Patterns and controls of chlorophyll-*a* and primary productivity cycles in the Southern California Bight

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Abstract

Factors that influence the magnitude and the depth of the chlorophyll maximum layer in the ocean off Southern California are explored using observations from the long-term California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. The data record is sufficiently long to reveal patterns not always evident from single stations or single cruises. Processes such as coastal wind-driven upwelling, geostrophic circulation, and annual physical and chemical cycles are illustrated to demonstrate their effect on euphotic zone nutrient availability, and subsequent phytoplankton biomass and primary productivity. In this area, where the influence of wind-driven upwelling is spatially restricted and advected waters are generally nutrient depleted, geostrophically induced upwelling and winter convection become important in determining spatial and temporal patterns of phytoplankton.
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1. Introduction

The California Current flows south along the coasts of California and Baja California, Mexico. The oceanography has been summarized in several papers (Hickey, 1979; Lynn and Simpson, 1987; Bray et al., 1999). At Pt. Conception, it diverges from the coast by as much as 100 km. Near 32°N, the current loops eastward, splitting as it approaches the coast (Haury et al., 1993). The main core continues equatorward along the Baja California coast, while the rest recirculates poleward as the inshore limb of the cyclonic Southern California eddy. The meandering current divides the California Current ecosystem into a productive nearshore region and an oligotrophic offshore region (Chavez et al., 1991; Hayward and Venrick, 1998). North of Pt. Conception, the nearshore area experiences significant wind-driven upwelling (e.g., Huyer, 1983; Kosro et al., 1991).

For more than 50 years, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been surveying the California Current ecosystem, making an extensive suite of physical, chemical and biological measurements. Recently, the portion of the ecosystem from Pt. Conception south to the Mexican border (the area now covered by CalCOFI surveys) has been subdivided into regions based, in part, upon the floristic composition (Venrick, 1998) and the seasonal cycles of the phytoplankton (Hayward and Venrick, 1998). The
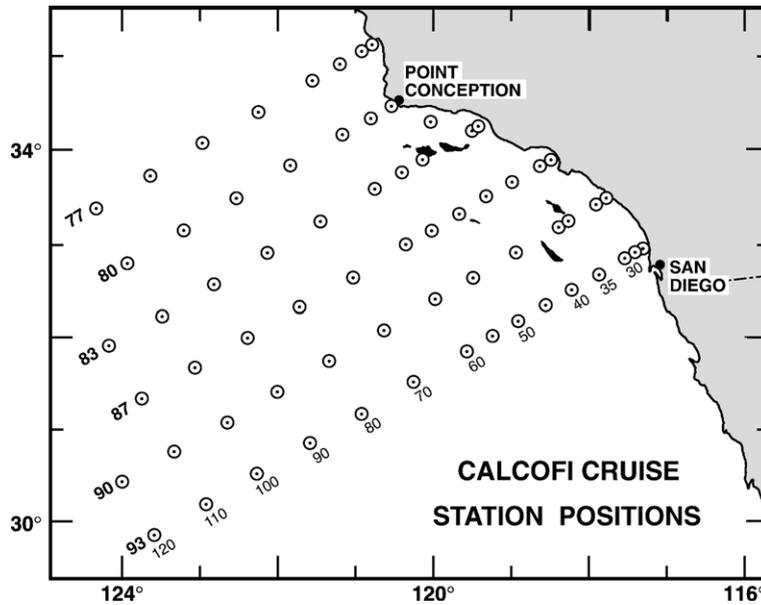
Fig. 1. Present CalCOFI station pattern. Line numbers are given along offshore edge. Station numbers are indicated below line 93.

current entering from the north is cold and fresh, but relatively low in nutrients (Chavez et al., 1991). Regular spring coastal upwelling is limited to a small region around Pt. Conception and the northern portion of the Southern California Bight (Hickey, 1979; Lynn and Simpson, 1987). Thus, most of the California Current ecosystem off southern California must be supported by nutrient input from sources other than coastal upwelling or advection.

The geographical and temporal coverage of the CalCOFI data set makes it ideal for exploring alternative sources of enrichment. With this large data set we have revealed some patterns not always evident at single stations, or during single seasons. In this paper we will present evidence that both the patterns of large scale circulation and the extent of winter mixing may be significant mechanisms for nutrient input over much of the area.

We start by reviewing the depths of the chlorophyll maximum and the top of the nitracline, and show that the concentration of chlorophyll in a deep layer is related to its depth. Using this relationship, we examine mechanisms that influence depth and concentration, including classic coastal wind-driven upwelling and geostrophic adjustment of the water column. Finally, the annual cycle of physical forcing may regulate winter nutrient input into the euphotic layer, setting the stage for phytoplankton growth for the following year. In regions with diminished coastal upwelling in the spring,

mechanisms such as geostrophy and winter convection appear to be important in regulating both spatial and temporal patterns of chlorophyll.

2. Methods

In 1950, the CalCOFI program initiated a standard sampling grid between the Oregon–California border and the southern tip of Baja California, Mexico. Large area, multi-ship surveys were carried out monthly for the first decade, and then less frequently until 1985 when the cruise frequency was changed to quarterly surveys restricted to the area between Pt. Conception and the U.S.–Mexican border (Fig. 1; Hewitt, 1988). Lines run perpendicular to the coast and are numbered from northwest to southeast. Stations are numbered out from the coast. Thus, the southwesternmost station is line 93, station 120 (93.120; Fig. 1).

The present CalCOFI sampling protocol is described in detail in the cruise data report series (e.g., Scripps Institution of Oceanography, 2002) and the CalCOFI web site (http://www.calcofi.org/newhome/publica-tions/Data_Reports/data_reports.htm). At each of 66 stations, a CTD cast is made to 500 m, bottom depth permitting. Water samples are collected with a Niskin rosette from 20 depths. All samples are analyzed for salinity, dissolved oxygen, and inorganic nutrients (silicate, phosphate, nitrate, and nitrite). The top of the nitracline is taken as the 1.0 μMol NO_3 depth, following

Cullen and Eppley (1981). Although we focus on nitrate here, the patterns of the other inorganic nutrients are consistent.

Chlorophyll samples are drawn from all samples above 200 m (usually 14), with a maximum vertical spacing of 10 m through the chlorophyll maximum layer; thus one sample is always taken within 5 m of the maximum concentration. Chlorophyll samples are filtered through Whatman GF/F filters and extracted in acetone in the dark and under refrigeration (Venrick and Hayward, 1984). Chlorophyll-a and phaeopigments are determined fluorometrically.

An irradiance profile is made once a day, preceding collection of samples for determination of primary productivity. The latter are collected from six irradiance levels between the surface (about 95%) and below 1% of the surface light intensity. Primary production is estimated from the uptake of radio carbon. Samples are collected shortly before local apparent noon and incubated between LAN and civil twilight in seawater-cooled on-deck incubators, with neutral density screens that simulate in-situ light levels at the depths of collection. Because these experiments are conducted only once per day, they are made on roughly one-fourth of the stations on a cruise, and, over all data, all stations have not been sampled equally for primary productivity.

Temperature, salinity, and dissolved oxygen have been sampled since 1949, while inorganic nutrients, chlorophyll-a, and primary productivity have been regularly measured only since 1984. For climatologies of the former, mean seasonal property variation is obtained by a least-squares regression of the data to annually periodic sinusoids, following the approach of Lynn (1967) and Chelton (1984), as described in Bograd and Lynn (2003). Since the time intervals between measurements are irregular, and typically consist of 3–4 month gaps, we restrict our harmonic analysis to include only the annual and semiannual harmonics. Because of the shorter lengths of the nutrient, chlorophyll and productivity data bases, mean annual cycles of these measurements are not based on harmonic mean curves, but on observed seasonal means.

3. Results and discussion

3.1. Relationship between the chlorophyll maximum layer and the nitracline

The vertical distribution of chlorophyll results from the requirements of phytoplankton for nutrients and light (e.g., Cullen and Eppley, 1981; Cullen, 1982). Under conditions of excess nutrients near the surface,

nutrient uptake by phytoplankton is rapid and net growth produces a near-surface biomass maximum. As growth continues, nutrient concentrations are reduced to the point that phytoplankton growth is restricted. Phytoplankton populations begin to sink and accumulate at depths where nitrate is more available, sacrificing ambient light for increased nitrate. This process continues, with the phytoplankton residing near the top of the nitracline and gradually eroding it until the process is reset by a new supply of near-surface nitrate or until growth, limited by light from above, is balanced by nitrate input from below (Venrick, 1993 and refs. therein). Such a phytoplankton cycle recurs in many environments and is usually characterized by a subsurface layer of maximum chlorophyll concentration. Above this maximum, phytoplankton growth is dependent upon some form of regenerated nitrogen. The general characteristics of this maximum layer as well as the scales of persistence differ greatly among environments. In eutrophic systems the chlorophyll maximum layer is often a maximum of biomass and productivity, and the evolution of the layer is frequently interrupted by advective and convective processes. In stable oligotrophic environments, the chlorophyll maximum layer may persist for years between nutrient limitation at shallower depths and light limitation below; the increase in chlorophyll in these conditions often results from an accumulation of pigments within cells—an adaptive response to extremely low light intensities. At these depths, the maximum layer is neither a biomass maximum nor a productivity maximum (Winn et al., 1995). Any event which results in upward shoaling of the relevant isopycnals will move a layer of light-limited but temporarily nutrient-sufficient phytoplankton into higher light intensities, facilitating nutrient assimilation and growth.

To illustrate the relationship between the chlorophyll maximum and nitracline depth across the CalCOFI region, we use the eight cruises from the 1998 El Niño and the 1999 La Niña years (two cruises per season). Of the 528 stations occupied on these cruises, 450 had a distinct subsurface chlorophyll maximum. The chlorophyll maximum layer depth was closely related to the depth where nitrate begins to increase (Fig. 2A). Over most of the depth range, the linear regression of the depth of maximum chlorophyll concentration against nitracline depth is a good fit ($r^2 = 0.83$). However the intercept is not zero, and, below 100 m, the chlorophyll maximum is generally shallower than the top of the nitracline. When the nitracline begins at the surface, the mean depth of the chlorophyll maximum is 12 m. At depth, the chlorophyll maximum is about 20 m
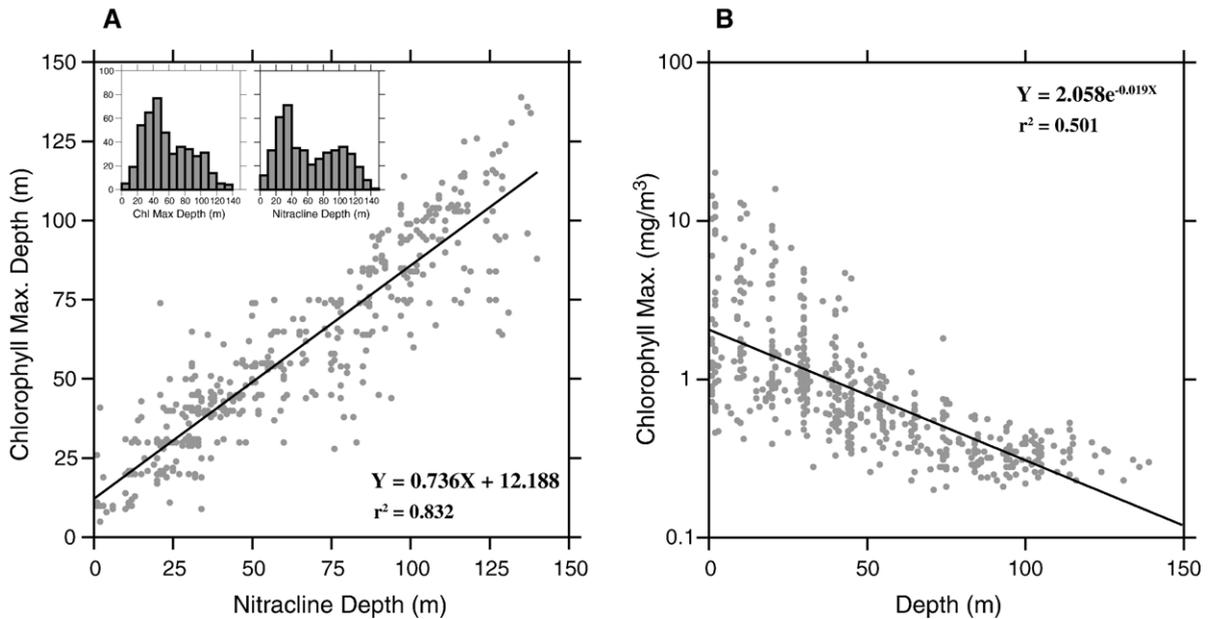
Fig. 2. (A) The depth of the chlorophyll maximum (m) versus the depth of the top of the nitracline (1.0 μM NO₃; m). The insets show the frequency distribution (# of total observations) of the depth of the chlorophyll maximum and top of the nitracline at 10 m intervals. Data in all plots are from quarterly cruises in 1998 and 1999; $n = 528$. (A) Linear fit. (B) Semi-log plot with exponential curve fit.

shallower than the nitracline, suggesting that, while the depth of the chlorophyll maximum layer is generally determined by a balance between the needs for light and for nutrients, at extremes of light, nutrient availability is sacrificed.

Histograms of the frequency of the depths of the chlorophyll maximum layer and of the top of the nitracline have a bimodal depth distribution (Fig. 2A, inset): the shallower values tend to be in the more eutrophic environment near Pt. Conception and inshore of the current, while the deeper ones are in the oligotrophic central Pacific environment offshore.

The concentration of chlorophyll in the maximum varies with the depth of the maximum layer. The relationship is exponential, reflecting the exponential decay of solar radiation in the ocean (Fig. 2B). The exponential regression explains about 50% of the variance; the fit improves slightly if the data are separated according to season. The ratio of surface chlorophyll intercepts between summer and winter (not shown) are close to the ratio of the seasonal variation in surface solar irradiance at the latitude of this data set.

The variability of chlorophyll maximum concentrations at a given depth increases as the depth shoals (Fig. 2B). This is likely the result of the increasing frequency of departure from steady state conditions, time lags both between enrichment and biomass, and between growth and grazing. Conversely, variance

diminishes at depth as phytoplankton growth approaches light-limited steady state.

3.2. Wind-driven coastal upwelling

Coastal upwelling is a process whereby long-shore winds drive near-surface waters offshore, lifting nutrient-rich deep waters to the surface, often stimulating surface phytoplankton blooms. Spring upwelling events are common along the central California coast north of Pt. Conception (e.g., Huyer, 1983; Kosro et al., 1991). In his classic paper on upwelling, Sverdrup (1938) used data taken on the early 1937 "Bluefin" cruises from a line of stations that is quite close to the northern boundary of the present grid (CalCOFI line 77). Sverdrup showed the abrupt change in isopycnal slopes that take place between late March and early May, and he demonstrated that the upwelled waters originate from no deeper than 200 m.

Using the 1998 CalCOFI data from this area, we examined the responses of nitrate and chlorophyll to a spring coastal upwelling event. In winter, the currents were poleward on the inshore part of the section, and slowly southward at the seaward end of the section (Fig. 3A). The main jet of the California Current was further offshore. There was a uniformly deep isothermal and isohaline mixed layer to about 80 m (Fig. 3A,D). Because subsurface isopycnals rise on the left-hand
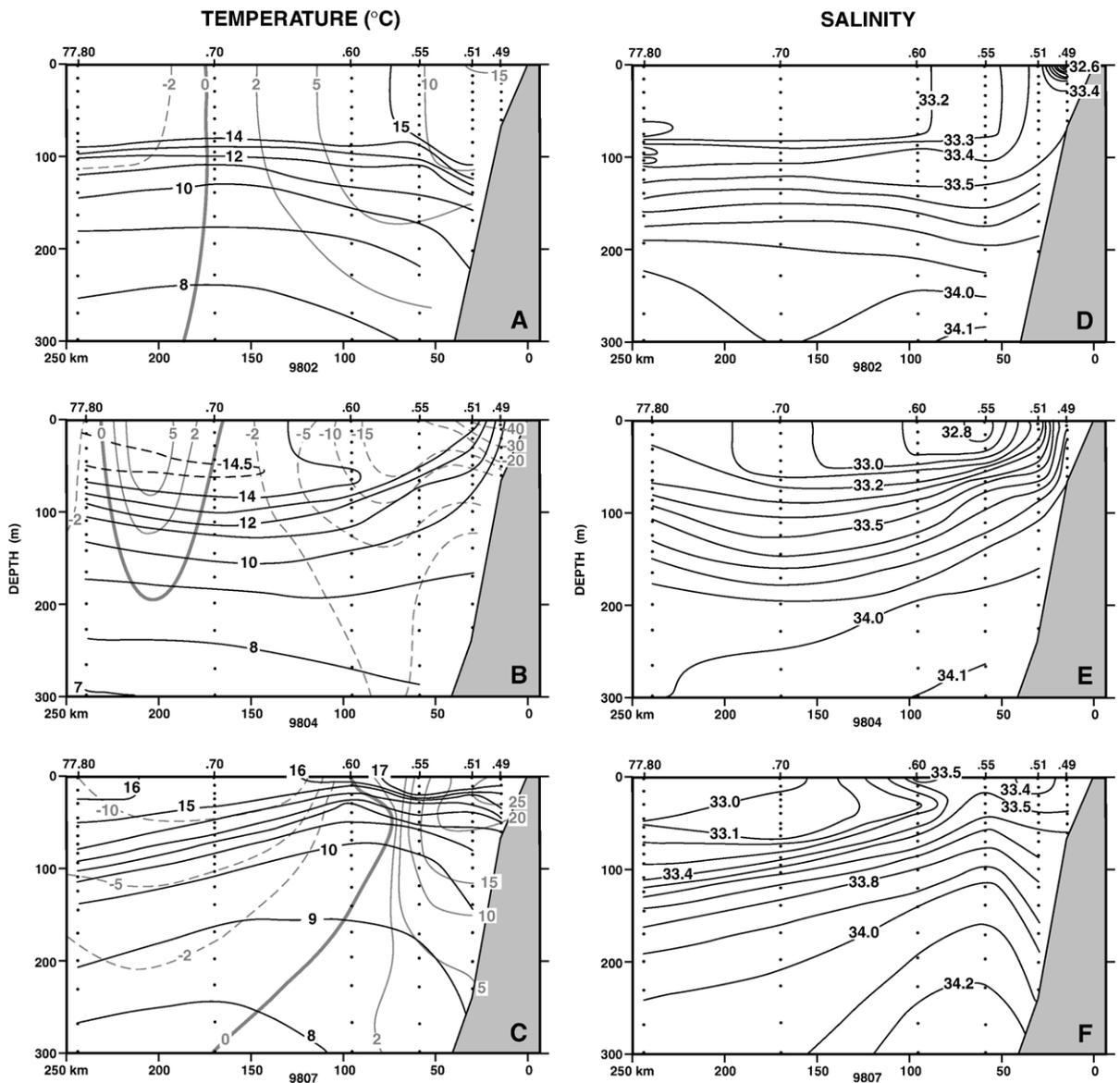
Fig. 3. Coastal upwelling in 1998 along line 77, just north of Pt. Conception; prior to upwelling (10–11 February), during upwelling (17–18 April), and following upwelling (23–24 July). (A–C) temperature section with the geostrophic current speeds (cm/s) superimposed. Solid contours indicate poleward flow, and dashed contours equatorward flow; (D–F) salinity, (G–I) nitrate, (J) chlorophyll-*a*.

edge of currents, and sink on the right, near the coast, the isotherms deepened, consistent with the geostrophic response to the poleward current. During the winter, the mixed layer nitrate was quite low (Fig. 3G). The shallow, low salinity, high nitrate water at the inshore station is presumably a result of local freshwater runoff. In winter, chlorophyll concentrations were relatively low, with highest concentrations in the mixed layer (Fig. 3J). The slight chlorophyll increase in the inshore reflected the elevated nutrients.

In spring, the near-shore currents had reversed and were flowing strongly equatorward (Fig. 3B) in response to the prevailing north winds. The near-shore isotherms and isohalines rose steeply near the coast (Fig. 3B,E), typical of wind-driven upwelling. Nutrients that had been at a depth of 150 m in the winter outcropped to the surface close to shore (Fig. 3H). Oxygen saturation (not shown) was less than 70%, also indicating the water originated from below the euphotic zone. Offshore, the nitracline remained as deep as or
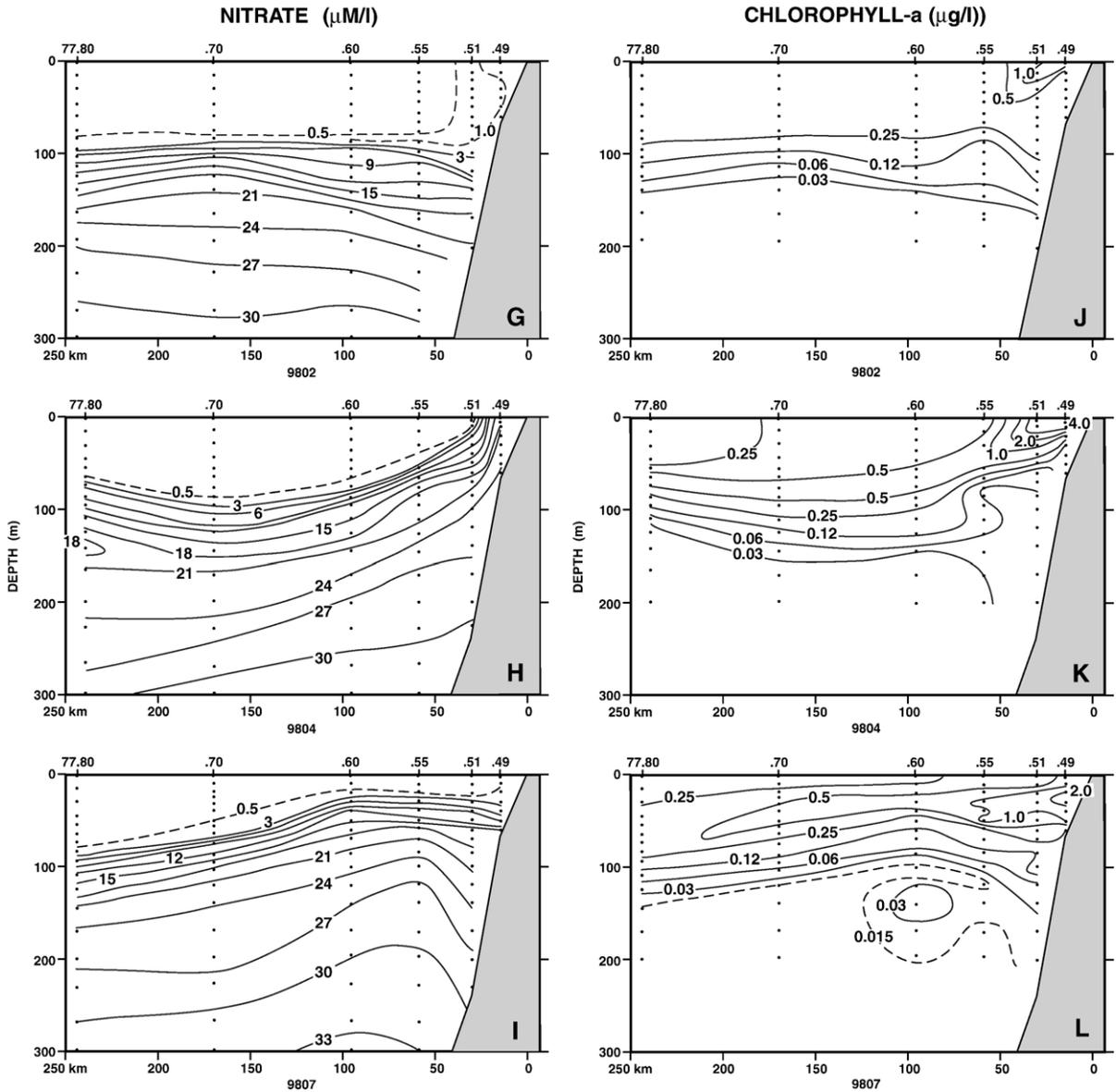
Fig. 3 (*continued*).

deeper than it had been in winter. Chlorophyll concentrations were increased at the inshore stations where the nitracline outcropped (Fig. 3K). The region strongly impacted by coastal upwelling is restricted to 50 km from the shore. At the offshore station, a subsurface chlorophyll maximum (0.82 µg/l) had developed at 85 m. Part of an offshore eddy is evident further offshore where isotherms and isohalines shoaled accordingly.

In summer, the near-shore current had reversed to poleward again (Fig. 3C), and the deeper isotherms and

isohalines again deepened towards the coast (Fig. 3C,F). The southward flow outside the islands caused isopycnals to slope upward toward the islands, while the northward flow along the coast caused the isopycnals to slope up toward the islands. As a consequence, the region between the poleward nearshore and the equatorward offshore currents showed a doming of the isohalines, typical for this region. Surface nitrate levels had returned to near-detection levels along the entire section (Fig. 3I). Surface chlorophyll had decreased, and a chlorophyll maximum layer had developed along the
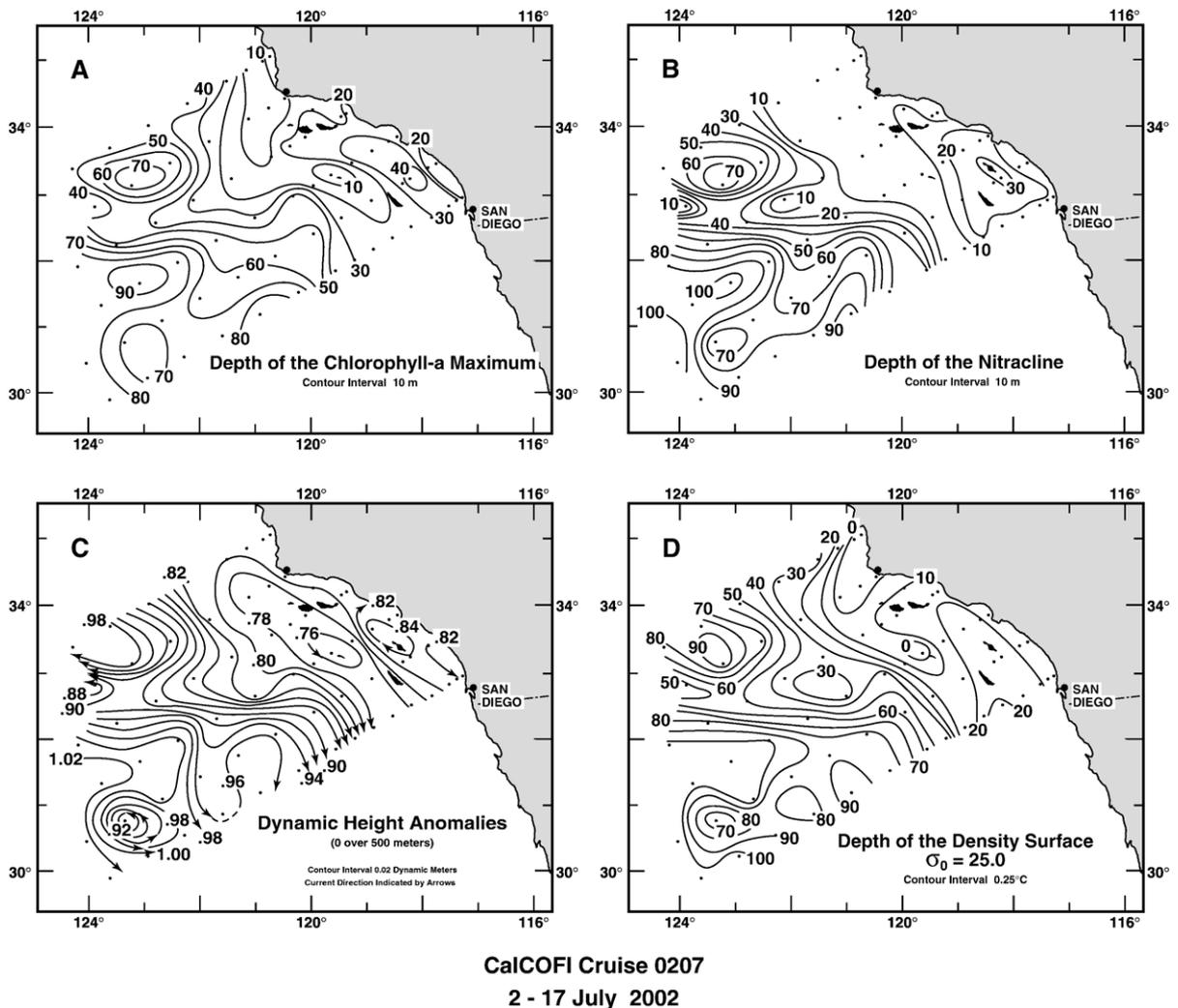
Fig. 4. CalCOFI cruise July, 2002: (A) depth of the chlorophyll maximum layer; (B) depth of the nitracline (where $NO_3 = 1.0$ μM); (C) surface currents based upon the dynamic height field, 0 over 500 m; and (D) depth of a constant density surface, where $\sigma_t = 25.0$.

entire section (Fig. 3L). At the inshore station, the layer occurred between 20 and 30 m and maximum concentration was 2.1 μg/l. Offshore the maximum remained at 85 m but the concentration had decreased by about half of the spring value.

3.3. Near-surface circulation

The depth of isopycnals, the nitracline and the chlorophyll maximum layer are influenced by circulation through geostrophic adjustment of the water column in response to the current field (Yentsch, 1974; Yentsch and Phinney, 1985; Hayward and Mantyla, 1990; Kosro et al., 1991). This is apparent from the elevation of isolines toward the center of the

offshore cyclonic eddy in the spring and from the doming of isolines between the poleward and equatorward flows in the summer (Fig. 3).

Spatial maps from two CalCOFI cruises illustrate these relationships more clearly. The surface flow is fastest where the dynamic height contours are closest together, and that is where the properties slope most strongly in depth. In July 2002 (Fig. 4), the map of dynamic height shows a typical pattern of meandering California Current flow, countercurrents and eddies (Fig. 4C). There is a current reversal along the outer edge of the Channel Islands where the inshore countercurrent encounters the southward flowing California Current. In addition there is an intense cyclonic eddy at the outer edge of line 90, an anticyclonic
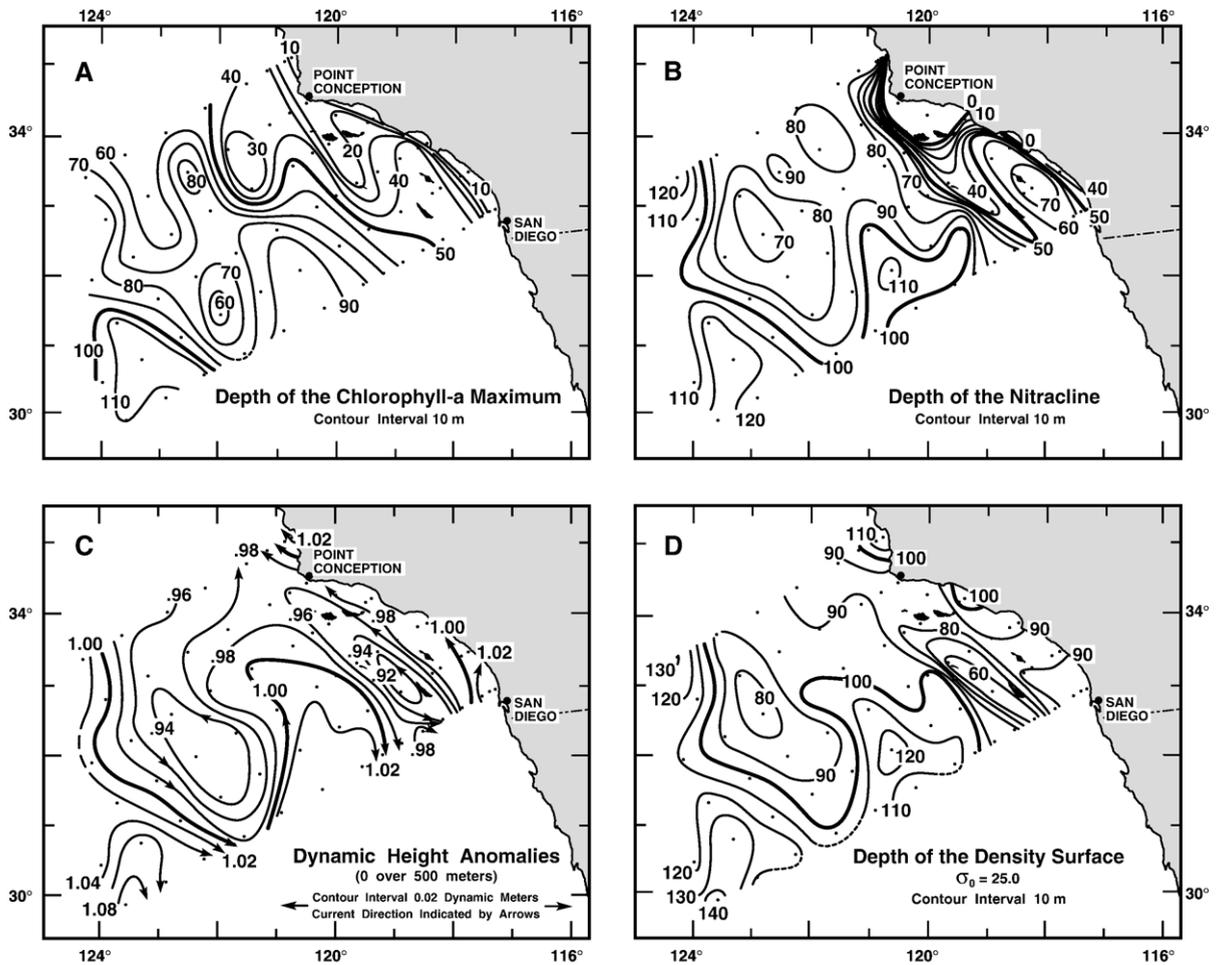
Fig. 5. CalCOFI Cruise February, 1998: A–D as in Fig. 4.

circulation at the outer edge of lines 77 and 80 and a cyclonic circulation at the end of line 80. Geostrophic adjustment causes isopycnal surfaces to reach minimum depths in a ridge along the outside of the Channel Islands (Fig. 4D). Inshore of the ridge, the cyclonic circulation within the Southern California Bight produces an elongated depression in density surfaces. The offshore cyclonic circulation features produce a doming of isopycnal surfaces while the anticyclonic feature produces a depression. Nitrate in excess of 1.0 μM reaches the surface in a broad band offshore of the Channel Islands, along the isopycnal doming (Fig. 4B). It is 20–30 m deeper within the Southern California Bight. The nitracline shoals within the offshore cyclonic circulation features and deepens within the anticyclonic circulation features. The depth of the chlorophyll

maximum layer reflects these vertical perturbations (Fig. 4A), and the maximum concentration changes as the simultaneous shoaling of light-limited phytoplankton and nutrients results in enhanced/reduced nutrient uptake and increased/decreased chlorophyll. Within the cyclonic eddy at 90.110, the nitracline and chlorophyll maximum layers shoal to 70 m from below 80 m. Chlorophyll at the maximum increases to 0.81 mg/m^3 from concentrations near 0.30 mg/m^3 on either side.

During February 1998 (Fig. 5), the circulation pattern showed two cyclonic eddies. The shoreward flow of the inshore eddy is formed by a strong nearshore countercurrent. The offshore eddy is formed by a large meander of the California Current jet. Between the two eddies is a region of anticyclonic flow. Isopycnals and the nitracline are deepest in the middle of the anticyclonic
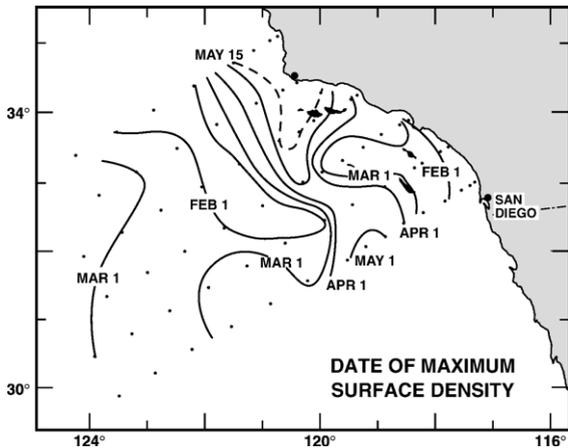
Fig. 6. Mean date of the seasonal maximum surface density at each CalCOFI station, for the period 1984–2004. The density maximum data vary from mid-January in the California Current jet, to mid-May in the upwelling area off Pt. Conception.

feature and are shallowest in the middle of cyclonic eddies. The depth of the chlorophyll maximum mirrors these domes and ridges (Fig. 5A). For instance, at

CalCOFI station 87.45, the chlorophyll maximum domes to 19 m. At this station, the maximum chlorophyll concentration increases to 0.76 mg/m^3 from 0.64 mg/m^3 at station 87.40 and 0.51 at station 87.50. Such geostrophic adjustments influence the mesoscale spatial patterns and may result in significant input of nutrients to the first trophic layer in this broad region which lacks nutrient input over most of the year.

3.4. The seasonal cycle

The annual cycle of mixing and irradiance drives a strong annual cycle of production in many oceanic ecosystems (e.g., Sverdrup, 1953; Miller et al., 1991). The amplitudes of seasonal cycles are reduced in the CalCOFI area. However, wind-driven convection may still be a significant source of nutrients because of the absence of stronger mechanisms of nutrient input. The mean timing of the maximum surface density (minimum SST) varies spatially (Lynn and Simpson, 1987). The maximum surface density may occur anywhere from 1 to 5 months after the winter solstice (Fig. 6), depending
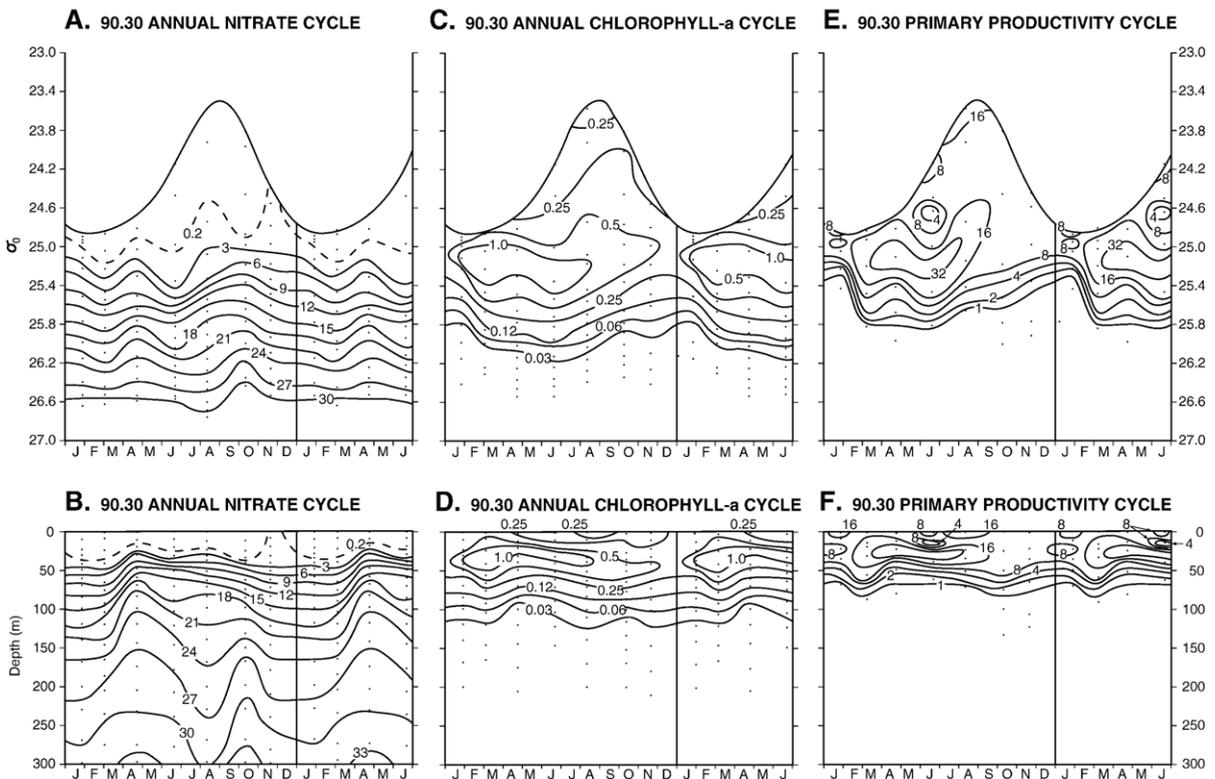

Fig. 7. Annual cycle of nitrate, chlorophyll-*a*, and primary productivity at station 90.30, based upon an arbitrary selection of occupations spread throughout the year, but from various years. Plots appear in pairs, the first with respect to density (σ_t=23.0–27.0) and the second with respect to depth (0–300 m). (A) Nitrate vs σ_t, and (B) nitrate vs depth; (C) Chlorophyll-*a* vs σ_t, and (D) chlorophyll-*a* vs depth (note the contour interval is either half or twice the adjacent contour, or unit exponents to the base 2); (E) Primary productivity vs σ_t (February and June data are from the near-by station 93.30), and (F) primary productivity vs depth.

upon the relative importance of winter convection and spring coastal upwelling in elevating deeper waters. Thus the mean maximum surface density around Pt. Conception and the inner edge of the California Current occurs from mid-April to mid-May, largely in response to the Ekman offshore transport. The offshore California Current and the nearshore southern California regions have the mean maximum surface density between mid-January and mid-February. This pattern is consistent with the different annual cycles of chlorophyll in these areas (Hayward and Venrick, 1998).

Station 90.30 was selected to illustrate the annual and interannual cycles of nutrients, chlorophyll and productivity (Fig. 7). Influence from coastal upwelling is rare in this portion of the Southern California Bight. Surface density is maximal during the winter, and surface nitrate appears when the seasonal convective overturning reaches the nitracline. This results in a small nitrate outcrop in November (Fig. 7A,B). Although wind-driven events can raise the nitracline to the surface in the northern coastal regions, over most of the CalCOFI area the seasonal near-surface low density water (the seasonal thermocline) appears to keep a cap on the denser waters below and minimize diffusive input of deeper nutrient-rich waters into the photic zone. In this area the nitrate versus temperature intercept occurs at a temperature that is close to the annual mean winter temperature minimum. Zentara and Kamykowski (1977) show nitrate vs temperature scatter plots over a wide range of latitudes, and point out that near-surface nitrate occurs at progressively cooler temperatures as latitude increases in tropical and temperate latitudes. It is likely that those temperatures represent the annual minimum mean winter surface values, and as the surface warms and a seasonal thermocline forms, nitrate becomes depleted.

Surface chlorophyll-a (Fig. 7C,D) is highest immediately after the winter maximum surface density, when the surface layers start warming and formation of the seasonal thermocline begins to stabilize the near-surface water. Surface chlorophyll is low during the summer and early fall when surface nitrate is undetectable. The subsurface chlorophyll maximum occurs near the depth of the first significant nitrate (e.g., Fig. 2A). After the late winter or early spring bloom, the layer of maximum chlorophyll gradually decreases in concentration and deepens through the year until fall and early winter.

The mean annual cycle of primary productivity (Fig. 7E–F) is similar to that of chlorophyll-a, with highest production from late winter to early summer, peaking at 1.3 gC/m^2/day in March. Minimum values of 0.4 gC/m^2/day occur in January. Production is confined to the top 75 m at this station. Although the available surface sunlight in summer is roughly twice as great as in winter, the highest production occurs prior to the summer season, at submaximal irradiance, when the maximum chlorophyll is closer to the surface.

The elevated chlorophyll-a and productivity at the surface seen in July (Fig. 7C–F) are unexplained. Typical July conditions over the CalCOFI area include warm surface water, a mixed layer shallower than 10 m, absence of measurable NO$_3$, and high surface irradiance. Over all stations, maximum productivity occurs most often near 14 m (36% of surface light; Table 1). It is shallower, occurring at near-surface light levels only 11% of the time, *except* in July when productivity peaks near the surface 26% of the time. The stations with elevated productivity in July are scattered throughout the CalCOFI area, both inshore and offshore of the California Current. On most of these July stations there is also a secondary productivity maximum below the surface near the nitracline that corresponds to the usual subsurface maximum. It is tempting to postulate a floristic change as a cause, perhaps surface blooms of nitrogen-fixing phytoplankton or cyanobacteria (e.g., Kahru and Mitchell, 2000; Wilson, 2003), but, to date, floristic analyses have not produced direct evidence for this (Venrick, 2000, 2002; Collier and Palenik, 2003).

Once the maximum winter convective overturn has occurred, and the nitracline has reached its shallowest depth, phytoplankton growth is largely set for the rest of the year, until the next year's photic zone nutrient replenishment (Nezlin et al., 2004). A logical consequence is that winters with shallower winter convection will mix less nitrate into the euphotic zone and support less production the rest of the year. Winters with deeper mixing will support higher production. We examine this hypothesis with data from station 90.35 during the period between mid-1997 to mid-1999, which includes the transition from an El Niño winter to a La Niña winter (Fig. 8). The surface waters after the La Niña winter of 1998–99 were much colder and denser than those of the El Niño winter of 1997–98, leading to deeper convection. The integrated chlorophyll-a in April 1999 exceeded 200 μg chlorophyll-a per m^2, compared to less than 50 μg chlorophyll-a per m^2 in April 1998. Increased chlorophyll production after this ENSO transition was also noted off of Baja California (Espinosa-Carreon et al., 2004) and off southern and central California (Bograd and Lynn, 2001; Chavez et al., 2002). Thus the relative severity of winter conditions may be one factor that controls the degree of nutrient availability in the photic zone (Townsend et al., 1994). In regions little influenced by coastal upwelling, such as the Southern California Bight, this nutrient source may be significant.

Table 1
Frequency of maximum productivity occurrence vs incubation light level, by month for all of the CalCOFI productivity casts since 1984

Month	n	Light level, percent of surface					
		95%	36%	17%	7%	2%	0.3%
Jan	58	9	57	17	15	2	0
Feb	62	11	37	23	27	2	0
Mar	47	4	47	25	11	13	0
Apr	51	4	53	20	14	10	0
May	44	7	46	34	9	4	0
Jun	7	(14)	(43)	(14)	(14)	(14)	(0)
Jul	109	26	49	16	8	2	0
Aug	76	9	54	16	20	1	0
Sep	54	15	46	30	4	6	0
Oct	71	14	48	23	15	0	0
Nov	67	10	57	25	8	0	0
Dec	0	–	–	–	–	–	–
AVG.%		11%	49%	22%	13%	5%	0

Total number of productivity measurements (n) made between 1984–2004 are given for each month. Frequency values for June (in parentheses) are based on a small sample size ($n=7$).

To further examine the hypothesis that winter mixing affects subsequent phytoplankton biomass, data from all stations shoreward of station 100 were examined for the relationship between the winter mean 10 m temperature and mean integrated chlorophyll-*a* the following year (Fig. 9). Cooler winters, with deeper mixing, have a tendency to lead to higher areal mean water column chlorophyll the following year. The greater number of data points at the warm end of the plot reflect the fact

that many of these cruises took place after the 1976–77 climate shift, following which El Niño events have been more common than La Niña events (McGowan et al., 2003). With only four CalCOFI cruises per year, the coldest event of the year or the timing of the subsequent growth could be missed. Thus the relationship in Fig. 9 might improve if more data were available on a finer temporal scale.

4. Conclusions

Phytoplankton biomass in the region of the California Current between Pt. Conception and the Mexican border exhibits considerable spatial and temporal heterogeneity. In this region, however, the mechanisms for nutrient input that drive patterns in many systems are only weakly expressed. In this paper, we have examined the influence of physical processes that are not necessarily unique to this region, but which become important in the relative absence of mechanisms such as coastal upwelling, horizontal advection and freshwater runoff.

The long-term CalCOFI data set includes measurements of physical and chemical parameters and chlorophyll-*a*, supplemented by estimates of primary productivity. The maximum chlorophyll in the water column is most often found near the top of the nitracline. The maximum concentration is largely dependent upon the ambient irradiance at this depth. Thus a major influence on the concentration of chlorophyll at the depth of the maximum is the proximity of the
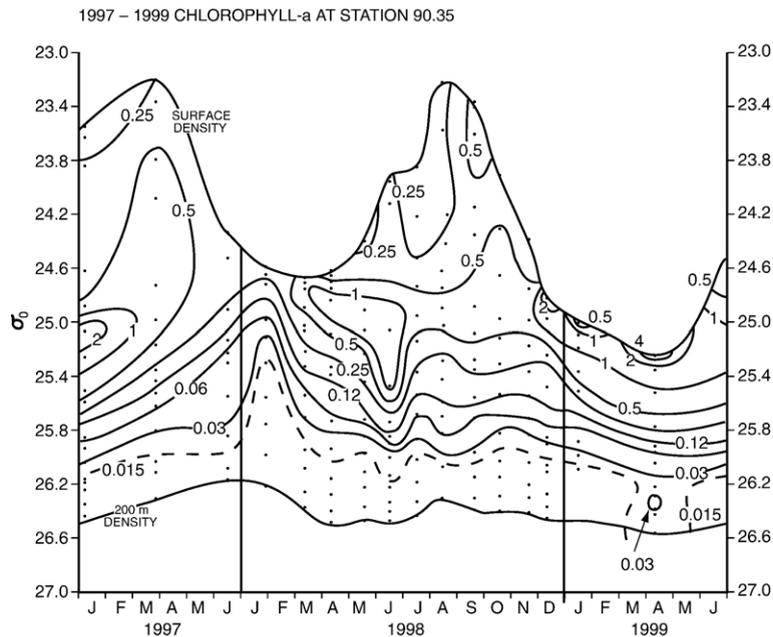

Fig. 8. Chlorophyll-*a* at station 90.35 from mid-1997 to mid-1999, plotted on a σ_t field, as in Fig. 7C.
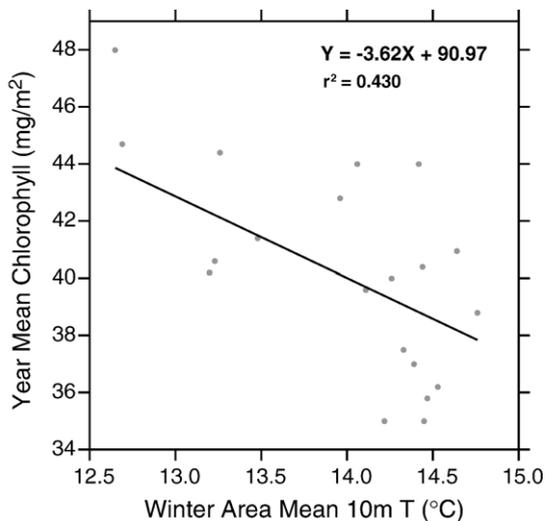
Fig. 9. Mean integrated chlorophyll-*a* (mg/m^2) versus the previous winter mean 10 m temperature, with linear fit. The chlorophyll is the mean of the four seasons following the winter lowest cruise temperature mean. Data are averaged over all stations inshore of station 100, for the period 1984–2004.

nitracline to the surface. Coastal upwelling is one way of elevating nutrients into the euphotic zone. However, in a region such as the Southern California Bight that is nutrient limited much of the year (Hayward and Venrick, 1998), current strength and orientation and the consequent geostrophic adjustment of isopycnal surfaces may also be important for providing nutrients to the photic zone. Thus, elevated near-surface chlorophyll values are often found adjacent to the strong flow, where the nitracline shoaling results from cyclonic circulation.

We emphasize that the effect of isopycnal shoaling on phytoplankton is not restricted to specific features such as eddies or frontal regions, but is a general feature of moving environments, where near-surface nutrients are depleted. Clearly, this mechanism alters the horizontal pattern of chlorophyll concentration in the CalCOFI area. To the extent that this response appears to be growth mediated, it must also represent introduction of new nutrients into the euphotic layer and new production. In a region such as the Southern California Bight that is nutrient limited much of the year (Hayward and Venrick, 1998), this mechanism of nutrient injection may be significant.

Winter convection appears to be a second mechanism for nutrient injection in this region. Away from the coastal upwelling near Pt. Conception, the deepest annual convective overturning occurs when the surface waters are coldest and densest. This mixes nutrients into the near-surface layer from deeper waters. The phytoplankton bloom begins immediately afterward, as the surface water begins to warm up and the seasonal thermocline develops. Nitrate is quickly stripped from the surface layer by the phytoplankton, and the surface layer remains isolated from the nitrate by the thermocline until the following winter convective overturning and replenishment. The depth and duration of winter convective overturning varies from year to year and, through the amount of nutrients mixed upward, controls the amount of chlorophyll produced the following year. Cooler than normal winters result in higher surface densities that can mix deeper into the nitracline. Greater winter surface nutrient enrichment results in more phytoplankton growth over the entire region that lasts for the rest of the year.

Acknowledgments

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