and positively corre-

TABLE 4.—Microzooplankton: relative density, May 1978-April 1979.

Taxon	mean ±1 SE	$n \cdot 1^{-1}$	%
copepod nauplii	15.14 ±	1.82	54.97
barnacle nauplii	0.56 ±	0.09	2.03
polychaete larvae	0.36 ±	0.08	1.31
tintinnids	6.56 ±	2.68	23.82
rotifers	1.24 ±	0.45	4.50
harpacticoid copepods	0.03 ±	0.02	0.11
ostracods	0.01 ±	0.01	0.04
gastropod veligers	0.04 ±	0.02	0.15
Peridinium	3.59 ±	1.45	13.03

lated with zooplankton density ($r = 0.27, P = 0.027$). All interpretation of the microzooplankton data was done under the assumption that estimates of volume filtered are accurate.

Environmental Variables

The mean surface water temperature during this study was 15.2°C. The coldest reading was 8.0°C at station 2 in January; the warmest was 22.5°C at station 1 in August (Fig. 2). Water temperature near the bottom varied from 8° to 21.5°C (mean = 15.0°C). Mean temperature stratification, the difference between the surface and bottom temperatures, was 0.2°C. Stratification was generally present June through October, especially at station 5. Mean stratification during these months was 0.5°C (Fig. 2). During February and March 1979 the surface temperature was lower, on average, than the temperature near the bottom thus showing the influence of air temperature on the surface water temperature. Surface salinity varied from 3 to 31‰ (mean = 23.6‰). Bottom salinity was 14-31‰ (mean = 24.8‰). The low readings for both surface and bottom salinity occurred at station 5 during March 1979. Surface salinity at station 1 was usually low, showing the influence of freshwater inflow at the south end of the Bay (Fig. 2). Salinity at station 6 was relatively high, showing the oceanic influence at the Golden Gate. Surface salinity at other stations reflected their relative positions between these two influences. The lowest surface salinity was always at station 5 due to the Sacramento River discharge. During March 1979, salinity at stations 4 and 6 also showed the effects of high freshwater discharge which lowered the salinity at station 5 to 3‰. Salinity was slightly lowered this month at station 3 in South Bay also. Surface salinity followed a seasonal pattern; it was high from July through January and low in the winter and spring months. Relatively high salinity corresponded to high temperature July through October. Salinity stratification was generally <2‰ except at station 5 where the average stratification was 4.7‰ (Fig. 2).

Surface salinity was negatively correlated with salinity stratification, ($r = -0.62, P < 0.001$), and positively correlated with Secchi depth ($r = 0.39$, $P = 0.001$). Salinity stratification was negatively correlated with Secchi depth ($r = -0.29, P = 0.012$).

Turbidity

Light penetration was lowest at stations 1 and 5, and highest at stations 6, 4, and 3 (Fig. 2). The mean depth of light penetration during this study was 1.1 m with a range of 0.1-2.5 m. The data suggest a weak seasonal trend with light transmission higher in summer and lower in winter. The variable with the strongest linear association with Secchi depth was zooplankton density. Light penetration was inversely related to zooplankton density ($r = -0.58$).

Relationships Among Varibles

Northern anchovy egg abundances were positively associated with surface temperature, temperature stratification, and Secchi disk depth and negatively correlated with zooplankton density (Table 5). Eggs were positively associated with larvae but this correlation was not significant at the 5% level ($P = 0.053$). Larvae were positively correlated with surface temperature and zooplankton density (Table 5). They were negatively correlated with Secchi depth. Thus, eggs and larvae both were significantly correlated with zooplankton and Secchi depth but in opposite directions: eggs were associated with clearer water and lower zooplankton density, larvae with more turbid water and higher zooplankton density.

Stepwise Multiple Regression

Surface temperature alone explained 65% of the variability in egg density ($r^2 = 0.651$). The combination of microzooplankton density with surface temperature explains an additional 1.5% of the variability of egg density. The addition of all other variables only increased the amount of variability explained to 68% ($r^2 = 0.678$). The predictive regression model using the independent variables whose addition to the model improved its prediction by more than 1% is

$$E = -2.20 + 0.317T - 0.502M$$

TABLE 5.—Bivariate correlations between northern anchovy eggs, larvae, and other variables. EGGS: log (eggs·m^{-3}); LARV: log (larvae·m^{-3}); ZOOP: log (zooplankters·m^{-3}); MICR: microzooplankton; TEMP: surface water temperature; SALI: surface water salinity; TSTR: temperature stratification; SSTR: salinity stratification; SECC: Secchi disk depth.

	EGGS	LARV	ZOOP	MICR	TEMP	SALI	TSTR	SSTR
LARV	0.23+							
ZOOP	−0.38**	0.29*						
MICR	−0.11	−0.02	0.27*					
TEMP	0.81**	0.31**	−0.46**	0.02				
SALI	0.18	0.08	−0.20	−0.16	0.19			
TSTR	0.40**	0.17	−0.25*	−0.02	0.46**	0.06		
SSTR	−0.10	0.07	0.05	0.09	−0.03	−0.62**	0.12	
SECC	0.35**	−0.34**	−0.58**	−0.34**	0.32**	0.39**	0.20	−0.29*

* Significant at $P = 0.05$.
**Significant at $P = 0.01$.
\+ $P = 0.053$.

where E = log (eggs/1,000 m^3 + 1)
T = surface temperature (°C)
M = log (microzooplankton/l + 1), (Table 6).

No single variable explained the majority of the variability in larval density (Table 7). Secchi depth was the single best predictor, accounting for 11% of the variance of larval density ($r^2 = 0.113$). The combination of surface temperature with Secchi depth increased the coefficient of determination to 0.306. All of the variables combined explained just 50% of the variability of larval density ($r^2 = 0.498$). Five variables improved the prediction of the set of independent variables by more than 1% when added to the model. The predictive equation for larval density based on using these five is

$$L = -0.842 - 0.591X + 0.126T + 0.515Z - 0.571M + 0.029S$$

where L = log (larvae/1,000 m^3 + 1)
X = Secchi depth (m)
T = surface temperature (°C)
Z = log (zooplankton/1,000 m^3 + 1)
M = log (microzooplankton/l + 1)
S = surface salinity (‰).

The results of the multiple regressions show that northern anchovy egg density could be predicted largely by surface water temperature. Larval density could not be predicted well by a single variable or by the five variables which, when combined, accounted for only 49% of the variability.

Spawning Stock Estimates

Based on estimates of egg production, the spawning stock biomass of northern anchovies in the part of San Francisco Bay sampled in this study ranged from undetectable in December 1978 and January 1979 (no eggs collected) to 696 t (metric tons) (767 short tons) in July 1978. If the area of the Bay which is <2 m deep were included, the estimate of July biomass would have been 2,030 t (2,240 short tons).

TABLE 6.—Stepwise multiple regression: northern anchovy egg density vs. biological and environmental variables.

Independent variable	Multiple r^2	Change in r^2
Surface temperature	0.651	0.651
Microzooplankton	0.666	0.015
Salinity stratification	0.670	0.004
Surface salinity	0.672	0.002
Secchi depth	0.675	0.003
Zooplankton	0.677	0.002
Temperature stratification	0.678	0.001

TABLE 7.—Stepwise multiple regression: northern anchovy larval density vs. biological and environmental variables.

Independent variable	Multiple r^2	Change in r^2
Secchi depth	0.113	0.113
Surface temperature	0.306	0.194
Zooplankton	0.392	0.085
Microzooplankton	0.459	0.067
Surface salinity	0.486	0.028
Salinity stratification	0.495	0.009
Temperature stratification	0.498	0.003

Length Frequencies of Larvae

Monthly samples could contain larvae from the current month and 2 previous ones because metamorphosis is not complete until 35 mm, age 74 days at 16°C (Hunter 1976). However, larvae longer than 15 mm were not taken at the standard stations from August through October, although eggs and smaller

larvae had been abundant since June (Fig. 4). Larvae >15 mm long were found over the shoals near station 3 in October and April (Fig. 5). Larvae longer than 15 mm were taken in the channel from November through February, months with little or no spawning. Large larvae and juveniles, which had apparently overwintered, were present when spawning resumed in March and April.

DISCUSSION

Previous suggestions that northern anchovy spawn in San Francisco Bay were based on the presence of small larvae (Eldridge 1977; Sitts and Knight 1979), juveniles (Smith and Kato 1979), or the spawning season in the California Current (Hubbs 1925). Anchovy eggs collected in this study provide conclusive evidence that the northern anchovy spawns in San Francisco Bay because eggs could not drift upstream to station 5 or into South Bay as far as station 1 or 2. Peak spawning based on the abundance of eggs was May through September when adult anchovies are known to be plentiful in the Bay (Aplin 1967).

Spawning in San Francisco Bay differed from anchovy spawning in the sea. Most spawning of the central subpopulation of northern anchovy in the California Current takes place January-April when the 10 m temperature is 14°-16°C; not June through October when water temperature is 16°-19°C

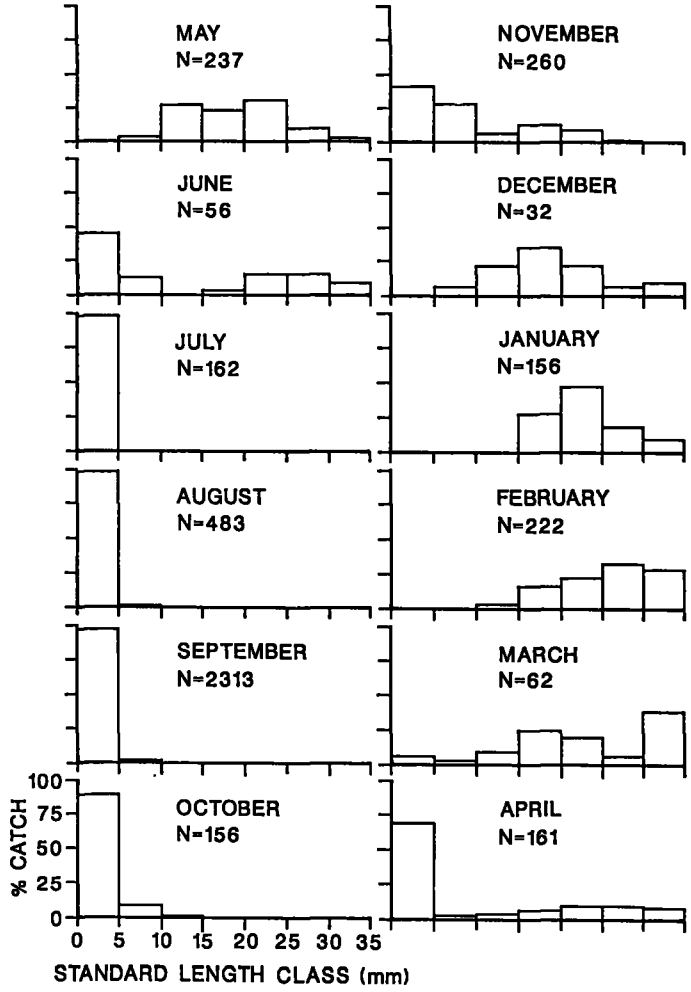

FIGURE 4.—Length-class frequencies of larvae and juvenile northern anchovies for each month of the study.

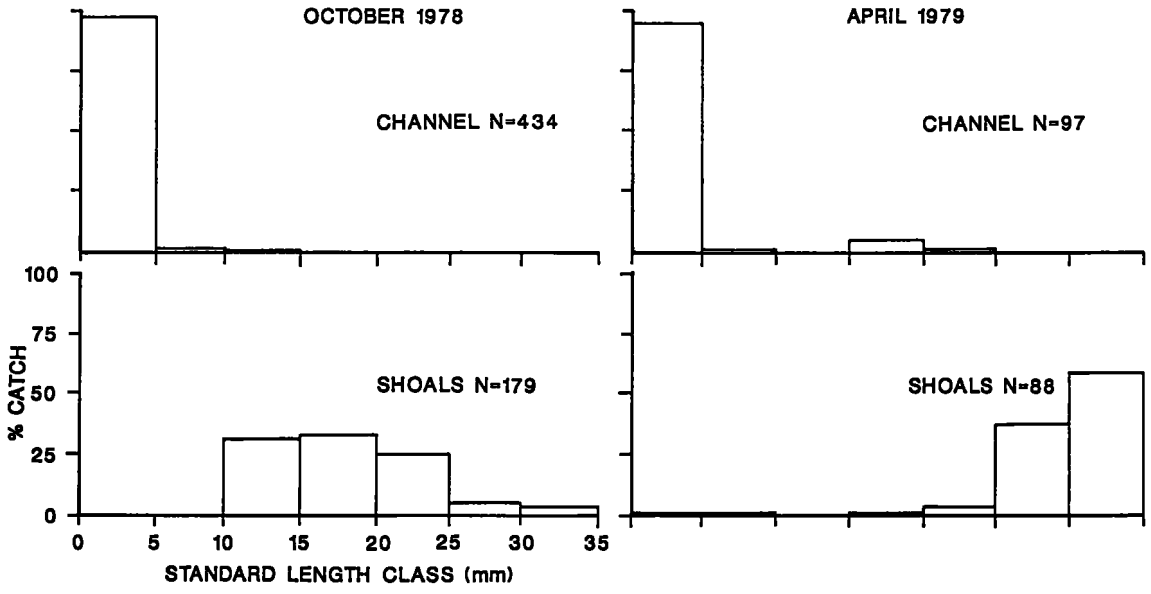

FIGURE 5.—Length-class frequencies of larvae and juvenile northern anchovies for October 1978 and April 1979 showing the different sizes caught in the channel versus those in shallow water.

(Smith and Lasker 1978). The northern subpopulation spawns off Oregon and Washington from mid-June to mid-August when 1 m temperatures are 14°-17°C (Richardson 1980). These two subpopulations overlap at San Francisco (Vrooman et al. 1981) and the spawning season in the Bay overlapped the spawning seasons of both subpopulations. But spawning in the Bay took place at higher temperatures than usual for either population in the ocean (13°-18°C, Brewer 1976). Few eggs were taken in the Bay from December 1978 to March 1979 when water temperature was below 13°C. However, at station 3 in March 1979, 477 eggs were taken at a water temperature of 11.5°C. Peak spawning in the Bay was in July, August, and September when the mean water temperature was 19.0°, 19.8°, and 19.2°C, respectively. The highest catch of eggs occurred at station 2 in July at 21.0°C. Eggs were also plentiful at station 1 in August at 22.5°C. During June, July, and August, eggs were least abundant at stations 4 and 6, where water temperature was relatively low. During September and October, egg densities at stations 4 and 6 peaked, as did water temperature at these stations. Sitts and Knight (1979) found larvae shorter than 4 mm at 18°-22°C in the Sacramento-San Joaquin estuary in July and August. Although much of the northern anchovy spawning took place in the Bay within the previously reported temperature range and some took place at low temperatures, most occurred in water warmer than in the coastal spawning regions. The strong correlation of egg abundance with temperature includes potential confounding effects of presumed seasonal influx of adults, apparent "preference" for spawning within the Bay, and differences in dilution due to tidal exchange which affected stations 4 and 6 more than the other stations. Therefore the correlations are descriptive, perhaps predictive, but not causal.

In the California Current, temperature, upwelling, and stable stratification of the water column are thought to interact to produce favorable conditions for anchovy larvae (Lasker 1975). In San Francisco Bay there is no upwelling, but salinity or freshwater outflow variability might influence ecological conditions. Freshwater flow may have an indirect effect by promoting blooms of certain phytoplankton or by retaining particles through estuarine circulation (Cloern 1979). Relatively high salinity coincided with warm temperatures at the beginning of the spawning season, but spawning ceased in November when water temperature decreased to 13°C, although salinity remained high until February. Sitts and Knight (1979) found larvae shorter than 10 mm at low salinity (<10‰) and relatively high temperature (>18°C). They found only large larvae (>10 mm) in November when water temperature fell below 13°C.

In this study, only temperature had a strong direct relationship with abundance of eggs and larvae;

peak abundance tracked the seasonal temperature cycle closely. Temperature stratification was most pronounced in June-October when spawning was greatest, especially at station 5 where salinity stratification was also most noticeable.

Offshore transport of eggs and larvae is believed to be one of the environmental hazards to anchovy reproductive success (Bakun and Parrish 1982). Peak spawning in the Bay took place in June-August, the months of greatest offshore directed Ekman transport at the latitude of San Francisco (Parrish et al. 1981). Larvae, retained in San Francisco Bay by estuarine circulation or behavior, would not be subject to offshore drift into areas of low plankton density. Therefore, they may have a higher probability of survival than larvae in the California Current and they might survive during bad years for oceanic larvae.

Within San Francisco Bay there were apparent differences between spawning habitat and larval habitat. Eggs and small larvae were more abundant in warm, clear, thermally stratified water with relatively less plankton; large larvae were found in shallow, warm, less stratified, plankton-rich water with reduced light penetration. Negative correlations between zooplankton and the eggs of zooplanktivorous fishes were attributed to predation on the zooplankton by de Ciechomski and Sanchez (1983). Cannibalism on larvae by adult northern anchovies and competition between adults and juveniles are two reasons why separate habitats would be adaptive. Because spawning and nursery habitats differ in location and environmental properties, it is not surprising that multiple regression variables measured in the spawning habitat did not predict larval abundance. It may be that spawning areas are selected by adults, perhaps for feeding (Brewer 1978) or for water clarity, while larger larvae seek different conditions where their survival is determined by other factors than those which affect first-feeding larvae. If variable mortality on the larger larvae determines eventual recruitment, then recruitment may be largely decoupled from spawning and first-feeding conditions. This could explain why predictions of recruitment from larval surveys (which do not adequately sample large larvae and juveniles) have not been reliable.

The conditions where larvae were more abundant are more characteristic of shallow nearshore water than of the California Current. Juveniles and young of the year are also relatively more abundant nearshore in California (Parrish et al. 1986). In 1978, when spawning was restricted to nearshore areas, apparent recruitment was high relative to 1979 when spawning was offshore (Hewitt and Methot 1982). The 1978 spawning season for California Current anchovy was not typical; storms prevented favorable conditions for larvae until March in southern California (Lasker 1981). Nearshore areas might be refugia during anomalous years and they could contribute a disproportionate number of recruits every year (Brewer and Smith 1982).

It might be argued that the 20-30 mm larvae found nearshore in the Southern California Bight (Brewer and Smith 1982) merely avoided the nets in standard CalCOFI tows, but I found a similar pattern with respect to length frequencies when comparing samples taken in the channels and in shallow water in San Francisco Bay. That is, larger larvae were found in shallower zooplankton-rich areas. Estuaries and nearshore areas may provide conditions favorable enough for survival of larvae and juveniles to compensate for low mean food density and for occasional years of unfavorable oceanographic conditions in the California Current.

San Francisco Bay northern anchovy larvae, especially those which overwinter, are subject to different ecological conditions than those in the California Current, thus they may have slightly different morphology and meristics (Hempel and Blaxter 1961; Blaber et al. 1981). The San Francisco Bay subspecies *Engraulis mordax nanus* Hubbs (1925) may be an ecotype of *E. mordax*.

A female northern anchovy has enough energy stored as fat for 17 of its 20 annual batches of eggs, but protein for egg production must come from feeding during the spawning season (Hunter and Dorr 1982). The primary food of northern anchovy, zooplankton, was abundant in the Bay. I found a mean density of 1 zooplankter/L with a 0.308 mm mesh net, but this is an underestimate of copepodites and small copepods because of the relatively large mesh size. By comparison, Hutchinson (1981) found at least order of magnitude greater densities at nearby stations over the same time period using 0.080 and 0.064 mm mesh nets. Anchovy feed by biting individual organisms or by filter-feeding if particle density is high enough. The laboratory-determined threshold for filter-feeding is 5-18 particles (0.236 mm wide) per liter (Hunter and Dorr 1982). My zooplankton density estimate, which was biased conservatively, is of the order of magnitude required to stimulate filter-feeding. Therefore, I conclude that zooplankton prey for adult northern anchovies were abundant in the Bay during this study.

For the Bay to be a good larval nursery area it should have abundant microzooplankton prey for lar-

vae. I found a mean density of 28.8 per liter using a 0.080 mm mesh net (probably a conservative estimate because of net clogging and meter malfunctioning). This is higher than would be expected in the California Current using the same mesh size (<1 per liter, Arthur 1977). It is comparable to the 36 per liter found with a finer mesh net (Arthur 1977). It is an underestimate of available prey for larvae because they consume particles as small as 0.040 mm, and there is a peak of biomass of small plankton in the California Current at 0.070 mm (Arthur 1977), just below the mesh size of my net. Sitts and Knight (1979) found a mean density of 32.3 copepod nauplii/L in a 1-yr study in the Sacramento-San Joaquin estuary using 0.060 mm mesh. Hutchinson (1981) found approximately 10 nauplii/L over the same period of time as this study. (I calculated this value from her data for density of nauplii at 1 m depth at her stations 19 and 30 which correspond to my stations 6 and 2.) My microzooplankton estimates did not adequately represent the rotifers, tintinnids, and other small larval prey which were collected in high numbers with finer mesh nets (Hutchinson 1981). These organisms are known to be eaten by northern anchovy larvae and I observed tintinnids in the guts of some larvae.

Larvae reared in the laboratory generally require more than 1,000 prey items/L for good survival, but some survival occurs at lower densities. Houde (1978) obtained 1% survival to metamorphosis of *Anchoa mitchilli* with a prey density of 27 per liter. Northern anchovy larvae in the sea which obtain enough food to survive also obtain enough to grow rapidly (Methot and Kramer 1979). The existence of dense patches of food has been suggested to account for the discrepancy between average food densities observed in the sea and those needed in the laboratory. Dense patches of larval prey might not be needed in the Bay where I found mean prey density higher than that typical of the California Current. However, dense patches of microzooplankton would be expected in the Bay because blooms of their prey, phytoplankton, occur (Cloern 1982). Dense patches of microzooplankton, undetected by my sampling design, would make San Francisco Bay a very good feeding area for larval northern anchovies. Because the water was warmer in the Bay than in the California Current, larvae could search a larger volume of water per unit time, they would encounter high densities of prey and would be expected to survive in greater numbers and to grow rapidly. Therefore, San Francisco Bay may be a good feeding area for larvae as well as for spawning adults.

To my knowledge, my estimates of spawning biomass of northern anchovies in the Bay are the first such estimates. Are they reasonable, and what are the implications of this biomass of anchovies in the Bay? The estimate based on egg abundance assumes that parameters estimated for California Current anchovies apply to San Francisco Bay anchovies. I argue they do because parameters for the estimate were obtained from anchovies at the peak of spawning in the California Current in 1978, the year my study began. I believe these parameter values may be applied to the anchovy population in San Francisco Bay because the seasonal pattern of spawning and abundance of anchovies in the Bay indicates that most of these anchovies are seasonal migrants from the California Current stocks. No actual measurements of batch fecundity of anchovy in the Bay have been taken so the values used are the best available. Errors in estimating egg and larval abundances are probably more important than small changes in the estimates of batch fecundity. The egg-based estimate could be high if adults leave the Bay immediately after spawning or if they spawn more frequently due to greater food availability. The estimate could be low if they spawn infrequently because the season is later than the regular spawning season in the California Current or if higher temperatures greatly increase metabolic needs.

The estimate is conservatively biased because I merely divided the number of eggs caught by the number of days to hatch at the measured temperature without considering mortality. During the months with peak egg abundance the estimated time to hatch was 2 d. If egg mortality was 0.184 da^{-1} (Picquelle and Hewitt 1984), then the estimate was approximately 25% low. The estimate would be high if eggs were present only in the channel and not over the area used to calculate total abundance. However, station 3, in shallow water near San Bruno Shoal in South San Francisco Bay, had high egg densities; therefore, eggs were distributed in some shallow-water areas. Stations 1 and 2, which had high egg densities, represented small areas, while stations 4 and 6 with low densities represented large areas. San Pablo Bay and the rest of the North Bay were not included in the biomass estimate. Potential biases in the egg-based stock estimate either cancel one another or give a conservative estimate.

My estimate is consistent with information from other studies. I found mean values of 3,360 eggs/1,000 m^3 and 259 larvae/1,000 m^3. Hutchinson (1981) found 4,730 eggs/1,000 m^3 (my calculations from her stations 19 and 30). Sitts and Knight (1979) calculated a mean larval abundance of 490 per 1,000

m^3. The estimates of larval densities are similar to estimates for the Southern California Bight nearshore CalCOFI area in 1978-79 (461 per 1,000 m^3, calculated from table 4 of Brewer and Smith 1982, assuming average tow depth = 210 m; two-thirds of the stations were >210 m according to their table 2). The mean density of eggs in the Bay was much higher than in the Southern California Bight nearshore CalCOFI area (310 per 1,000 m^3, Brewer and Smith 1982). The seasonal northern anchovies fishery in the Bay took approximately 481 tons for frozen and live bait (Smith and Kato 1979). My estimate is adequate to permit such a yield.

Northern anchovy females need a daily ration of 4-5% of their body weight of copepods per day to support growth and reproduction (Hunter and Leong 1981). Approximately 5% of caloric intake goes into growth. Using these values, 38.35 tons of copepods per day would be consumed by the July biomass of 767 tons of anchovies. Growth would be about 1.92 tons per day. Doing similar calculations for each month and summing for the 12 mo of this study result in an estimate of 3,260 tons of copepods consumed and a net annual production of 158 tons of anchovy growth. If the egg estimates based on the area of the Bay, including the shallow areas were used, the consumption of copepods and growth estimates would be approximately doubled. These calculations are a first order estimate of the impact of a carnivorous planktivore on zooplankton in the Bay. The energy converted to anchovy growth would be removed from the Bay, so the estimate of net growth is also a minimum estimate of a sink for Bay production as growth of a transient consumer. In San Francisco Bay where plankton production from a limited area is being consumed by a large, transient anchovy population, grazing by anchovy could conceivably limit zooplankton abundance seasonally. Although it is impossible to distinguish between grazing and interannual differences without estimates of zooplankton production, zooplankton was more abundant in winter 1978-79 when adult anchovies were absent.

A large biomass of planktivores could have other effects on the ecology of the Bay. Selective feeding by clupeoids on larger organisms in lakes can affect the zooplankton community structure (Brooks and Dodson 1965). Northern anchovy schools can also have an impact on nutrient cycling. Smith and Epley (1982) calculated that ambient ammonium concentration would be nearly doubled behind an anchovy school in the Southern California Bight. McCarthy and Whitledge (1972) estimated that nitrogen excretion by the Peruvian anchoveta is an order of magnitude greater than zooplankton excretion, so fish excretion may be the major source of regenerated nitrogen nutrients for phytoplankton production. These high nitrogen inputs would be patchy (Blaxter and Hunter 1982) and their importance would depend on whether or not background levels of nutrients were limiting. Nutrients may not be limiting in San Francisco Bay where light penetration and residence time control phytoplankton dynamics (Cloern 1979). Laboratory studies of copepod productivity, anchovy predation, and nutrient regeneration are needed to define quantitatively the impact of the northern anchovy on plankton dynamics in the Bay. A complete description of the trophic role of anchovy in the Bay should include estimates of zooplankton consumption by larvae, cannibalism by adults, and predation on adult and larval anchovies.

CONCLUSION

San Francisco Bay is a favorable area for northern anchovy spawning because it has abundant food for adults, protection from advective loss for eggs, and abundant food for larvae. There is apparent habitat partitioning between spawning adults and larger larvae which could adaptively reduce predation and competition. Recruitment to the California Current stocks may be determined more by events in the nursery habitat of larvae and juveniles than by conditions favorable for spawning adults and first-feeding larvae; therefore, further work in estuaries and nearshore areas is warranted.

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LITERATURE CITED

APLIN, J. A.
1967. Biological survey of San Francisco Bay, 1963-1966. Calif. Fish Game, Mar. Resour. Oper. Lab. Ref. No. 67-4, 131 p.

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74: 517-530.
1977. Distribution, size, and abundance of microcopepods in the California Current System and their possible influence on survival of marine teleost larvae. Fish. Bull., U.S. 75: 601-611.

BAKUN, A., AND R. H. PARRISH.
1982. Turbulence, transport, and pelagic fish in the California and Peru current systems. CalCOFI Rep. 23:99-112.

BLABER, S. J., D. P. CYRUS, AND A. K. WHITFIELD.
1981. The influence of zooplankton food resources on the morphology of the estuarine clupeid *Gilchristella aestuarius* (Gilchrist, 1914). Environ. Biol. Fish. 6:351-355.

BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 1-223.

BREWER, G. D.
1976. Thermal tolerance and resistance of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:433-445.
1978. Reproduction and spawning of the northern anchovy, *Engraulis mordax*, in San Pedro Bay, California. Calif. Fish Game 64:175-184.

BREWER, G. D., AND P. E. SMITH.
1982. Northern anchovy and Pacific sardine spawning off Southern California during 1978-1980: preliminary observations on the importance of the nearshore coastal region. CalCOFI Rep. 23:160-171.

BROOKS, J. L., AND S. I. DODSON.
1965. Predation, body size, and composition of plankton. Science 150:28-35.

CLARKE, T. A.
1983. Comparison of abundance estimates of small fishes by three towed nets and preliminary results of the use of small purse seines as sampling devices. Biol. Oceanogr. 2:311-340.

CLOERN, J. E.
1979. Phytoplankton ecology of the San Francisco Bay system: the status of our current understanding. *In* T. J. Conomos (editor), San Francisco Bay: the urbanized estuary, p. 247-264. AAAS Pac. Div., San Franc., CA.
1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? Mar. Ecol. Prog. Ser. 9:191-202.

CONOMOS, T. J., AND D. H. PETERSON.
1977. Suspended particle transport and circulation in San Francisco Bay: an overview. *In* M. Wiley (editor), Estuarine processes, Vol. 2, p. 82-97. Acad. Press, N.Y.

DE CIECHOMSKI, J. D., AND R. P. SANCHEZ.
1983. Relationship between ichthyoplankton abundance and associated zooplankton biomass in the shelf waters off Argentina. Biol. Oceanogr. 3:77-101.

ELDRIDGE, M. B.
1977. Factors influencing distribution of fish eggs and larvae over eight 24-hr samplings in Richardson Bay, California. Calif. Fish Game 63:100-116.

HEMPEL, G., AND J. H. S. BLAXTER.
1961. The experimental modification of meristic characters in herring (*Clupea harengus* L.). J. Cons. Perm. Explor. Mer 26:336-346.

HEWITT, R. P., AND R. D. METHOT JR.
1982. Distribution and mortality of northern anchovy larvae in 1978 and 1979. CalCOFI Rep. 23:226-245.

HOUDE, E. D.
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395-411.

HUBBS, C. L.
1925. Racial and seasonal variation in the Pacific herring, California sardine, and California anchovy. Calif. Fish Game, Fish Bull. 8, 23 p.

HULL, C. H., AND N. H. NIE (editors).
1981. SPSS update 7-9. McGraw-Hill Book Co., N.Y.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

HUNTER, J. R., AND H. DORR.
1982. Thresholds for filter feeding in northern anchovy, *Engraulis mordax*. CalCOFI Rep. 23:198-204.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.

HUTCHINSON, A.
1981. Zooplankton species composition and abundance in the South Bay, 1978-1979. U.S. Geol. Surv. Open File Rep. 81-132.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177:322-354.
1981. Marine fish larvae. Univ. Wash. Press, Seattle, 131 p.

LUND, J. W. G., C. KIPLING, AND E. D. LECREN.
1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11:143-170.

MCCARTHY, J. J., AND T. E. WHITLEDGE.
1972. Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*). Fish. Bull., U.S. 70:395-401.

MCGOWAN, M. F., AND F. H. BERRY.
1984. Clupeiformes: development and relationships. *In* H. G. Moser et al. (editors), Ontogeny and systematics of fishes, p. 108-126. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1, 760 p.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engralis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Fish Game, Fish Bull. 157, 235 p.

MONTGOMERY, D. C.
1976. Design and analysis of experiments. John Wiley & Sons, N.Y., 418 p.

MURPHY, G. I., AND R. I. CLUTTER.
1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. SPSS: statistical package for the social sciences. 2d ed. McGraw-Hill Book Co., N.Y.

PARKER, K.
1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78:541-544.

PARRISH, R. H., D. L. MALLICOATE, AND K. F. MAIS.
1986. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:483-496.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

PICQUELLE, S. J., AND R. P. HEWITT.
1984. The 1983 spawning biomass of the northern anchovy. CalCOFI Rep. 25:16-27.

RECKSIEK, C. W., AND H. W. FREY.
1978. Biological, oceanographic, and acoustical aspects of the market squid, *Loligo opalescens* Berry. Calif. Fish Game, Fish Bull. 169:1-185.

RICHARDSON, S. L.
1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855-876.

SCURA, E. D., AND C. W. JERDE.
1977. Various species of phytoplankton as food for larval northern anchovy *Engraulis mordax*, and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fish. Bull., U.S. 75:577-583.

SITTS, R. M., AND A. W. KNIGHT.
1979. Plankton ecology in the Sacramento-San Joaquin estuary. Water Sci. Eng. Pap. No. 4509, 145 p. Univ. Calif. Davis, Davis, CA.

SMITH, D. L.
1977. A guide to marine coastal plankton and marine invertebrate larvae. Kendall/Hunt Publ. Co., Dubuque, IA.

SMITH, P. E., AND R. W. EPPLEY.
1982. Primary production and the anchovy population in the Southern California Bight. Limnol. Oceanogr. 27:1-17.

SMITH, P. E., AND R. LASKER.
1978. Position of larval fish in an ecosystem. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:77-84.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. No. 175, Rome.

SMITH, S. W., AND S. KATO.
1979. The fisheries of San Francisco Bay: past, present, and future. *In* J. T. Conomos (editor), San Francisco Bay: the urbanized estuary, p. 445-468. AAAS Pac. Div., San Franc., CA.

TYLER, J. E.
1968. The Secchi disk. Limnol. Oceanogr. 13:1-6.

VROOMAN, A. M., P. A. PALOMA, AND J. R. ZWEIFEL.
1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*. Calif. Fish Game 67:39-51.

WANG, J. C.
1981. Taxonomy of the early life stages of fishes: fishes of the Sacramento-San Joaquin estuary and Moss Landing Harbor-Elkhorn Slough, California. Ecological Analysts, Inc., Concord, CA., 168 p.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes - a general model. Fish. Bull., U.S. 74:609-621.