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THE RELATION BETWEEN OCEANOGRAPHIC CONDITIONS AND LARVAL ANCHOVY FOOD IN THE CALIFORNIA CURRENT: IDENTIFICATION OF FACTORS CONTRIBUTING TO RECRUITMENT FAILURE

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Evidence is offered in this paper to suggest that monitoring the extent and aggregation of potential larval fish food particles over a spawning season along with pertinent environmental parameters may be a practical way to predict the relative degree of pelagic fish recruitment and the strength of the resultant year class.

To discover the extent, both horizontal and vertical, of larval anchovy feeding areas and how these change with time and a variety of oceanographic and meteorological conditions, a survey of inshore and offshore particle distribution was made off southern California from September 1974 through September 1975. The temporal and spatial picture of the anchovy larva's micro- and macro-environment was expected to suggest whether conditions were good for larval anchovy feeding and hence whether good or bad recruitment might be expected on the basis of larval food distribution.

In an earlier study it was shown that it is possible to establish whether a body of water is a good or poor feeding ground for first-feeding larval anchovy, *Engraulis mordax*. Sufficiently high numbers (> than 30 particles/ml) of proper-size food organisms (cells approximately 40 µm diameter) have to be present for successful feeding.

Food was abundant within 5 km off the California shore in chlorophyll maximum layers prior to January 1975. Gyral circulation caused a widespread distribution of food throughout the Southern California Bight in January. In February 1975, a major upwelling event occurred in this area. The proper-size food particles, mostly dinoflagellates, which were abundant before the upwelling, were dissipated because of it. Smaller particles in the form of a variety of diatoms supplanted the dinoflagellates. Laboratory and field experiments have shown that regardless of their concentration, small diatoms do not provide the caloric requirements of first-feeding anchovy larvae. Upwelling continued through the early spring and summer months of 1975 and diatoms persisted. Early spring was the end of the anchovy spawning season. The data suggest that the timing of onset and the duration of upwelling are crucial determinants for survival of larvae and the resultant year classes of the northern anchovy.

INTRODUCTION

It is known from well-studied fisheries, e.g., the Atlanto-Scandian herring (*Clupea harengus*) that there is often no correlation between the size of a spawning stock and the size of its resultant year class (Hjort, 1926). Although pelagic and benthic fishes can produce enough eggs to replace their own individuals lost by natural and fishing mortality, often there are population collapses which cannot be correlated with the amount of spawning. On the other hand, there are also examples of exceptionally large pelagic fish year classes which have been produced from relatively small spawning stocks (Simpson, 1956).

Even when no fishery exists, great changes in the magnitude of pelagic fish populations may occur. For example, large fluctuations in the population size of the Pacific sardine (*Sardinops caerulea*=*S. sagax*) and northern anchovy (*Engraulis mordax*) in the California Current have taken place recently (Smith, 1972) as well as over the last 150 years, as shown by Soutar and Isaacs (1974) from sedimentary records off California.

An estimation of recruitment into an upcoming year class from the statistical information available on the size of the spawning stock can be unreliable. This was particularly evident when the Peruvian anchoveta (*Engraulis ringens*) fishery collapsed in 1973. The catch of anchovies fell drastically below the previous years' catches, from 10 million metric tons annually to less than 5 million metric tons. The panel of experts on stock assessment of the Peruvian anchoveta recognized that two years of poor recruitment touched off the collapse of that fishery, in common with the decline and disappearance of other formerly

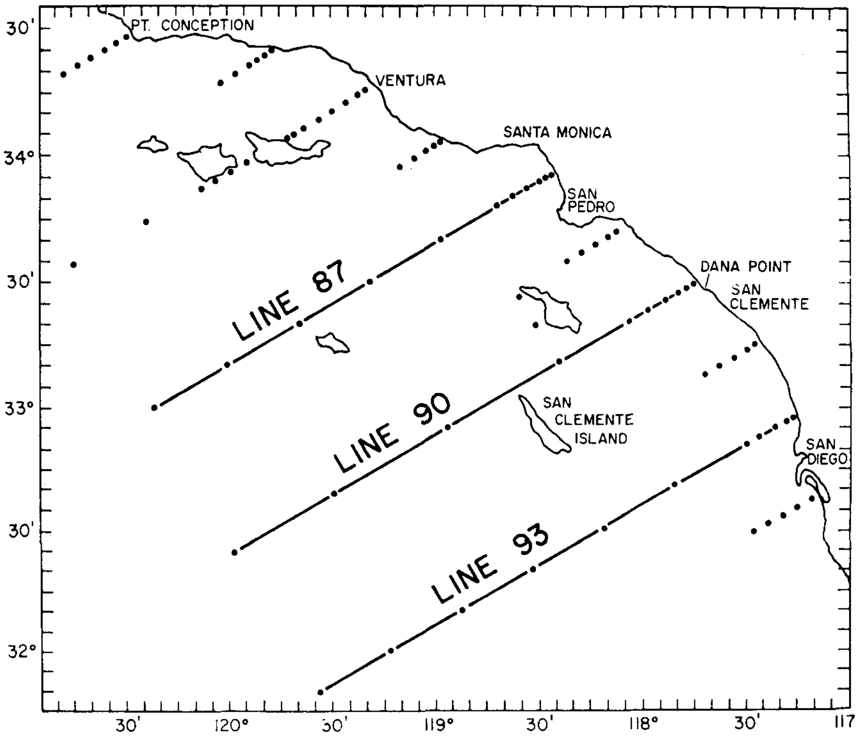

Figure 182. Basic sampling stations for the Southern California Bight. Inshore stations are located 1, 2 and 4 km from the shore.

great fisheries such as the Atlanto-Scandian herring, the Pacific sardine, the Hokkaido herring and the Japanese sardine (Murphy, 1974).

Thus despite the ability of fishery scientists to recognize the failure of recruitment into a fishery after-the-fact, there is still a lack of understanding of the mechanisms that determine year-class strength in pelagic fish populations. To manage a fishery, fishery scientists would like to be able to predict whether and to what degree any particular spawning will result in successful recruitment. For maximum economic exploitation, managers would like to know how small a spawning stock may be to ensure subsequently a reasonably large year class.

In an earlier study (Lasker, 1975), I showed from a combination of laboratory and field work that there are criteria for characterizing a body of water as a good or poor feeding ground for first-feeding larval anchovy, *Engraulis mordax*. The present study describes the results of an environmental survey of the California Current based on this earlier work and delimits the area and time when first-feeding anchovy larvae can feed sufficiently to ensure survival. Evidence is offered to suggest that monitoring the extent and aggregation of potential larval fish food particles over a spawning season along with selected environmental parameters may be a practical way to predict the relative degree of anchovy recruitment and the strength of the resultant year class. Sette (1943) in a prescient article anticipated that a meteorological-oceanographic connection might be used to predict recruitment. Data given in this paper add strength to his premise.

THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

The northern anchovy (*Engraulis mordax*) spawns in the California Current, a broad sluggish (12 km/day) southward moving current along the U.S. west coast and Baja California, Mexico (Kramer and Ahlstrom, 1968) which is characterized by gyres (Jones, 1971). The central sub-population of the northern anchovy, recently estimated at 3 to 5 million metric tons in its spawning area of 80000 km^2 (Smith, 1972) in 1974–1975, supported a 40000 metric ton

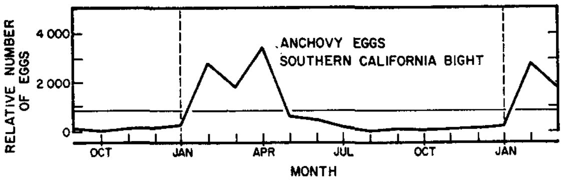

Figure 183. Annual spawning cycle (appearance of anchovy eggs) in the Southern California Bight; 8 year average from 1953 to 1960 (from Lasker and Smith, in press).

fishery in Mexico and a 110000 metric ton fishery in California. Mexico has announced its intention to exploit this resource at 500000 tons annually (Keir and Melcer, 1975).

The anchovy is highly fecund and a mature female is capable of producing thousands of eggs at a single spawning. Yet the larvae produced from eggs die at an exponential rate in the sea. Lasker and Smith (in press) have shown that on the average there is only 0·06% survival at 20 days of larval age for the northern anchovy, with 40 or more additional days still to go until metamorphosis, depending on temperature. Various explanations for this enormous mortality have been suggested. Hjort's hypothesis (1914), that for a larva to survive it must have the correct food in the right density when it starts to feed and that the success of a subsequent year class depends on this, has not been disproven and continues to be one of the most reasonable explanations for differential larval survival (May, 1974). Hjort's idea as restated by May (1974) is that the strength of a year class is determined by the availability of planktonic food shortly after the larva's yolk-sac has been exhausted.

Laboratory work on northern anchovy has shown that relatively high densities of food particles are needed by first-feeding anchovy larvae to account for: 1) their inefficient ability to capture food during the first few days of feeding (Hunter, 1972), 2) their relatively high metabolic requirement (Vlymen, 1974),

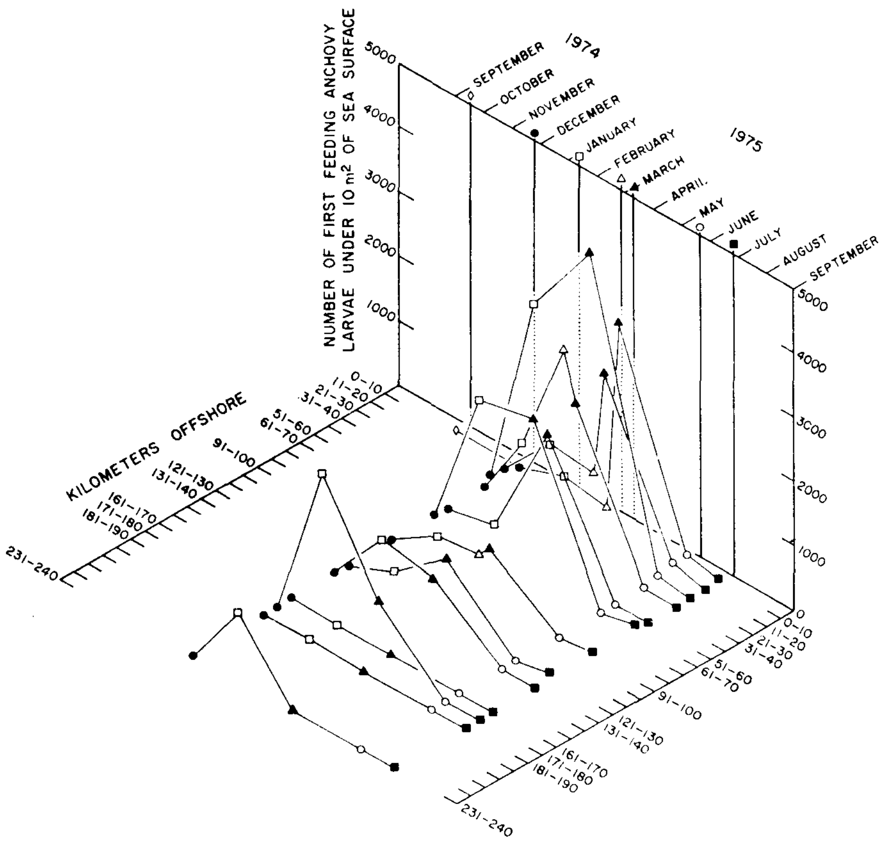

Figure 184. Spatial and temporal distribution of first-feeding northern anchovy larvae in the Southern California Bight and offshore zone. Symbols identify particular cruises as indicated on the abscissa.

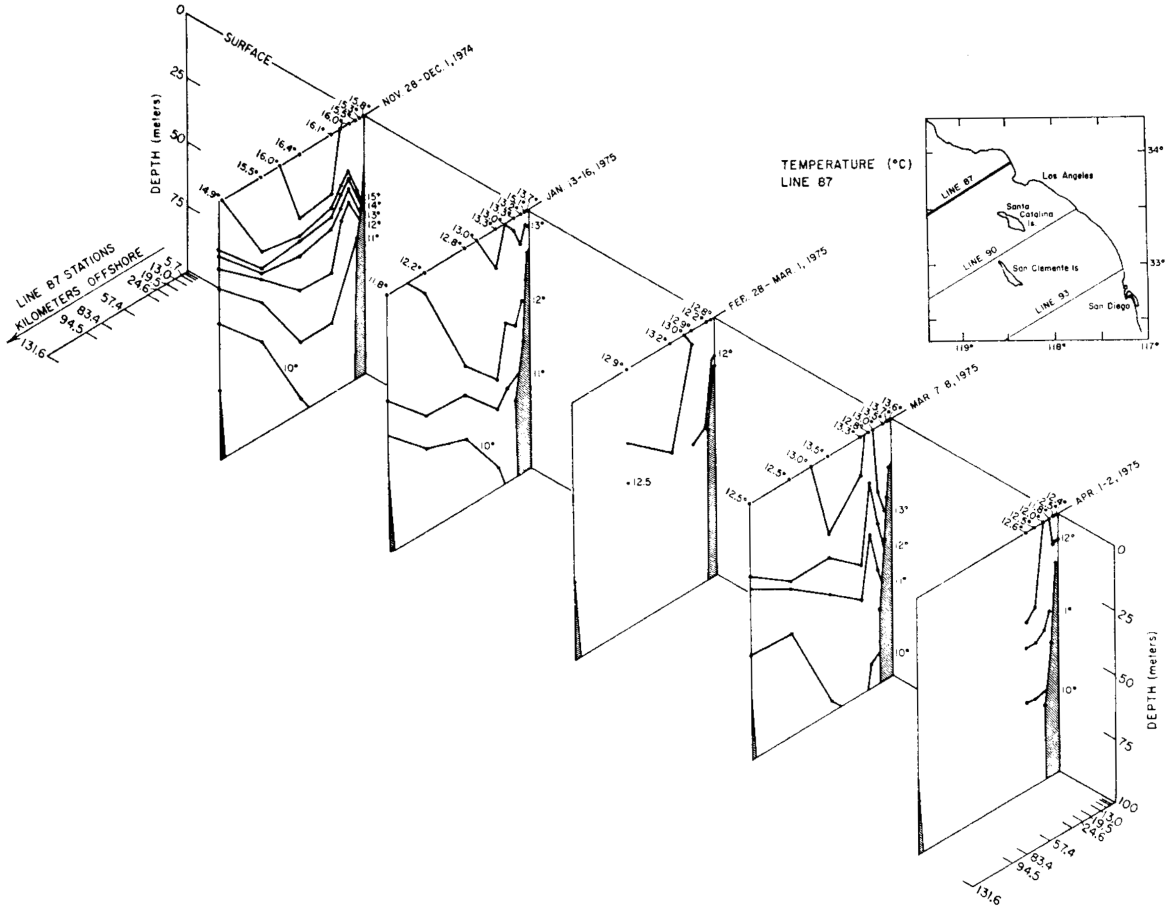

Figure 185. Temperature profiles during five cruises from November 1974 to April 1975. Line 87 extends from Santa Monica Bay, California to offshore.

3) a small mouth size restricting the maximum particle size that can be taken, and 4) the cessation of feeding at night (Arthur, 1976). Hunter (in press) has calculated that approximately 230 food particles of about 50 µm in diameter (e.g., the size of the unarmoured dinoflagellate, *Gymnodinium splendens*) would have to be consumed per day by a first-feeding anchovy larva to meet its metabolic requirement.

TEST AT SEA OF HJORT'S HYPOTHESIS

In an earlier investigation (Lasker, 1975), laboratory-hatched first-feeding anchovy larvae were allowed to feed in natural sea water in March and April 1974 and in various densities of *Gymnodinium splendens* in the laboratory. Both experiments showed that a full or partial filling of the gut over an 8-hour period required between 20 and 40 cells per millilitre in the larva's environment. Cells smaller than 30 µm in "effective diameter"[1] were taken only occasionally (Lasker, 1975). Sufficiently high numbers of proper-size food organisms were found chiefly in well-developed chlorophyll maximum layers adjacent to the California coastline. A stormy period was effective in eliminating the chlorophyll maximum layer and in diluting the potential food organisms (in this case the unarmoured dinoflagellate, *Gymnodinium splendens*) below the critical density needed for feeding. An unusual finding was that the dinoflagellate population extended for at least 100 km along the shore.

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[1] Coulter Counter (Model Ta) was used to record the volumes of individual particles. Despite the fact that particles are varied in shape, in this study, sizes were recorded by "effective diameter" as if all particles sampled were spheres.

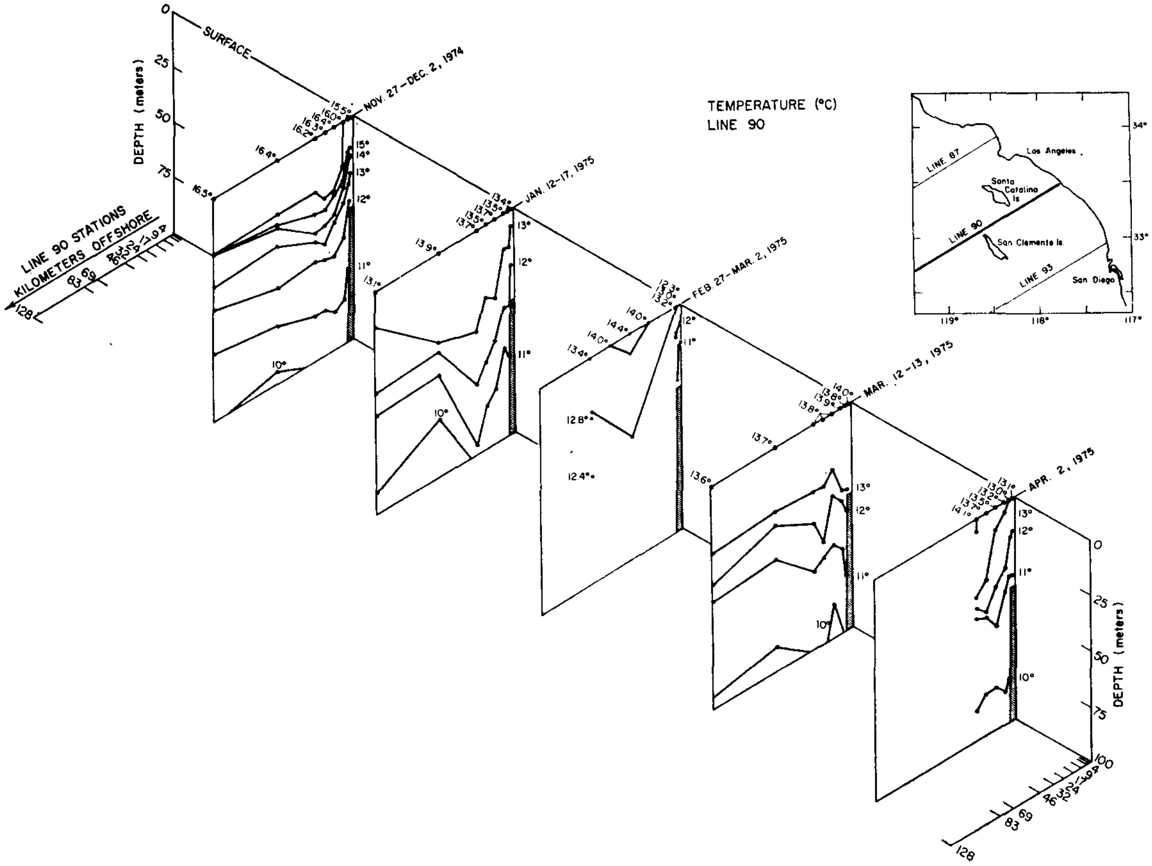

Figure 186. Temperature profiles during five cruises from November 1974 to April 1975. Line 90 extends from Dana Point, to offshore between Santa Catalina and San Clemente Islands.

The seaward extent of this huge "patch" was not ascertained (Lasker, 1975; Kiefer and Lasker, 1975).

The threshold for larval anchovy successful first-feeding was therefore defined as the presence of at least 30 cells/ml of particles 30 to 50 µm in effective diameter. Successful recruitment depends on the existence of sufficient areas containing such particles at proper densities and co-occurring with first-feeding anchovy larvae.

OBJECTIVES

To discover the extent, both horizontal and vertical, of larval anchovy feeding areas and how these change with time and a variety of oceanographic and meteorological conditions, a survey of inshore and offshore particle distributions was made off southern California from September 1974 through September 1975. This period spanned a complete anchovy spawning season which normally occurs from January to May (Fig. 183). The temporal and spatial picture of the anchovy larva's micro- and macro-environment was expected to suggest whether conditions were good for larval anchovy feeding and hence whether good or bad recruitment might be expected on the basis of larval food distribution.

Specifically, the following were measured: 1) the extent, persistence and patchiness of organisms causing chlorophyll maximum layers, 2) the relationship of these organisms to the distribution of first-feeding anchovy larvae, 3) the concentration of > 20 µm "effective diameter" particles and their size distribution, 4) the relationship of phyto- and microzooplankton patches to environmental conditions, e.g.,

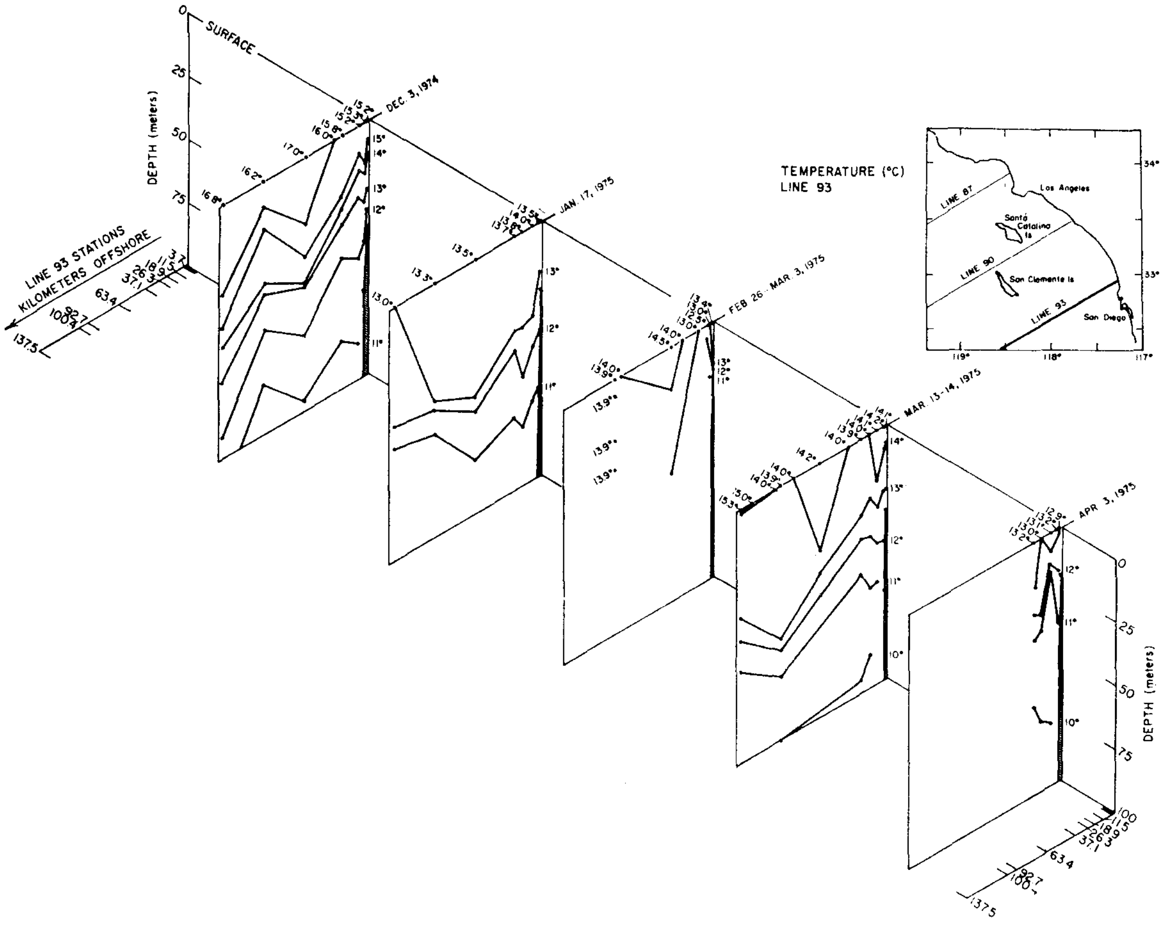

Figure 187. Temperature profiles during five cruises from November 1974 to April 1975. Line 93 extends from Del Mar, California to offshore.

storms and upwelling, and 5) the nutritional value of the dominant larval anchovy food organisms.

METHODS

An intensive sampling pattern in the inshore zone (Fig. 182) was established during the regular California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey using the RV "David Starr Jordan". This was done to determine the seaward extent of chlorophyll maximum layers shallower than 30 m. Thirty metres depth was chosen because Ahlstrom (1959) (data summarized by Hunter and Sanchez, 1976) showed that over 80% of northern anchovy larvae smaller than 12 mm long are found in water shallower than 30 m, while most yolk-sac and newly feeding larvae are nearer the surface. Cruises of the RV "David Starr Jordan" were held about monthly from September 1974 through September 1975.

A 3/4 h.p. - 110 V submersible centrifugal pump[2] was used with 30 m of 2·54 cm inside diameter flexible hose deployed over the ship's side to detect chlorophyll and particle concentrations. A stream of water was ducted to a Turner fluorometer onboard and the chlorophyll depth profile recorded. Samples of water (200 ml) were taken from just under the surface and from the chlorophyll maximum layer for particle

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[2] Prosser Industries, Inc., 900 E. Ball Road, Anaheim, California 92803 Pump No. 9-911-7.

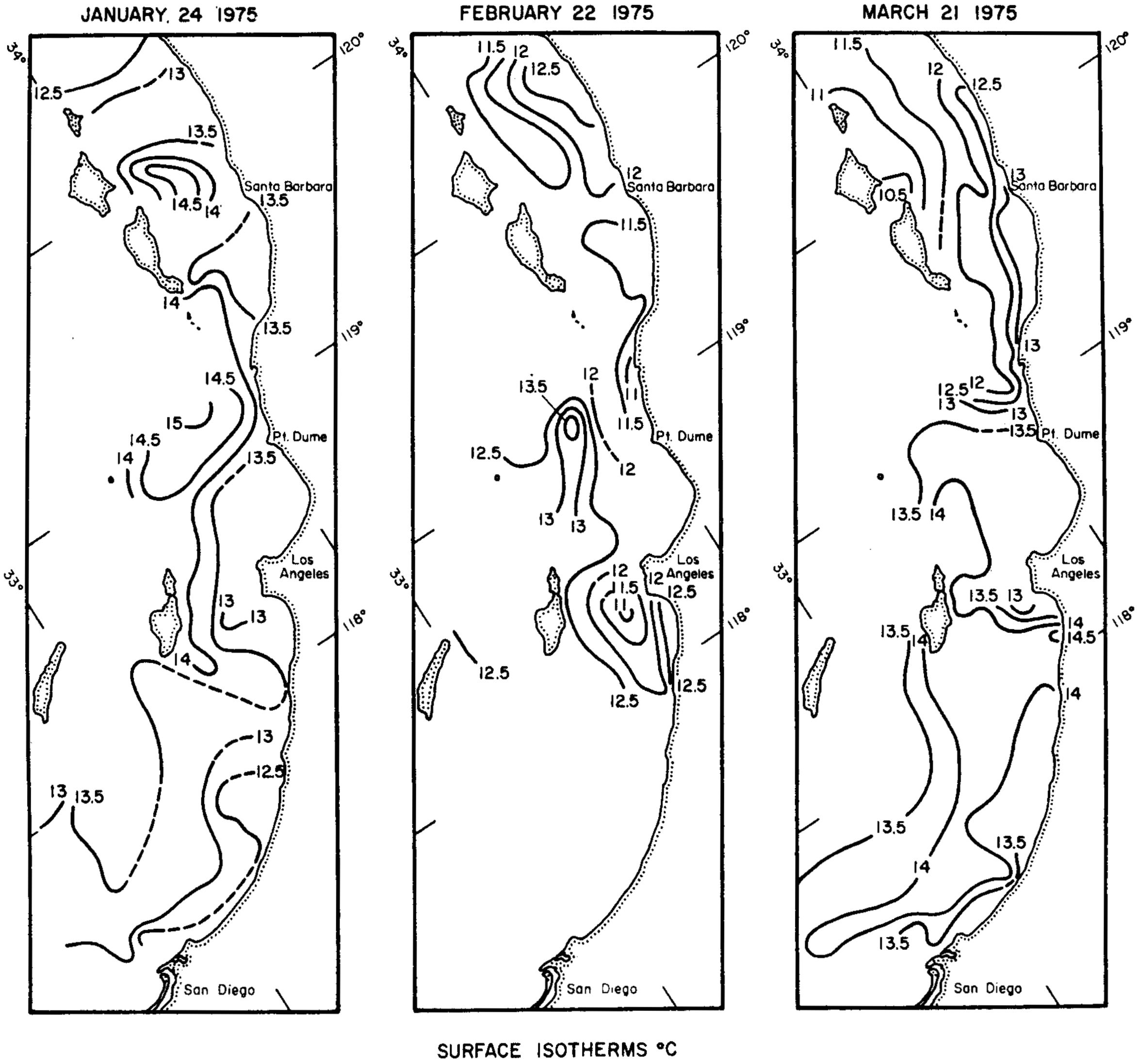

Figure 188. Surface isotherms obtained by U.S. Coast Guard overflights with an infra-red radiometer.

counting and sizing with a 16-channel Model Ta Coulter Counter using a 280 µm pore and for determining the chlorophyll *a* component (Kiefer and Lasker, 1975). When no subsurface chlorophyll maximum was found, a water sample was taken routinely from 15 m depth. In each instance an additional 500 ml water sample was preserved with strontium-chloride-fortified-formalin as described by Beers and Stewart (1970) for later microscopic examination. No particles smaller than 20 µm effective diameter were counted with the Coulter Counter, but all particles having at least one dimension, 20 µm or longer, were identified and counted microscopically. The latter usually included most of the diatom species found in the Southern California Bight.

Anchovy larvae were collected in oblique plankton tows with a 1 m mouth diameter plankton net (mesh size, 0·505 mm). Larvae were sorted from other

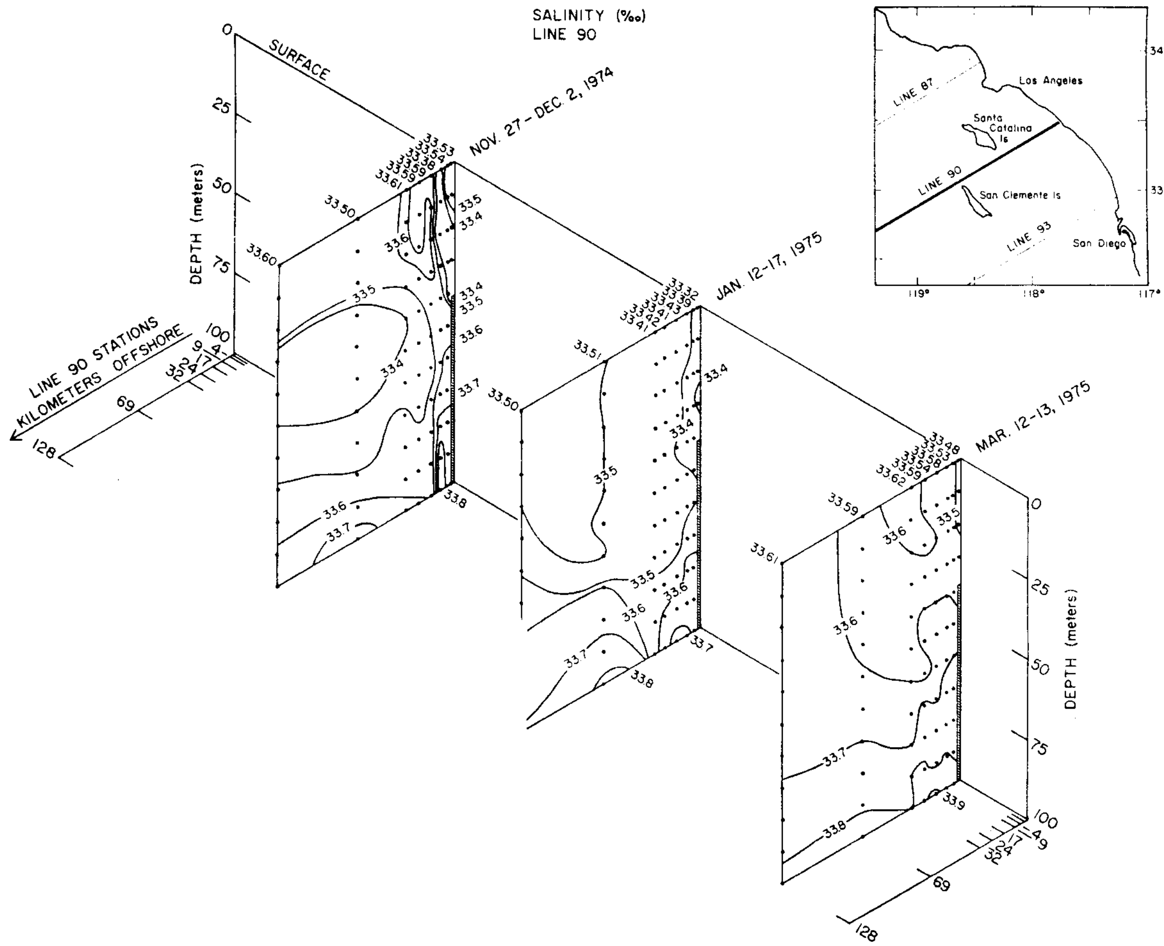

Figure 189. Isohalines along line 90, November 1974 to March 1975.

plankton, measured and counted. Details of these operations are given by Kramer et al (1972). Larval anchovy concentrations are given as numbers of larvae under 10 m^2 of sea surface.

Salinities and temperatures with depth were recorded at each station with a Plessey STD. In September 1974, February 1975 and June 1975, cruises by the Food Chain Research Group of the Scripps Institution of Oceanography occupied three regular CalCOFI transects and their information supplements that obtained by the RV "Jordan".

The CalCOFI basic station plan (Anon, 1963) shows the major stations occupied on every CalCOFI cruise. The three transects studied most intensively in this investigation were Lines 87, 90 and 93. The relative positions of these three transects are also shown in Figure 182.

OCEANOGRAPHY OF THE SOUTHERN CALIFORNIA BIGHT DURING THE 1974–1975 NORTHERN ANCHOVY SPAWNING SEASON

Annual spawning season

The distribution and aggregation of larval food, composed of microplankton > 30 µm effective diameter, is greatly affected by currents, turbulence, upwelling and downwelling. Therefore, oceanic conditions in the Southern California Bight were closely monitored during the 1974–1975 spawning of the

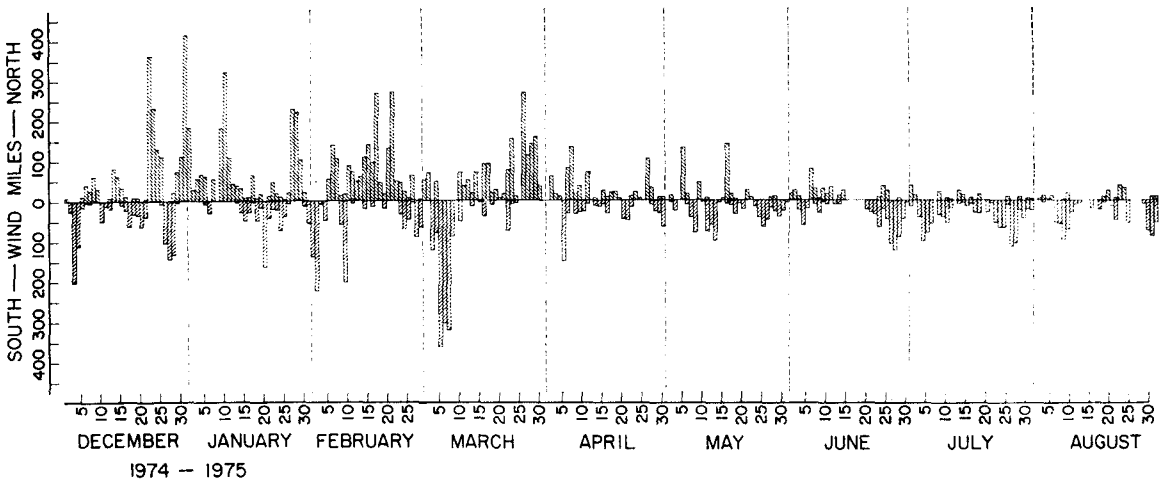

Figure 190. North and south wind miles at San Clemente Island. Wind miles were calculated by multiplying hours and wind speed. Major upwelling was noted on February 22 after about a week of northerly winds.

northern anchovy. Usually, spawning by the northern anchovy occurs over the winter and early spring months, but mostly during February, March and April (Fig. 183). This temporal spawning pattern was repeated in 1974–1975 (Fig. 184). The February–March 1975 spawning in the Southern California Bight was substantially greater than it had been in the previous five years (Smith, pers. comm.).

When plankton tows were made to sample anchovy larvae and their food, vertical profiles of water temperature and salinity were taken simultaneously. A weather station on San Clemente Island provided wind and storm data.

WATER TEMPERATURES OF THE SOUTHERN CALIFORNIA BIGHT

Stable water temperatures were characteristic of the Southern California Bight from September 1974 through early December 1974. For example, surface temperatures over the entire Bight were between 15°C and 17°C along the three major transects in the Bight, lines 87, 90 and 93 (Figs 185, 186 and 187) the first week of December. A sharp thermocline extended from the shore out to approximately 10 km and the entire length of the bight, about 300 km. Surface cooling was particularly evident when the 12–17 January cruise was held. A deep (25–50 m) mixed layer of 12° to 13°C developed along line 87, and at 13° to 14°C along lines 90 and 93. In February, 11°C was common inshore and was indicative of a major upwelling event (Fig. 188).

SALINITY STRUCTURE OF THE SOUTHERN CALIFORNIA BIGHT

Southern California Bight water was generally less saline in mid-January (33·3–33·4$^{0}/_{00}$ S) inshore than it was in early December (33·5–33·6$^{0}/_{00}$). No strong upwelling was evident. The hyposaline condition (33·3–33·4$^{0}/_{00}$) (Fig. 189) can be explained by a southward flow next to the coast, associated with a clockwise gyre typical of winter circulation in the southern part of the Bight (Jones, 1971).

UPWELLING

Strong upwelling began in February in the Bight after the onset of northerly winds (Fig. 190) and was clearly evident from the appearance of depressed temperatures (11°–12°C) inshore coincident with the appearance of diatoms (see following section).

A series of storms with strong southerly winds started on 3 March and lasted one week. The appearance of higher salinities inshore indicated a northerly flow of water and convergence (downwelling) throughout the Bight. After this stormy period, upwelling recommenced as shown by the generally colder water inshore and the upward thrust of the colder (11° and 12°C) isotherms in April (Figs 185, 186 and 187). Similar upwelled conditions prevailed through the following spring and summer months.

These data show that there was a typical winter circulation in the Southern California Bight. Generally calm conditions presaged the annual anchovy spawning cycle. January in particular was not stormy but

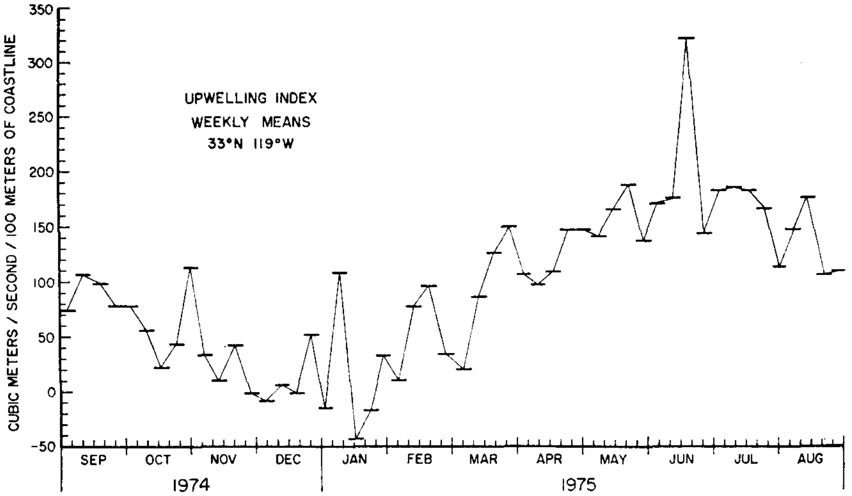

Figure 191. Upwelling index, September 1974–September 1975, calculated at San Clemente Island for the Southern California Bight. Upwelling is given as flow of water in m^3 s^{-1} 100 m^{-1} of coastline (Bakun, 1975).

there was sufficient water circulation and surface cooling in the Bight to obliterate the thermocline and, as will be seen from the following section, to distribute potential larval fish food throughout the Bight. Northwest winds (Fig. 190) prior to the 26 February to 3 March sampling cruise presumably caused divergence of water from the inshore zone resulting in a significant upwelling which was reversed in the days that followed. This alternation of upwelling and relaxation over a 2-week period was associated with a thorough mixing of the upper isothermal (13°–14°C) layer. Two weeks later, in early April, upwelling was firmly established once more and continued throughout the rest of the spring and summer. This alternation of upwelling and relaxation, as shown by temperature profiles, is also reflected by Bakun's (1975) upwelling index for the 3° square encompassing the Southern California Bight and measured at 33°2′N 118°36′W, at the northern tip of San Clemente Island, 55 m elevation (Fig. 191). Infra-red satellite photographs of the Southern California Bight and Baja California showed that upwelling had commenced at least as early as 21 February 1975 and extended as far south as Vizcaino Bay at that time, 723 km from Los Angeles, California. This encompassed virtually the entire larval anchovy's feeding grounds.

POTENTIAL LARVAL ANCHOVY FOOD PARTICLES IN THE SOUTHERN CALIFORNIA BIGHT, 1974–1975

In March 1974, at the height of the 1973–1974 anchovy spawning season, the unarmoured dinoflagellate *Gymnodinium splendens* (30–50 µm effective diameter) was the dominant organism inhabiting inshore chlorophyll maximum layers (Lasker, 1975). By September 1974, in the same inshore areas, the common red tide organism, the armoured dinoflagellate *Gonyaulax polyedra* dominated the chlorophyll maximum layers. *G. splendens* was no longer seen. The areal extent and temporal persistence of *G. polyedra* was striking; an apparently continuous layer about 300 km long, and 5 km wide, extended from at least Point Conception to San Diego ranging in concentration from 20 to 2000 cells/ml in the chlorophyll maximum until January 1975 when *G. polyedra* in relatively high concentrations was distributed throughout the Southern California Bight. Table 14 and Addendum summarize phytoplankton and microzooplankton species and relative densities along line 90 from September 1974 through July 1975. The spatial and temporal distribution of dinoflagellates and diatoms is shown graphically in Figure 192.

From September 1974 until early February 1975, *G. polyedra* was the numerically abundant organism in the size range eaten most often by first-feeding anchovy larvae. The high number of particles displayed do not occur throughout the water column, but rather appear either at the surface or in well-defined chlorophyll maximum layers, most 15–20 m below the surface. In January (Fig. 193), *G. polyedra* was no longer confined to within a few kilometres of the shore, but was prevalent in high concentrations, i.e. > 35 cells/ml, throughout the Bight, presumably distributed by the usual winter gyral movement of

Table 14. Species composition and relative numerical abundance of phytoplankton and microzooplankton along line 90 from September 1974 through September 1975. All stations were within 9·5 km. Stations and depths selected for this table had the highest overall concentrations of organisms. Note the disappearance of *Gonyaulax polyedra* and the appearance of diatoms after the early February sampling, presumably as a result of a major upwelling event.

Key; Cells/ml: 0·1–0·9 (+); 1–9 (++); 10–99 (+++); 100–999 (++++).

DATE DISTANCE FROM SHORE (KM) AND DEPTH (M)	DINOFLAGELLATES												DIATOMS																									
	Gonyaulax polyedra	Ceratium furca	Ceratium fusus	Dinophysis caudata	Peridinium spp.	Prorocentrum micans	Ceratium spp.	Dinophysis spp.	Gymnodinium spp.	Misc. Unarmored Dinoflagellates	Misc. Armored Dinoflagellates	Oxytoxum spp.	Nitzschia spp.	Rhizosolenia spp.	Biddulphia sp.	Chaetoceros spp.	Thalassiothrix frauenfeldii	Unidentified Chain Diatoms	Asterionella japonica	Thalassiosira spp.	Skeletonema costatum	Eucampia zoodiacus	Coscinodiscus spp.	Ditylum brightwellii	Thalassionema nitzschioides	Misc. Diatoms (≥ 20 µ)	Unidentified Cells (20-50 µm)	Unidentified Cells (50-100 µm)	Silicoflagellates	Coccolithophores	Ciliates	Tintinnids	Holotrichs	Copepod nauplii	Radiolarians & Foraminiferans	Unidentified particles (20-50 µm)	Unidentified particles (50-100 µm)	Unidentified particles (>100 µm)
Sept. 13-20, '74 0.93 km (3m)	+++	++	+	++	++	++	++																			++	++	+				+	++		++	+++	++	
Nov. 26-Dec. 19 '74 1.85 km (13.5m)	++++		++	++	++		++					++		++													+++	++		++			++			++	++	
Jan. 12-Feb. 3 '75 9.45 km (14m)	++++	++			++		++				++		+++	++	++	++	++									++	++	++		++	+				+	+++	++	++
Feb. 26-Mar. 3 '75 0.93 km (1m)	++	++			++		+		++	++++			++++	++		+++	++	++		++	+++					++	++	++	++		+	+	+			++	++	++
Mar. 6-26, '75 1.85 km (30m)								+		+			+++	++		++	+++	++			+	++	+			++	++	++	+	+	++	+	++	+		+++	++	+++
Apr. 1-3, '75 1.85 km (17.5m)										++			+++	+++	++	++++	++++		+++	++++	+++	++		+++	+++	+++	++									+++	+++	++
May 15-26, '75 4.08 km (15m)					+		+			++	+			+	+											+	+	+	+		++	++	++	+		+++	++	++
June 16-24, '75 0.93 km (12 m)		++			++	++	+	++	++	++		+	+++	++	++	+++		+++								+	++	+			+	++	+	+		++	++	++
June 24-July 7, '75 4.08 km (10 m)	++	+			+	+++	++	++		++		+	+++	++	++	++		++	++		+	++++				++	++	+			+	++	+		+	++	++	++
Sept. 6-14, '75 0.93 km (Surface)	++	++	++		++	++	++	+	++	++	++	++															++	+	+		++		+	+		+++	++	++
Sept. 13-22, '75 1.85 km (22 m)								+						+													+								+	++	++	+

water[3] (Schwartzlose, 1963) and favourable conditions for reproduction. First-feeding anchovy larvae appeared in the Bight in January. Twenty-five first-feeding larvae of 253 examined in that month had discrete particles in their intestines; sixteen of the twenty-five contained *Gonyaulax*.[4] Five weeks later, as a result of an upwelling which encompassed the entire Bight, the number of particles with effective diameters of 30 µm and larger over the entire area was reduced

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[3] Advection of southerly water cannot be dismissed as a possibility.

[4] While particle size and density are limiting characteristics for larval anchovy survival, the nutritive value of the food particles may also be an important factor. A number of feeding experiments with laboratory cultured *G. polyedra* and laboratory hatched *E. mordax* larvae showed that first-feeding larvae did not grow well on *G. polyedra* as a sole diet, whereas they can on the unarmoured dinoflagellate *Gymnodinium splendens* (Scura and Jerde, 1977). A dominant, but nutritionally inadequate, food for anchovy larvae provides an additional cause for unfavourable survival of an anchovy year class.

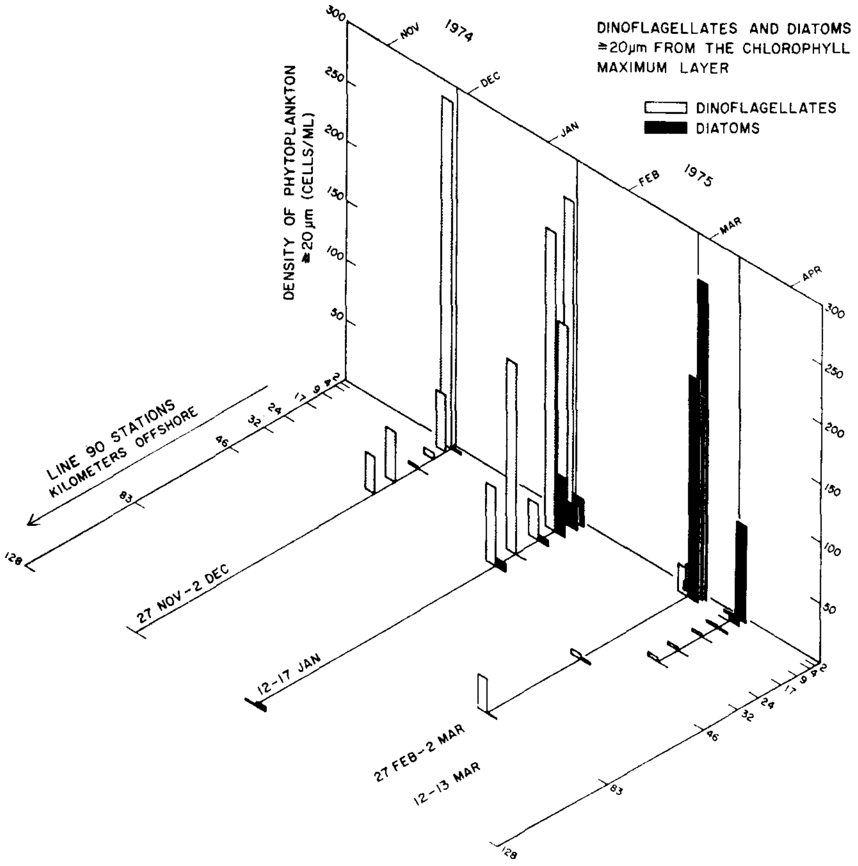

Figure 192. A comparison of diatom and dinoflagellate abundance along line 90 over the anchovy spawning season.

far below that necessary for first feeding and survival by anchovy larvae. This is shown graphically in Figure 194.

The importance of this event and its possible effect on survival of fish larvae should be emphasized. Chlorophyll *a* measurements (Fig. 195) and the replacement of dinoflagellates by diatoms show clearly the response to the major upwelling in the Bight during February and March 1975. However, my own laboratory and field results, and the work of Arthur (1976) and Berner (1959) show that anchovy larvae have a particle size threshold for feeding; small diatoms, whether in chains or as single cells and regardless of concentrations are usually not large enough to be seen or are ignored for other reasons by first-feeding anchovy larvae.

Thus, despite the obvious benefit to phytoplankton production that upwelling brings to coastal waters, the disruption of well-defined layers and aggregations of suitable larval fish food organisms is undoubtedly detrimental to the larvae relying on such aggregations. In other words, those oceanographic features which favour stability in inshore waters can be classified as favourable for anchovy larval fish feeding, while those which cause instability should be considered to be detrimental to larval survival. Nelson et al (1976) showed in a different environmental context that menhaden larvae which depend on nursery grounds in estuaries for food are carried into the estuaries during downwelling periods. In this instance, upwelling also acts to the detriment of larval survival but by a different mechanism.

Hunter (in press) has shown that northern anchovy larvae can exist and grow until they are 6 mm in length on particles approximately 40 μm in diameter, e.g., *Gymnodinium.* The larvae remain 6 mm in length as long as there are 40 μm particles in high enough concentrations on which they can subsist. It is im-

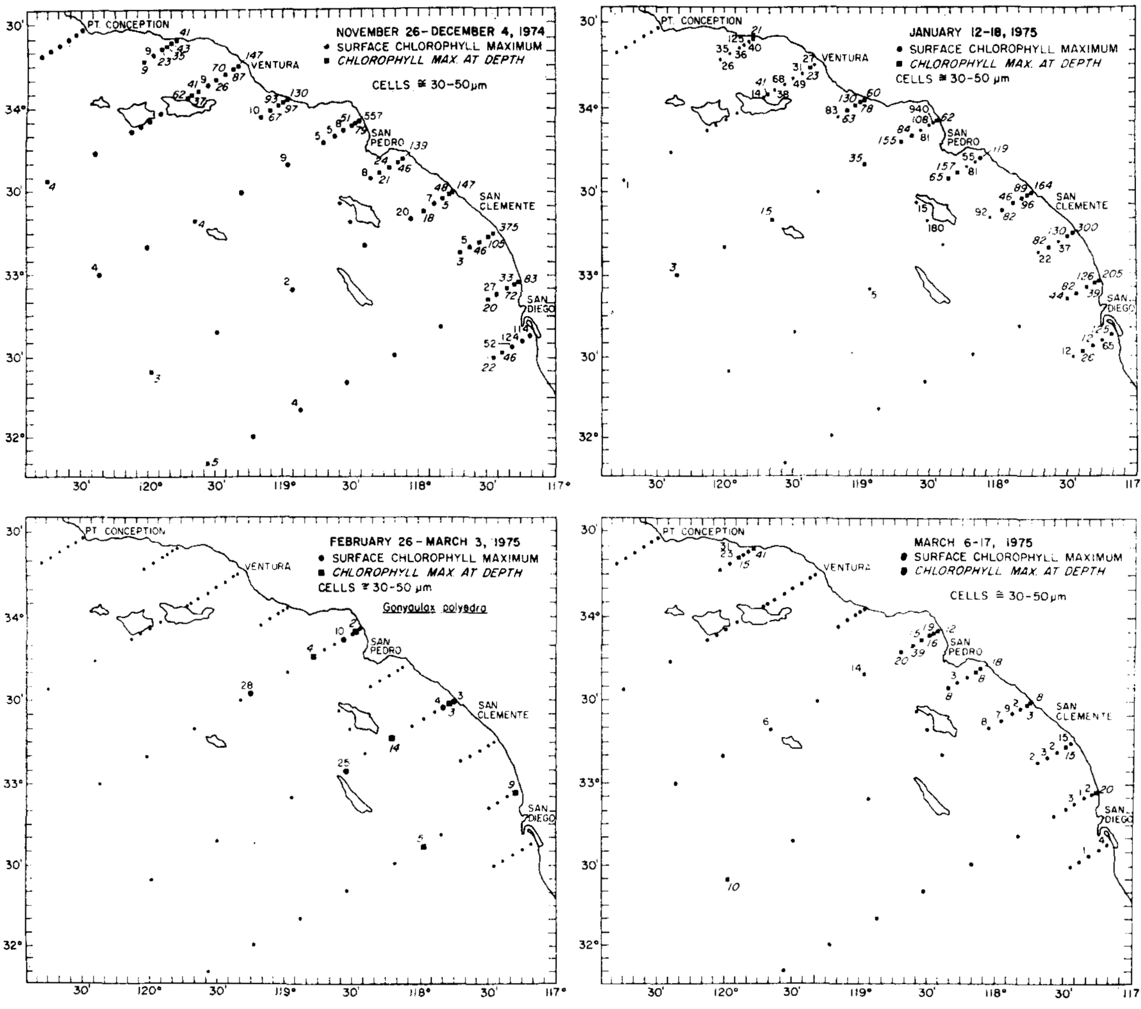

Figure 193. The distribution of maximum counts of 30–50 μm particles in the Southern California Bight from November 26 1974 to March 17 1975. Note the inshore prevalence of these particles in late November and their widespread distribution in January.

possible for them, because of physical limitations, to capture enough of these small particles once they have attained this size to do any more than maintain their metabolic requirement. However, should larger particles become available to them, enabling them to grow larger than 6 mm, this larger size precludes an ability to resort solely to small particles once again and the larva becomes locked into eating larger particles to meet its metabolic requirements. The implications of this are profound, i.e. from 6 mm on, anchovy larvae must encounter relatively high densities of larger particles to ensure their survival, yet these densities have not often been found in the sea. In other words, high densities of microzooplankters larger than 50 μm in diameter must exist, but are not reported in the literature.

Counts of micronauplii were made for samples taken along line 90 with a plankton pump to see if minimum numbers, as calculated by Vlymen (1977), would be found during the spawning season of the anchovy. Concentrations of nauplii as high as this were encountered rarely. For example, only two inshore water samples taken from the chlorophyll maximum layer, 0·9 km apart, showed 280 and 117 micro-

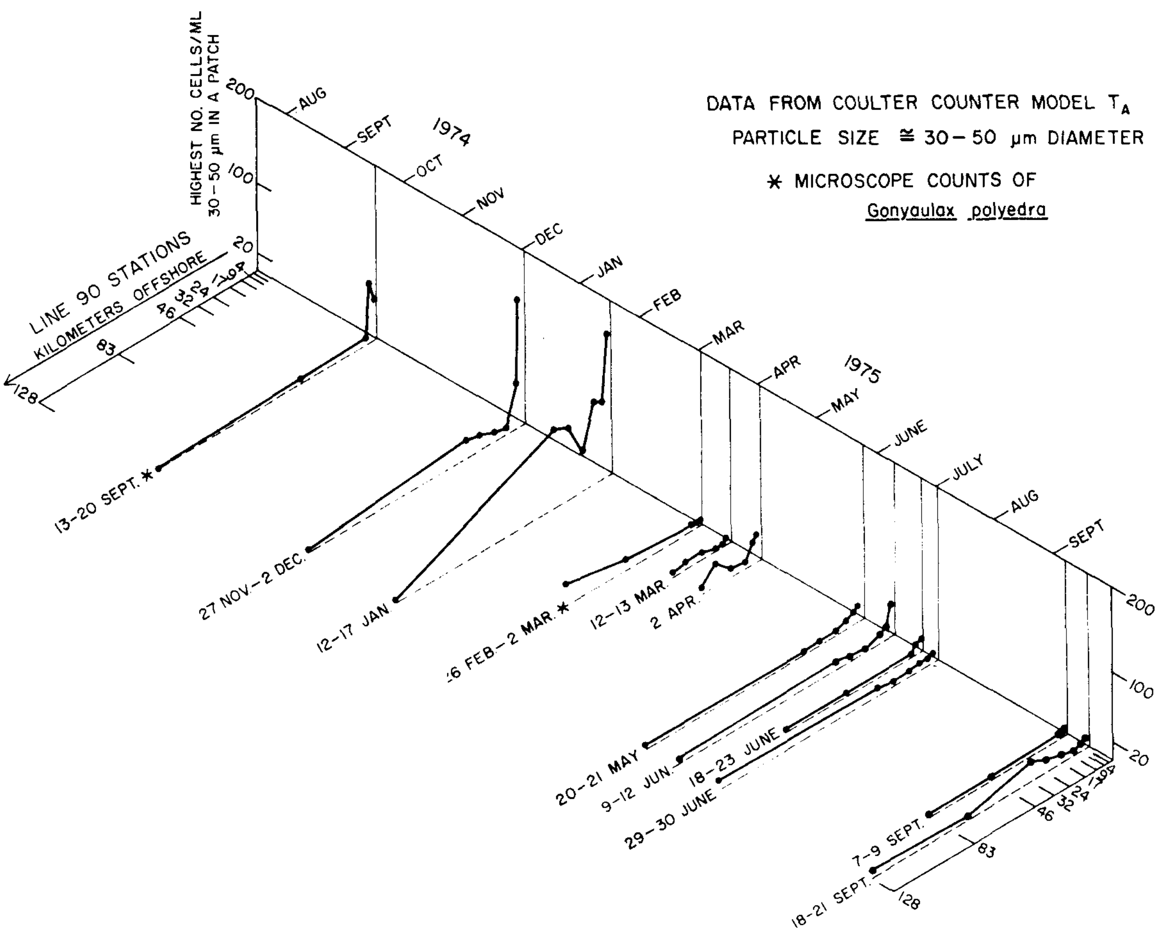

Figure 194. Spatial and temporal distribution of the highest number of 30–50 µm diameter particles found in the water columns throughout the Southern California Bight from September 1974 through September 1975. Note the high inshore particle concentrations in December and January.

zooplankters per litre, respectively. Both samples had the same size frequency distribution of organisms which included nauplii, copepod, post-nauplii and polychaete larvae. Nauplii were present in the greatest number in each sample (Fig. 196). Upwelling regions, as described in this paper, when they stimulate reproductive activity in copepods and other small plankters provide the necessary forage for anchovy larvae larger than 6 mm in length. If a larva grows to a larger size despite a dilution of its initial food during the upwelling process, the chances for survival may increase if regions of high naupliar and other microzooplankton densities are established in the wake of an upwelling event.

Throughout this study, concentrations of phytoplankton and zooplankton have been reported as they were taken with a plankton pump, which undoubtedly reduces concentrations of organisms at the opening of the pump and as water travels through the pipe to the shipboard laboratory. Thus, the key to defining microstratification, clumping and patchiness is the solution of a sampling problem for the particles which serve as food for fish larvae. Without doubt, there will be many areas found in the larval anchovy spawning ground which emulate the highest concentrations of organisms we have sampled with the techniques at hand. The spatial distribution and temporal persistence of high larval food concentrations is an important

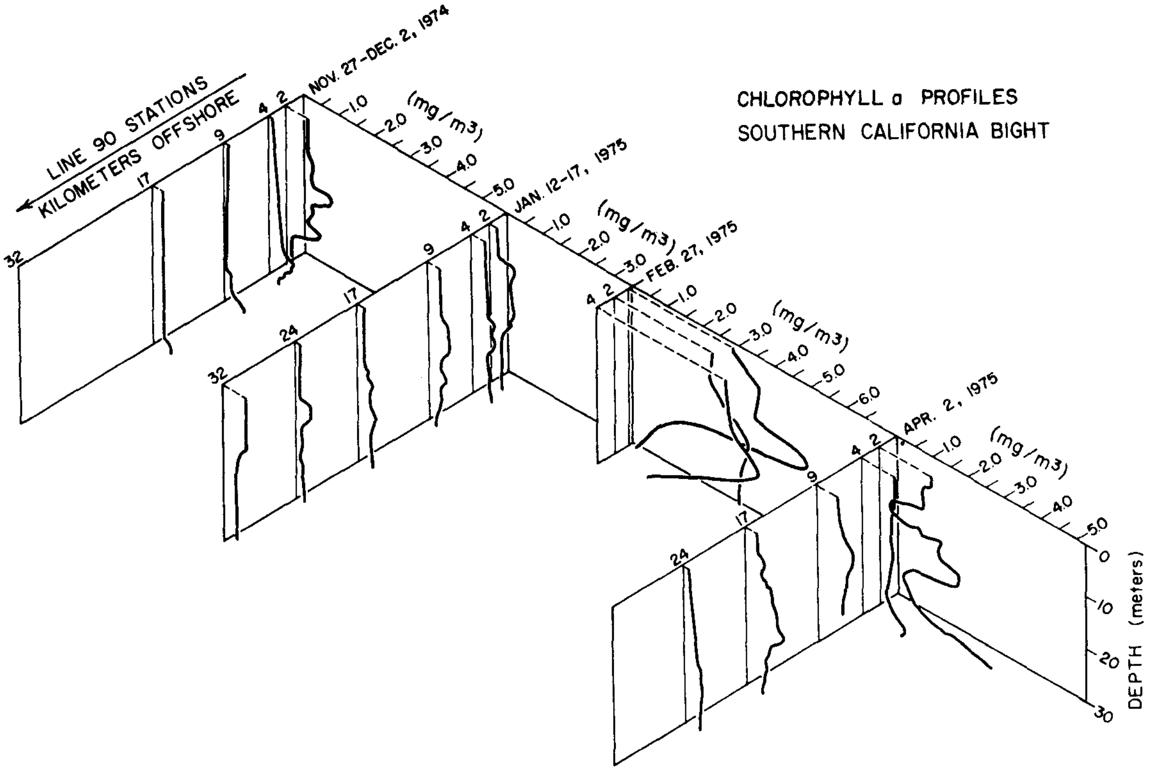

Figure 195. Chlorophyll *a* profiles for line 90 from November 1974 through early April 1975. High chlorophyll *a* in February is due to a diatom bloom (see Table 14).

area of study for elucidating the stock and recruitment relationship.

ACKNOWLEDGEMENTS

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SUMMARY

1) Northern anchovy larvae require at first feeding, relatively high densities of 30–50 μm particles for metabolism and growth. During the 1975 anchovy spawning season, dinoflagellates met these conditions in the main inshore spawning area of the anchovy off California.

2) Stable oceanographic conditions which foster stratification are needed to maintain high densities of dinoflagellates.

3) When particle sizes and concentrations were monitored over a complete anchovy spawning season in the Southern California Bight, it was seen that upwelling and storms could disrupt dinoflagellate layers. In February 1975, a massive upwelling throughout the Southern California Bight diluted dinoflagellate concentrations far below that needed by first-feeding anchovy larvae for metabolism and growth.

4) Despite the obvious value of upwelling to total algal productivity the diatoms which are first produced in numbers are too small or unacceptable behaviourally as food for first-feeding anchovy larvae.

5) Anchovy larvae can sustain themselves and grow to 6 mm on small particles. Once this size is attained further growth depends on large particles being eaten. Once larger particles are eaten the larva cannot rely on small particles any longer but must continue to seek and find large ones to maintain its metabolism.

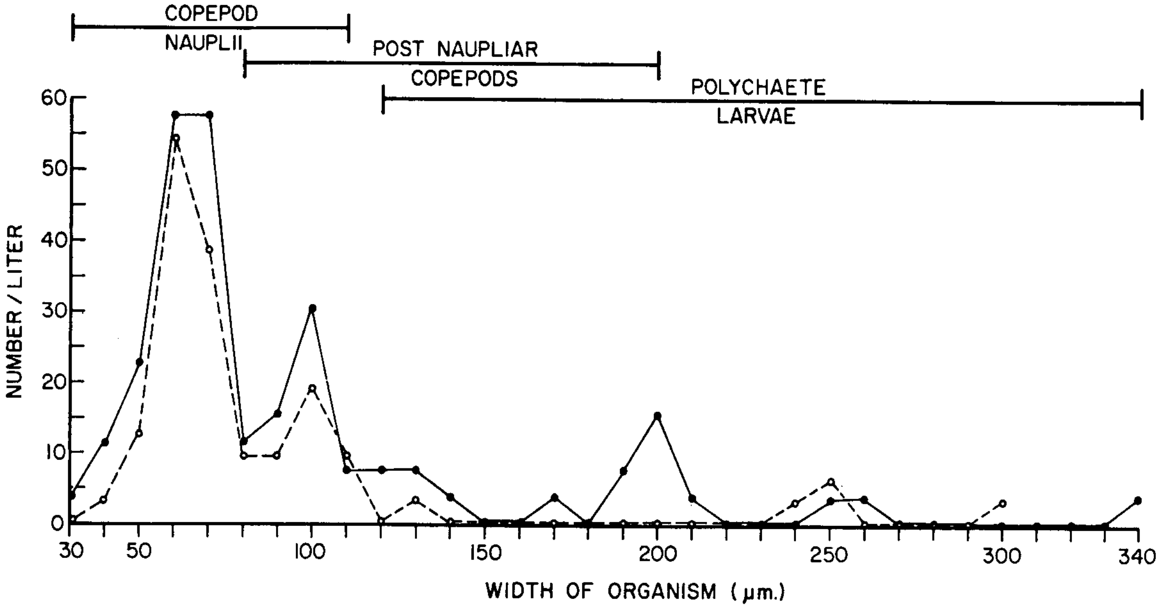

Figure 196. Width frequency distribution of two samples of microzooplankton taken in March 1976, 0·8 km apart within 2 km of the shore. Closed circles indicate the sample taken nearest the shore.

6) Microzooplankters are generally larger than 40 μm in width but were rarely found in high enough concentration to serve as food for larger anchovy larvae.

7) The most dominant dinoflagellate present during the 1975 anchovy spawning season was found to be nutritionally deficient in laboratory experiments.

8) The presence of a nutritionally inadequate dominant food as well as a massive upwelling in the midst of the anchovy spawning season suggests inadequate feeding conditions for the 1975 year class of anchovy during larval development. If this hypothesis is correct, the 1975 year class of the northern anchovy will be a relatively poor one.

ADDENDUM

A RÉSUMÉ OF PHYTOPLANKTON DISTRIBUTION FROM SEPTEMBER 1974 THROUGH SEPTEMBER 1975

September 1974

In the cruise period 13–20 September 1974, microscope counts revealed that *Gonyaulax polyedra* was the dominant species of phytoplankton in the Southern California Bight, with the highest density (about 2000/ml) in Santa Monica Bay (line 87), 67/ml off Dana Point (line 90) and 20/ml off Del Mar (line 93). *G. polyedra* was concentrated in the inshore zone along line 87, within 5–6 km offshore and within 3·7 km for lines 90 and 93.

Other organisms common in the Bight at the same time were the dinoflagellates *Ceratium furca* and *Prorocentrum micans*. *C. furca* averaged 10/ml on line 87 with a maximum of 27/ml. Lines 90 and 93 never had more than 2/ml of *C. furca* in September 1974. *Prorocentrum micans* averaged ≤ 5/ml for lines 87, 90 and 93. The maximum *P. micans* for line 87 was ~ 15/ml; ~ 10/ml for line 90 and ~ 6/ml for line 93.

Diatoms larger than 20 μm in effective diameter were not found at every station. Assorted diatom species were occasionally found in low concentrations (≤ 2/ml) along lines 87, 90 and 93. Highest densities were found on line 90, 1 km offshore with a maximum of 7/ml and 1·9 km offshore on line 93 with a maximum of 15/ml.

The density of *G. polyedra* in Santa Monica Bay was high enough to be seen as a red tide, 1 and 2 km offshore, with chlorophyll *a* concentrations of 27 and 36 mg/m^3 respectively. There was an average chlorophyll *a* content of 0·73 mg/m^3 along lines 90 and 93.

October 1974

On a special 1-day cruise 1 month later on 17 October 1974 off Dana Point (line 90), plankton pump samples were taken only from the inshore zone within a boundary extending 9 km offshore to delineate the seaward extent of the *G. polyedra* aggregations. *G. polyedra* was still the dominant species with *C. furca* second in number as it had been the previous month near line 90. *Gonyaulax* was concentrated within the first 7·4 km from shore, with a maximum number of 57/ml. However, it dropped off quickly in number at about 8·3 km offshore. *Ceratium furca* was also concentrated within the first 7·4 km offshore with a maximum of 29/ml dropping off sharply at 8·3 km to ≤ 2/ml.

Diatoms larger than 20 μm effective diameter remained sparse (≤ 2·5/ml), except for two inshore stations which had densities of 20/ml and 6/ml, half of which were species of *Nitzschia*.

November–December 1974

A month later, sampling from 26 November to 19 December 1974 showed that *Gonyaulax polyedra* remained the dominant species in the Southern California Bight. The number of *G. polyedra* was uniformly high at all the inshore stations, with densities of around 100/ml. Santa Monica Bay (line 87) again had the highest concentrations (870/ml).

C. furca continued to be found in small numbers, ≤ 5/ml over the entire Bight. No other dinoflagellates were in notably high concentrations.

Diatoms were, on the average, less than 1% of the number of dinoflagellates in the same size range along lines 83 (off Ventura, California) and 90, while line 87 had 8% diatoms to dinoflagellates.

The average chlorophyll *a* content for each line was ≤ 1 mg/m^3, with the exception of line 87, which averaged 1·63 mg/m^3. The maximum chlorophyll *a* for each transect was less than 4·0 mg/m^3, again with the exception of line 87, which had a maximum of 10·37 mg/m^3. As indicated in the previous section describing the oceanography of the Southern California Bight, no turbulent conditions were prevalent which could have disrupted the dinoflagellate concentrations.

January–February 1975

In the following month during 12 January to 3 February 1975, *G. polyedra* was not only found in high concentrations (~ 100/ml) at the inshore stations, but occurred as far as 25 km offshore along lines 87 and 90, in relatively high numbers (see Fig. 193).

Diatoms[5] increased moderately in number in the entire Bight averaging 55/ml in chlorophyll maximum layers on line 81·5, 46/ml along line 87, and 17/ml along line 90. Diatoms became fewer in number beyond Station 90·30 (17 km from shore).

The average chlorophyll *a* content throughout the Southern California Bight was higher than in December. Transects north of Dana Point had an average of about 2 mg/m^3 chlorophyll *a* and < 1·5 mg/m^3 south of Dana Point. The maximum chlorophyll content, depending on the transect, varied from 1·5 to 4·3 mg/m^3 (Fig. 195).

Water circulation in January favoured the horizontal distribution of *G. polyedra* throughout the Southern California Bight resulting in a large increase in areal distribution of this potential larval fish-food organism.

26 February–3 March 1975

By the sampling period 26 February to 3 March, there had been a sharp decline in the *G. polyedra* populations. Less than 10/ml were found within 18·5 km off the shore along lines 87, 90 and 93, while in general cell numbers above 25 cells/ml were only found far offshore (46 km) (Fig. 193).

Diatoms were higher in number than in January and were concentrated in the inshore zone. Various species of *Nitzschia* were most abundant in the Bight: *N. pacifica*, *delicatissima*, *pugens* and others. Species of *Chaetoceros* were also common at stations where diatoms were > 80/ml, while the number of dinoflagellates was less than one quarter the number of diatoms. Line 90 had about 200 diatom cells or chains within 4 km offshore, while line 93 had 52 cells or chains per millilitre about 2 km offshore. This was the result of the strong upwelling period during February (see section on oceanography) characterized by cold water close inshore.

The chlorophyll *a* content became significantly higher inshore. The average chlorophyll *a* for lines 87, 90 and 93 were from 3 to 5·5 mg/m^3. Line 87 had the highest maximum value of 15 mg/m^3 about 2 km offshore. Lines 90 and 93 had the highest maximum value of 15 mg/m^3 about 2 km offshore, and maxima of 5 and 8 mg/m^3 respectively within 2 km offshore (see Fig. 195).

6–26 March 1975

The 6 March to 26 March cruise period was the height of the northern anchovy spawning season (see following section). However, *G. polyedra* continued to diminish in number during March and reached a low concentration of 3/ml along line 90. This was characteristic of dinoflagellate concentrations throughout the entire Bight.

The diatoms *Chaetoceros* and *Nitzschia* species re-

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[5] Species of *Chaetoceros* and *Nitzschia* were the most common diatoms over the whole Bight. With respect to chain diatoms, each cell was counted microscopically as a single organism in those species whose single cell size was ≥ 20 μm in any dimension. Species with cells < 20 μm long were counted by chains. For example, because *Chaetoceros* cells are less than 20 μm long, the concentration per millilitre reflects the number of *Chaetoceros* chains, not individual cells in each chain.

mained common although in lower number than in the previous weeks. Along line 90, the diatom concentration peaked at 2 km offshore at 81 cells or chains per millilitre dropping to an average of 2/ml for the next 23·7 km offshore. The diatom populations on each sampled transect showed similar species composition and numbers (Table 14).

1–3 April 1975

In early April, *G. polyedra* had virtually disappeared from the Southern California Bight and the entire region was dominated by diatoms. The number of diatoms increased from March in the inshore zone. On line 87, a station ~2 km offshore had a count of 76 diatoms/ml with a great deal of detritus < 20 µm in diameter in the water. At ~3·5 km offshore, diatoms increased to 858/ml. On line 88·5 at a station ~5 km offshore, the density of diatoms was 480/ml increasing to > 1000/ml about 8 to 9·5 km offshore. Line 90 had diatoms > 1000/ml 2 km offshore with small detritus 10–30 µm. Diatoms dropped to ~300/ml, 4 km offshore and then to < 271/ml from 9–32 km offshore. Line 95 had over 3600 diatoms/ml within 3·7 km offshore. About 3500/ml of these diatoms were a chain diatom identified as a species of *Leptocylindricus* (diameter 4–7 µ). Species of *Chaetoceros* and *Thalassiothrix frauenfeldii* were the most common and abundant species of the Bight, with the exception of *Leptocylindricus* which was found in dense concentrations only along line 93. Of the total number of cells with diameters from 16·0 to 161 µm, the majority of cells (40–60%) fell in the 16–20 µm size range for lines 87, 90 and 93. Cells with effective diameters of 30–50 µm, i.e. the size required by anchovy larvae at first feeding were frequently high, i.e. > 30 particles/ml in the Bight; but these were due to diatom chains and are not eaten by anchovy larvae (Lasker, 1975).

Dinoflagellates were less than 2% the number of diatoms at each station along lines 87, 88·5, 90 and 93 except for those at which the numbers of diatoms dropped to ≤ 27/ml. At these stations, both diatoms and dinoflagellates were similarly low in density.

The average chlorophyll *a* content in the beginning of April was ~25% lower than the February–March cruises for line 90 with 2·4 mg/m^3 and line 93 with 3·8 mg/m^3. Maximum chlorophyll values for lines 90 and 93 were ~8 and 6 mg/m^3, respectively. Line 87 decreased also from an average of ~5·5 mg/m^3 in February–March to ~2 mg/m^3 in April. From line 88·5 through 91·5, the average chlorophyll was around 2–5 mg/m^3 with a maximum of 7–8 mg/m^3.

15–26 May 1975

Not a single *G. polyedra* was identified along line 90 during the May cruise.

Particle counts for 30–50 µm particles were even lower than during the April 1975 cruise. For example, along line 87 there was an average of 7/ml to 25 km offshore. Line 90 averaged only 17/ml within 4 km offshore. Line 93 had particle counts averaging 10/ml within 26 km offshore.

The diatom "bloom" of early April had dissipated by mid-May. On line 90, diatoms were 18/ml 2 km offshore. Further offshore the number of diatoms dropped to < 3/ml to as far as 32 km offshore.

Dinoflagellate concentrations were very low, < 7/ml, averaging < 2/ml for line 90. Not one species of dinoflagellates was especially common; mostly miscellaneous unarmoured dinoflagellates were present.

The average chlorophyll *a* content for the Bight was $< 1·5$ mg/m^3 during this period.

16 June–5 July 1975

Between 16 and 24 June particle counts for 30–50 µm particles were ≤ 40/ml for lines 87, 90 and 93 with the exception of a station on line 87, about 1 km offshore which had 129/ml. Microscope counts of water from this station showed a large number of armoured dinoflagellates: *Ceratium dens, C. furca, Dinophysis* sp. and *Peridinium* sp.

On lines 90 and 93, dinoflagellates numbered, on the average, 3·5/ml with a maximum inshore of 12/ml. Species of *Prorocentrum, Ceratium, Gymnodinium*, and *Peridinium* were identified.

Within 2 km offshore there was an average of 44 diatoms/ml. At 46 and 83 km, diatoms averaged in number about 90/ml. Chain diatoms, *Chaetoceros* and *Nitzschia*, comprised the inshore diatoms. Farther offshore (46–83 km), *Nitzschia* was most numerous.

The chlorophyll *a* content had increased since the mid-May cruise. Line 87 had an average of ~5 mg/m^3; line 90, an average of 3 mg/m^3. Line 93 remained about the same with an average of 2 mg/m^3.

The particle counts, species identification and chlorophyll *a* measurements were repeated for the entire Bight from 24 June through 7 July 1975. No major differences were seen in any of the measurement parameters.

6–22 September 1975

No cruises were held during late July or August. In September, low numbers of 30–50 µm particles prevailed. Very low dinoflagellate counts were characteristic.

20 October–2 November 1975

Repeating the pattern of the previous year, a dinoflagellate bloom was evident in October. All along the coast from line 83 down to line 95, microscope counts revealed *Gymnodinium uberrimum* (40–

60 µm) to be the dominant organism. *G. uberrimum* numbered 40–50/ml along line 90 within 4 km offshore and was present in lesser concentrations (2–4/ml) out to 32 km offshore. Line 95 had 64/ml 4 km offshore. At a nearshore station on line 83, the density of *G. uberrimum* was 1363/ml.

Diatoms were slightly higher than during the 13–22 September cruise, especially in the inshore zone. Line 90 had a maximum of 15/ml. Line 83 had 28/ml. *Nitzschia* was the most common species.

There appeared to be an unusually high number of coccolithophores along line 90 from 9 km to 17 km offshore. The density of these organisms was 15–19/ml. In past cruises, coccolithophores did not number more than ~5/ml.

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