ESTIMATION OF THE EFFECTS OF ENVIRONMENTAL VARIATIONS ON THE EGGS AND LARVAE OF THE NORTHERN ANCHOVY

REUBEN LASKER AND PAUL E. SMITH

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Expanded studies of stock and recruitment at the Southwest Fisheries Center have led to additional objectives for laboratory and field work concerning the northern anchovy, *Engraulis mordax*. In addition to monitoring the stock size of the spawning portion of the anchovy population, we have begun to examine the possible causes and rates of larval mortality.

In this paper we show that the sampling effort required to measure changes in larval survival must be much greater than that used to monitor anchovy spawning biomass, i.e., closer intervals of sampling (in time and space) will be needed over relatively broad areas. Although existing sampling techniques are probably adequate to accomplish this, we show that there still remains the need to refine our statistical methods for analyzing larval age groups, data required for assigning larval mortality rates.

Changes in anchovy spawning are compared to seasonal and annual variations in sea water temperature, vertical temperature gradients, upwelling, California Current speed, flushing rate of the Southern California Bight, and secondary production. It appears that the usual habit of the anchovy to spawn in the southern California area in winter, alters radically in some years. The cause for this is not yet known. Quarterly apparent mortality rates are assembled for the years of greatest environmental changes in the southern California regions for anchovy eggs and larvae (to 6.25 mm).

New biological information needed for analyzing the causes of anchovy larval mortality has been assembled. For example, first feeding anchovy larvae require abundant food in a narrow size range and of particular species. *Gymnodinium splendens*, a naked dinoflagellate about 40 μm in diameter, supports growth when it occurs in concentrations of 20 or more cells per ml. Tests with laboratory reared larvae have confirmed the existence of suitable strata of larval food organisms in nearshore waters which are associated with chlorophyll maximum layers at 15–30 m depth. Storms were observed to disperse the food organisms until they were too low in number to support larval growth.

INTRODUCTION

Review of Field and Laboratory Research on California Anchovy, and the CalCOFI Program

In the last two decades (1955–1974) the northern anchovy, *Engraulis mordax*, supplanted the Pacific sardine, *Sardinops caerulea*, in biomass and in the commercial and live bait fisheries off the California coast (Baxter, 1967; Messersmith, 1969; Ahlstrom, 1966). The northern anchovy is now the chief forage fish for most of the large sport and commercial fishes of the California Current and represents a large, underutilized fishery resource, probably exceeding in biomass the former sardine population.

Estimates from a number of sources (see Messersmith, 1969, for a resume; Smith, 1972) agree that the standing stock of the northern anchovy off California and Baja California exceeded 4 million metric tons in the 1960's. This large population is the result of a rapid increase in numbers of anchovies since 1950 to 1951 when the population was estimated to be less than 1 million metric tons (Smith, 1972). This dramatic increase in numbers and biomass of the anchovy took place while the Pacific sardine population declined to a point where fishing was no longer profitable and when the standing stock of sardines was reaching a low point of less than 10,000 metric tons in 1965 (Smith, 1972) from which it had not recovered in the ensuing 8 years.

Loukashkin (1970) has shown that *E. mordax* is chiefly zooplanktivorous; thus, this large biomass of anchovies undoubtedly has had an impact on the food web, in particular on the secondary production and standing stock of zooplankton of the California Current. It also seems likely that the management of fisheries on the northern anchovy will be complicated by radical shifts in the success of year classes contributing to the fishery.

The fundamental objectives of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program in the California Current region have been to measure the changes in biomass of the major pelagic fish populations inhabiting the region and to find explanations for these changes. Recent major reviews of the CalCOFI program including Marr (1960), Murphy (1966), Ahlstrom (1965, 1968), Smith (1972), and Soutar and Isaacs (1974) permit one to conclude that the major changes in the biomass of several populations in this region have been adequately monitored. In addition, it appears that changes in biomass which have been observed cannot yet be explained in terms of fishing effort, competition among species, or environmental variations.

Most changes in biomass of populations studied

through monitoring a fishery appear to be due to changes in the success of recruitment to the fishable population. For example, spawning success varied independently of the spawning stock size of the sardine population by 7 times, from 1932 to 1957 (Murphy, 1966, p. 77). There is reason to believe similar changes occurred in spawning success of the anchovy (Soutar and Isaacs, 1974) during the last century.

In a renewed attempt to explain changes in biomass, we intend to examine the food requirements of the anchovy at all stages in its life cycle, to describe the incidence of suitable feeding areas in the ocean, and to discuss how changes in food requirements and feeding might affect recruitment. Where it is applicable, suggestions are made to change present sampling programs in order to provide additional information for evaluating changes in the environment as these might induce changes in the anchovy population, e.g., changes in growth rate, mortality, and fecundity. Because of the existence of considerable information on food requirements at the larval stage, and records of larvae from most of the northern anchovy spawning area since 1951, we have chosen to describe in detail the parameters which seem necessary for estimating the effects of environmental variations on survival and growth of anchovy eggs and larvae. We anticipate this will guide future workers who may need to establish similar criteria for studying biomass fluctuations in other fish populations.

ASSESSMENT OF ANCHOVY EGGS AND LARVAE AND ITS RELATIONSHIP TO THE SPAWNING BIOMASS

The amount of effort required for the efficient assessment of eggs and larvae is different when the objective is to monitor the size of the spawning stock than when the objective is to analyze mortality which occurs during the planktonic phase of a fish's life cycle. The surveys now being conducted in CalCOFI have been designed to monitor the spawning biomass. Estimates of mortality require more precise sampling and the evaluation of some major biases. It is the purpose of the following to define sampling requirements for each of these objectives from the long data record from CalCOFI surveys, and from some intensive investigations of local sampling variability.

Pelagic Pattern

The chief obstacle to effective sampling is the intensity of adult anchovy schooling behavior when spawning. In areas where spawning is taking place, newly spawned eggs at densities of hundreds per square meter may be within a few hundred meters of areas where there are no eggs at all. Dispersal of these eggs from the spawning sites is apparently very slow, with identifiable traces of this pattern persisting for the entire time that the larvae are
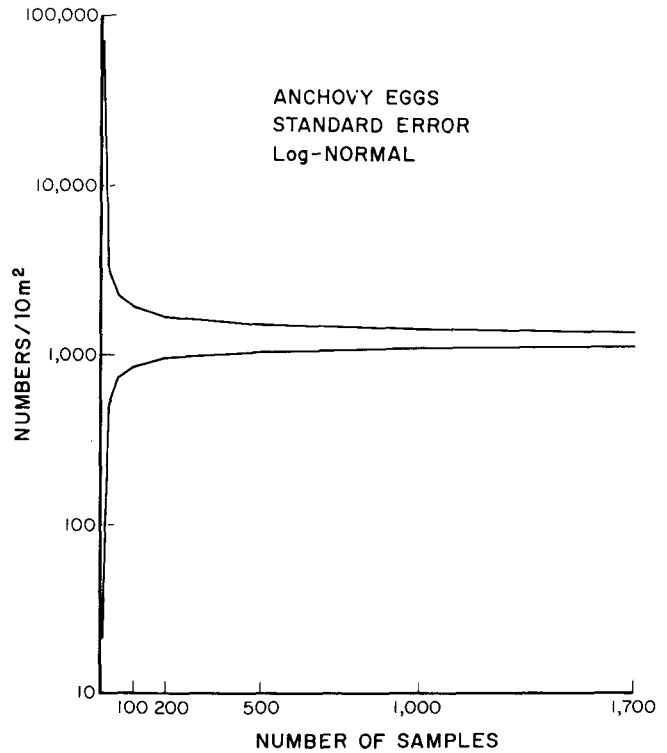
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FIGURE 1. The relationship between standard error and number of samples for anchovy eggs using a log-normal transformation. Single sample variability at the origin indicates the intensity of patchiness.
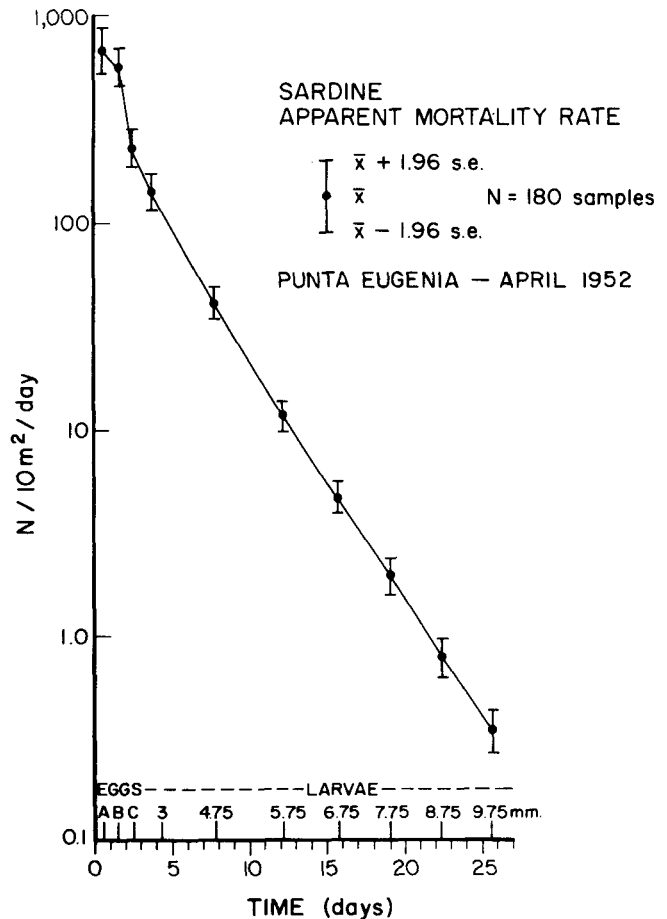

FIGURE 2. Apparent mortality rate of Pacific sardine eggs and larvae, N = 180.

vulnerable to the net. It seems likely that schooling behavior begins before the larvae have been entirely dispersed from the schooling behavior of the adults.

Regardless of the cause of pelagic pattern, the effect on sample precision must be overcome for the purposes of estimating the amount of spawning and determining the fate of the spawn. Precision may be increased by increasing the sampling effort and maintaining a rigorous sampling quality control. This is particularly important in the sampling of log-normal distributions common in the sea. For 10% sample confidence limits, when eggs are sampled, about 500 samples per space-time unit (Figure 1) need to be collected. To obtain a 25% sample confidence limit, which is adequate for determining rapid mortality rates (Figure 2), fewer than 100 samples may suffice (Figure 3). Satisfactory results in monitoring spawning biomass have been obtained in CalCOFI using as few as 30 samples per space-time unit.

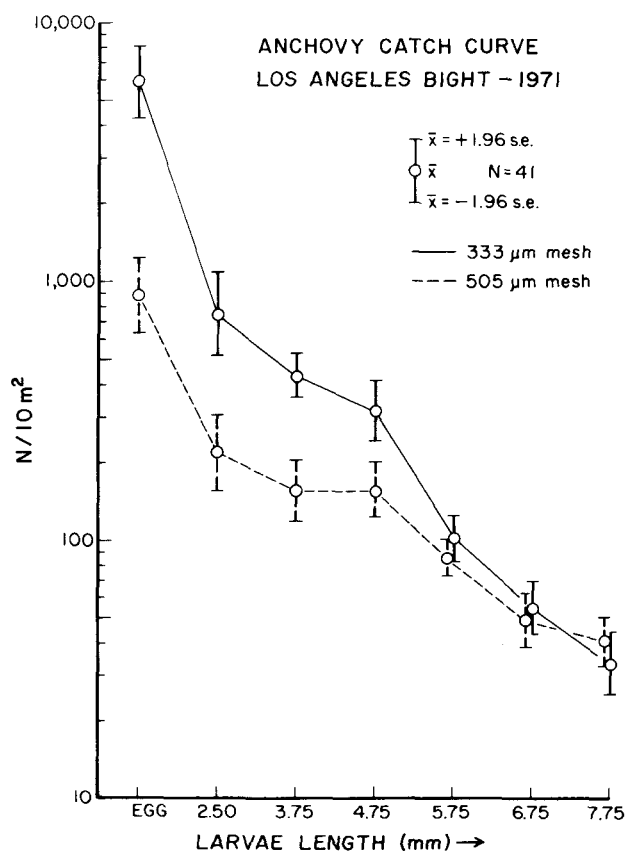For estimation of spawning, the most important bias is due to the loss of eggs and small larvae through the meshes of the plankton net. Lenarz (1952) found that a few paired tows of nets with different meshes are adequate for quantifying this bias. For determining the fate of the spawn, the most important bias is the growing tendency of larvae to avoid the net. No suitable solution is now available for this avoidance problem (Clutter and Anraku, 1968) but bongo nets and other higher speed bridle-free nets can materially increase the number of larger larvae collected.

The issue of assigning confidence limits to data derived from counts of eggs and larvae of pelagic fish has rarely been treated satisfactorily (Bagenal, 1955; Harding and Talbot, 1973). Among the pressing problems is evaluating mortality rates between two adjacent age classes when the variance of the number of fish in each age class is changing and the older class has been dispersed over a wider area than the younger class. While analysis of the existence of a difference can be attempted using log-transformed data, estimating the magnitude of the difference must be accomplished using the original arithmetic means. As pointed out by Cassie (1968, p. 109), "means obtained from log-transformed data are, after taking anti-logarithms, geometric means which will be smaller than the corresponding arithmetic means." Observations containing small and uniform proportions of "O" observations are satisfactorily treated in logarithmic transformations by adding a constant to each value, usually "1". However, in larval sampling, there are trends in the proportion of "O" observations. Therefore, the standard practice of adding "1" and taking the logarithm is not applied because it has not been adequately studied under these conditions.

FIGURE 3.   An example of the discrimination between the catch of anchovy eggs and larvae using two net meshes, N = 41.

Seasonal and Annual Changes in Spawning, Environmental Parameters, and Apparent Larval Mortality

A sample of existing data has been assembled to illustrate the magnitude and timing of spawning and other seasonal events as well as examples of changes between years. These seasonal and annual changes may be used as guides to design improved surveys and devise analytical techniques for the assessment of larval mortality and some of its causes. The area and time period chosen for these examples is the Southern California Inshore or SCI (Smith, 1972) for the years 1953 through 1960. This area was chosen because it was sampled thoroughly and regularly. The time interval was chosen to span two unusual climatic events; in 1956 the ocean off southern California was colder than average and in 1958 it was warmer than average.
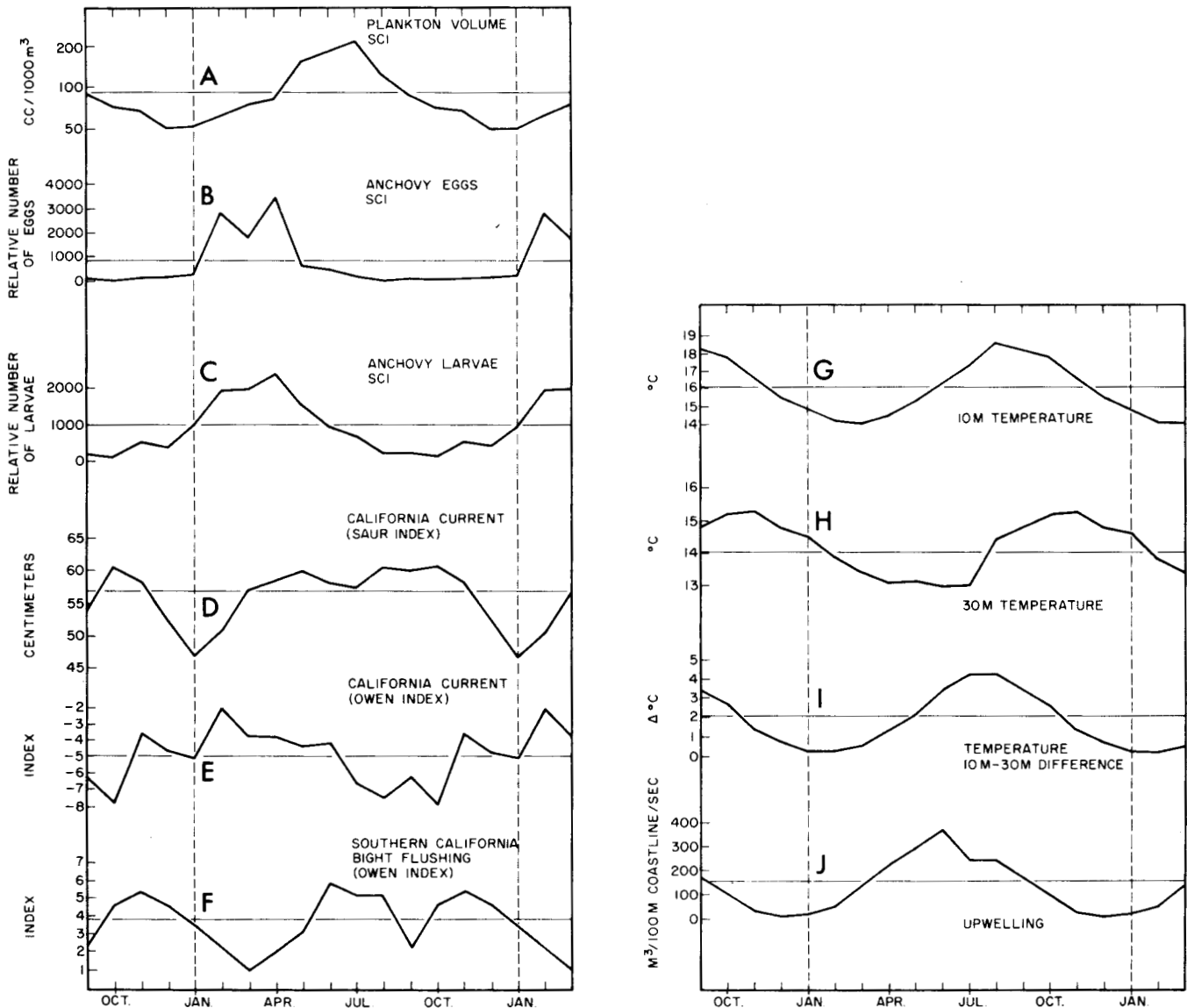
FIGURE 4.   Average annual cycles (1953–1960) in the Southern California Inshore region. Six months are repeated for cycle emphasis; a) plankton volume, b) anchovy eggs, c) anchovy larvae, d) the California Current (Saur, 1972), e) the California Current south of Pt. Conception within the CalCOFI grid (Owen, National Marine Fisheries Service, La Jolla, Pers. comm.), f) Southern California Bight Flushing Index (Owen, National Marine Fisheries Service, La Jolla, pers. comm.), g) 10-meter temperatures, h) 30-meter temperatures, i) temperature difference between 10 and 30 meters, j) upwelling (Bakun, 1973).
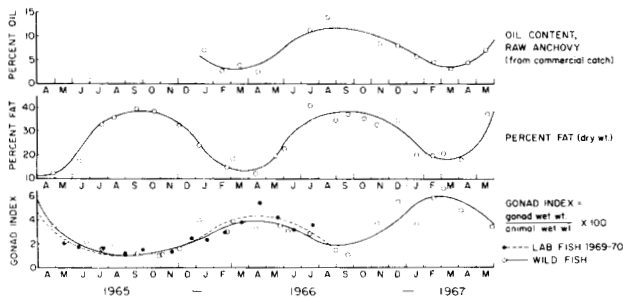

FIGURE 5.   Annual northern anchovy fat and gonad cycles for 1965–1967. Oil content is from the commercial catch in California (data provided by Roland Finch, National Marine Fisheries Service, Terminal Island). Laboratory fish were kept in an outdoor pool at the La Jolla Laboratory of the Southwest Fisheries Center under ambient light and temperature conditions.

The seasonal maxima of anchovy spawning in the Southern California Inshore region appear to be in February, March, and April. The minima are in August, September, and October (Figures 4B, C). Maximum spawning coincides with the minimum temperature at 10 m depth. The temperature at 30 m decreases after the spawning maximum and coincides with upwelling (Bakun, 1973) which reaches a peak in June. Anchovy spawning also coincides with the maximum rate of increase in the 1953 to 1960 upwelling index. The lowest zooplankton standing stock is coincidental with the upwelling minimum in December although the zooplankton peak in July appears 1 month after the upwelling maximum. The fastest rate of increase in

fat content of anchovy adults coincides with the zooplankton maximum (Figures 4A and 5). Average conditions for California Current strength by sea level difference approximations (Saur, 1972) and by geostrophic calculations (Owen, National Marine Fisheries Service, La Jolla, pers. comm.) do not agree closely (Figures 4D, E). Exchange of water between the rather permanent eddy in the Southern California Inshore region and the California Current (Owen's Southern California Bight Flushing Index, Figure 4F) appears to be at a minimum during the height of anchovy spawning. This indicates that water and spawned eggs and larvae are moving out of the Southern California Inshore region at a relatively slow rate. An 8 year average of each environmental and biological variable was calculated (Figures 4A–J and 5).

6). The increase in estimates of the abundance of larvae appears to be rather gradual in the annual census estimate for all anchovy larvae in the entire California Current sampling grid in all seasons. There is an increase in the total abundance of larvae in the winter quarter generally parallel to the annual estimates. The abundance of anchovy larvae in the winter quarter in both the Southern California Inshore and Offshore regions indicate this is a major spawning area for anchovy (Figure 6). The considerable changes in the fraction of the total larval population in these combined regions in this season suggest that studies of survival will need to be conducted over an even bigger area than the 35,000 square nautical miles represented.
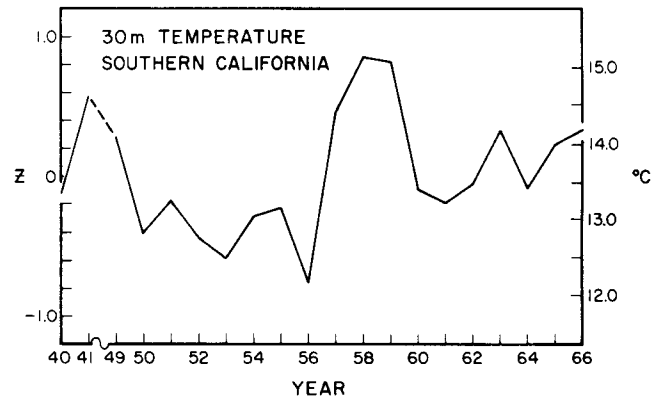
FIGURE 7.   Thirty (30) meter annual average temperature for the Southern California Inshore zone, Z is the normalized standard deviation of the variable.
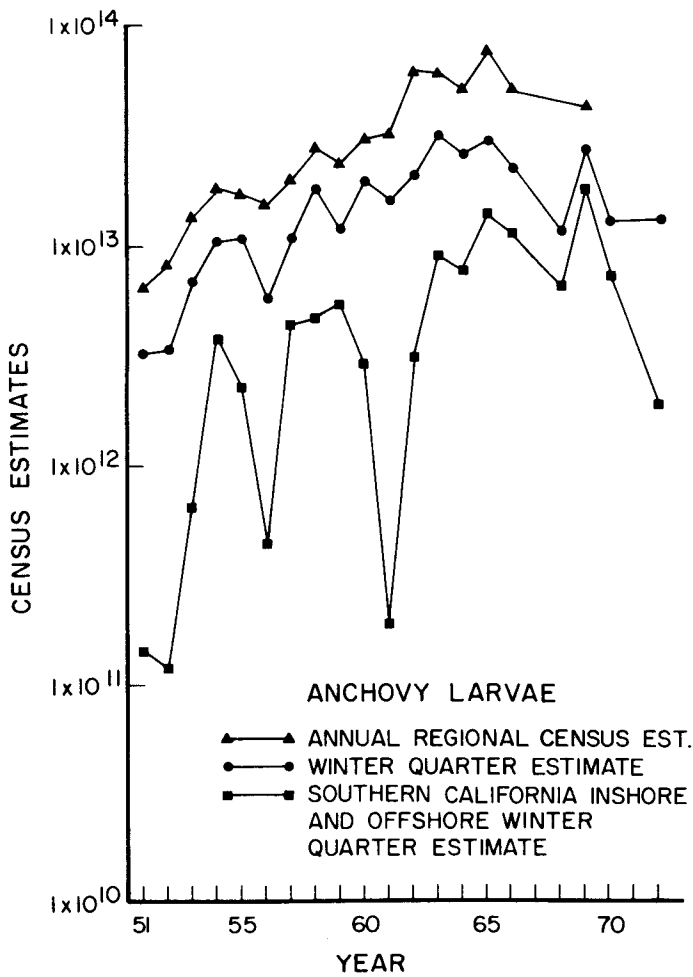

FIGURE 6.   Time series of regional census estimates of anchovy larvae (Smith, 1972).

Five additional time series have been selected to illustrate the magnitude and extent of coincidence of annual variations in spawning and other routinely measured environmental data. Three curves represent the abundance of anchovy larvae (Figure

FIGURE 8.   Zooplankton volumes, 1953–1960 for Southern California Inshore and Offshore regions. Carbon equivalents were obtained by multiplying wet volume figures by 0.056 (Cushing, 1971).

The time series of temperature at 30 m depth illustrates major climatic shifts in the Southern California Inshore region (Figure 7). Yet there 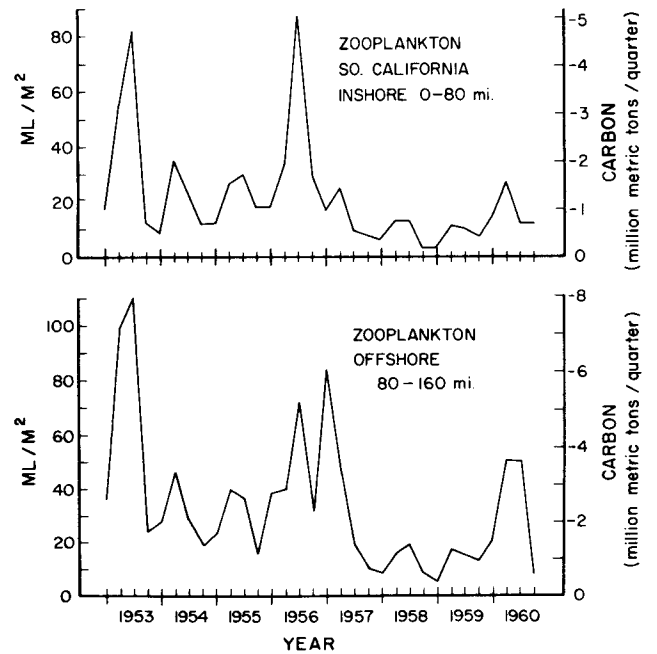does not appear to be any obvious direct control exerted by temperature over spawning. Lastly, two curves illustrate Southern California Inshore and Offshore zooplankton standing crop as well as estimates of secondary production by the "Cushing" method (1971) over the same reference period (Figure 8). Estimates of zooplankton production do not offer obvious explanations for major shifts in the amount or location of spawing. We conclude from these time series that over gross areas, changes in temperature and zooplankton production do not offer promising leads for finding cause and effect mechanisms which determine survival of larvae and recruitment to the parent stock.

Mortality rates for larvae in the sea are of special interest because these are needed to measure the effects of environmental variations on recruitment. These rates are difficult to derive because there have been few attempts to assign ages to the various size categories of larvae in our samples (Ahlstrom, 1954).

Hatching time, however, is a function of temperature and as a first approximation, the ratio of hatching time at ambient temperature to that at 15°C has been used to adjust each egg and larval count. The regional census estimates of the eggs and various sizes of anchovy larvae have been assembled from the adjusted data. The numbers of eggs and larvae also have been corrected for an escapement bias described by Lenarz (1972). Quarterly estimates of egg and larval abundance in the Southern California Inshore region have been made (Table 1). The parameters of the least squares fit made to the simple exponential equation:

$$N_t = N_o e^{-zt}$$

where:

N_t = is an estimate of the number of eggs or larvae at time "t" in days

N_o = is the ln N at time zero, and

z = is the instantaneous rate of apparent mortality.

TABLE 1

Larval anchovy mortality rate by quarter (QTR) for each year (YR), 1953 to 1960.*

YR-QTR	Eggs 1.5 days old	2.50 mm larvae 3.8 days old	3.75 mm larvae 5.6 days old	4.75 mm larvae 7.5 days old	5.75 mm larvae 9.8 days old	r_1	r_2	z_1	$(N_0)_1$	z_2	$(N_0)_2$
53-1	1328	536	195	80	65	-.949	-.975	.3538	7.3889	0.3870	7.6431
2	355	201	83	47	15	-.996	-.993	.4188	6.8694	.3824	6.5866
3	493	1951	406	431	191	-.904	-.619	.3407	8.4987	.1623	7.1354
4	787	3197	1426	661	279	-.999	-.622	.4034	9.5563	.1755	7.8147
54-1	2482	3718	1725	964	462	-.997	-.902	.3408	9.4441	.2294	8.5927
2	2560	1494	256	133	61	-.957	-.976	.5046	8.8311	.4820	8.6584
3	3420	1585	434	264	129	-.969	-.985	.3964	8.6142	.4081	8.7040
4	475	500	193	84	39	-.994	-.962	.4216	7.7061	.3307	7.0116
55-1	3679	1707	1251	649	330	-.994	-.997	.2808	8.5859	.2854	8.6208
2	1879	1079	671	321	170	-.997	-.997	.3140	8.1948	.2954	8.0534
3	312	2461	597	307	170	-.961	-.486	.4273	9.1169	.1545	7.0320
4	187	86	137	36	21	-.866	-.913	.2829	5.8879	.2596	5.7106
56-1	1627	102	154	31	19	-.882	-.927	.3355	6.2490	.5001	7.5068
2	4631	2321	828	318	166	-.987	-.992	.4392	9.2664	.4225	9.1390
3	597	188	162	204	148	-.467	-.773	.0261	5.3340	.1356	6.1709
4	598	130	70	62	27	-.973	-.957	.2433	5.7584	.3432	6.5214
57-1	34741	3147	1989	1220	338	-.979	-.960	.3643	9.5757	.5067	10.6639
2	25402	5608	2050	1108	592	-.983	-.979	.3644	9.8443	.4488	10.4889
3	685	1721	382	200	137	-.934	-.824	.4030	8.5926	.2574	7.4798
4	1001	58	98	100	47	-.271	-.743	.0397	4.5401	.2821	6.3925
58-1	9668	3746	2044	760	376	-.995	-.997	.3933	9.7277	.3972	9.7573
2	3540	3627	1329	827	495	-.971	-.960	.3183	9.2015	.2632	8.7803
3	84	396	189	156	80	-.978	-.231	.2489	6.8242	.0472	5.2831
4	793	255	25	11	10	-.874	-.941	.5098	6.7669	.5771	7.2808
59-1	2227	1345	1103	207	93	-.967	-.959	.4856	9.2588	.4035	8.6317
2	3269	1581	1058	702	434	-1.000	-.995	.2143	8.1694	.2387	8.3558
3	41	372	87	41	21	-.968	-.487	.4621	7.3690	.1663	5.1092
4	196	398	97	19	8	-.984	-.906	.6609	8.3060	.4576	6.7524
60-1	1957	2411	948	390	186	-.993	-.945	.4259	9.3003	.3178	8.4747
2	6846	1172	757	532	293	-.998	-.945	.2262	7.9225	.3508	8.8747
3	127	247	75	76	37	-.923	-.804	.2811	6.3177	.1761	5.5153
4	53	48	6	5	1	-.955	-.956	.5867	5.7329	.4986	5.0596
n	32	32	32	32	32						
x̄	3626	1481	651	342	170	-.995	-.997	.3550	8.5562	.3722	8.6876
s	7351	1416	653	346	165						

* Low values of z_1 and z_2 indicate high survival or low mortality; high values, the opposite. The intercept, N_0, is an *index* of the size of the spawning population, proportional to the logarithm of the amount of spawning which took place in each quarter. No extrapolation nor prediction should be conducted from these slopes and intercepts without refitting curves with non-linear least squares; for example, the Marquardt algorithm or equivalent.

r_1, z_1 and $(N_0)_1$ = without eggs.

r_2, z_2 and $(N_0)_2$ = with eggs.

Sample values for eggs and larval lengths through 6.25 mm and the age of each stage are listed (Table 1). Parameter estimates r_1, z_1, and $(N_0)_1$ exclude the egg sample variable whereas r_2, z_2, and $(N_0)_2$ include the variable. One may see from the correlation coefficient, r, that the simple exponential model more effectively describes the sample data at the height of spawning in winter and spring quarters than in the summer and fall quarters. The sample variation is better described when the egg census estimate data are omitted. From the tabular summary, it is evident that the number of eggs from sample to sample varied proportionately more than did the larvae.

BASE REQUIREMENTS FOR FEEDING, GROWTH, AND SURVIVAL OF ANCHOVY LARVAE

Numbers of research papers have appeared from the Southwest Fisheries Center, La Jolla, California, which developed criteria for growth and survival of anchovy larvae (Hunter, 1972; Hunter and Thomas, 1974; Kramer and Zweifel, 1970; Lasker, 1964; Lasker et al., 1970; Lasker, 1975; O'Connell and Raymond, 1970; Theilacker and Lasker, 1974; Theilacker and McMaster, 1971; Thomas, Dodson and Linden, 1973).

Feeding of larvae in relation to biological and physical environmental conditions has been the main area of investigation in order to examine the hypothesis that variations in year class strength are probably due to differential mortality of larvae when they first begin to feed; i.e., that a lack of food at the time of first-feeding may be the main cause of huge mortalities and result in small year classes (Hjort, 1914).

The northern anchovy has been and can be continually matured sexually and spawned in captivity at the Southwest Fisheries Center (Leong, 1971) which provides investigators with ample eggs and larvae for experimental work. Some of the studies referenced above have been done with laboratory produced larvae. These investigations have shown us that the following criteria need to be met for reasonable success in laboratory survival and growth of *Engraulis mordax* larvae. Another discussion of these criteria may be found in Lasker (1975).

The size of the food particle at first-feeding must neither be too small nor too large. Berner (1959) examined stomach contents of northern anchovy larvae from field collections and found that particles of food in the intestines of first-feeding larvae ranged from 24 to 186 μm long. However, over 70% of the food was between 60 and 80 μm long. This seems to be controlled by the mouth gape of the larva as borne out by laboratory feeding studies. Algal cells between 10 and 20 μm in diameter are not eaten by first-feeding anchovy larvae while particles of 40 μm and larger are eaten without difficulty. Organisms the size of the rotifer *Brachionus plicatilis*, which

range from 99 to 281 μm long and 66 to 182 μm wide can be taken by a small proportion of first-feeding anchovy larvae (Theilacker and McMaster, 1971; Hunger, 1972).

The number of food particles per unit volume in the first-feeding anchovy's environment must be above a minimum concentration. O'Connell and Raymond (1970) showed that a minimum density of micronauplii (about 1/ml) was needed for anchovy larvae to survive in laboratory experiments. Hunter (1972) has shown that there is a minimum density of algal cells that must be present if an anchovy larva is to obtain enough nutrients for metabolism, but his calculation is about 10X lower than the minimum number of cells we find to be necessary (i.e., about 20 to 40 cells/ml) for metabolism, growth, and to account for capture inefficiency in the laboratory.

Not all food organisms capable of being eaten by anchovy larvae support growth and survival. In the laboratory only one phytoplankter, *Gymnodinium splendens*, of a number tested, suppported growth of first-feeding anchovy larvae. However, larvae fed a variety of foods, such as found in wild plankton, invariably grow faster and survive better than those fed single species of organisms in the laboratory, but only when the plankton was concentrated to increase the density of the food organisms per unit volume (Kramer and Zweifel, 1970). Hunter (1972), who analyzed Arthur's (1956) data, pointed out that phytoplankton comprises at least 32% of the diet of first-feeding anchovy larvae. We know from rearing experiments that some nauplii (e.g. from the harpacticoid copepod *Tisbe furcata;* Hunter, National Marine Fisheries Service, La Jolla, unpublished) support good growth in first-feeding larvae, while other invertebrate larvae do not (Lasker et al., 1970).

The frequency of feeding strikes, and thus the success in capturing food is greater with high densities of food organisms. Hunter (1972) showed that feeding success at first-feeding for anchovy larvae is only about 10% of the feeding strikes made. Recently, Hunter and Thomas (1974) studied the feeding behavior of anchovy larvae in patches of *Gymondinium splendens* and found that the larvae fed more frequently inside the patch than outside. This differential feeding was related to the density of the food organisms in the larva's area.

Recent Observations at Sea

Lasker (1975) used first-feeding anchovy larvae produced by laboratory spawned fish to detect concentrations of larval fish food *in situ* along the California coast. First-feeding larval anchovies, whose development was controlled by temperature manipulation aboard ship, were placed in samples of Southern California Bight water taken from the surface and from chlorophyll maximum layers, usually 15 to 30 m below the surface. Feeding by larvae in water from the surface was minimal in all

experiments but extensive feeding occurred in water from the chlorophyll maximum layers when these contained phytoplankters having minimum diameters of approximately 40 μm and which occurred in densities of 20 to 400 particles/ml. In March and April 1974, the chlorophyll maximum layer along the California coast from Malibu to San Onofre (a distance of about 100 km) consisted chiefly of a bloom of the naked dinoflagellate *Gymnodinium splendens,* a food organism known to support growth in anchovy larvae. Copepod nauplii and nonliving particles were never in high enough concentration or of the proper size to be eaten by the larvae. A storm which caused extensive mixing of the top 20 m of water obliterated the chlorophyll maximum layer and effectively destroyed this feeding ground for larval anchovy.

ADULT PHYSIOLOGY

Lenarz and Hunter (National Marine Fisheries Service, La Jolla, pers. comm.) have demonstrated that there is a distinct seasonal trend in anchovy egg size and that the size of larvae at 3 days of age is related to the original egg size. Whether smaller larvae are at a disadvantage in the sea is not known but knowledge of when adults spawn is probably essential information in later studies of recruitment.

We know also from MacCall (California Department of Fish and Game, La Jolla, pers. comm.) that the apparent mortality rate of adults from the southern subpopulation (see below) is higher than that of the central subpopulation. These examples have prompted us to examine some pertinent features of cyclic phenomena in the physiology of the adult northern anchovy.

Subpopulations

Unpublished work by Vrooman and Paloma (MS)[1] gives good immunological evidence for the existence of three distinct subpopulations of the northern anchovy off the west coast of the United States and Baja California, Mexico. Presumably, these reproductively separate races do not interbreed. One population is centered chiefly off lower Baja California, another, the so-called central subpopulation which contains the major portion of the stock, ranges from northern Sebastian Vizcaino Bay, Baja California, to San Francisco, California, while a northern subpopulation extends from San Francisco to at least Newport, Oregon. A considerable amount of information is available on the year class strength and biomass of the central California subpopulation (Vrooman and Smith, 1971; Smith, 1972; Soutar and Isaacs, 1974).

Lasker (1970) showed that there is a reciprocal relationship between the amount of fat in the body of the Pacific sardine, *Sardinops sagax caerulea,* and the maturation of the gonad, as measured by the

[1] Vrooman, Andrew M. and Pedro A. Paloma. MS. Subpopulations of northern anchovy *Engraulis mordax* Girard.

gonad index (i.e. wet weight of the gonad divided by the wet weight of the fish X100). Shul'man (1960) in his review on lipids in fish stated that this is to be expected in most temperate fish. The same kind of relationship exists in the northern anchovy (Figure 5). Note that oil extracted from the commercial catch also reflects this cyclic phenomenon. We have also plotted mean gonad indices from anchovies kept in an outdoor tank at the La Jolla Laboratory. All of the fish came from the central subpopulation. Lipid deposition reaches a maximum in the anchovy during the summer, and a minimum during the peak of the spawning season (February, March, and April).

Laboratory experiments (Leong, 1971) have shown that northern anchovy gonad maturation can be induced by exaggerating winter light conditions. For example, 4 hours of light and 20 hours of darkness insures maintenance of high gonad indices (i.e. GI = 5% or higher) for as long as this light regime is maintained. Thus, this winter-early spring spawning fish's reproductive activity seems keyed to the seasonal light regime.

LARVAL ANCHOVY SURVIVAL

Recent work by Lasker (1975) has shown a correlation between the vertical stratification of suitablysized phytoplankters and the appearance of first-feeding anchovy larvae. The importance of the extent of these phytoplankton stratified patches, both horizontally and vertically, cannot be overestimated. We believe that virtually all survival of first-feeding anchovy larvae is linked to these favorable areas.
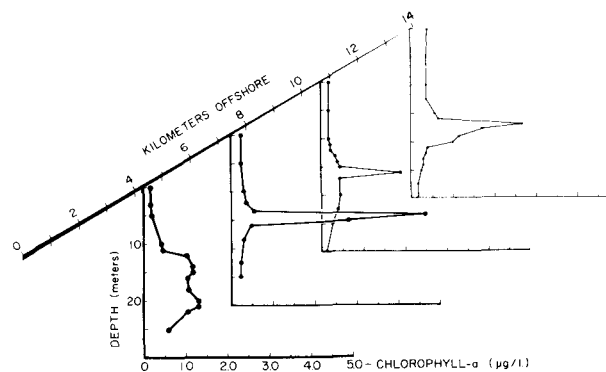

Figure 9.   Chlorophyll maximum layer in an offshore transect at a right angle to the shore at San Onofre, California, April 22-23, 1974. The chief component of the layer was a 10 μm diameter green flagellate (Lasker, 1975).

Two examples of vertical and horizontal structure of phytoplankton patches, one taken in April 1974 and the other in October 1974 off San Onofre, California, were obtained (Figures 9 and 10). Results emphasize the vertical distribution of a 10 μm green flagellate (Figure 9) and the horizontal, vertical, and size distribution of a patch characterized by a 30 to
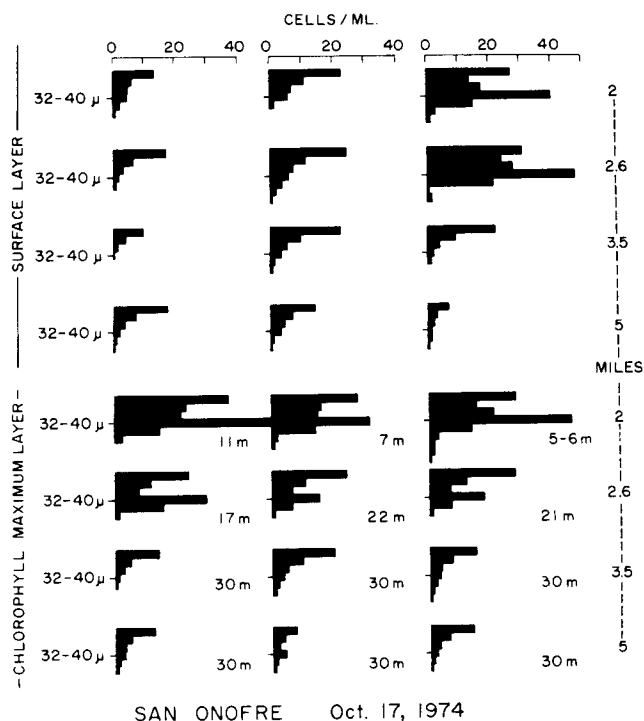
Figure 10. Particle size distribution from 12 adjacent stations off San Onofre, California, October 17, 1974. Five size groups are shown in histograms for each station; these are, top 16–20 μm, followed by 20–25 μm, 25–32 μm, 32–40 μm, 40–50 μm, and 50–64 μm.

40 μm dinoflagellate, *Gonyaulax polyedra* (Figure 10).

Quantitative studies of the food requirements of larvae and the feeding capability of predators on larvae (Hunter, 1972; Lillelund and Lasker, 1971; Theilacker and Lasker, 1974) indicate that average conditions in the sea are insufficient in food supply and sufficient predatory capability exists to consume the entire spawn. We have seen above that spatial patterns in the vertical and horizontal planes results in nursery patches for first-feeding anchovy larvae. Cursory examination of the patchy distribution of predatory organisms such as euphausiids and chaetognaths indicates that most of the predatory capability is concentrated in a relatively small proportion of the ocean, thus the spaces between patches of predators serve as a refuge for the survival of sufficient numbers of larvae for maintenance of population. The major criteria for survival of larvae appears to be related to coincidence rather than abundance alone; that is, a patch of larvae will survive if it coincides with an adequate patch of food organisms and also if it does not coincide with a patch of predators adequate to destroy the larval patch. These conditions also lead one to infer that the major influences on larval survival depend not on adequate production alone, but a stable oceanographic environment which will permit and maintain a discrete pattern of distribution of larval food, larvae, and the predators on larvae.

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