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FACTORS CONTRIBUTING TO VARIABLE RECRUITMENT OF THE NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IN THE CALIFORNIA CURRENT: CONTRASTING YEARS, 1975 THROUGH 1978

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Studies on the distribution of first-feeding larval anchovy and their food were made to test the hypothesis that the upper mixed layer of the ocean must be in a stable (non-turbulent) state for survival of enough larval anchovy to insure the production of a good year-class. Turbulent conditions destroy food aggregations and dilute potential food organisms to below feeding threshold concentrations of first-feeding larval anchovies. Surveys during the anchovy spawning season of 1975, 1976, and 1978 provided data supporting this hypothesis. Food of first-feeding larval anchovies became limiting when storms (1978) or drastic upwelling (1975) occurred which diluted food aggregations. A complicating factor was that nutritionally inadequate larval fish food could be occasionally overwhelmingly dominant in the larva's environment (1975). The drought year (1976) was characterized by stable conditions in the Southern California Bight and produced one of the best of the last 16 anchovy year-classes; 1975 produced one of the worst. Partial success of the anchovy year-class in 1978 is predicted based on the onset of stable conditions and food aggregations in the latter part of the spawning season.

INTRODUCTION

THE STOCK AND RECRUITMENT PROBLEM[1]

In recent years the stock and recruitment problem has become an active area of investigation as part of fishery studies throughout the world; of particular interest to fishery scientists are ways to predict future fish year-class sizes and how to determine the causes of the huge variability often seen in year-classes which cannot be ascribed to the size of the spawning stock. In the last decade work toward elucidating these mechanisms has been based chiefly on Hjort's (1914) suggestion that the strength of a year-class of fishes is most probably established through differential larval mortality during the earliest larval feeding stages and is dependent upon the amount and kind of food

[1] Briefly stated, the following questions are asked: 'What are the major factors controlling reproduction and larval survival, and what is the impact of reduced stock size on the strength of future recruitment into a year-class?' Figure 1 shows the wide fluctuation in spawning biomass of the Northern anchovy that can occur even in adjacent years.

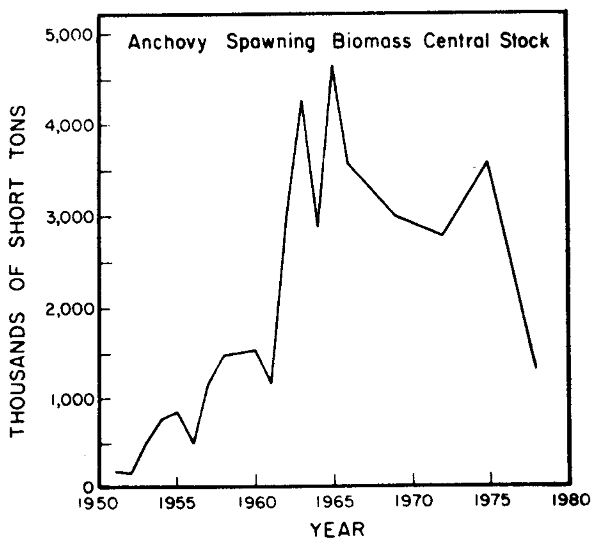

Figure 1. Variation in Northern anchovy biomass with time. Data provided by Dr Paul E. Smith.

available to the larvae when they first begin to feed. Other hypotheses have been suggested; for example, predators may have a great depressant effect on larval populations because early larvae are particularly vulnerable to a variety of vertebrate and invertebrate predators (see Hunter, 1976). With respect to food and predators, Lasker and Smith (1977) concluded that "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."

In recent years, correlative techniques have established relationships between physical and chemical factors in the environment and the strength of various fish year-classes, e.g., Pacific mackerel (Parrish and MacCall, 1978; Parrish et al., in press) and Atlantic menhaden (Nelson et al., 1977), but even these are usually explained by indirect effects on larval survival, e.g., larval drift into good or poor feeding areas. Density dependency, i.e., on the average, the larger the stock the greater the resulting year-class, is also considered to be a viable hypothesis by many fishery scientists.

TEST OF HJORT'S HYPOTHESIS

In 1975 I presented results of field experiments which indicated that Hjort's (1914) hypothesis might be tested by establishing the threshold number of particles needed for feeding by a larval fish, by determining the vertical and horizontal distribution of suitable food particles in the larva's environment, and by monitoring the temporal and spatial changes that occur in larval food concentrations, eventually correlating these with the resultant year-class (Lasker, 1975).

Although the "threshold-for-feeding" idea was tested only for the larval anchovy (*Engraulis mordax*), it may be applicable to other fishes for which it can be determined that a minimum concentration of food is needed for the larvae to feed and survive. Not all areas of the ocean can supply the required levels of food for all fish larvae, and I showed (Lasker, 1975) that in the Southern California Bight, anchovy larvae are dependent for survival mainly upon the inshore environment for an above-threshold number of nutritious particles. Offshore areas were seen to be particularly sparse in the kinds and sizes of particles needed by first-feeding larval anchovy. I suggested that storms might be an important mechanism for disrupting larval food aggregations, because in April 1974 after a storm I recorded a dramatic reduction in chlorophyll (Fig. 2) and potential larval fish food particles per unit volume.

An extensive survey of the Northern anchovy's environment was made in 1975 and the results were reported recently (Lasker, 1978). These suggested that strong upwelling, when it occurred during the anchovy spawning season, could be destructive to the establishment of a new year-class because it disrupted aggregations of suitable food particles and caused dilution of the particles to concentrations below the threshold needed by larval anchovy for first feeding.

Another important factor in survival of first-feeding anchovy larvae was suggested by Lasker et al. (1970) and confirmed by Scura and Jerde (1977) when they showed that the particles eaten by the anchovy larva and usually represented by dinoflagellates or microzooplankton of various kinds, were not always nutritionally complete. Above-threshold numbers of food organisms usually appeared when dinoflagellates were in bloom proportions or when they were other aggregating mechanisms (e.g., diurnal migration) which permitted particle number per unit volume to exceed the threshold for larval anchovy feeding. If the

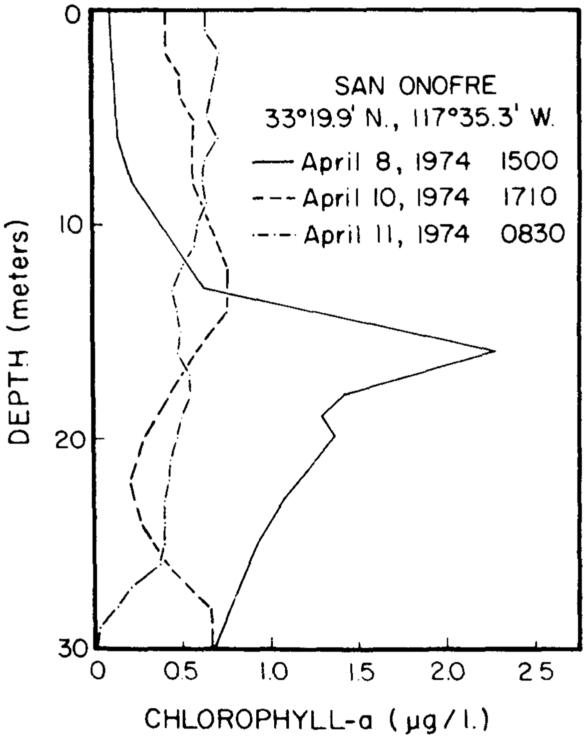

Figure 2. Reduction in chlorophyll before and after a storm. A major contributor to the chlorophyll maximum on 8 April was the dinoflagellate *Gymnodinium splendens*, (after Lasker, 1975).

dominant particle was nutritionally inadequate and also the chief food source for the larva, then a large mortality might be expected. This was suggested (Lasker, 1978) when the dominant particle in the larval anchovy's environment during the 1975 spawning season was found to be the dinoflagellate, *Gonyaulax polyedra*, and which Scura and Jerde (1977) showed to be an inadequate food for survival and growth of first-feeding anchovy larvae.

Upwelling brings nutrients to the surface and results in high levels of primary productivity in the surface layers of the sea and particularly in water adjacent to the shore. This is a common course of events in the Southern California Bight but enhanced productivity does not necessarily ensure good larval fish feeding conditions despite the fact that above-threshold-for-feeding concentrations of particles, usually a variety of diatoms, are prevalent during these events. Behaviorally, the anchovy larva ignores or rejects diatoms, probably because diatoms are spiny and filamentous. These phytoplankters are rarely found in the anchovy larva's intestinal contents (Arthur, 1976; Berner, 1959; Scura and Jerde, 1977).

TEST OF THE "STABILITY" HYPOTHESIS

In early 1978, California experienced unusual climatic conditions during the winter months. Storms were frequent and intense: precipitation in Southern California set a 20-year record, e.g., San Diego experienced 56 cm (22 inches) of rain as opposed to the 100-year average of 25 cm (10 inches). In this paper I present the results of an oceanographic survey made in the Southern California Bight during the stormy year of 1978 and compare the distribution of larval anchovy food with that found in 1975, a year of relative calm but also characterized by a geographically extensive upwelling along the coast in the midst of the anchovy spawning season. From the temporal and spatial descriptions of the Southern California Bight in 1975 and 1978 and with additional data from 1976, I draw conclusions on the hypothesis I have proposed, that stability of the ocean's upper layers during the anchovy spawning season is essential for larval fish food aggregation, a prime requisite for larval anchovy survival and thus a successful year-class. Readers are referred to my recent paper (Lasker, 1978) for details on the anchovy fishery and the methods employed in obtaining the information on oceanographic, meteorological and biotic conditions described in the following.

FLUCTUATIONS IN YEAR-CLASS STRENGTH OF THE NORTHERN ANCHOVY

There has been an active fishery on the Northern anchovy out of the California port of San Pedro for some years. The catch has been sampled and apportioned according to age and the percent year-class composition determined by the California Department of Fish and Game who have published their results in a series of articles (Collins, 1971; Collins and Spratt, 1969; Spratt, 1972, 1973; Sunada, 1975).[2] Table 1 indicates the percent composition of anchovy year-classes from the 1965 through 1977 seasons. The variability in strength of year-classes is quite evident. For example, the strong year-classes of 1970, 1971, and 1972 show up clearly as large percentages of the year-class composition in years succeeding the establishment of each year-class; by comparison, 1974 and 1975 were relatively poor. I anticipated a poor 1975 year-class because of the dominance of the dinoflagellate *Gonyaulax* as the major food particle in the larval anchovy's environment. Also the advent of strong upwelling during the latter half of the spawning season destroyed any food aggregations that might have been beneficial for feeding and prevented others from forming except inedible diatoms. As I pointed out earlier, the dinoflagellate *Gonyaulax polyedra* is known, from laboratory experiments (Scura and Jerde, 1977), to be a poor food for anchovy larvae. The 1976 year-class showed up very strongly in the fishery in 1977. This was earlier than any other "zero" group of northern anchovy since 1969. These fish were either born earlier or growth was extremely rapid after the usual spawning period.

Table 2 provides a ranking of the proportionate contribution of 16 Northern anchovy year-classes to the fishery off California. The 1975 year-class was one of the worst of this record while the 1976 year-class was one of the best. In this ranking, 1977 appears poorer than average. Data for 1978 is not available at this writing (January 1979), but the environmental data presented in this paper will provide the basis for a prediction of the relative future contribution of the 1978 year-class to the fishery. Notably, 1976 and 1977 were energetically quiet years off southern California, characterized by drought, high barometric pressure, no storms, and many cloudless days, and contrasted strongly with 1978, a very stormy year. This will be discussed in the next section.

[2] Since the central subpopulation of the Northern anchovy straddles the U.S.-Mexico border, in recent years the Mexican fishery out of Ensenada, Baja California, has also been sampled and apportioned by age. Data for the 1976 and 1977 year-classes are from Sunada (pers. comm.).

Table 1. Percent composition of Northern anchovy year-classes in the commercial catch from 1965 to 1977. (Data provided by John Sunada, California Depattment of Fish and Game.)

	Age in years						
Season	0	I	II	III	IV	V	VI
1965–66	4.5	14.7	48.5	23.4	7.5	...	...
Year-class ——→	1965	1964	1963	1962	1961	1960	1959
1966–67	6.9	22.9	38.1	23.0	7.5	...	...
Year-class ——→	1966	1965	1964	1963	1962	1961	1960
1967–68	...	...	...	...	...	...	...
Year-class ——→	1967	1966	1965	1964	1963	1962	1961
1968–69	18.5	45.9	23.4	8.2	4.3	...	...
Year-class ——→	1968	1967	1966	1965	1964	1963	1962
1969–70	27.0	27.8	35.2	8.3	...	...	...
Year-class ——→	1969	1968	1967	1966	1965	1964	1963
1970–71	4.0	32.1	40.2	20.1	3.1	...	...
Year-class ——→	1970	1969	1968	1967	1966	1965	1964
1971–72	11.3	50.8	26.7	8.5	2.4	...	...
Year-class ——→	1971	1970	1969	1968	1967	1966	1965
1972–73	9.3	25.7	47.6	14.4	2.4	0.4	...
Year-class ——→	1972	1971	1970	1969	1968	1967	1966
1973–74	6.9	20.3	35.3	30.7	6.2	1.0	...
Year-class ——→	1973	1972	1971	1970	1969	1968	1967
1974–75	4.6	18.5	39.5	26.4	9.6	1.3	...
Year-class ——→	1974	1973	1972	1971	1970	1969	1968
1975–76	2.4	10.5	37.3	34.1	12.0	3.2	...
Year-class ——→	1975	1974	1973	1972	1971	1970	1969
1976–77	27.7	12.1	16.2	27.8	13.4	2.5	...
Year-class ——→	1976	1975	1974	1973	1972	1971	1970
1977–78	10.6	37.7	20.3	14.0	14.0	2.4	0.2
Year-class ——→	1977	1976	1975	1974	1973	1972	1971

THE OCEAN ENVIRONMENT

TEMPERATURE, SALINITY AND UPWELLING

In 1975, surface temperatures in January, February and March were about a degree cooler than the 1950–78 mean of 14.7°C in the Southern California Bight and the adjacent California Current. In fact, a large pool of 13° to 14°C water extended from Pt. Conception to Baja California and over 100 km seaward. Salinity was close to the long-term mean of about 33.5 ‰ . Conditions were drastically different in 1978. Storms and heavy precipitation characterized December 1977 through mid-March 1978. Salinity was extremely low, 33.2 – 33.3 ‰ , over the entire area for the first 3 months of 1978. This may not be entirely explained by precipitation and run-off, although this may have been the dominant factor (McLain et al., 1979, R. Lynn, pers. comm.). Surface temperatures were much warmer than normal in 1978; nearly 16° C in January and 15° to 16° C in March, 1° C above the long-term mean (Eber, 1977). Bakun (1973, 1975) has published upwelling indices for the entire west coast of the United States. Upwelling indices are values of Ekman transport derived from atmospheric pressure differences and are expressed in cubic meters of upwelled water per second per 100 m of coastline. Figure 3 shows upwelling indexes for January 1977 to March 1978 compared with a 32-year (1946–77) time series. Locations in the Gulf of Alaska are toward the top of the figure, while those off Baja California are toward the bottom. Note that the stormy period from December 1977 through mid-March 1978 coincided

Table 2. Northern anchovy year-classes are ranked by using the annual deviation from the mean of the proportionate contribution of each anchovy year-class to the fishery (Paul E. Smith, personal communication).

Year-class	Rank	Year-class	Rank
1962	5	1971	8
1963	3	1972	6
1964	12	1973	10
1965	13	1974	14
1966	15	1975	16
1967	4	1976	1
1968	9	1977	11
1969	7		
1970	2		

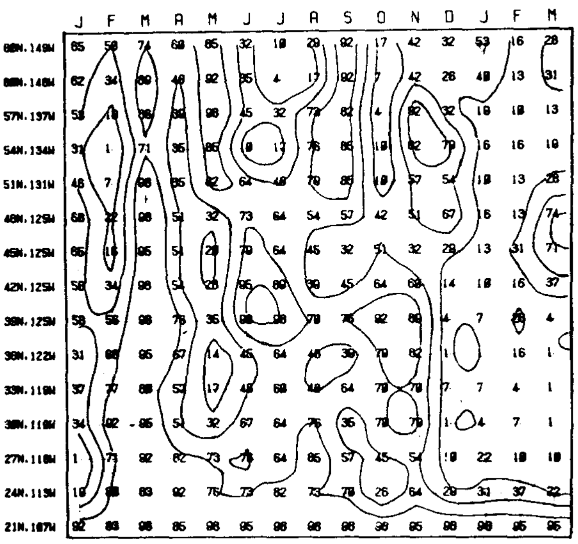

Figure 3. Monthly upwelling index values for January 1977 to March 1978, in percentiles of the frequency distribution made up of the 32 values for each month and location in a 32-year (1946–77) time series. Locations in the Gulf of Alaska are toward the top of the figure; those off Baja California are toward the bottom. The contour interval is 25 percentiles. Values above the 50th percentile indicate stronger than normal upwelling while those below indicate weaker than normal upwelling (A. Bakun, personal communication).

with very low upwelling index values from as far north as 39° N, 125° W to as far south as 27° N, 116° W, i.e., from Cape Mendocino to Vizcaino bay, California, a distance of 1600 km. This encompasses the area of Northern anchovy central subpopulation spawning (Vrooman and Smith, 1971).

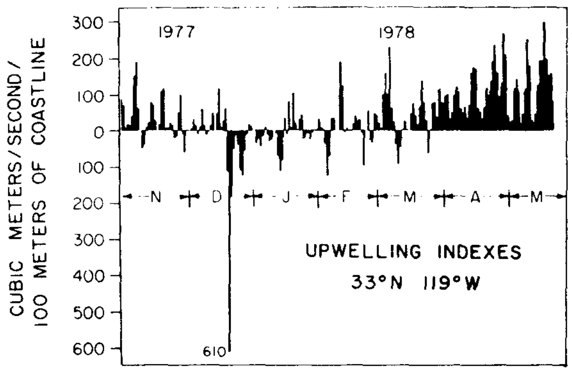

Figure 4. Upwelling index at San Clemente Island approximately 65 miles off the southern California coast and indicative of oceanographic events in the Southern California Bight. The major downwelling response in December 1977 was due to a violent storm. Other downwelling episodes are indications of additional stormy periods. Note their virtual cessation by mid-March 1978.

WINDS OVER THE ANCHOVY'S SPAWNING GROUNDS

In 1975, wind from the north (southward) early in the year was much more frequent and prolonged than in early 1978 and resulted in intense upwelling. While there was a major storm pulse in the first few days of March 1975, storms were much more frequent and intense in 1978, as evidenced by frequent and intense northward winds and the concomitant decrease in southward winds. The strongest initial stormy event was very evident in the San Diego area as illustrated by a major downwelling pulse shown in Bakun's indexes for 33° N 119° W (Fig. 4). This mid-December 1977 event presaged turbulent conditions in the mixed layer of the Southern California Bight which persisted and were maintained by successive stormy events through most of the 1978 anchovy spawning season until mid-March.

Because of the importance of both upwelling and storms to the disruption and dilution of larval anchovy food aggregations, a quantitative analysis of wind was investigated as a possible simple way to characterize the energy available to induce turbulence in the upper mixed layer of the ocean. In Table 3, the mean cube of the wind speed, which is roughly proportional to the mechanical energy available for inducing turbulent mixing (Niiler and Krause, 1977; Elsberry and Garwood, 1978) for two locations (central California coast north of Pt. Conception: 36° N 122° W and San Clemente Island; 33° N 119° W), is presented. While there is not a perfect coherence between the two

Table 3. Mean cube of the wind speed over four spawning seasons (1974–75 to 1977–78) of the Northern anchovy. 36° N, 122° W is representative of the California coast north of Pt. Conception; 33° N, 119° W of the Southern California Bight.

Spawning season	Dec	Jan	Feb	Mar	Apr	Dec–Feb Average
	Mean cube of the wind speed at 36° N 122° W					
1974–75	416	274	534	756	538	408
1975–76	232	132	186	495	644	183
1976–77	42	110	121	539	580	91
1977–78	583	621	375	334	230	526
	Mean cube of the wind speed at 33° N 119° W					
	Dec	Jan	Feb	Mar	Apr	Dec–Feb Average
1974–75	281	314	300	598	529	298
1975–76	250	185	280	661	603	238
1976–77	90	220	266	622	644	192
1977–78	413	192	267	338	391	291

locations, the similarities are apparent and consistent. For example, 1976 and 1977 were much less windy years than 1975 and 1978, particularly when averages of wind cubed for December through February are compared. The highest wind cubed index of the 1977–78 series at 33° N 119° W was in December 1977, a particularly stormy month. Winds at 36° N 112° W, when compared to previous years, were also exceptionally strong in December 1977.

An analysis of these wind events suggests the following: (1) winters of the drought years 1975–76 and 1976–77, when anchovies were spawning, were characterized by much lower cumulative wind speed cubed over the Southern California Bight, the chief spawning ground of the Northern anchovy; and (2) the winter of late 1977 and early 1978 was characterized by unusually strong storm winds, which were potentially disruptive to stratification in the upper mixed layer of the Southern California Bight.

To summarize, the winters of 1976–77 and 1975–76 were consistently relaxed, low-energy situations while the winter of 1977–78 was marked by intense, highly fluctuating northward wind stress episodes. The winter of 1974–75 was relatively high in cumulative southward wind energy although upwelling did not commence strongly in the Southern California Bight until mid-February.

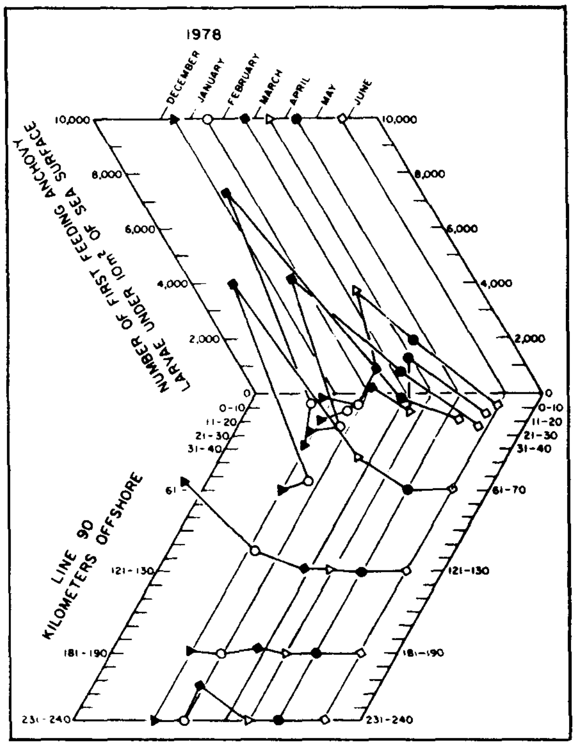

Figure 5. First-feeding larvae under 10 m² of sea surface plotted by distance from shore and time from December 1977 through June 1978 for CalCOFI line 90. Refer to Figure 9 for geographic locations of CalCOFI lines.

BIOLOGICAL CONSEQUENCES OF UNUSUALLY STORMY CONDITIONS IN THE SOUTHERN CALIFORNIA BIGHT

TEMPORAL AND SPATIAL SPAWNING DISTRIBUTION OF THE NORTHERN ANCHOVY, 1978

Figure 5 shows the seasonal and seaward distribution of first-feeding anchovy larvae found in the Southern California Bight over the 1978 spawning season, as indicated from plankton tows taken along

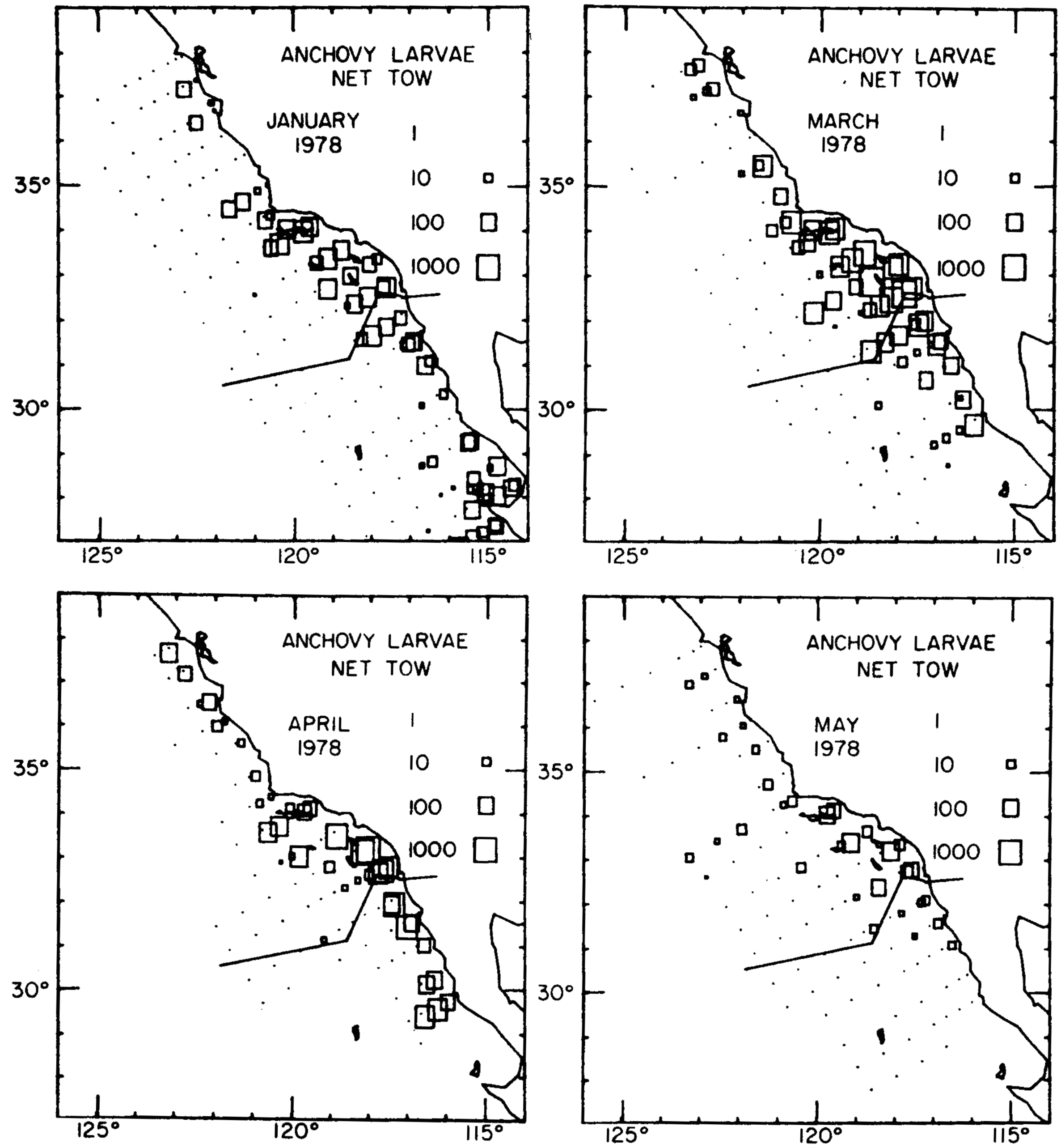

Figure 6. Larval anchovy distribution during the 1978 spawning season. Each dot indicates an occupied but "zero larvae" station. The line extending from land is the Mexico-U. S. border. (Graphs courtesy of Dr Paul E. Smith).

CalCOFI line 90[3]. An interesting feature of this graph is the comparatively low number of larvae which appeared inshore during January, February, and March. Figure 6 shows that anchovy spawning was extensive throughout the Southern California Bight during the entire season but was minimal offshore.

[3] Geographic locations of sampling transect lines are shown in Figure 8.

THRESHOLD PARTICLE CONCENTRATIONS FOR FIRST-FEEDING ANCHOVY LARVAE

Lasker (1975) determined that between 14° to 15° C, 30–40 particles per ml, are needed in the larval anchovy's local environment to provide for gut filling in a reasonable time period (8 h). Confirmation of this threshold based on metabolic needs and prey capture efficiencies was given by Lasker and Zweifel (1978) where they simulated the percent survival of anchovy larvae after the first day of feeding in various concentrations of organisms at 14° C. From these results, it seems unlikely that the threshold for feeding can be as low as 20 particles per ml. However, in this study, because higher temperature decreases the threshold for feeding (Lasker, 1975) and slightly higher temperatures prevailed in the Southern California Bight in 1978, larval anchovy survival is discussed in terms of a threshold of 20 particles per ml for first feeding.

PARTICLE DISTRIBUTION WITH DISTANCE, DEPTH AND TIME IN THE SOUTHERN CALIFORNIA BIGHT

The number of particles per ml are plotted against time and distance from shore for the two major lines sampled (lines 87 and 90) during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises during the anchovy spawning season in 1978 (Fig. 7). Except for Santa Monica Bay (inshore stations, line 87), which had reasonably high numbers of 30–50 μm diameter particles before the major December 1977 storm, the entire Southern California Bight was literally devoid of food particles suitable for first-feeding larval anchovy during January, February, and early March. Stable conditions which became established in mid-March were reflected in bloom conditions of some organisms, particularly *Gymnodinium splendens*, a food known to be nutritious for first-feeding anchovy larvae (Fig. 8). Figure 8 also shows clearly that the storm event of December 20 (see Fig. 4) destroyed the aggregation of dinoflagellates which would have been good feeding for larval anchovies. In fact, it wasn't until March 13–18 that above-threshold-for-feeding concentrations of dinoflagellates began to appear at these inshore stations. Diatoms became more prevalent after this period of time but probably did not contribute to larval feeding success because, as noted before, these are not eaten by Northern anchovy larvae. The results of continued turbulence are also evident in low particle concentrations over the entire Southern California Bight recorded from December to March 1978; elevated particle concentrations show up in mid-March after general relaxation of stormy conditions (Fig. 9).

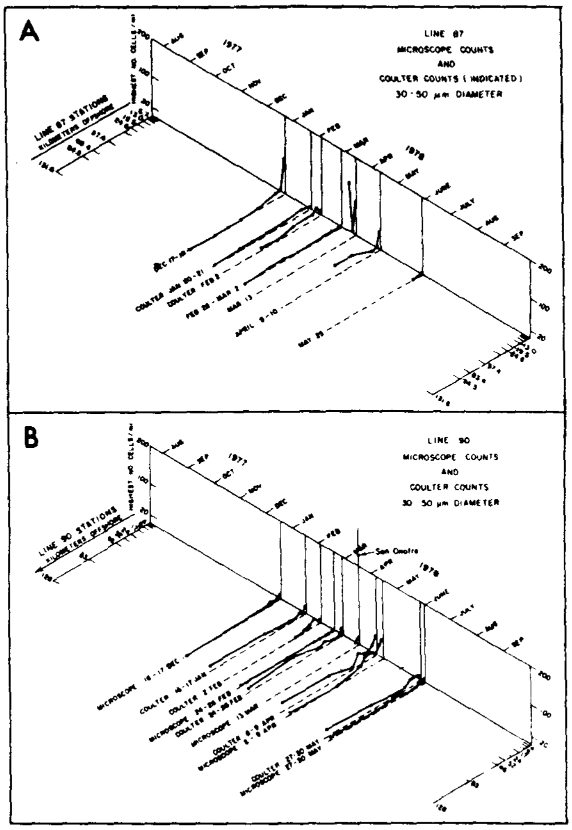

Figure 7. Particle distribution with time and distance from shore, lines 87 and 90. Refer to Figure 9 for geographic location. Note the depressed particle numbers below threshold for larval first-feeding until March at the inshore stations. The >200 particles/ml at San Onofre was a patch of *Gymnodinium splendens*.

A similar picture is seen in the distribution of chlorophyll along line 90 and shown in Figure 10. Whatever chlorophyll maximum layer existed on 16–17 December 1977, it was completely obliterated right after the major storm event and no reasonable quantity of chlorophyll appeared until late February in the most inshore stations. Chlorophyll was much more prevalent during the 8–9 April transect of the Bight and became layered in the following months, reflecting stable (i.e., non-turbulent) conditions. This indicates that storms kept the upper 30 m of the Southern California Bight well mixed and diluted with respect to particles but once storms ceased, recovery was relatively rapid and stratification of phytoplankton became firmly established by April. April spawning in the inshore zone was the highest of the year (Fig. 5) and despite poor conditons for larval

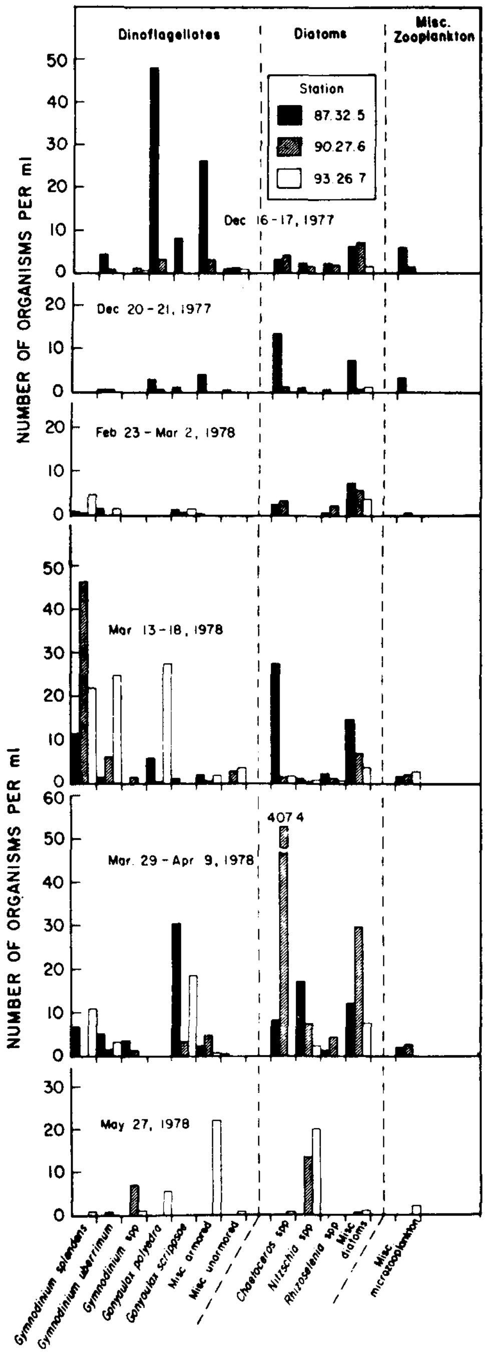

Figure 8. Diatoms, dinoflagellates and miscellaneous zooplankton >20 μm diameter at three inshore stations in the Southern California Bight. The storm of 20 December reduced aggregations well below larval anchovy first-feeding threshold levels (i.e., <20/ml).

anchovy survival during January, February, and early March, the stable conditions prevailing from mid-March through April probably avoided a failure of the 1978 year-class.

EVIDENCE OF DELAYED LARVAL ANCHOVY SURVIVAL, 1978

Two ancillary lines of evidence seem to indicate that the anchovy achieved a partial spawning success late in the 1978 spawning season. First of these is the appearance of small anchovies in schools in June and July, although these could not be caught by commercial fishermen because of their small size. The minimum size for fishing by regulation in the southern California area is 12.7 cm total length, although smaller fish are caught by bait dealers along the coast. Age structure of two samples of these small fish, as deduced from daily rings on their otoliths (Brothers et al., 1976), shows that most of them were born after mid-March (R. Methot, pers. comm.) (Fig. 11).

Second, a small bird, Xantus' murrelet (*Endomychura hypoleuca*), which nests on some of the Channel Islands off California, feeds heavily on late larvae of Northern anchovy. In 1976, clutch initiation started in early March and in 1977 in late March. In 1978, it was almost early May before clutch initiation started (Fig. 12). This suggests a lack of food for this highly specialized feeder, possibly due to a delay in the survival of anchovy larvae (G. Hunt, pers. comm.).

1976 AND 1977 SPAWNING SEASONS

Eggs and larval surveys were not conducted in 1976 and 1977, but, as noted earlier, the 1976 Northern anchovy year-class was one of the best of the 16 year-classes from 1961 through 1977. Reid et al. (1978) provide some information of phytoplankton aggregation in the Southern California Bight in 1976 which showed that there was strong vertical stability and a sharp chlorophyll maximum layer throughout the inshore areas of the Bight. The most significant taxa in the chlorophyll maximum layer were the dinoflagellate *Exuviella* sp. and the photosynthetic ciliate *Mesodinium rubrum*, both of a size easily seen and consumed by *E. mordax* first-feeding larvae. I conducted a survey of the Bight for threshold numbers of larval anchovy food organisms in March 1976 over the CalCOFI grid and the results (Fig. 13) showed above-threshold concentrations of particles, consistent with calm seas, prolonged stability and aggregation of motile phytoplankters. Reid et al. (1978) listed a wide variety of organisms which were found in the area and concluded that there were elongate bands of phytoplankton oriented parallel to the shore. My results show that concentrations of these organisms were highest inshore as well.

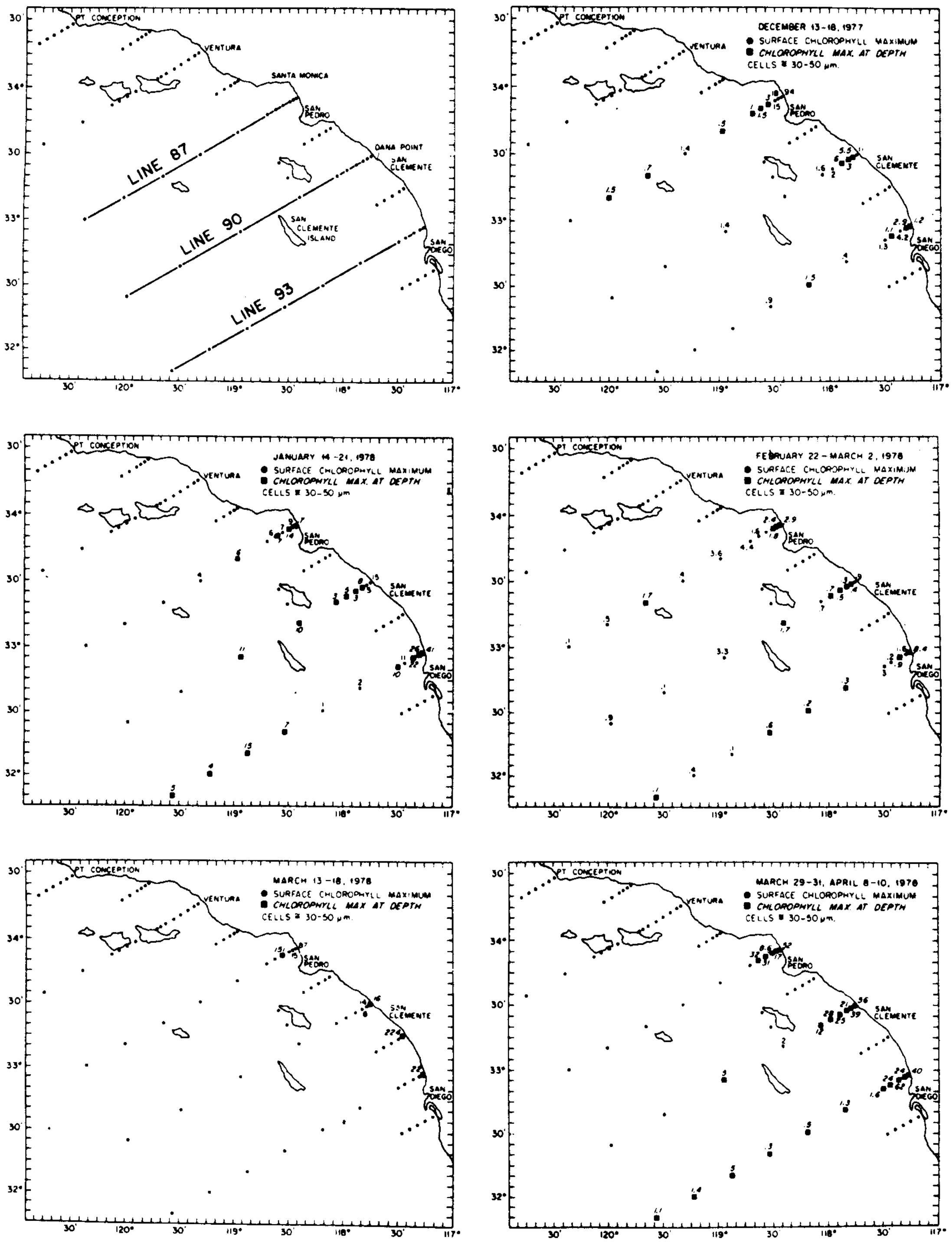

Figure 9. Particle distribution in the Southern California Bight during the 1978 anchovy spawning season. Numbers are cells per milliliter. Storms kept concentrations of particles in the 30–50 μm size range below threshold for larval anchovy first feeding. Calm conditions in mid-March presaged phytoplankton aggregations.

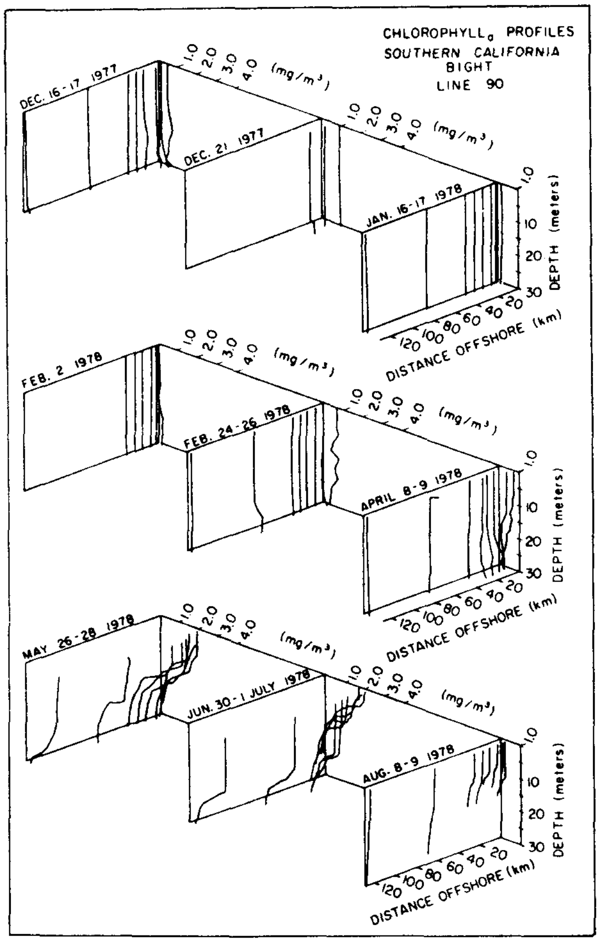

Figure 10. Vertical chlorophyll profiles with time and depth along line 90 (San Onofre, California) throughout the anchovy spawning season.

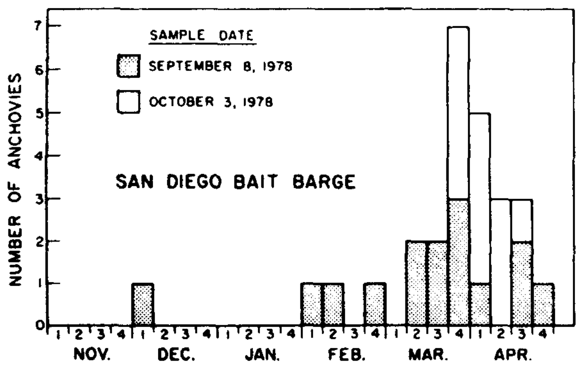

Figure 11. Birthweeks of pre-recruit anchovies caught in September and October 1978 (R. Methot, pers. comm.).

Figure 14 shows the results of particle counts in the 30–160 μm diameter range, taken on 16–17 March 1976 in a tight station pattern along shore from Encinitas, California to La Jolla, California, a distance of 15 km. A complete microscopic analysis of 10 samples from the chlorophyll maximum at the northernmost station showed that dinoflagellates were dominant, averaging 35 cells per ml, and *Exuviella* sp. constituted 68% of these. Copepod nauplii averaged 20 per liter and the globular dinoflagellate *Noctiluca* sp. numbered 54 cells per liter. Diatoms did not exceed 10 per ml. From what we know of the threshold concentrations of phytoplankton needed for larval anchovy first feeding (i.e., >20 cells/ml of dinoflagellates), March 1976 exemplified excellent feeding conditions. Unfortunately, no consistent sampling was possible in 1977 during the anchovy spawning season, so no clues are available to assess the 1977 year-class.

PRODUCTIVITY AND YEAR-CLASS STRENGTH

Cumulative productivity (data collected and analyzed by Dr Richard W. Eppley of Scripps Institution of Oceanography) is given in Figure 15 for the Southern California Bight from 1974 through 1978. The poor anchovy year-class of 1975 corresponded with a generally elevated productivity in the Bight, undoubtedly brought about by the extensive upwelling that year. This was also reflected in chlorophyll measurements taken at the same time by Lasker (1978). The year of the very good year-class, 1976, was a relatively poor one for primary production in the Bight. My interpretation of these events is that primary productivity *per se* is less essential to larval survival than prolonged stability of the upper mixed layer (no upwelling, no storms) which allows for aggregation by vertical and horizontal migration of motile larval anchovy food organisms, probably dinoflagellates. Stability also provides conditions conducive to the deliberate hunting-feeding behavior of the larval anchovy. High production is usually also indicative of diatom production, which is not a favorable condition for successful feeding by first-feeding anchovy larvae.

DISCUSSION

This study, with others (Lasker, 1975, 1978), has shown that food of first-feeding larval anchovies becomes limiting when storms or drastic upwelling occurs and dilutes food aggregations. A complicating factor is that often nutritionally inadequately larval fish food can be overwhelmingly dominant in the

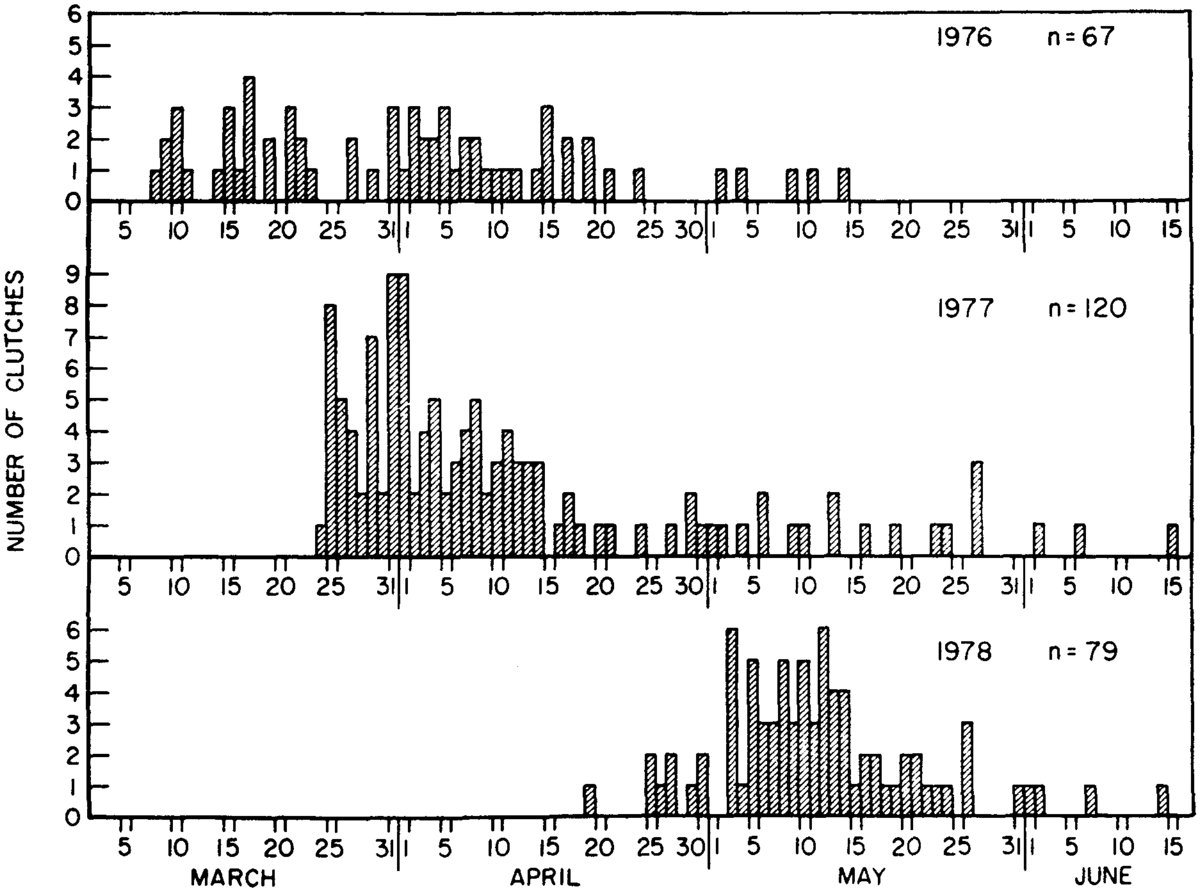

Figure 12. Clutch initiation dates (1976–78) for Xantus' murrelet (*Endomychura hypoleuca*) (G. Hunt, pers. comm.), nesting on Channel Islands in the Southern California Bight.

larva's environment despite otherwise favorable oceanographic conditions. Several conditions seem to be necessary for the survival of first-feeding anchovy larvae; these are stability of the water column and aggregation of nutritionally suitable food organisms coinciding with the production of anchovy larvae in time and space.

The years investigated and compared in this paper, 1975–78, provided interesting comparisons. In early 1975, the weather and seas of the Southern California Bight were relatively calm, but a nutritionally poor food organism, *Gonyaulax polyedra*, was the dominant one available to first-feeding anchovy larvae. Upwelling in the latter half of the spawning season swept out *G. polyedra* but replaced it with diatoms which the larvae do not eat. The result of these events was one of the poorest year-classes of anchovies in the last 16.

The drought year 1976 had calm seas and very little upwelling during the anchovy spawning season. Dinoflagellates were plentiful, diatoms were sparse, and stratification was strong. The resultant year-class was one of the best of the last 16. No data are available to assess the 1977 year-class.

In early 1978, southern California had one of the stormiest seasons on record. Stratification was non-existent until March. A poorer-than-average year-class is expected because only a portion of the spawning season could have resulted in good survival. Early evidence is that most pre-recruits were born after March 1978.

Correlating year-class strength with oceanographic, meteorological and biological parameters that affect larvae requires a lag of 2 years between collection of environmental data and information on the magnitude of the resultant year-class as obtained from

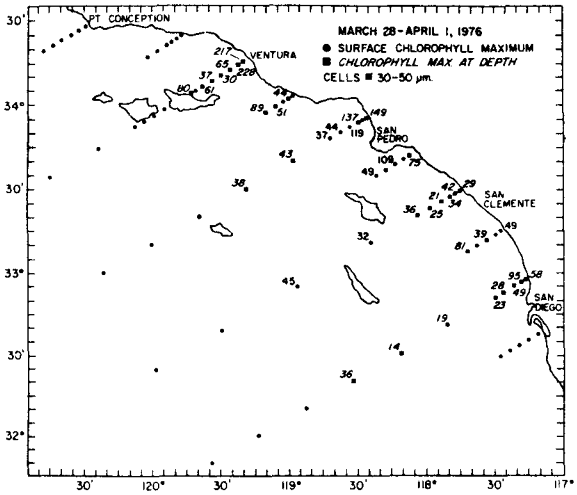

Figure 13. Particle distribution (30–50 µm) over the CalCOFI grid, March 1976. Numbers are cells per milliliter. Note the uniformly high particle concentrations during this period of calm and drought.

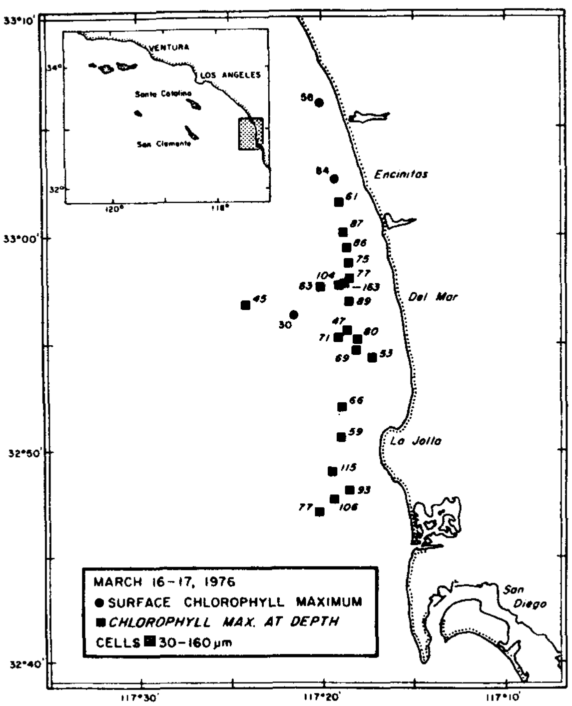

Figure 14. Particle distribution from an along-shore transect (30–160 µm), March 1976 in the Southern California Bight. Numbers are cells/milliliter.

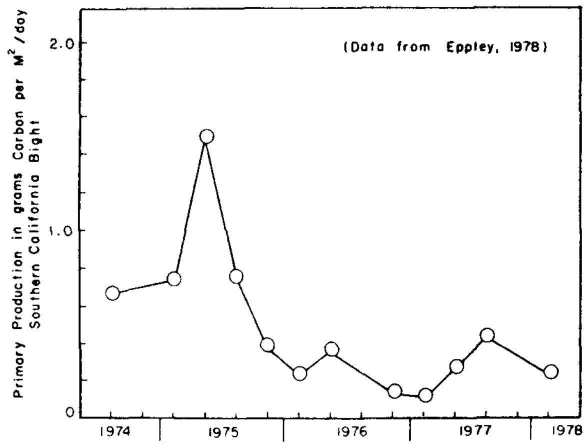

Figure 15. Cumulative carbon production of the Southern California Bight, 1974 through 1978 (R. Eppley, pers. comm.).

the fishery. The difficulty of this task precludes obtaining the statistics necessary to test the "stability" hypothesis vigorously in a short span of years, particularly with an annually spawning fish. The prediction of year-class strength probably depends on knowledge of wind stress, direction, duration, number of repeat episodes, and the depth of the ocean in which stress is translated into turbulence and mixing. The extent and speed of restratification after wind events is also important and is currently an active area of investigation (Garwood, 1977).

As far as larvae are concerned, the biotic components of their environment are equally as important for survival, e.g., the degree of patchiness of larvae, their food, and predators. However, if we can establish quantitatively the interactions suggested in this paper between weather, ocean, biota, and fishery, the results may give insights needed to understand the important relation between stock and recruitment, and provide the information needed to permit a prediction of the magnitude of an incoming year-class.

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REFERENCES

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.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–1971. NOAA Tech. Rept. NMFS SSRF-671, 103 pp.

Bakun, A. 1975. Daily and weekly upwelling indices, west coast of North America, 1967–73. NOAA Tech. Rept. NMFS SSRF–693, 114 pp.

Berner, L., Jr. 1959. The food of the larvae of the northern anchovy, *Engraulis mordax*. Bull. inter-Amer. Trop. Tuna Comm., 4: 1–22.

Brothers, E. B., Mathews, C. P., and Lasker, R. 1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U. S., 74: 1–8.

Collins, R. A. 1971. Size and age composition of northern anchovies (*Engraulis mordax*) in the California reduction and canning fisheries, 1968–69 season. Calif. Fish and Game, 57(4): 283–289.

Collins, R. A., and Spratt, J. D. 1969. Age determination of northern anchovies, *Engraulis mordax*, from otoliths. *In* The northern anchovy (*Engraulis mordax*) and its fishery, 1965–68. Calif. Dep. Fish and Game, Fish. Bull., (147): pp. 39–53.

Eber, L. E. 1977. Contoured depth-time charts (0 to 200 m, 1950 to 1966) of temperature, salinity, oxygen and sigma-t at 23 CalCOFI stations in the California Current. Calif. Coop. Oceanic Fish. Invest. CalCOFI Atlas No. 25, 231 pp.

Elsberry, R. L., and Garwood, R. W., Jr. 1978. Sea surface temperature anomaly generation in relation to atmospheric storms. Bull. Amer. Meteorological Soc., 59: 786–789.

Garwood, R. W., Jr. 1977. An oceanic mixed layer model capable of simulating cyclic states. J. Phys. Oceanogr., 7: 455–468.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer, 20: 1–228.

Hunter, J. R. (ed.). 1976. Report of a Colloquium on larval fish mortality studies and their relation to fishery research, Jan. 1975. NOAA Tech. Rept. NMFS Circ-395, 5 pp.

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.

Lasker, R. 1978. The relation between oceanographic conditions, and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 173: 212–230.

Lasker, R., Feder, H. M., Theilacker, G. H., and May, R. C. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5: 345–353.

Lasker, R., and Smith, P. E. 1977. Estimation of the effects of environmental variations on the eggs and larvae of the Northern anchovy. Calif. Coop. Oceanic Fish. Invest. Repts. 19: 128–137.

Lasker, R., and Zweifel, J. R. 1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. *In* Spatial pattern in plankton communities, Ed. by J. H. Steele, Plenum Publ. Corp., New York. pp. 329–354.

McLain, D. R., Favorite, F., and Lynn, R. J. 1979. Marine environmental conditions off the Pacific coast of the United States, January 1977 to March 1978. Mar. Fish. Rev. 41: 48–69.

Nelson, W. R., Ingham, M. C., and Schaaf, W. E. 1976. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrranus*. Fish. Bull., U. S., 75: 23–41.

Niiler, P. P., and Krause, E. B. 1977. One-dimensional models of the upper ocean. *In* Modeling and Prediction of the Upper Layers of the ocean. Ed. by E. B. Kraus, Pergamon Press, New York, 323 pp.

Parrish, R. H., and MacCall, A. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish and Game Fish Bull. 167, 110 pp.

Parrish, R. H., Nelson, C. S., and Bakun, A. In Press. Larval transport mechanisms and reproductive success of fishes in the California Current. Fish. Bull., U. S.

Reid, F. M. H., Stewart, E., Eppley, R. W., and Goodman, D. 1978. Spatial distribution of chlorophyll maximum layers off southern California. Limnol. Oceanogr. 23: 219–226.

Scura, E. D., and Jerde, C. W. 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.

Spratt, J. D. 1972. Age and length composition of northern anchovies, *Engraulis mordax*, in the California reduction fishery for the 1969–70 season. Calif. Fish and Game, 58(2): 121–126.

Spratt, J. D. 1973. Age and length composition of northern anchovies, *Engraulis mordax*, in the California reduction fishery for the 1971–72 season. Calif. Fish and Game, 59(4): 293–298.

Sunada, J. S. 1975. Age and length composition of northern anchovies, *Engraulis mordax*, in the 1972–73 season California anchovy reduction fishery. Calif. Fish and Game, 61(3): 133–143.

Vrooman, A. M., and Smith, P. E. 1971. Biomass of the subpopulations of Northern anchovy, *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Repts., 15: 49–51.