Remote-sensed analysis of the influence of 1997–1998 El Niño on the California pelagic ecosystem

Nikolay P. Nezlin, William M. Hamner[1],
and Louis D. Zeidberg[1]

ABSTRACT - The influence of the 1997–1998 El Niño event on coastal California was evaluated via multidisciplinary analysis of remote-sensed data. We processed and analyzed the time-series of surface chlorophyll concentration, sea surface temperature, and wind stress in eight small regions off central and southern California. Seasonal summer minima of remote-sensed chlorophyll concentrations were observed in all zones of the region under study during the entire periods of observations (1978–1986 for Coastal Zone Color Scanner [CZCS] and 1997–2000 for Sea-viewing Wide Field-of-view Sensor [SeaWiFS]), suggesting that nutrient limitation is regulated by the strength and depth of the seasonal pycnocline. Seasonal maxima of chlorophyll were observed during summer in upwelling zones, during spring in the regions adjacent to upwelling zones, and during winter in the southern area, far from upwelling zones. The main factors stimulating the growth of phytoplankton biomass were the intensity of coastal upwelling and wind stress. The 1997–1998 El Niño event coincided with a complete collapse of the squid fishery. This collapse was preceded by a significant decrease in remote-sensed phytoplankton biomass. Sea surface temperature increased first in the Southern California Bight and then in the more northern upwelling zones without significant changes of wind pattern. The variations observed during the El Niño event were consistent with a deepening of the pycnocline resulting from downwelling waves propagating northward along the coast. This excess stratification likely results in reduced nutrient flux into the euphotic zone; however, the precise mechanism that led to collapse of the squid fishery requires further investigation.

INTRODUCTION

The California coastal ocean is well studied in terms of both hydrology (Hickey 1979; Lynn and Simpson 1987, Hickey 1992, Bray *et al.* 1999, Brink *et al.* 2000) and the influence of meteorological and hydrological processes on plankton development (Chelton *et al.* 1982, Strub *et al.* 1990, Thomas and Strub 1990, Abbott and Barksdale 1991; Roemmich and McGowan 1995; Hayward and Venrick 1998). Nonetheless, the remote-sensed observations obtained by SeaWiFS radiometer since September 1997 (Acker *et al.* 2002) enable more comprehensive analyses of regional phytoplankton dynamics. Using SeaWiFS, seasonal variations of remote-sensed chlorophyll concentrations can be traced for a several-year period. This ability can be especially helpful in analyzing the catastrophic effects of El Niño events, such as the one that occurred during the second half of 1997 and the first half of 1998 (Chavez *et al.* 1999, McPhaden 1999, Kahru and Mitchell 2000).

El Niño Southern Oscillation (ENSO) events affect the California coastal ecosystem by influencing global patterns of sea surface temperature (SST) (Chavez *et al.* 1998, Chavez *et al.* 1999, McPhaden 1999). The initialization of an ENSO event is associated with bursts of westerly winds in the western Pacific Ocean that blow surface water eastward along the equator. As a result, warm water of the upper mixed layer accumulates over the equator due to Ekman transport (right-hand directed in the northern hemisphere and left-hand directed in the southern hemisphere). This, in turn, raises the sea surface height and deepens the thermocline over the equator. The bulge of warm water on the equator moves eastward due to the action of equatorial Kelvin waves. These Kelvin waves reach the west coast of South America and propagate poleward as two coastally trapped waves. When the northward wave reaches California, it causes a deepening of pycnocline and an increase of SST resulting from the accumulation of heat in the upper mixed layer. The

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[1] *Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, 621 Charles E. Young Drive South, Box 951606, Los Angeles, CA 90095-1606*

increase of SST results in increased evaporation, accumulation of water vapor in the atmosphere, and resulting torrential rains and floods along the coast. Although El Niño events also affect atmospheric circulation patterns (atmospheric teleconnection), the deepening of the thermocline (oceanic teleconnection) is the feature of an El Niño event that has the greatest effect on the coastal ecosystem.

During the analysis of seasonal cycles of phytoplankton, it was presumed that light and nutrients limit phytoplankton growth (Longhurst 1995). During the summer, a strong pycnocline limits phytoplankton growth by hindering penetration of nutrients upward into the well-illuminated (euphotic) upper mixed layer. During winter, the erosion of the pycnocline due to increased wind stress and cooling of the ocean surface results in a higher rate of nutrient input and a winter maximum of phytoplankton growth typical for subtropical oceans, including offshore California waters (Chavez 1995). In high- and mid-latitude ocean zones and coastal regions where low-water transparency decreases the thickness of the euphotic layer, the deepening of the pycnocline and/or its complete destruction in winter also result in dispersion of algae cells into deeper, darker water layers where growth is limited by light. Consequently, an analysis of the seasonal cycles of phytoplankton must take into account the meteorological and hydrological factors influencing the stability and depth of the pycnocline, with special concern for wind stress.

This study used remote sensing data to understand the effects of El Niño on phytoplankton of the coast of central and southern California. The goals of the study were:

- To describe the seasonal cycles of phytoplankton biomass in different regions of coastal California
- To determine whether nutrient limitation resulting from water stratification was a major factor regulating seasonal variations of phytoplankton
- To discern the differences between the typical seasonal cycles of phytoplankton biomass and the cycles observed during the El Niño event of 1997–1998
- To analyze the hydrological and meteorological factors responsible for phytoplankton and squid fishery suppression during El Niño

METHODS

The study area for this project extended from 32ºN to 37º 30’N (Figure 1). To more clearly discern patterns in the data, the study area was divided into eight smaller regions: northern open ocean (NO), southern open ocean (SO), northern coastal (NC), southern coastal (SC), the open part of Southern California Bight (SCB), San Diego (SD), Santa Monica Bay (SM), and Santa Barbara Channel (SB).

The relationship between phytoplankton and physical oceanographic properties was investigated using remote-sensed data on surface chlorophyll concentration, sea surface temperature, and wind stress, collected at different scientific centers (NASA Goddard Space Flight Center [GSFC] and Jet Propulsion Laboratory [JPL], National Climatic Data Center [NCDC], and National Centers for Environmental Prediction [NCEP]). In addition, we evaluated field data from the CalCOFI program and data on the landings for the California market squid, *Loligo opalescens*, from the California Department of Fish and Game.

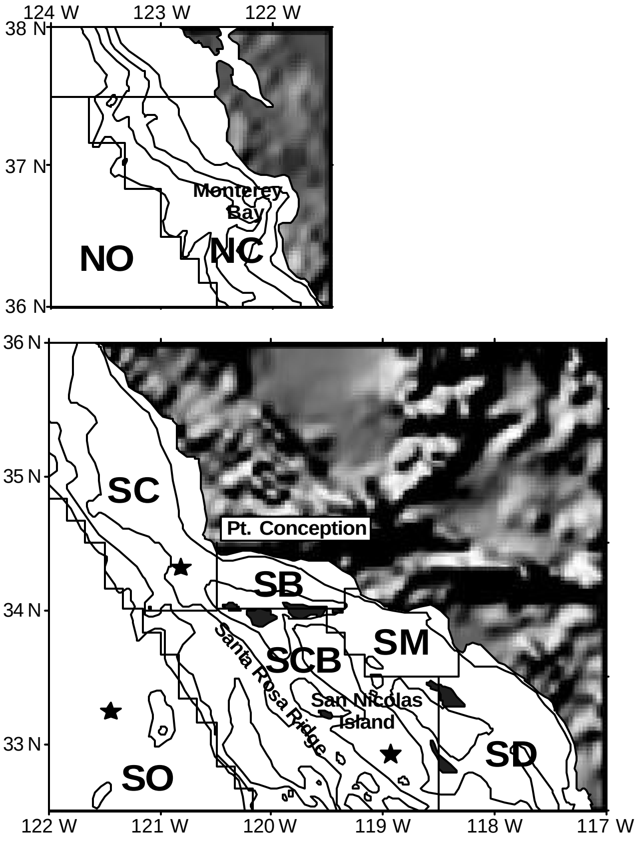


Figure 1. The scheme of regions used for time-series analysis. NO— Northern Open Ocean; SO — Southern Open Ocean; NC — Northern Coastal; SC — Southern Coastal; SCB — the open part of Southern California Bight; SD — San Diego; SM — Santa Monica Bay; and SB — Santa Barbara Channel. Stars indicate CalCOFI stations used for analysis.

The remote-sensed data on surface chlorophyll concentrations were obtained from NASA GSFC Distributive Active Archive Center (DAAC). We used 8-d averaged Level 3 standard mapped images (SMI) data of SeaWiFS surface chlorophyll calculated during reprocessing #3 (Version 3). Level 3 SMI SeaWiFS chlorophyll data are interpolated to a regular grid of equidistant cylindrical projection of 360°/4096 pixels (about 9.28 km) resolution. The SeaWiFS observations of chlorophyll were compared to seasonal variations of surface plant pigment concentrations measured by CZCS between November 1978 and June 1986. These data were obtained from the GSFC DAAC as regular monthly averaged grids of 360°/2048 pixels (about 19 km) resolution. Taking into account differences between the algorithms for estimating pigment concentrations in CZCS and SeaWiFS, we avoid direct comparison of absolute values.

Surface chlorophyll concentrations derived from satellite measurements are subject to significant inaccuracy associated with limitations of remote-sensed observations. Therefore, remote-sensed data are not compared directly to *in situ* absolute values of chlorophyll concentration; rather, the remote-sensed observations are used to analyze/compare general patterns in the cycles of phytoplankton development. Accordingly, the terms "remote-sensed surface chlorophyll concentration," "chlorophyll biomass," and "phytoplankton biomass" are used as synonyms, taking into account the correlation between remotely sensed surface pigment concentrations and total pigment concentrations in the water column (Smith and Baker 1978) and the good correlation between satellite and *in situ* chlorophyll observations off California (Chavez 1995).

Wind stress was calculated using meteorological information from the NCEP and supplied by GSFC DAAC as ancillary information for SeaWiFS users. These data were averaged over 8-d periods similar to SeaWiFS chlorophyll data.

Seasonal cycles of sea surface temperature were estimated from multi-channel sea surface temperature (MCSST) data collected since November 1981 by advanced very high resolution radiometers (AVHRR) and obtained from the Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory (JPL PODAAC Product 016). Only the data collected during nighttime (descending pass) were used to avoid the short-period SST variations resulting from heating of the thin ocean surface layer.

Daily air temperature data were obtained from the National Climatic Data Center at the National Oceanic and Atmospheric Administration (NCDC NOAA). The values for the "upwelling index" (i.e., the Ekman offshore drift calculated from 6-h fields of atmospheric pressure) were obtained from the Pacific Fisheries Environmental Laboratory (PFEL).

Seasonal cycles of phytoplankton dynamics, sea surface temperature, wind stress, and air temperature were calculated by averaging 8-d periods over the entire period of observations and smoothing (twice) using a 5-point running average. The "climatic" seasonal variations of SST and air temperature were subtracted from temperature data collected during the period January 1997–December 2000 to analyze variations in terms of anomalies (i.e., deviations from seasonal averages) rather than absolute values.

The conclusions based on the analysis of remote sensed data were validated using the data on vertical distribution of water density (σ_θ), chlorophyll, and nutrients obtained from the CalCOFI program. The data were used from three stations (Figure 1) located at 32°54.7–55.8'N, 118°55.4–56.7'W; 33°13.7–15.0'N, 121°25.8–27.7'W; and 34°17.6–20.0'N, 120°47.9–49.4'W.

Landings data for the California market squid, *Loligo opalescens*, were obtained from the California Department of Fish and Game (CDFG). The CDFG collects information on total weight of squid caught from an area of 10 x 10 nautical miles from the coastline to 200 nautical miles offshore. These data were averaged for the Southern California Bight and the Monterey Bay Basin, with the boundary along 36°N latitude.

RESULTS

Patterns of climatically averaged surface chlorophyll concentration off southern California vary spatially and seasonally (Figure 2). In December-January, chlorophyll concentrations were typically <2 mg/m^3 in the entire study region, except the most northern zone. In February, chlorophyll concentration increased in the southern part of the upwelling zone and in the Santa Barbara Channel. Between April and September, increased upwelling resulted in high chlorophyll concentration to the north of Point Conception and in the northern part of the Southern California Bight. However, in the latter case, the bloom continued through August.

The time-series of phytoplankton biomass in

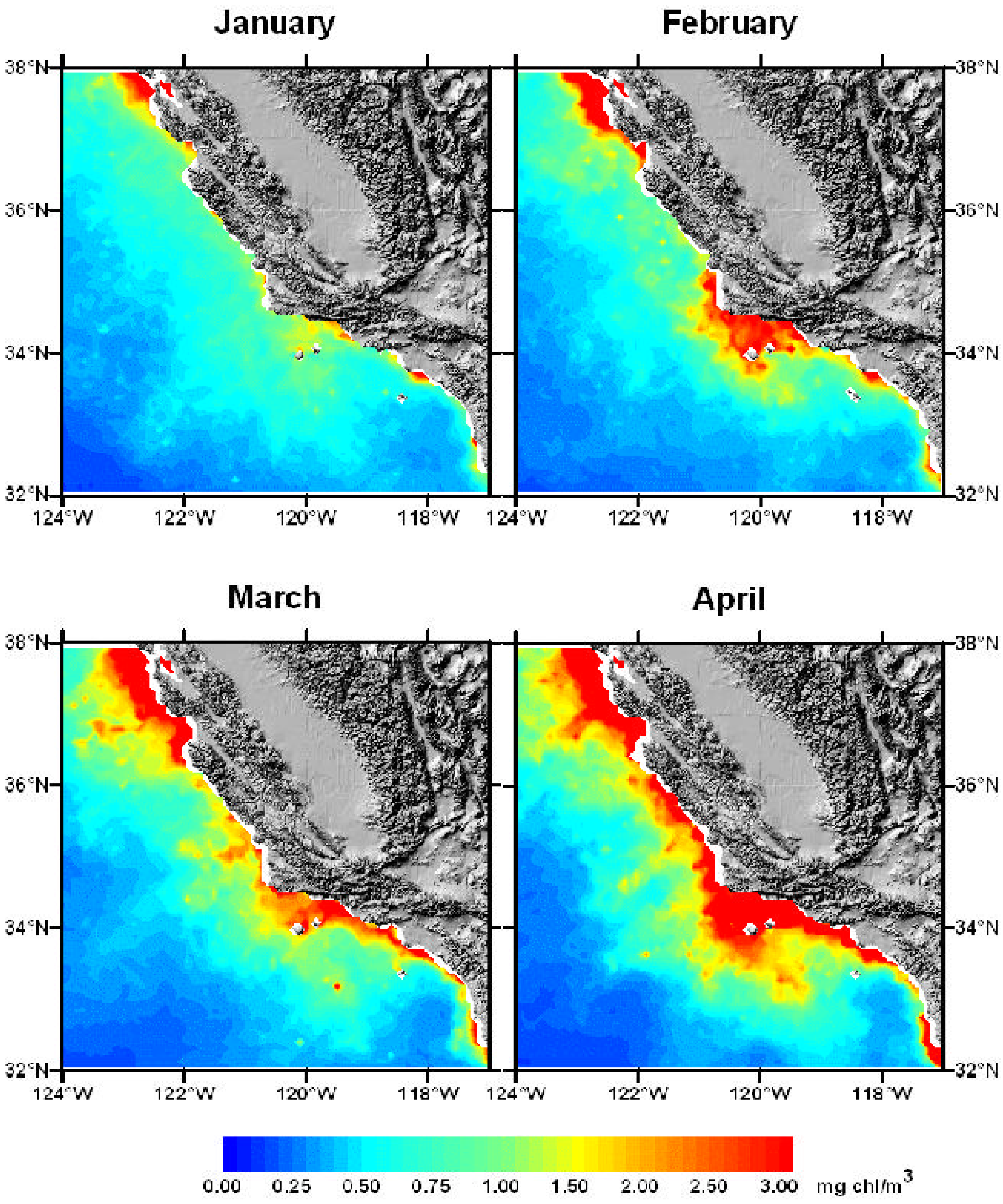
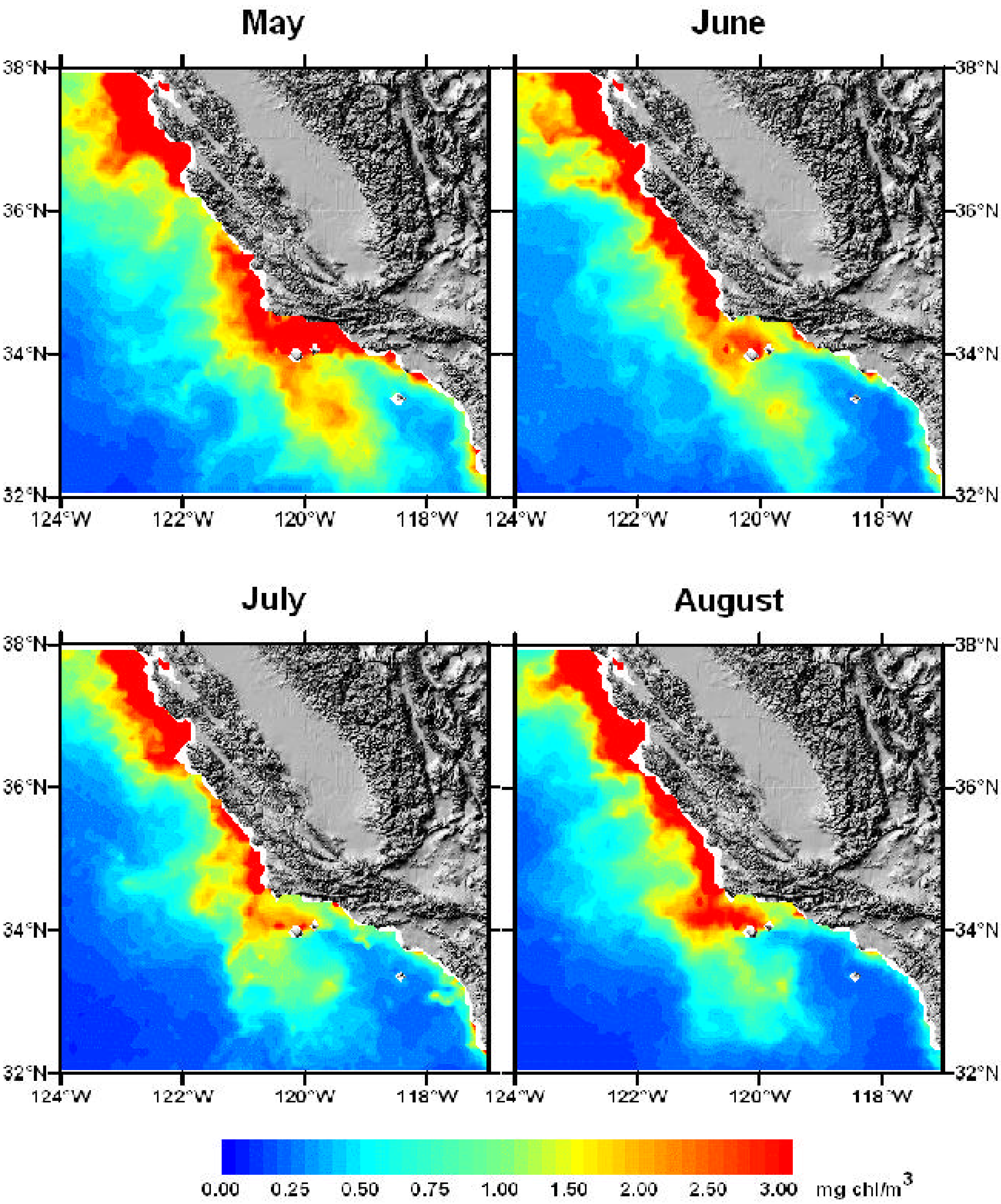


Figure 2. Climatically averaged (1997–2000) surface chlorophyll concentration measured by SeaWiFS radiometer off central and southern California.



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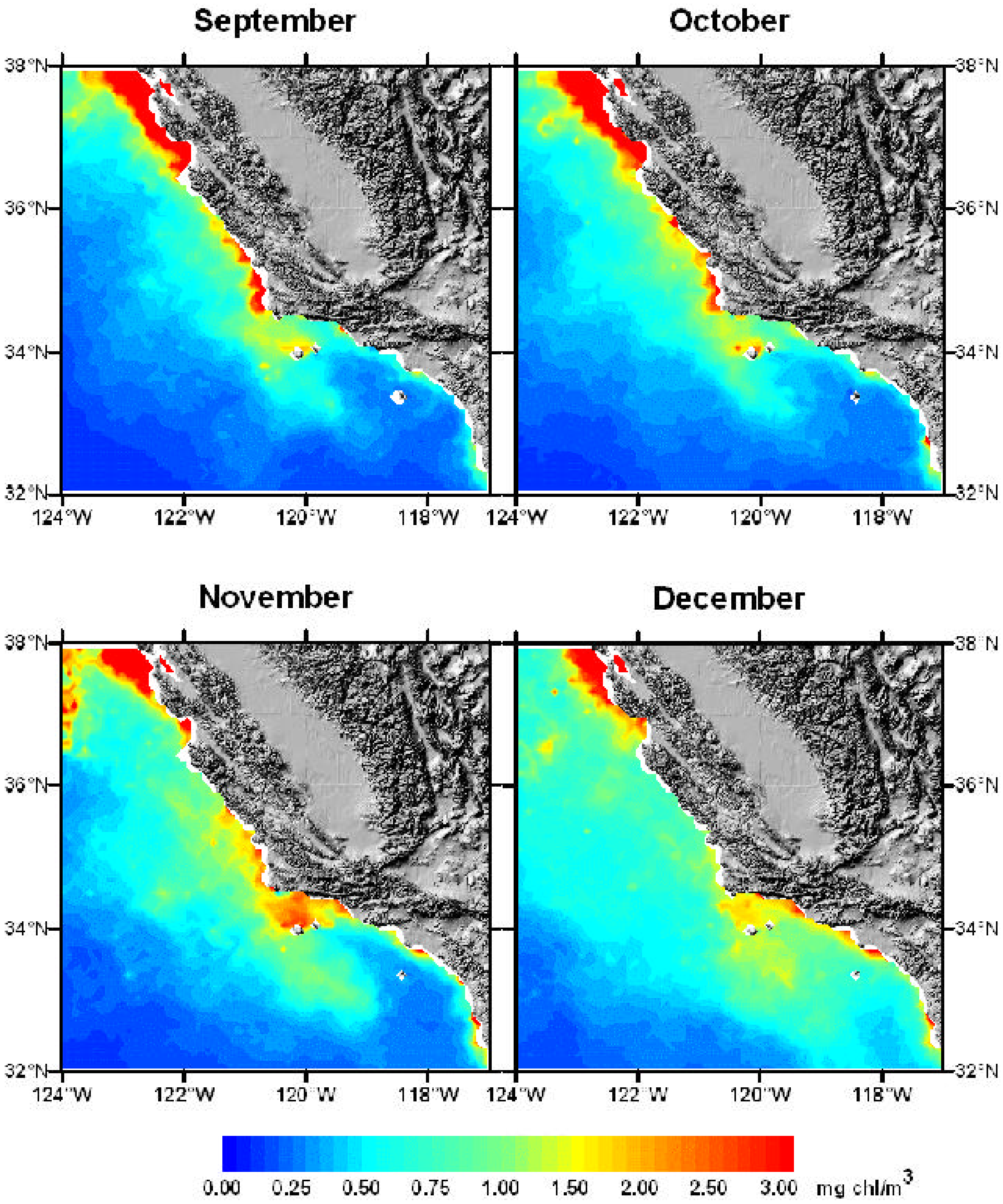

Figure 2 (continued).

different regions (Figure 3) shows a phytoplankton bloom during the spring-summer season to the north of Point Conception, and one late summer minimum and late spring maximum in the Southern California Bight. During the second half of 1997 and the first half of 1998, i.e., during the El Niño event, the chlorophyll concentration in all eight small regions (Figure 4) showed significant changes. The phytoplankton biomass decreased during the autumn seasons of 1997 and 1998. However, during the winter-spring season (between these two minima), the chlorophyll concentration was comparable to the climatically averaged level.

Typical absolute values of wind stress vary regionally (Figure 5). In northern regions (NO and NC), maximum wind stress occurs in summer. In southern regions, there typically are two periods of maximum wind stress, the first in December and the second in early summer. Wind stress in the southern zone of SCB is typically low all year round. During the El Niño event period, the wind stress pattern remained unchanged in all regions except the most southern ones, where there was an increase in wind stress (Figure 5, SM and SD).

The variations of sea surface temperature between 1997 and 2000 (Figure 6) in all regions analyzed reveal a strong interannual pattern of deviations from the long-term mean values. Between summer 1997 and summer 1998, the SST anomalies were positive (i.e., SST was relatively higher than normal). Thereafter, SST gradually decreased until late summer 1999, when it increased again. This pattern is reflected in the interannual variations of phytoplankton biomass, especially in the offshore regions NO and SO (Figure 4), where the chlorophyll concentration during 1999 exceeded the climatic means.

Air temperature in the Southern California Bight fluctuated noticeably in 1997–2000 (Figure 7). Summer 1997 was warm (anomaly +2.0°C), the spring and early summer 1999 were cold (anomaly from -1.5°C to -2.0°C). Peaks of air temperature anomalies were evident in May–June 1997, in September–October 1997, and in August 1998.

The intensity of offshore Ekman wind drift (Figure 8) exhibited “sine curve”-type seasonal variations with a maximum in early summer and a minimum in winter. Both to the north (36°N) and to the south (33°N) of Point Conception, the intensity of the “upwelling index” in autumn 1997 (i.e., during the onset of El Niño) did not change as compared to average climatic values. Two short periods of abrupt decrease of the upwelling index occurred at 36°N in November 1997 and February 1998.

The deepening of the pycnocline and the decrease of phytoplankton biomass is evident from CalCOFI observations (Figures 9 and 10). The depth of the pycnocline at the station located in the Southern California Bight was rather shallow in summer 1997 (just before the beginning of the El Niño event), but it deepened to about 60 m, as compared with about 40 m in autumn of 1998 and 1999. During winter 1998, the pycnocline at the coast of California was both deeper (50–80 m) and more pronounced than during other winter seasons, and similar features were still evident during the spring of 1998. In summer 1998, the pycnocline was still pronounced and rather deep, but its general properties were comparable with summer 2000. The vertical profile of phytoplankton was also reflected in the position of the nutricline (Figure 10). During autumn 1997, the concentrations of all main nutrients below the pycnocline were lower than those typically observed in other autumn seasons. The vertical distribution of specific density, phytoplankton, and nutrients at other CalCOFI stations was similar to Figures 9 and 10.

The typical squid fishery season (Figure 11) in the Southern California Bight is in winter (from October to April); near Monterey Bay, it is in spring-summer (from April to August), coinciding with spawning periods. Normal spawning patterns were observed in 1997 and 2000; however, starting from mid-1997 to mid-1998, the squid fishery off California decreased to almost zero. The squid fishery in the Southern California Bight started to recover in late 1998. A second, larger fishing period occurred in 1999, from March through July in the Southern California Bight, atypical for this region. In contrast, squid landings in the Monterey Basin remained low through 1998–1999. The squid fishery in both the Southern California Bight and the Monterey Basin appear to have fully recovered by 1999–2000.

DISCUSSION

The general pattern of remote-sensed phytoplankton biomass (Figure 2) reflects the main features of both productivity and hydrography of the region. The most productive area off the California coast is the upwelling zone north of Monterey Bay, and the mean chlorophyll concentrations gradually decrease offshore. In the Southern California Bight, the most productive zone is the Santa Barbara Channel (SB in

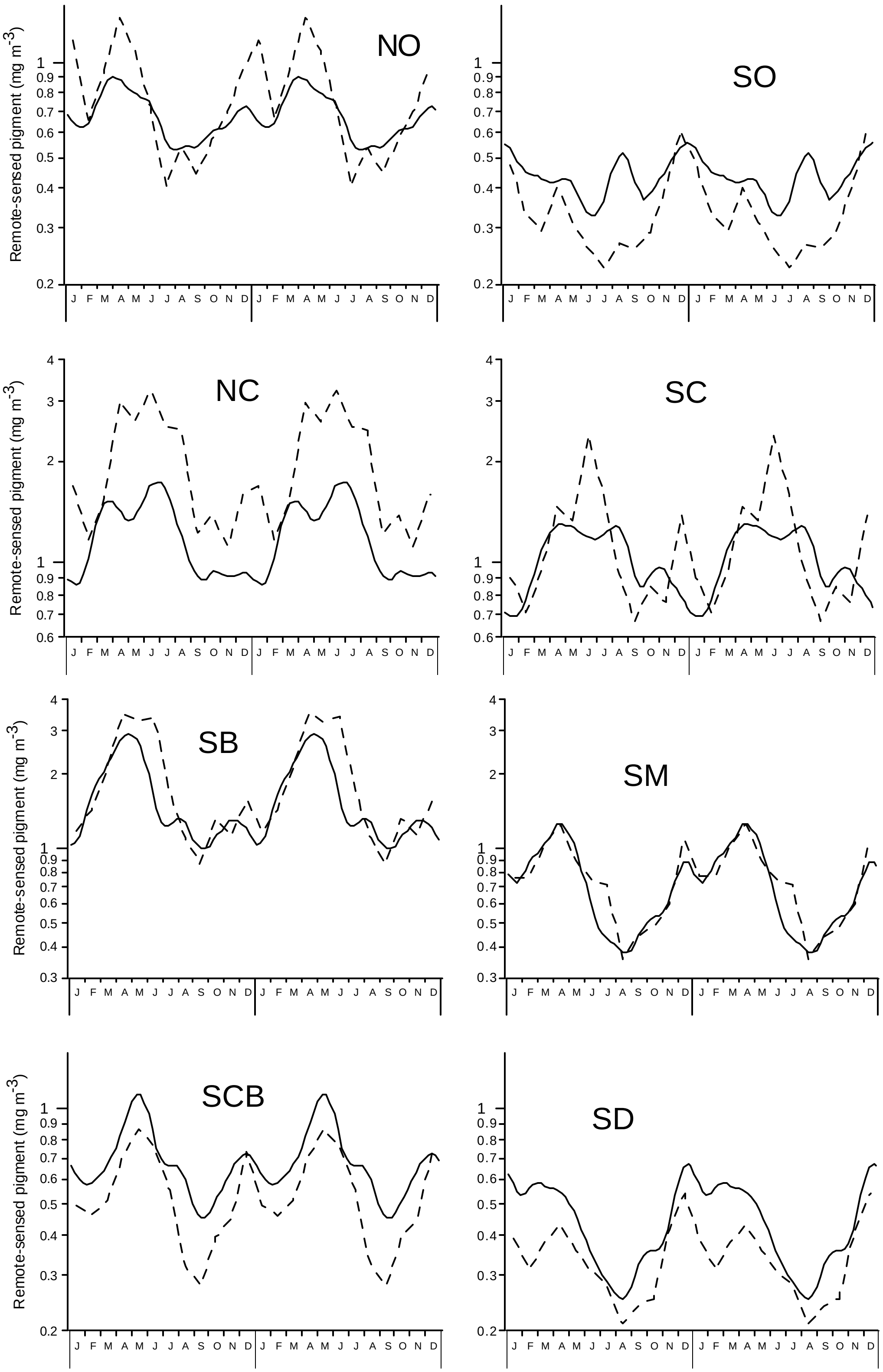

Figure 3. Seasonal cycles of remote-sensed phytoplankton dynamics. Solid line indicates SeaWiFS observations averaged over September 1997–December 2000. Dashed line indicates CZCS observations averaged over November 1978–June 1986. The abbreviations of the regions are indicated in Figure 1.

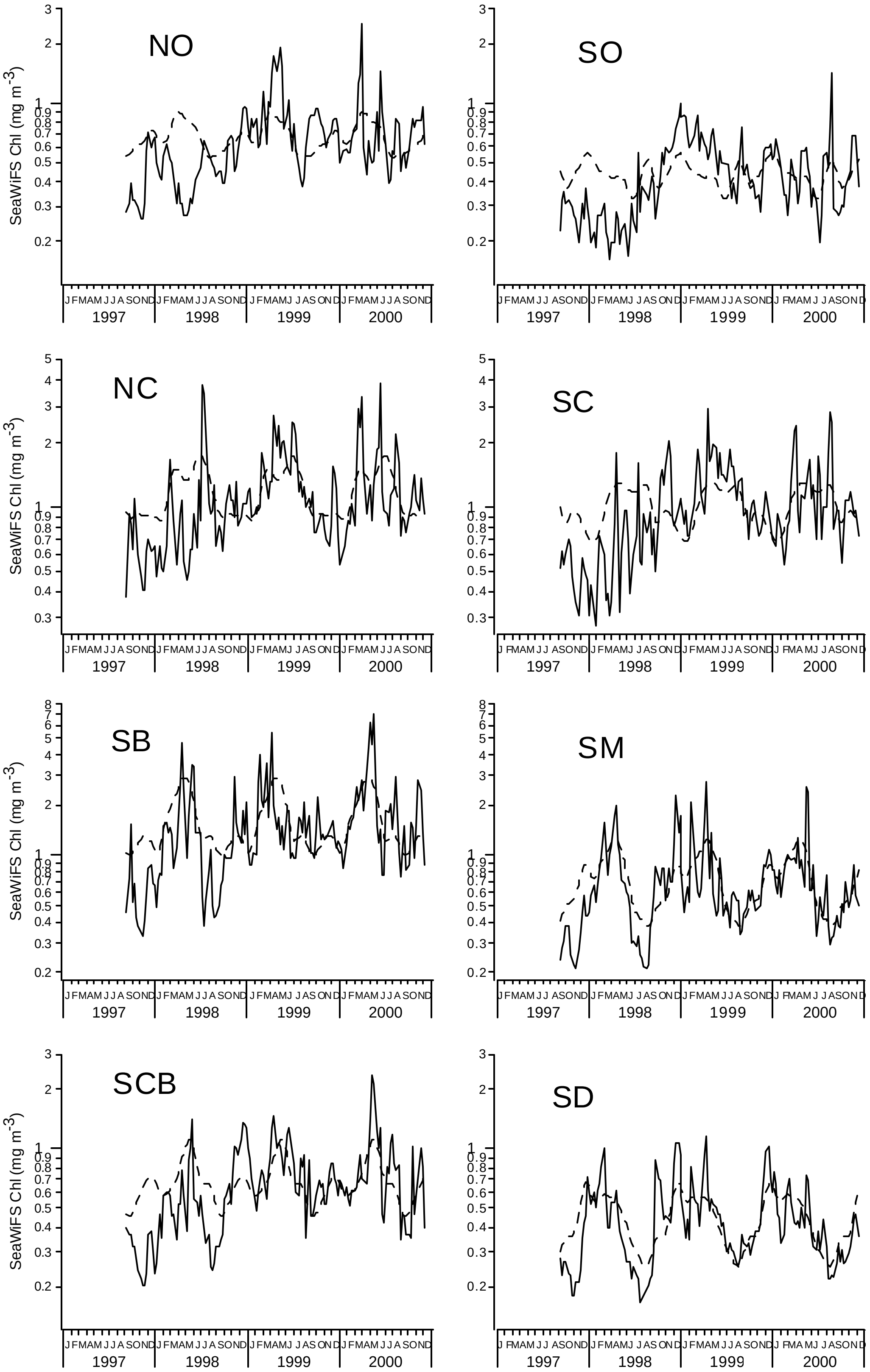

Figure 4. Variations of remote-sensed surface chlorophyll during 1997–2000. The abbreviations of the regions are indicated in Figure 1. The dashed line indicates the seasonal cycle averaged over the entire period of observations (similar to Figure 3).

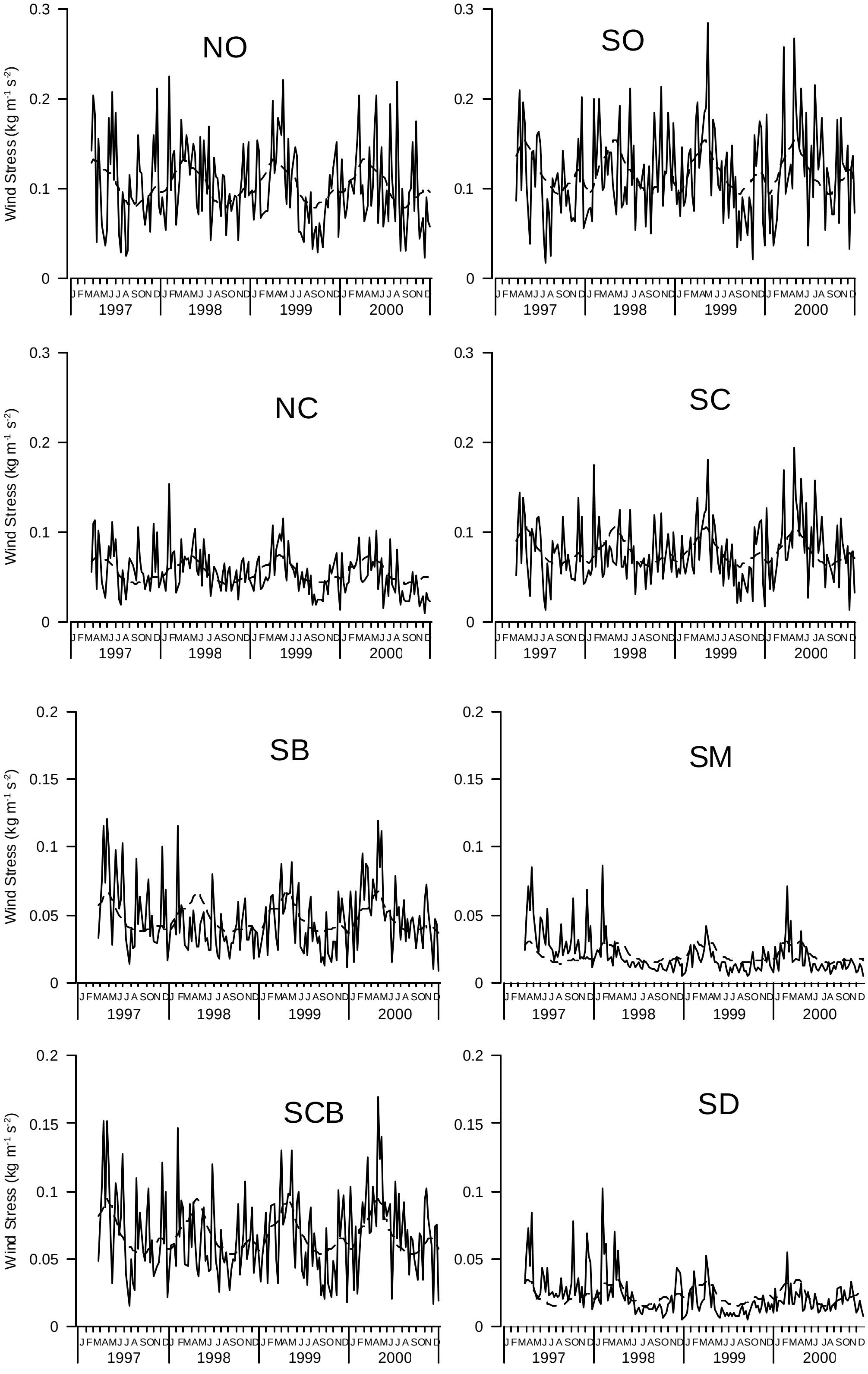

Figure 5. Variations of wind stress during 1997–2000. The abbreviations of the regions are indicated in Figure 1. The dashed line indicates the seasonal cycle averaged over the entire period of observations (similar to Figure 4).

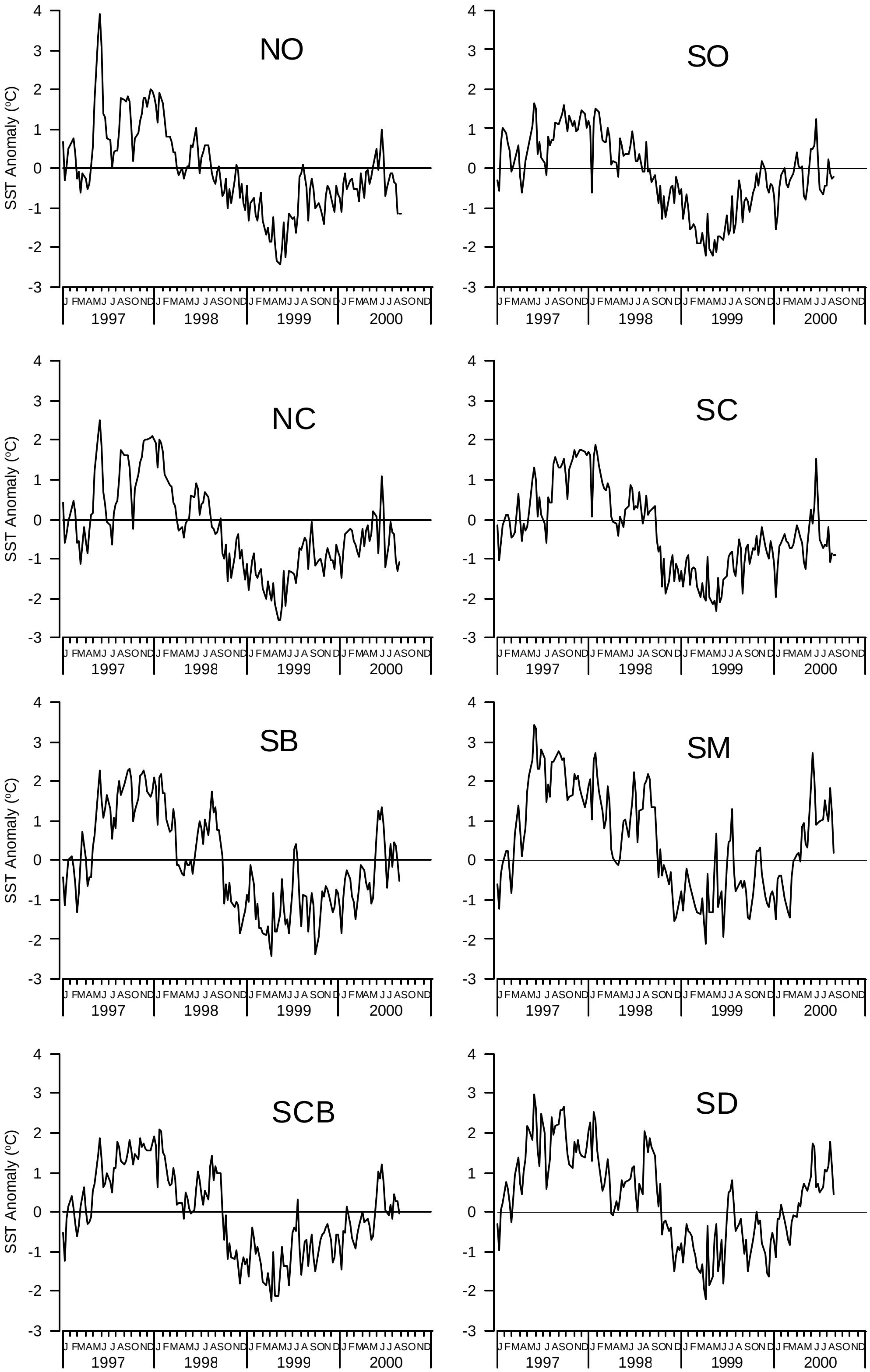

Figure 6. Variations of sea surface temperature anomalies during 1997–2000 referred to the period 1981–1996. The abbreviations of the regions are indicated in Figure 1.

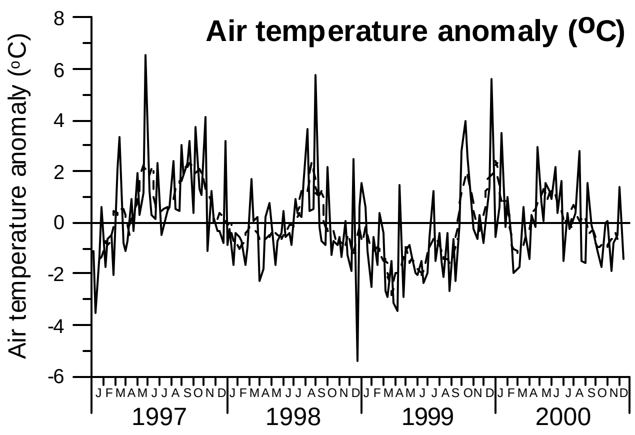

Figure 7. Variations of air temperature at San Nicholas Island during 1997–2000 referred to the period 1994–2000. Dashed line is a 5-point running average.

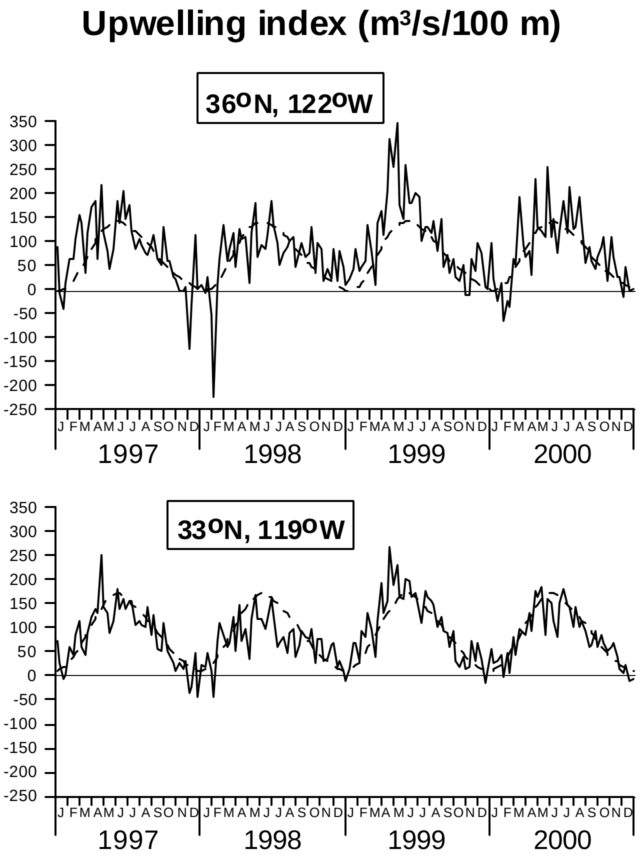

Figure 8. Upwelling index at two locations (36°N, 122°W and 33°N, 119°W) during 1997–2000 (data from PFEL). Dashed line indicates climatic cycle averaged over 8-d periods.

Figure 1). A tongue of chlorophyll-rich water also penetrates southeastward along the Santa Rosa Ridge toward San Nicolas Island (~33°15'N, 119°30'W), reflecting the southerly direction of the main jet of the California Current. This chlorophyll-rich area was documented previously in CZCS data (1978–1986) (Pelaez and McGowan 1986, Smith *et al.* 1988). Low levels of chlorophyll are transported eastward along 32°N (Thomas and Strub 1990) and then from southeast to northwest by the Southern California Countercurrent. This pattern of spatial distribution of remote-sensed chlorophyll is in accordance with the general cyclonic circulation in SCB.

Typical Seasonal Cycles of Phytoplankton Dynamics

Differences in the seasonal patterns of phytoplankton dynamics to the north and to the south of Point Conception can be explained by the difference in physical processes regulating phytoplankton growth in these regions.

Wind stress appears to be a principal source of seasonal variations of phytoplankton biomass to the north of Point Conception. Phytoplankton biomass in the central California coastal zone (NC and SC, Figure 3) typically increases during the spring-summer season; this seasonality results from the dynamics of upwelling (Huyer 1983) caused by seasonal variations of offshore Ekman wind drift (Bakun and Nelson 1991) (see also Figure 8). The absolute values of wind stress in these regions were also high in summer (Figure 5).

The seasonal pattern of chlorophyll in the open ocean was also regulated by wind stress. In the northern open ocean (NO), two maxima of chlorophyll were evident, in December (lower) and in March–May (higher). The SeaWiFS-observed seasonal pattern of chlorophyll in the southern part of open ocean (SO) was disrupted by an anomalous maximum in August, not observed in the CZCS data. Taking into account the general low values of phytoplankton biomass in this zone and the short period of observations (3 years, 3 months), this maximum may result from an atypical penetration of near-shore chlorophyll-rich water rather than a regular seasonal feature. The seasonal pattern of wind stress in these two regions also had two maxima, but the first of these was in December (Figure 5) and thus was not responsible for the anomalous maximum of phytoplankton noted above (Figure 4).

In contrast to the pattern seen in the upwelling zone, the Southern California Bight typically mani-

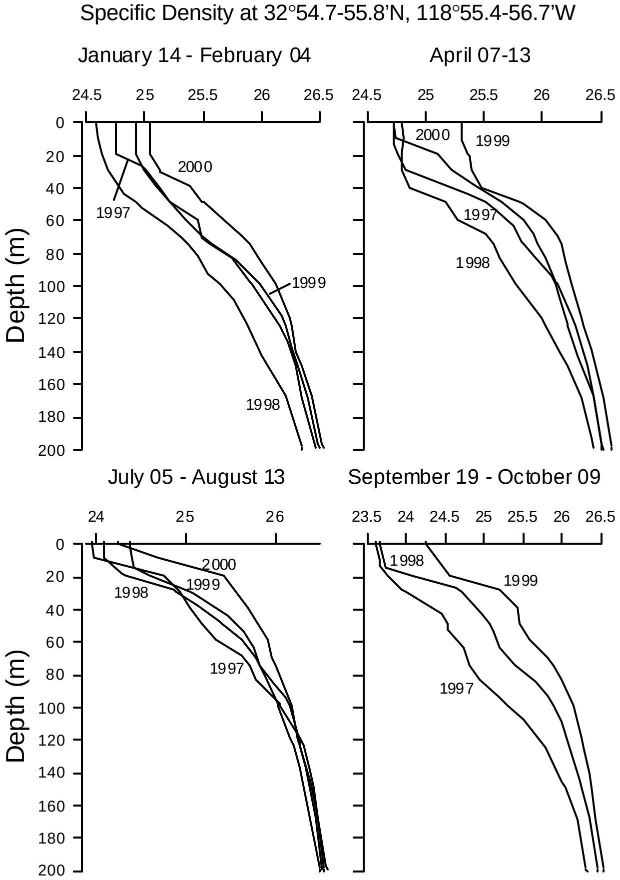

Figure 9. The depth of pycnocline at CalCOFI station (32°54.7–55.8'N, 118°55.4–56.7'W) during 1997–2000. The vertical profile of σ_θ during El Niño event is indicated by a thick line.

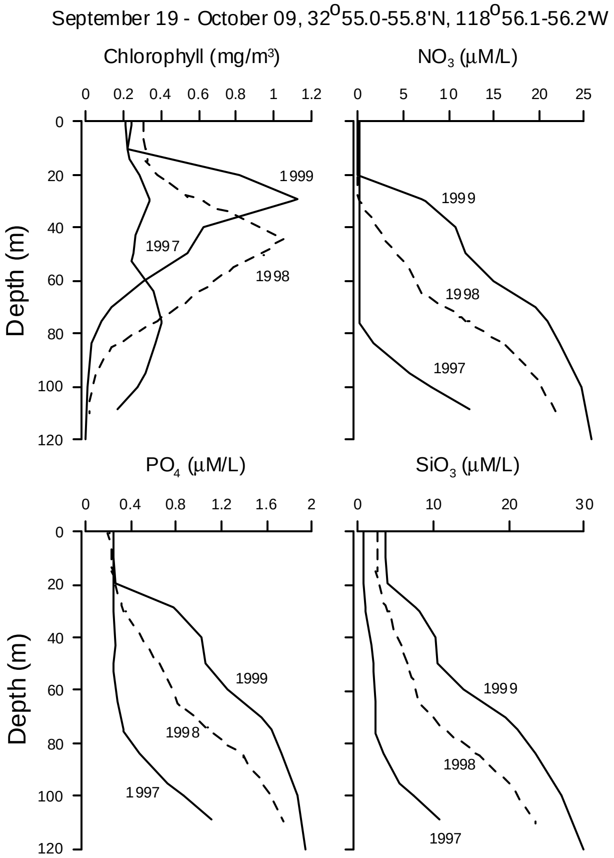

Figure 10. Vertical distribution of chlorophyll and nutrients at CalCOFI station (see Figure 9) during the autumn seasons of 1997–1999.

fested one late-summer minimum of phytoplankton, noted before from the 1978–1986 CZCS data (Michaelsen *et al.* 1988, Strub *et al.* 1990, Thomas and Strub 1990). The seasonal cycles of phytoplankton in the most southern near-shore regions of San Diego (and also to a lesser extent in Santa Monica Bay) manifested a typical subtropical cycle, with a phytoplankton minimum in summer and an extended maximum during winter-spring (from December to May). Wind stress in the San Diego region and Santa Monica Bay was quite low all year round (Hickey 1992, Winant and Dorman 1997). Consequently, the fall phytoplankton bloom was the result of winter cooling of sea surface rather than the influence of wind stress.

The spring maximum in phytoplankton observed in the northern part of the Southern California Bight requires an explanation. Although observed in spring, this particular bloom seems to have nothing in common with typical to mid-latitude "vernal blooms" of phytoplankton resulting from the formation of a seasonal thermocline (Sverdrup 1953). In the Southern California Bight, near-surface stratification is maintained even during the winter season (Hickey 1993); hence, the period of light limitation in winter is absent. Two periods of maximum wind stress are typical for SCB, the first in December and the second in early summer. This pattern seems to result from the higher absolute values of wind stress in the southern offshore area, in contrast to weak winds at the coast, caused by the year-round sheltering by the coastal mountain range (Dorman and Winant 1995). The phytoplankton maximum in SB in April coincides with the maximum of wind stress. This indicates that the bloom in April results not from formation of a thermocline, but from erosion of the thermocline and enrichment of the upper mixed layer with nutrients. Furthermore, the general pattern of water circulation

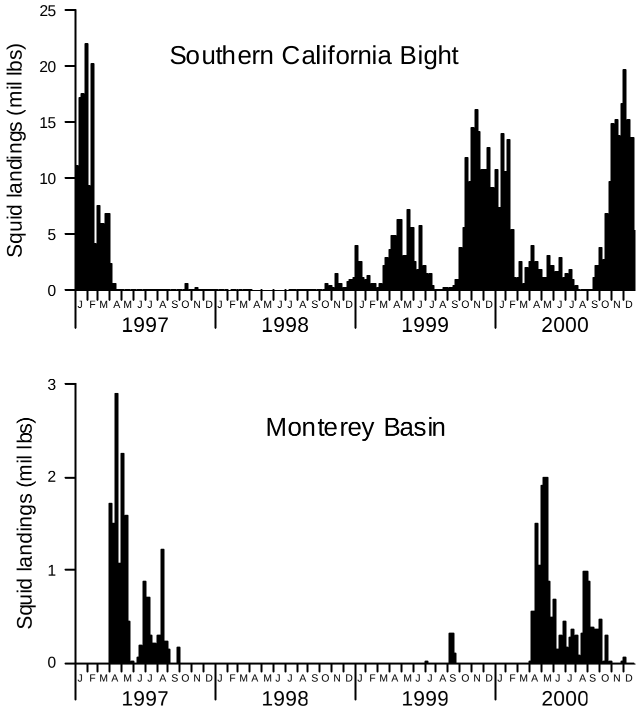

Figure 11. Squid landings during 1997–2000 in the Southern California Bight and Monterey Basin.

in the Southern California Bight implies that during spring the Southern California Countercurrent weakens and a branch of the California Current moves eastward through the Santa Barbara Channel (Harms and Winant 1998, Bray *et al.* 1999, DiGiacomo and Holt 2001). This current must transport waters rich in chlorophyll and nutrients from the Point Conception upwelling zone into the Southern California Bight, and it favors the increase of phytoplankton biomass there.

These general differences between the seasonal cycles of phytoplankton in the Southern California Bight (maximum in winter-spring) and in the Monterey Basin (maximum in summer) appear directly responsible for the seasonality in the squid fishery in these two regions. The seasonal cycles of zooplankton biomass averaged over 1950–1979 (Chelton *et al.* 1982) also revealed the difference: the period of high zooplankton was February–July in the Southern California Bight and April–September (two months later) in the Monterey Basin. The interannual variations of zooplankton biomass in the California region are well correlated with primary production (Smith and Eppley 1982). Although details of the relations between seasonal dynamics of phytoplankton and large carnivores like squids need further investigations of intermediate links in the food chain, the winter-spring fishery for squid in southern California co-occurs with winter cooling and incursion of California Current whereas the spring-summer fishery for squid in Monterey Bay is correlated with the coastal upwelling season.

Changes in Seasonal Dynamics of Phytoplankton During the 1997–1998 El Niño Event

The time-series of remote-sensed surface chlorophyll in all eight small regions show significant changes from the second half of 1997 to the first half of 1998. During the El Niño event (Figure 4), in the northern open ocean (NO) the chlorophyll concentration was half of the typical level during September–November 1997 and April–May 1998. In the southern open ocean (SO), the chlorophyll values were also lower during the El Niño period when compared with the typical seasonal cycle, and there were no evident maxima of phytoplankton during the El Niño period. Phytoplankton biomass in both coastal regions (NC and SC) resembled the patterns observed offshore (NO and SO), but coastal zones were much more heterogeneous. The lowest phytoplankton biomass was observed from November to January, when winter maxima normally occur in the neighboring northern open ocean region. Therefore, offshore transport was probably not the reason for the winter offshore maxima. Similarly, the pattern of wind stress in both the open ocean and the coastal zones did not reveal any changes during the 1997–1998 El Niño, indicating that wind stress is not the cause of lower phytoplankton biomass.

In all four regions within the Southern California Bight, the seasonal pattern of phytoplankton biomass variation did not change during the El Niño period, nor did the absolute values of chlorophyll concentration during the winter-spring period of “blooming.” Nevertheless, during the usual periods of summer minima in 1997 and 1998, the magnitudes of chlorophyll biomass decreased by about twice the normal amount. This pattern was more pronounced in all three near-shore regions (SB, SM, and SD) and less pronounced in the central part of SCB. We hypothesize that these decreases in chlorophyll resulted in lower zooplankton levels and could have inhibited squid spawning (Zeidberg and Hamner 2002).

The El Niño-related deviations in SST compared to normal patterns were reflected by interannual variations of phytoplankton biomass, especially in both offshore regions NO and SO (Figure 4), where the chlorophyll concentration during 1999 evidently exceeded the climatic means. Similar relations between water temperature and productivity in the California Current were noted before (Reid 1962, Colebrook 1977, Eppley *et al.* 1978, Chelton *et al.* 1982, Smith and Eppley 1982).

The peaks of SST in May–June 1997, in September–October 1997, and in August 1998 (Figure 6) coincided with the peaks of air temperature (Figure 7). In contrast, the increase of SST during the winter 1997–1998 (about +2°C) was not in accordance with the variations of air temperature. This warming does not result from air-sea surface interaction, it was driven hydrographically, perhaps related to weakening of upwelling. In the Southern California Bight, the rise of SST not related to air temperature began earlier; in contrast, in northern regions the increase of SST in winter started about two months later, indicating northward propagation of sea surface warming, perhaps with coastally trapped waves.

The wind stress in the Southern California Bight increased during the El Niño period in the SM and SD regions (Figure 5), during the time of minimum wind stress reported by Winant and Dorman (1997). This indicates that decreases of wind stress were not the reason for the decreased interannual variability of phytoplankton biomass.

The Hydrographical and Meteorological Factors Responsible for the Effect of the 1997–1998 Southern California El Niño

It is generally presumed that El Niño in California results from meteorological factors. However, the data for the 1997–1998 El Niño do not wholly support this assertion. Analysis of remote-sensed variations of phytoplankton biomass related to sea surface temperature and wind stress off the coast of California indicate that the deviations from normal patterns were not the result of weakening of southward wind and upwelling. First, variations of the upwelling index observed during the winter of 1997–1998 were too small and short to explain the significant increase of SST and decrease of phytoplankton biomass in the second half of 1997 and 1998. Second, the influence of El Niño on phytoplankton biomass was most pronounced during the periods when the development of phytoplankton in regions distant from the upwelling zone (in the Southern California Bight) was minimal. Third, the intensity of wind stress in 1997–1998 was not significantly weaker than during latter periods, and in the southern part of the Southern California Bight it was even higher. Fourth, the SST increase, not explained by air/sea surface interaction, was well pronounced and observed earlier in the regions distant from the zone of coastal upwelling.

The general features of oceanic teleconnection were evident from the remote-sensed observations during the 1997–1998 El Niño event off California. An increase of SST was observed first of all in the southern part of the region under study, and only two months later did warm water penetrate north into the zone of coastal upwelling (Figure 6). The wind pattern changed slightly, in terms of both wind stress and upwelling index, but the intensity of offshore Ekman transport was not markedly changed (Figure 8). Unlike the meteorological patterns discussed above, the zones off California where a pronounced pycnocline regulates phytoplankton growth were subject to significant modification by El Niño, which most likely affected oceanic stratification.

CalCOFI observations supported our speculations on the deepening of the pycnocline and the nutricline, and the decrease of phytoplankton biomass in the California costal zone. Lower concentrations of all main nutrients in autumn 1997 confirm that there was more pronounced nutrient limitation during autumn 1997 resulting from a pycnocline located below the nutricline as opposed to above it, as is typically the case (Eppley *et al.* 1978, 1979). During the 1997–1998 El Niño event, a deeper and steeper nutricline limited phytoplankton growth in the euphotic layer.

The results of our analysis support, expand, and clarify the results of previous investigations on the relationship between phytoplankton development and hydrographic and meteorological factors. Eppley *et al.* (1978) revealed an inverse correlation between standing stocks of phytoplankton and the depth of the nitrate vertical gradient in the Southern California Bight; the latter was related to near-shore water temperature anomalies. The authors supposed that these variations were coupled to climatic changes over vast areas of the Pacific Ocean, but the absence of detailed long time-series data at that time hindered them in relating these variations to El Niño events.

Fiedler (1984) and Strub *et al.* (1990), using CZCS data, described a pattern of the 1982–1983 El Niño similar to the 1997–1998 El Niño observed in our study. For example, their correlations between wind stress and pigment concentration were slight; the large-scale decrease in pigment concentration was stronger and longer lasting in the south than in the north, and a positive SST anomaly propagated northward at a speed comparable to the theoretical phase speed of coastal trapped internal Kelvin wave (100 km day^{-1}). However, these authors took into account only two physical factors influencing phytoplankton dynamics, upwelling caused by wind and horizontal advection of nutrients, and they did not consider the importance of pycnocline depth and/or atmospheric cooling in winter.

Hayward (2000) analyzed the impact of the 1997–1998 El Niño on hydrological and biological characteristics off southern California. He indicated the main mechanism of El Niño influencing phytoplankton growth: the decrease of vertical flux of nutrients through a deepened thermocline ("bottom-up trophic forcing"). However, he compared the El Niño period with other years using vertically integrated chlorophyll averaged over each entire CalCOFI cruise. However, averaged high values (from regions NC, SC, and SB, where influence of El Niño was slight) and low ones (from regions SD and SO, where influence of El Niño was strong) resulted in the erroneous conclusion that there was almost no decrease of chlorophyll concentration; when, in fact, it was substantially lower, as seen by SeaWiFS.

The most comprehensive analysis of the physical mechanism forcing the onset of the 1991–1993 El Niño and its influence on phytoplankton dynamics was conducted by Chavez (Chavez 1996) near Monterey Bay. Using a series of hydrological and biological observations, he revealed the propagation of coastally trapped Kelvin waves linked to the atmospheric events in the Western Pacific. The resulting deepening of the thermocline led to changes in circulation, positive sea surface temperature anomalies, low nutrient levels in the upper ocean waters, and depressed primary productivity. The maintenance of El Niño off California, in contrast to the conditions present during its onset, was partly reinforced by local atmospheric forcing. A similar pattern was described on the basis of CalCOFI observations in 1991–1993 by Lynn *et al.* (1995).

The collective results of this and previous studies strongly suggest that the basic features of seasonal dynamics of surface chlorophyll off California during the 1997–1998 El Niño event are best explained by patterns of hydrographical variability, wherein a deepening of the pycnocline and excess stratification results in reduced nutrient flux into the euphotic zone. Finally, although fluctuations in phytoplankton biomass have been correlated with changes in squid landings, the mechanism of the disruptive impact of El Niño on the biology of commercial fishery species, such as squids, needs further investigation.

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