

THE PHYTOPLANKTON OF THE SANTA BARBARA BASIN: PATTERNS OF CHLOROPHYLL AND SPECIES STRUCTURE AND THEIR RELATIONSHIPS WITH THOSE OF SURROUNDING STATIONS

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ABSTRACT

A twelve-year series of chlorophyll data from the CalCOFI station in the Santa Barbara Basin (SBB) shows that pigment is consistently concentrated in the upper 25 m. The annual maximum tends to be in April or May. When temporal fluctuations of mixed-layer chlorophyll are compared with the fluctuations at other CalCOFI stations, the stations most similar lie to the south and west of the SBB. There is one nonadjacent station to the north. Chlorophyll fluctuations west of stations 60 or 70 are negatively correlated with fluctuations at the SBB station.

Phytoplankton species at the SBB during April 1993 and April 1995 were typical upwelling diatoms. When the species structure at the SBB is compared with that at other CalCOFI stations, the stations with similar species structure tend to be those with similar temporal patterns of chlorophyll fluctuations. Species structures of the off-shore stations have negative correlations with structure at the SBB.

INTRODUCTION

The Santa Barbara Basin (SBB) is an area of roughly 575 km² in the central portion of the elongate Santa Barbara Channel, southeast of Point Conception, California. The channel and basin have been the site of many research programs (Baumgartner et al. 1992; Thunell et al. 1995; Hendershott and Winant 1996; Schimmelman and Lange 1996; Osgood and Checkley 1997). Much of the interest has been prompted by the existence of varved sediments within the basin (Lange et al. 1996; Schimmelman and Lange 1996). These are a consequence of a unique combination of hydrography, biology, and bottom topography, and they have unusual potential for fine-scale reconstruction of climatological and oceanographic history (Schimmelman and Lange 1996).

The accuracy of such reconstruction will depend in part on the degree to which the deposition within the basin can be related to regional oceanographic conditions and to larger-scale processes. On the one hand, the complicated hydrography of the SBB (Harms and Winant 1998) indicates that near-surface conditions in the SBB are highly variable on small spatial and tempo-

ral scales and may not always be closely related to conditions outside the basin. On the other hand, sedimentary records from the SBB do appear to reflect historic large-scale phenomena (Lange et al. 1990), suggesting that generalizations are valid, at least over sufficiently broad scales.

Since the early 1950s, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has regularly occupied a station in the SBB as a part of its routine survey of the California Current. To my knowledge, no study has directly compared phytoplankton of the near-surface waters of the SBB with those of the rest of the stations in the CalCOFI grid in order to examine similarities and differences on scales of kilometers and years.

Two recent studies have examined patterns of mixed-layer chlorophyll and floristics from the CalCOFI region. The SBB station provided data for both studies. But because of the synthesis of a large amount of data, the contribution of this one station cannot be identified specifically. Because of the interest in this local region, it is appropriate to examine the data from the SBB station directly.

The first study included an analysis of near-surface chlorophyll concentrations between January 1984 and July 1995 (Hayward and Venrick, in press). On the basis of the temporal fluctuations, three cohesive regimes within the CalCOFI area were identified (fig. 1). Within each regime, primary production is regulated by a different combination of physical processes. Most relevant to the present study is the northern inshore regime, which includes the SBB station at the northern edge. At these stations, chlorophyll in the mixed layer typically peaks between March and May when the euphotic zone is enriched by isopycnal shoaling, which brings nutrient-rich water to the surface.

In the second study (Venrick 1998) the distributions of phytoplankton species in the mixed layer were examined for two spring bloom periods: April 1993 and April 1995. In these years, a spring flora recurred and dominated the northern inshore regime.

The following study extends the previous analyses to examine the conditions at the SBB station with three objectives: to confirm the seasonal cycle of chlorophyll, to determine the species composition during two spring bloom periods, and to determine how large a region is

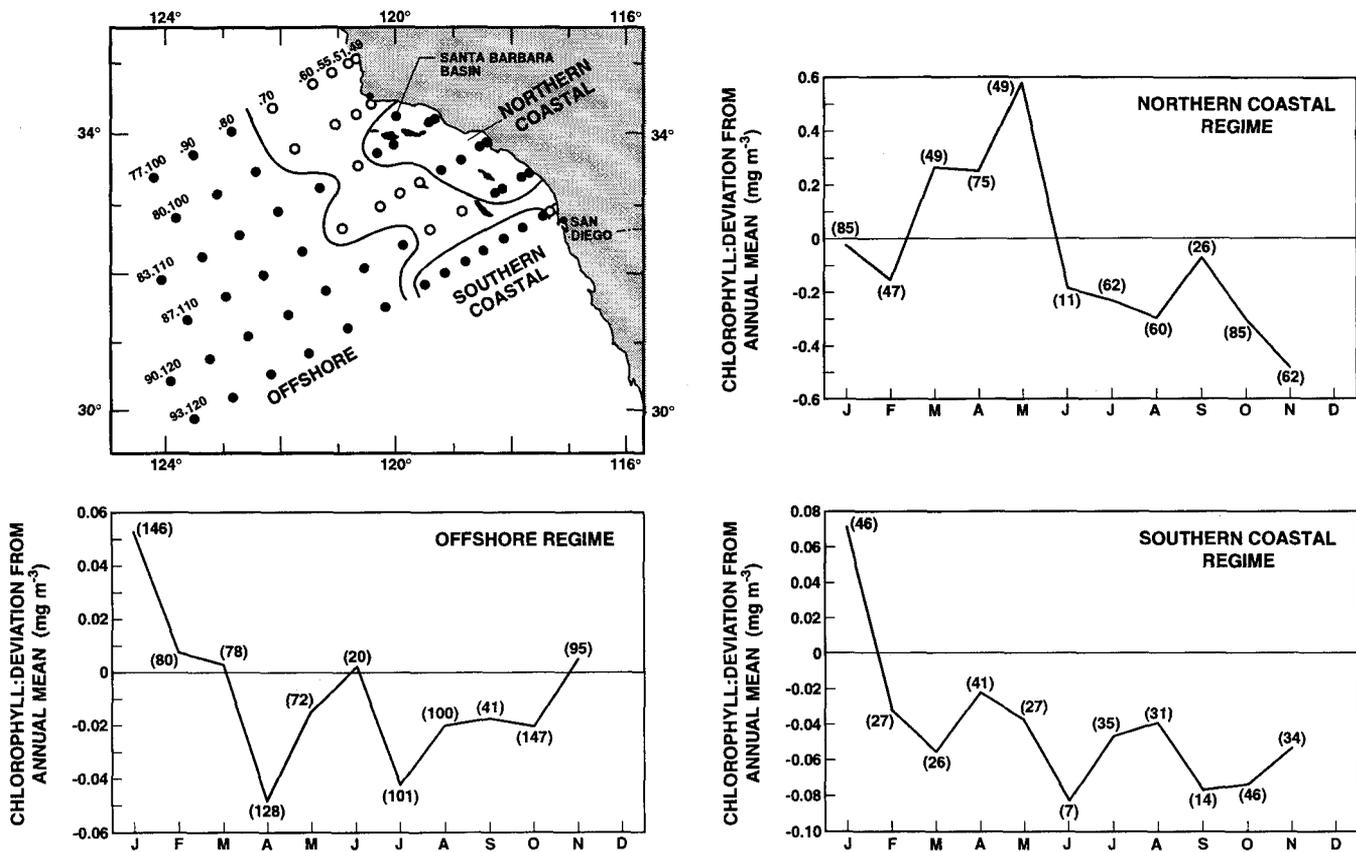


Figure 1. Location of three environmental regimes defined by Hayward and Venrick (in press). The near-surface chlorophyll concentrations at stations within each regime have similar patterns of fluctuations over time. The boundary between regimes fluctuates, so that 16 stations (open circles) are alternately in one regime or another and cannot be classified. The average seasonal variations of chlorophyll within each regime are expressed as the difference between the annual mean at each station and the cruise value, averaged over all stations within a region within a month. Numbers in parentheses indicate the numbers of values in each mean.

represented by chlorophyll fluctuations in the SBB on the interannual scale, and by floral structure on the quasi-synoptic scale.

METHODS

All samples were collected at standard CalCOFI stations. Station positions are given in CalCOFI data reports (e.g., SIO 1993, 1995). For convenience, station numbers have been rounded to the nearest whole number. Thus, station 40.6 on line 83.3 is designated as 83.41.

Since 1984, chlorophyll concentrations have been routinely determined from 10 to 14 depths in the upper 200 m. Samples are filtered through Whatman GF/F filters, extracted in acetone, and analyzed fluorometrically. Details of the procedure are given in CalCOFI data reports (e.g., SIO 1993, 1995). During this period, cruises have occurred quarterly, except for 1984 when there were six cruises. Fifty cruises in 12 years (8401 to 9510) are included in this study. On each of these cruises, a single station was occupied in the SBB, usually station 82.47. The target location of this station is 34°16.5'N,

120°15'W. Past stations have been within 15 km of this position.

In April 1993 (cruise 9304) and April 1995 (cruise 9504), phytoplankton samples of 125 ml were collected from the second bottle of the routine hydrocasts. Samples were preserved with neutralized formalin and enumerated under an inverted microscope. The volume counted varied from 0.17 ml to 100 ml. The entire amount settled was counted at 100× for the larger or rarer taxa, and one-sixth of the volume was counted at 250× for small species.

The sample from the second depth comes from the mixed layer when a mixed layer exists. This is the only depth, other than the surface, that has a consistent relationship with the vertical density structure across a broad range of hydrographic regimes. Over the 12-year period, the second depth varied between 3 m and 22 m, with a mean of 12.2 m. At the SBB, the mean depth was 10.8 m.

In order to compare the SBB station to the other stations in the CalCOFI grid, Spearman's nonparametric

correlation coefficients (ρ) were calculated between data from the SBB station and from each other station. In the analysis of chlorophyll, the data correlated were the temporal sequences of mixed-layer chlorophyll concentration. In the floristic analyses the data were the rank order of abundance of phytoplankton species from the mixed layer.

In these analyses, ρ is used as a qualitative index of similarity. The numbers of correlations are so great that some are likely to be "significant" by chance alone (multiple testing). Thus the actual probability of any one value cannot be directly evaluated. The null distribution of Spearman's ρ is a function of sample size, and sample size varies with each station pair (i.e., the number of cruises that sampled both stations during the 12-year period, or the number of species in their combined species list). Thus values of ρ based upon samples of different sizes cannot be directly compared. To correct for the effect of sample size, the magnitude of a correlation was evaluated by reference to standard statistical tables. It is important to keep in mind that, in spite of reference to statistical tables, I am interested in relative strengths of relationships and their patterns, rather than statistical significance.

RESULTS

Temporal Patterns of Chlorophyll

The SBB station is one of 7 stations near Point Conception that has a mean mixed-layer chlorophyll in excess of 2 mg m^{-3} (fig. 2). It had the fourth highest single chlorophyll concentration observed during this study: 22.3 mg m^{-3} at 1 m depth in April 1995. The maximum chlorophyll concentration was 29.9 mg m^{-3} at 21 m at station 87.33 in March 1987. Concentrations exceeding 22.3 mg m^{-3} were also found at station 83.41 in May 1985 and at station 77.55 in July 1990.

Elevated chlorophyll concentrations at the SBB station are restricted to the upper 25 m (fig. 3). There is no recurring or persistent subsurface maximum such as characterizes offshore waters (Venrick et al. 1973) or waters farther south in the Southern California Bight (Cullen and Eppley 1981).

Values integrated to 200 m are variable (fig. 4), ranging between 20 mg m^{-2} (Aug. 18, 1985) and 553 mg m^{-2} (April 17, 1995). An estimate of the seasonal cycle is obtained by subtracting from each datum that year's annual mean value (fig. 5). Maximum annual deviations occur between April 11 and May 17. Only four of ten deviations in that period are markedly elevated, although nine of the ten are above the annual mean. Minimum deviations occur between August and January. Maximum values in the spring are characteristic of the northern inshore regime defined by Hayward and Venrick

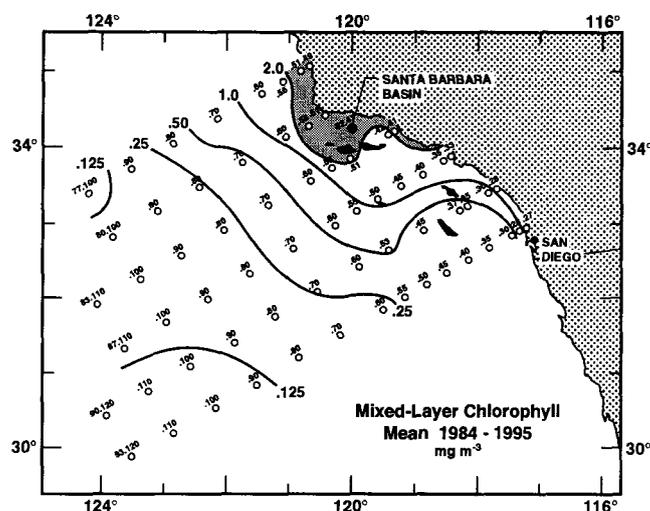


Figure 2. Mean chlorophyll concentration in the mixed layer, 1984-95.

(fig. 1), although some stations in this regime have peak concentrations as early as March. The probability that the four highest annual deviations would occur during the spring (March-May) if, in fact, there is no spring bloom is vanishingly small ($p = 8.7 \times 10^{-10}$).

To make the following analysis comparable to the floristic analysis to follow, I have restricted it to the chlorophyll in the second depth of the routine CalCOFI hydrocasts. At the SBB station, this sample most frequently (44%) contains the maximum chlorophyll in the water column, and the concentration from this depth explains 65% of the variability of the total chlorophyll (Spearman's $\rho = 0.81$; I do not give a probability here because of the lack of independence of the two sets of data). Presumably, fluctuations of chlorophyll at the second depth indicate fluctuations in biomass as well as do fluctuations at any single depth.

I have examined the geographical area sharing the pattern of chlorophyll at the SBB station by calculating Spearman's rank order correlation coefficient between the sequence of chlorophyll at the SBB station and the sequence at each of the 65 remaining CalCOFI stations. The highest coefficients of similarity (" $p \leq 0.001$ ") define a group of 9 stations, which, with one exception, lie south and west of the SBB (fig. 6). The boundary of this cluster is similar to that of the northern inshore regime defined by Hayward and Venrick (fig. 1). On the other hand, the correspondence with the high chlorophyll stations (fig. 2) is weak. The next contour of similarity (" $p \leq 0.05$ ") includes most of the nearshore stations, east of station 70 in the north but restricted to the immediate coast along lines 90 and 93. This boundary corresponds to the 12-year mean chlorophyll contour of 1.0 mg m^{-3} (fig. 2). Thirty-seven of the 65 CalCOFI stations have positive correlations with the SBB. These

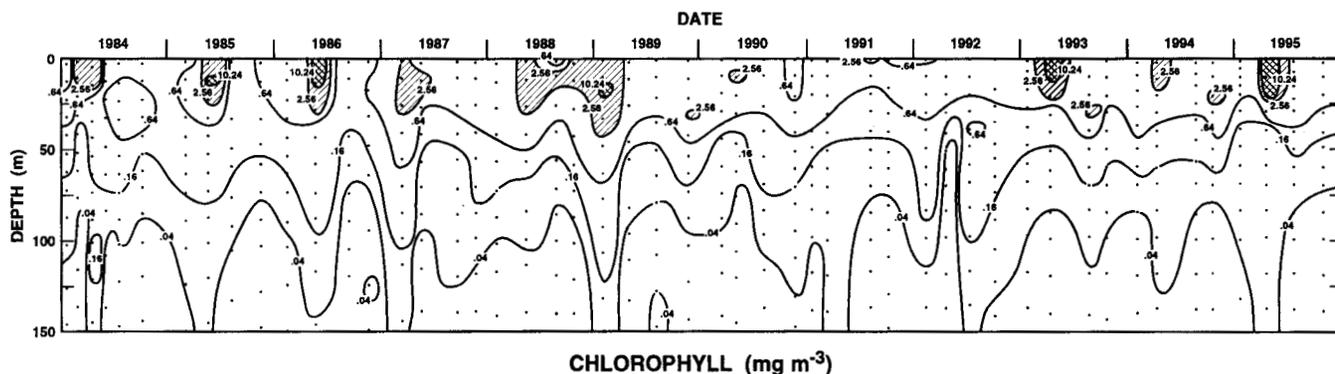


Figure 3. Time/depth plot of chlorophyll concentration at the Santa Barbara Basin station, 1984-95.

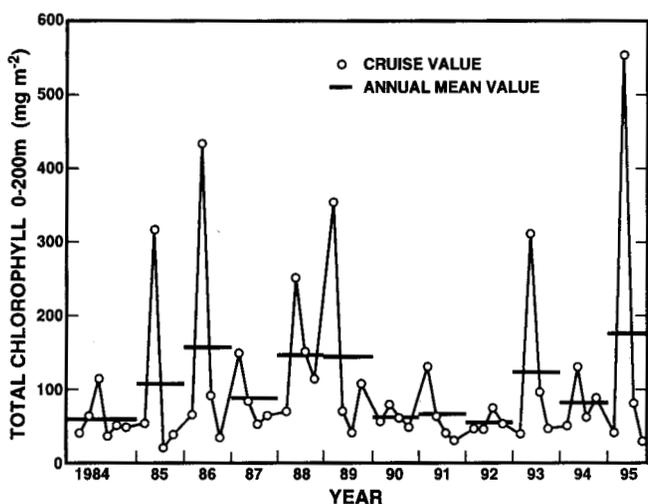


Figure 4. Temporal variability of integrated chlorophyll, 0-200 m, at the SBB station. Horizontal lines indicate annual means.

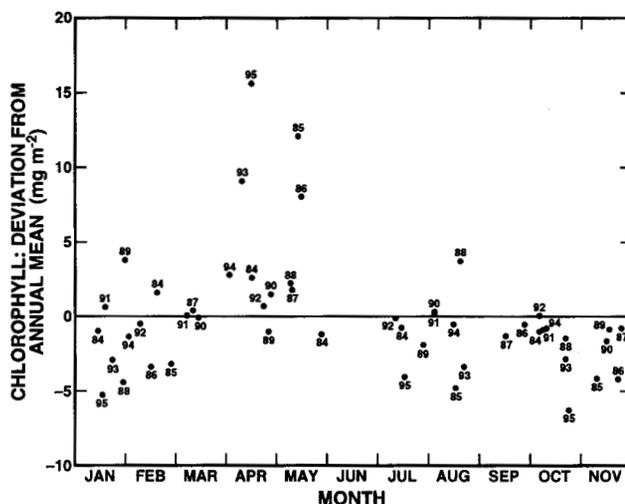


Figure 5. Seasonal cycle of integrated chlorophyll, 0-200 m, at the SBB station. Values are deviations from the annual mean value, by month. Numbers indicate the year.

stations are the inshore portion of the CalCOFI grid. Farther offshore, all but two stations have low but negative correlations with the SBB station. These offshore stations fall in the offshore regime defined by Hayward and Venrick (in press).

Within the region delimited by a positive relationship with SBB (fig. 6), only the SBB station and station 87.45 have eight high correlations with other inshore stations ($p \leq 0.001$). No other inshore station has more. From this perspective, we may say that the fluctuations of mixed-layer chlorophyll at the SBB station are as representative of fluctuations in the inshore region as are those at station 87.45, and are more representative than chlorophyll fluctuations from other stations.

Spring Species Composition

El Niño conditions prevailed during most of 1993. However, during the spring of 1993, there was a brief return to more normal circulation patterns (Hayward et al. 1994), so that the environmental characteristics of

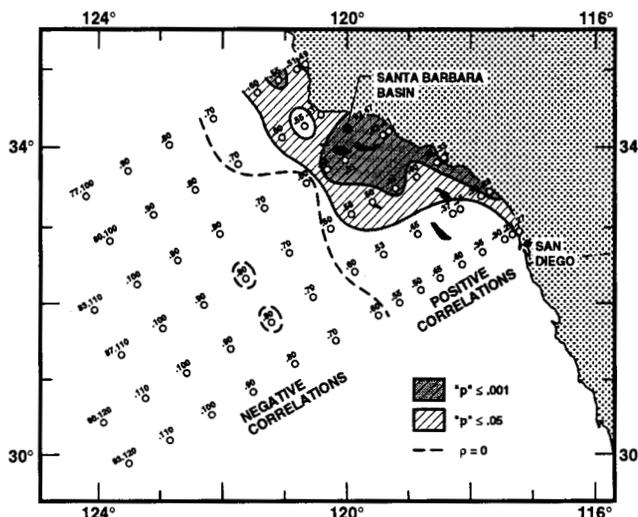


Figure 6. Similarity map for chlorophyll. Contours indicate positive correlations (Spearman's ρ) between chlorophyll fluctuations at the SBB station and surrounding stations at two "probability levels," uncorrected for multiple testing. Dashed contour is the boundary between positive and negative correlations.

station 82.47 in April 1993 were similar to those of April 1995 (fig. 7). The pycnocline began near 20 m, and most chlorophyll was shallower. The major differences between years were the lower nitrate and higher chlorophyll in 1995. The profiles suggest that the SBB in 1993 was sampled earlier in the development of the bloom, and that differences between years may be artifacts of the time of sampling.

Temperature, oxygen, nitrate, and chlorophyll data indicate that the most recent upwelling occurred near stations 77.49 and 80.51 in 1993 and near stations 77.49, 77.51, and 80.51 in 1995 (Venrick 1998). Some portion

of the water at the SBB station may have been advected from the north. Conditions during these cruises are discussed more fully by Hayward et al. (1994, 1995, 1996). Data have been published in cruise reports (SIO 1993, 1995).

A total of 39 species was identified at the SBB station during the April cruises of 1993 and 1995 (table 1). There were 2,556 cells ml⁻¹ comprising 27 identified species in April 1993; three additional species were recognized in uncounted material. In 1995 there were 4,181 cells ml⁻¹ comprising 25 species. Both flora were dominated by species of *Chaetoceros* in the subgenus *Hyalochaetae*. Five coccolithophorids but no dinoflagellates were present. The major differences between the two floras were the absence of *Skeletonema costatum* in 1993 and the dominance of *Chaetoceros socialis* in 1995. Despite the differences, the correlation between rank orders of abundance of the two spring floras was significant ($\rho = 0.34$, $p < 0.05$). Such temporal consistency is not normal in the CalCOFI pattern. Between the two sampling periods, only three other stations (77.80, 77.55, and 83.55) had a similar consistency of flora over time. It is unlikely that there is anything special about these four stations; more likely, they are random artifacts of the large numbers of possible correlations.

Spearman's ρ was used to examine the floral similarities between the SBB station and the remaining CalCOFI stations. In general, stations with similar patterns of chlorophyll fluctuations over time (fig. 6) have similar species composition (fig. 8). However, the patterns derived from floristics are less spatially and temporally cohesive. The stations most similar to the SBB station were different in 1993 and 1995; the only stations to be correlated with the SBB station with " p " ≤ 0.05 in both years were stations 83.55, 87.50, and 87.33. Relationships with other stations changed; station 83.51 was similar to the SBB station in 1993 ($\rho = 0.40$, " p " ≤ 0.01) and not in 1995 ($\rho = 0.13$, " p " $> .20$). Also, the stations most similar to the SBB station are not always adjacent to it.

The floristic patterns reflect the hydrography. The similarity between SBB and 87.70 in 1993 corresponded to a well-developed offshore eddy that is reflected in the maps of dynamic height and 10 m chlorophyll values. The eddy had transported offshore a parcel of nearshore water and flora. The discontinuous flora along line 83 in 1995 was related to a meander in the California Current, which brought offshore flora into stations 80.60 and 80.55. This is more evident in the 10 m chlorophyll and temperature map (SIO 1995) than in the dynamic heights, perhaps indicating a near-surface feature.

In this study, a negative correlation of species structure usually indicates species replacement. The stations that were negatively related to the SBB station were as abundant as stations with positive relationships. Out of

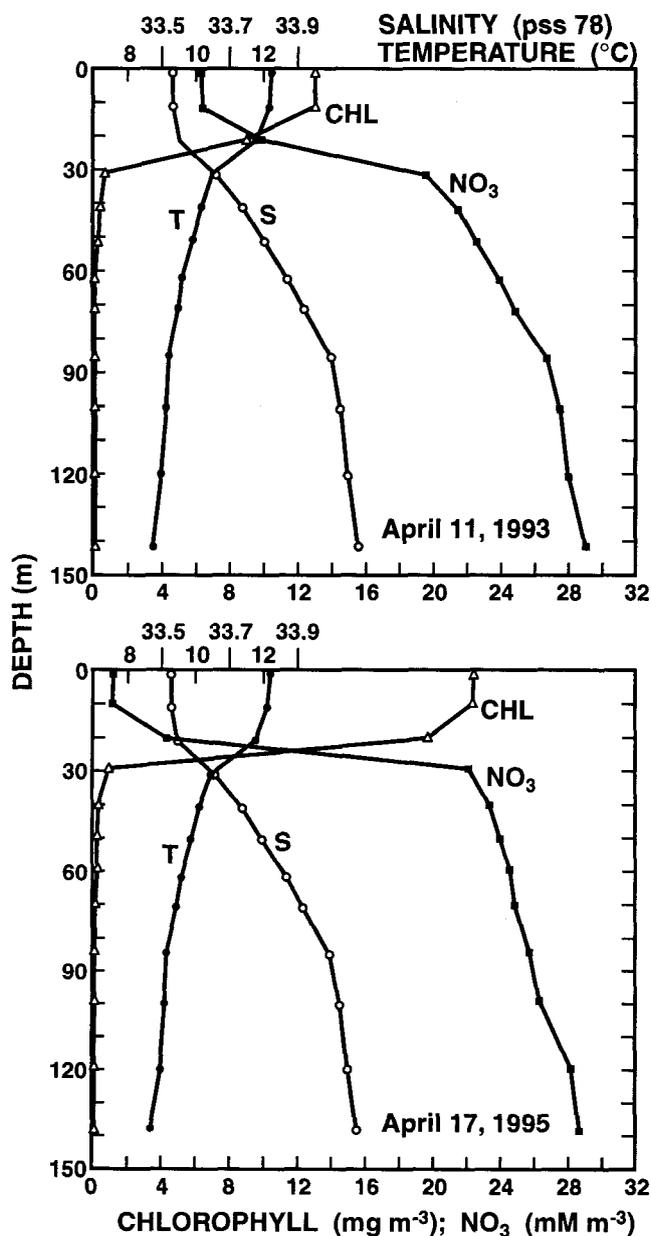


Figure 7. Environmental characteristics at the SBB station, April 1993 and 1995.

TABLE 1
Species Found in the Santa Barbara Basin (CalCOFI Station 82.47) in April 1993 and April 1995,
Listed According to Mean Dominance

Code number	Species	Cells ml ⁻¹		
		1993	1995	Mean
1	<i>Chaetoceros socialis</i> Lauder	147	2,031	1,089.0
2	<i>Chaetoceros debilis</i> Cleve	636	499	567.5
3	<i>Chaetoceros radicans</i> Schutt	566	145	355.5
4	<i>Pseudo-nitzschia</i> spp.—delicate forms	356	82	219.0
5	<i>Skeletonema costatum</i> (Grev.) Cleve	0	277	138.5
6	<i>Pseudo-nitzschia</i> spp.—robust forms	44	231	137.5
7	<i>Chaetoceros didymus</i> Ehrenb.	49	195	122.0
8	<i>Chaetoceros costatus</i> Pavillard	209	0	104.5
9	"Epiphytic cylinder"	114	54	84.0
10	<i>Chaetoceros compressus</i> Lauder	84	54	69.0
11	<i>Gephyrocapsa oceanica</i> Kämt. (Grindley & Tayler)	49	82	65.5
12	<i>Thalassiosira cf. aestivalis</i> Gran	5	118	61.5
13	<i>Gephyrocapsa</i> spp.	16	82	49.0
14	<i>Fragilariopsis pseudonana</i> Hasle (Hasle)	82	0	41.0
15	<i>Bacteriastrium delicatulum</i> (Cleve)	54	18	36.0
16	<i>Cylindrotheca closterium</i> (Ehrenb.) Lewin & Reimann	16	54	35.0
17	<i>Chaetoceros</i> cf. <i>vanheurcki</i> (Gran)	24	45	34.5
18	<i>Dactyliosolen phuketensis</i> (Sundstrom) Hasle	24	23	23.5
19	<i>Thalassiosira cf. anguste-lineata</i> (A. Schmidt) Fryxell & Hasle	0	45	22.5
20	<i>Thalassiosira cf. bioculata</i> (Grunow) Ostenfeld	0	45	22.5
21	<i>Emiliana huxleyi</i> (Lohm.) Hay & Mohler	+	27	13.5
22	<i>Thalassiosira cf. eccentrica</i> (Ehr.) Cl.	0	23	11.5
23	<i>Thalassiosira rotula</i> (Meunier)	22	0	11.0
24	<i>Dactyliosolen fragilissima</i> (Bergon) Hasle	19	0	9.5
25	<i>Dactyliosolen blavyanus</i> (H. Perag.) Hasle	0	18	9.0
26	<i>Hemiaulus sinensis</i> (Grev.)	0	14	7.0
27	Pennate 1	10	0	5.0
28	<i>Leptocylindrus danicus</i> Cl.	0	9	4.5
29	<i>Lauderia annulata</i> Cl.	8	0	4.0
30	<i>Chaetoceros affinis</i> Lauder	5	0	2.5
31	<i>Amphiprora</i> spp.	5	0	2.5
32	<i>Ditylum brightwellii</i> West (Grun.)	0	5	2.5
33	<i>Thalassiosira cf. nordenskiöldii</i> Cleve	0	5	2.5
34	<i>Chaetoceros</i> "fine aequatorialis"	3	0	1.5
35	<i>Actinocyclus</i> "small curvatus"	3	0	1.5
36	<i>Anoplosolenia brasiliensis</i> (Lohm.) Deflandre	3	0	1.5
37	<i>Haslea wawriake</i> (Hust.) Simonsen	3	0	1.5
38	<i>Mastogloia woodiana</i> Taylor	+	0	+
39	<i>Helicosphaera carterae</i> (Wallich) Kämtner	+	0	+
Total		2,556	4,181	3,367.5
	Unidentified cells			
	<i>hyalochaete</i> spp.	745	784	764.5
	spores	0	5	2.5
	<i>Thalassiosira</i> spp.	35	5	20.0
	Pennate diatoms	5	23	14.0
Overall total		3,374	4,998	4,186.0

+ indicates that the species was present in the material but not seen in the fraction counted.

48 and 51 comparisons in 1993 and 1995, 22 and 31 pairs were negative. The boundary between negative and positive correlations varied, but the alongshore orientation agreed with the boundary defined in figure 6 on the basis of positive and negative relationships between temporal patterns of chlorophyll. Both of these, in turn, corresponded with the boundary region between coastal and offshore regimes defined by Hayward and Venrick (fig. 1).

DISCUSSION

Seasonal Cycle

There is a great deal of variability in the chlorophyll data series (figs. 3 and 4). Although much of this may be due to the complicated hydrography in the region, some portion almost certainly arises from sampling error due to the interaction of cruise timing with the seasonal cycle. For instance, the absence of a peak in the spring of 1994

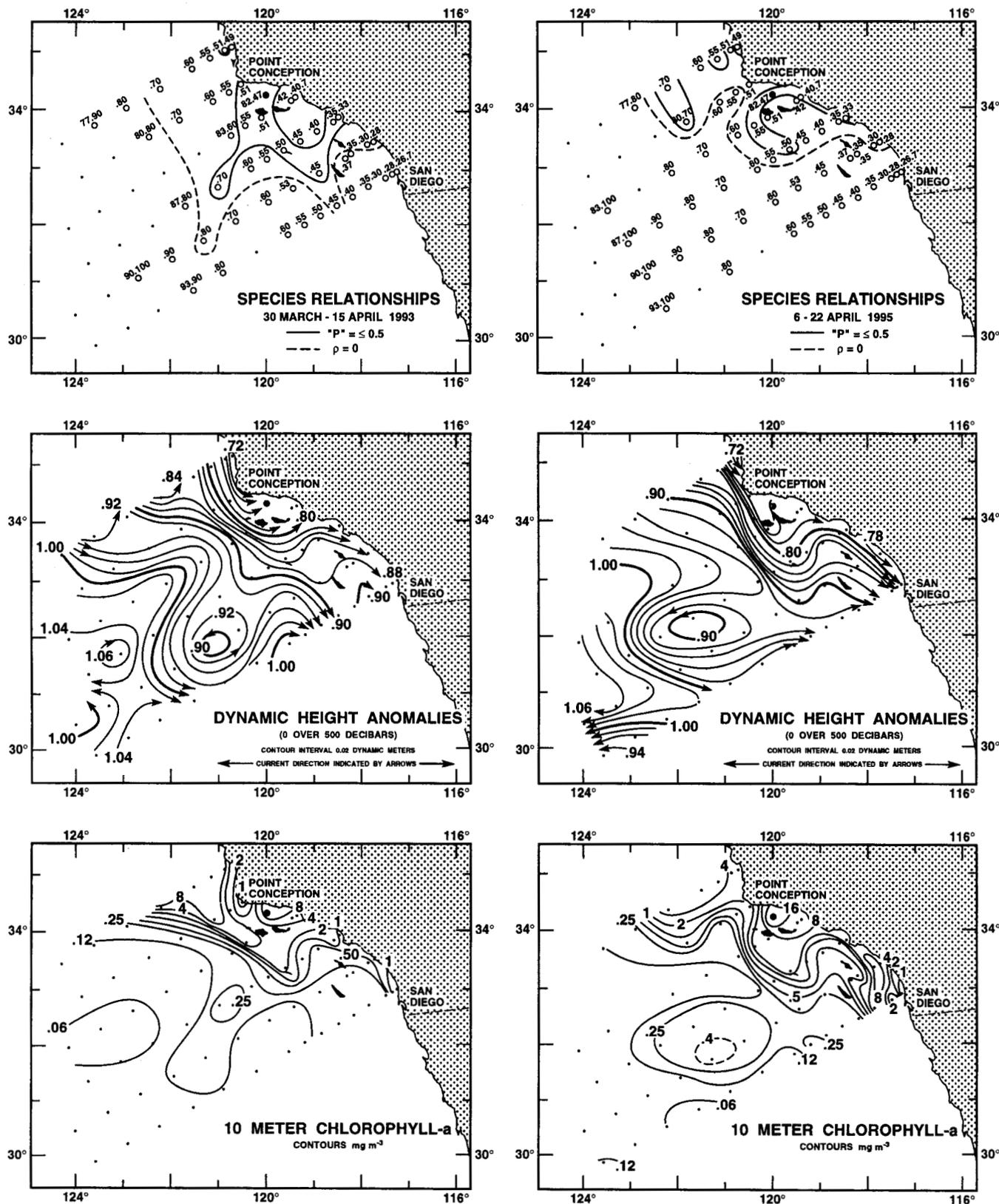


Figure 8. Similarity maps for species structure together with maps of dynamic heights and 10 m chlorophyll concentrations for 1993 and 1995 (SIO 1993, 1995). Solid contours of similarity indicate the positive correlation (Spearman's ρ) between the order of dominance of species at the SBB station and surrounding stations at " $\rho \geq 0.05$, uncorrected for multiple testing. Dashed contour shows boundary between positive and negative correlations. Stations without floristic samples are unlabeled.

may indicate only that the cruise did not coincide with the spring bloom in the SBB. This sampling error is reflected in both seasonal and interannual variabilities.

With some simplifying assumptions, the sampling error may be used to estimate the probable duration of the spring peak. I define a bloom as an integral chlorophyll concentration greater than 7 mg m^{-2} above the annual mean. There were four such values between April 11 and May 17 (fig. 5). I assume that the peak occurs each year during a 40-day period (e.g., April 10 and May 20); this period was sampled by ten cruises. I also assume that the number of days of elevated chlorophyll is the same each year (although they do not need to be sequential), and that the timing of cruises relative to the chlorophyll peak is random, so that each cruise during that period is equally likely to sample a chlorophyll peak. Then, from the binomial distribution, the 90% confidence interval for bloom duration is between 9 and 24 days. If we permit some years without blooms, this interval becomes longer. For instance, if we assume we sampled every bloom (i.e., six years had no blooms), the shortest likely bloom duration is 18 days. If we assume a bloom each year but enlarge the possible bloom period to include March, then the corresponding 90% confidence interval is 11–33 days. Calculations such as these suggest that the spring bloom at the SBB station (when it occurs) is likely to be longer than one week and shorter than six weeks.

Spring Species Composition

A spring flora—dominated by *Chaetoceros* species in the subgenus *Hyalochaetae*, *Skeletonema costatum*, and *Pseudo-nitzschia* spp.—appeared during April of both 1993 and 1995. These species are the quintessential components of enriched flora throughout temperate oceans (Venrick 1998).

A continuing goal of my work is to provide information on species composition in the water column which can be compared with species from sediment traps and near-surface sediments (e.g., Lange et al. 1997). I need many more than two phytoplankton samples over varying scales of time and space to make this comparison meaningful. Nevertheless, a preliminary observation may be warranted.

On the basis of sediment trap data collected in 1994 from the SBB, Lange et al. (1997) characterized the spring bloom by a high flux of diatom resting spores in the genus *Chaetoceros*, most notably spores of *C. radicans*. In the mixed-layer samples of the present study, species in the genus *Chaetoceros* were dominant, and *C. radicans* was among the top five species in both 1993 and 1995 (table 1). For correct interpretation of the sedimentary record, it is not necessary for the spring flora to be preserved unaltered, only that key elements be preserved and that any transformations between water and sedi-

ment be quantified. *Chaetoceros radicans* may prove to be one such key element.

Generality

The area represented by the phytoplankton of the SBB has been examined with different data sets over different time scales. The floristic data are nearly synoptic in each of two years. On this scale there is clearly a great deal of heterogeneity. The stations most similar to the SBB station differ between the two sampling periods, and the floral structure at the SBB fluctuates. Generalizing details from the spring flora of the SBB to surrounding stations at any one point in time is risky.

On the other hand, the analysis of changes in chlorophyll over a 12-year period indicates a group of stations primarily to the south and west of the SBB station that show a common pattern of biomass fluctuations, visible above the small-scale complexity of the area. This is due, at least in part, to a common seasonal cycle. With the present sampling frequency, we cannot define the seasonal cycle accurately enough to examine the residual interannual variability. It is reasonable to expect (but in no way proven) that the floristics behave over time in a way similar to chlorophyll. That is to say, there is a group of stations, including the SBB station, that tend to have similar spring flora on a decadal scale in spite of considerable heterogeneity between years.

Clearly this study is a small fraction of the ideal study. The floristic analyses are limited to April. There is no reason to expect similar results during different seasons, especially since the circulation within the SBB and the rest of the California Current has a strong seasonal component (Hickey 1979; Harms and Winant 1998). Data from additional years are needed. Finally, the study should be expanded to other trophic levels.

Perhaps the most important result from this study is that the SBB represents only a fraction of the CalCOFI area, regardless of the data type or sampling scale. This is the area that roughly corresponds to the northern in-shore regime as defined by Hayward and Venrick (in press). Stations in the offshore regime are clearly unlike the SBB. This places limitations on the generalizations that can be made from Santa Barbara Basin data, at least on scales shorter than interdecadal.

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LITERATURE CITED

- Baumgartner, T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. Calif. Coop. Oceanic Fish. Invest. Rep. 33:24-40.
- Cullen, J. J., and R. W. Eppley. 1981. Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance. Oceanol. Acta 4:23-32.
- Harms, S., and C. D. Winant. 1998. Characteristic patterns of the circulation in the Santa Barbara Channel. J. Geophys. Res. 103:3041-3065.
- Hayward, T. L., and E. L. Venrick. In press. Nearsurface pattern in the California Current: coupling between physical and biological structure. Deep-Sea Res. II 45.
- Hayward, T. L., A. W. Mantyla, R. J. Lynn, P. E. Smith, and T. K. Chereskin. 1994. The state of the California Current in 1993-1994. Calif. Coop. Oceanic Fish. Invest. Rep. 35:19-35.
- Hayward, T. L., D. R. Cayan, P. J. S. Franks, R. J. Lynn, A. W. Mantyla, J. A. McGowan, P. E. Smith, F. B. Schwing, and E. L. Venrick. 1995. The state of the California Current in 1994-1995: a period of transition. Calif. Coop. Oceanic Fish. Invest. Rep. 36:19-39.
- Hayward, T. L., S. L. Cummings, D. R. Cayan, F. P. Chavez, R. J. Lynn, A. W. Mantyla, P. P. Niiler, F. B. Schwing, R. R. Veit, and E. L. Venrick. 1996. The state of the California Current in 1995-1996: continuing declines in macrozooplankton biomass during a period of nearly normal circulation. Calif. Coop. Oceanic Fish. Invest. Rep. 37:22-37.
- Hendershott, M. C., and C. D. Winant. 1996. Surface circulation in the Santa Barbara Channel. Oceanography 9:114-121.
- Hickey, B. M. 1979. The California Current system—hypotheses and facts. Prog. Oceanogr. 8:191-279.
- Lange, C. B., S. K. Burke, and W. H. Berger. 1990. Biological production off southern California is linked to climatic change. Clim. Change 16:319-329.
- Lange, C. B., A. Schimmelmann, M. Yasuda, and W. H. Berger. 1996. Marine varves off southern California. SIO Ref. 96-22.
- Lange, C. B., A. L. Weinheimer, F. M. H. Reid, and R. C. Thunell. 1997. Sedimentation patterns of diatoms, radiolarians, and silicoflagellates in Santa Barbara Basin, California. Calif. Coop. Oceanic Fish. Invest. Rep. 38:161-170.
- Osgood, K. E., and D. M. Checkley Jr. 1997. Observations of a deep aggregation of *Calanus pacificus* in the Santa Barbara Basin. Limnol. Oceanogr. 42:997-1001.
- Schimmelmann, A., and C. B. Lange. 1996. Tales of 1001 varves: a review of Santa Barbara Basin sediment studies. In Paleoclimatology and paleoceanography from laminated sediments, A. E. S. Kemp, ed. Geol. Soc. Spec. Pub. 116, pp. 121-141.
- SIO. Scripps Institution of Oceanography. 1993. Physical, chemical and biological data. CalCOFI cruise 9301, 12-27 January 1993 and CalCOFI cruise 9305, 30 March-15 April 1993. SIO Ref. 93-26.
- . 1995. Physical, chemical and biological data. CalCOFI Cruise 9501, 4-21 January 1995 and CalCOFI Cruise 9504, 6-22 April 1995. SIO Ref. 95-33.
- Thunell, E. R., E. Tappa, and D. M. Anderson. 1995. Sediment fluxes and varve formation in Santa Barbara Basin, offshore California. Geol. 23:1083-1086.
- Venrick, E. L. 1998. Spring in the California Current: the distribution of phytoplankton species in April 1993 and April 1995. Mar. Ecol. Prog. Ser. 167:73-88.
- Venrick, E. L., J. A. McGowan, and A. W. Mantyla. 1973. Deep maxima of photosynthetic chlorophyll in the Pacific Ocean. Fish. Bull. 71:41-52.