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# Vertical motion of the thermocline, nitracline and chlorophyll maximum layers in relation to currents on the Southern California Shelf

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## ABSTRACT

A continuous four-day time series of nitrate concentration, temperature, chlorophyll fluorescence, and currents, sampled at fixed depths, revealed that distributions of temperature and nitrate could be accounted for by vertical motions in the water column associated with the semidiurnal internal tide and internal waves. A probable mixing event was observed: the transport of nitrate into the surface-layer associated with shear instabilities generated by internal waves. On temporal scales of less than a few hours, the variation of chlorophyll fluorescence could also be explained by vertical advection. However, on longer scales, swimming behavior of the phytoplankton assemblage (dominated by *Ceratium spp.*), along with vertical motions in the water column, appears to account for the vertical distribution of chlorophyll. These results indicate that the nitracline maintains a stable relationship with the density structure of the water column on a scale of days, whereas the subsurface chlorophyll maximum can change significantly over several hours.

## 1. Introduction

Primary production in the Southern California Bight is largely regulated by the input of nutrients to the euphotic zone (Eppley *et al.*, 1979). The depth of the sharp vertical gradient of nitrate concentration (nitracline) is indicative of nutrient supply; it is determined by the balance of vertical mixing of nitrate from below and the uptake of nitrate by phytoplankton in the euphotic zone. This balance is manifest in the negative correlation between depth of the nitracline and primary production (cf. Herbland and Voituriez, 1979; Eppley *et al.*, 1979): both primary production and standing stocks of phytoplankton are higher on the Southern California Shelf (<10 km width) than 20-100 km offshore, just as the nitracline is shoaler nearshore (Eppley *et al.*, 1978). Nutrient regeneration by the benthos may augment the input

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of nutrients to the euphotic zone in shallow waters (Hartwig, 1976; Rowe *et al.*, 1975), but enhancement of vertical mixing near the coast should also be considered (Riley, 1967; Eppley *et al.*, 1979).

The nitracline is more than an expression of productivity in the water column: it is an ecologically important feature in vertical profiles, dividing nutrient-limited from nutrient-saturated strata (Dugdale, 1967) and perhaps representing a zone of optimal potential for growth of phytoplankton (Jamart *et al.*, 1977). As might be expected if growth rates were highest near the nitracline, subsurface maxima of chlorophyll *a* (chlorophyll maximum layers) are generally associated with the nitrate gradient and are prominent features of vertical profiles in stratified waters (reviewed in Cullen, 1982). However, the coincidence of chlorophyll maximum layers and the nitracline may be explained by any of several mechanisms (Richerson *et al.*, 1978; Cullen, 1982), each of which has different ecological implications.

It has been demonstrated that the movements of water on the Southern California Shelf can have a large effect on the distributions of phytoplankton and nutrients at the frequencies of internal waves (Armstrong and LaFond, 1968). However, records of more than several hours duration were not analyzed and thus the response of biological and chemical features to forcing at tidal frequencies has not been measured. Given that the influence of internal waves on the spatial distributions and on the primary production of phytoplankton has been examined theoretically over several temporal scales (Kamykowski, 1974), it is important to determine, with data from the field, the influence of physical motions on biological processes over a wide band of frequencies. In doing so, however, it is important to remember that the influence of physical transport processes on chemical or biological features can be direct or biologically-mediated (cf. Denman and Platt, 1975; Platt, 1978), depending on scale: on relatively short temporal or spatial scales, nitrate and chlorophyll can behave as passive contaminants whereas, over longer scales the increased importance of phytoplankton growth and nutrient uptake leads to variation of biological and chemical properties somewhat independent of the physical variance spectrum. The boundary between these two subranges of temporal or spatial scale is the critical scale, analogous to that defined by Kierstead and Slobodkin (Kierstead and Slobodkin, 1953; Platt, 1978). Although considerable progress has been made relating the distributions of phytoplankton to horizontal turbulence (e.g. Gower *et al.*, 1980 and references therein), vertical structure *per se* has been less often characterized as a function of scale (Denman, 1977), and to our knowledge, data from the field have not been analyzed to determine critical scales for the vertical distribution of chlorophyll and nutrients.

We will consider here the coastal environment on the Southern California Shelf, where the bottom slope is rather steep, 0.017 (dimensionless) compared to the broad, gently sloping shelf on the U.S. east coast (Winant and Bratkovich, 1981), resulting in relatively energetic motions of cross-shore currents at tidal frequencies.

The stratification of the shelf waters, particularly in summer, contributes to the baroclinic nature of these motions. The cross-shelf currents at the surface are 180° out of phase with those at the bottom, resulting in velocity shear at the thermocline, a condition conducive to mixing of nutrients from the bottom water into the nutrient-depleted surface layer (cf. Winant and Olson, 1976).

We have obtained and studied continuous and simultaneous measurements of currents, temperature, nitrate concentration and chlorophyll fluorescence. Our first purpose was to examine the hypothesis that over the time scale of the investigation, chlorophyll (hence phytoplankton) and nitrate are passively transported along with water motion on the Southern California Shelf. An alternative hypothesis was that there existed within the temporal scale of our study a critical scale beyond which biological processes dominated physical processes in determining the variation of nitrate or chlorophyll. The second purpose of our study was to search for episodic injection of nitrate into the nitrate-depleted surface layer. It seemed quite possible that shear instabilities associated, for example, with internal waves (cf. Woods and Wiley, 1977; McGowan and Hayward, 1978; Haury *et al.*, 1979) might be revealed in the record of nitrate. The occurrence of such injection of nitrate into the surface layer nearshore, if demonstrated, could help explain more rigorously a physical-biological coupling of relatively long scale: the gradients of phytoplankton stocks and primary production off the Southern California Coast (Eppley *et al.*, 1978).

## 2. Methods

The observations reported here were made on the narrow Southern California Shelf at a station in 30 m of water (Fig. 1). The edge of the shelf, near the 60 m isobath, is located approximately 4 km from the coast. Offshore, the Gulf of Santa Catalina is characterized by depths of about 1000 m. The slope, which provides the transition between the Gulf and the shelf, has a gradient of about 0.1.

*a. Current meters.* Three instrumented moorings were deployed on a cross-shelf transect located near the city of Del Mar, California. These were in depths of 60 m, 30 m, and 15 m (Winant and Bratkovich, 1981). Only data from the 30 m mooring are reported here: in 30 m depth, instruments were located at 3 m, 12 m, 19 m, and 27 m beneath the surface. The current meter array was deployed during a 45-day period, between 27 July and 11 September, 1978.

*b. Continuous measurements of nitrate concentration, temperature, and chlorophyll fluorescence.* Hoses were attached to a weighted line suspended from the R/V *E.B. Scripps* at 6 m and 11 m depth in a 30 m water column about 100 m south of the 30 m current meter array. Peristaltic pumps (Little Giant GH-300) on deck provided water from each depth to a Turner Designs model 10-005 fluorometer and to an autoanalyzer for continuous nitrate measurement (actually nitrate + nitrite;

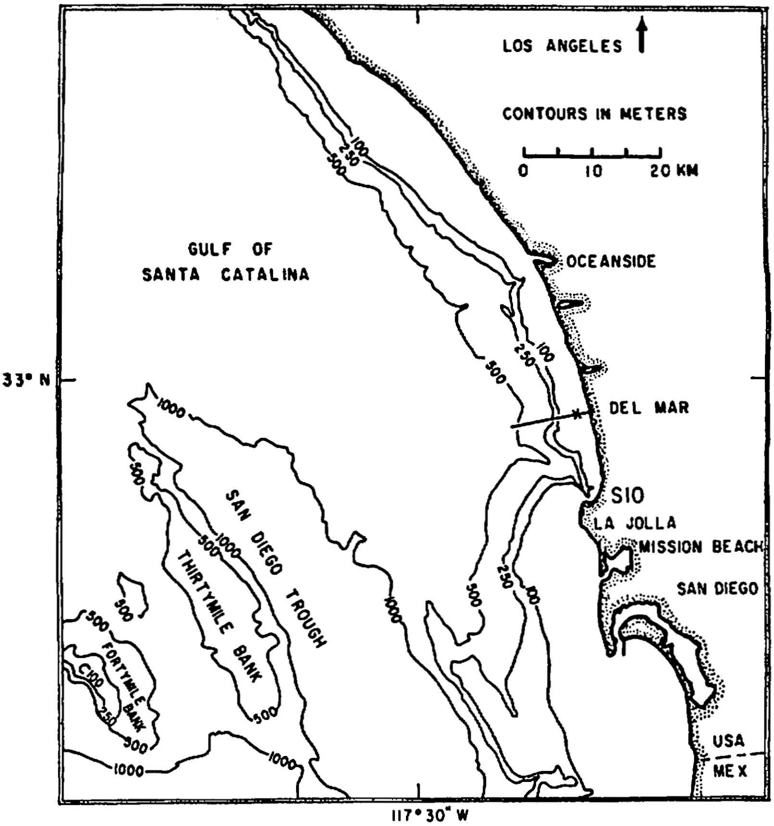


Figure 1. Bathymetry of the study site. The station was at 30 m depth on the line drawn offshore of Del Mar, California.

Strickland and Parsons, 1972; Anderson and Okubo, 1982). A thermistor recorded temperature at 11 m. All three signals were recorded for 4 days, 11-14 August, 1978, on cassette tapes using a Hewlett-Packard system 45 and an interface designed and constructed by C. R. Booth. At intervals the fluorometers and autoanalyzers were calibrated: distilled water served as the blank for the instruments, standard nitrate solutions were used for the autoanalyzers, and calibration of the fluorometers by fluorometric measurement of extracted chlorophyll *a* (Strickland and Parsons, 1972) were performed, usually in duplicate. The flow rate of water through the system ($l \cdot s^{-1}$) was measured and the lag time (s) was determined simultaneously by dye tracer. The product of the two measurements is the volume of the system (l). Lag time was determined often during the experiment by dividing the volume of the system by the measured flow rate.

The sampling depths of 6 m and 11 m were chosen from historical data (12 previous cruises) such that the upper intake would be in the nitrate-depleted layer and the lower intake would be in the upper portion of the nitracline. We expected measurable nitrate at 6 m only at intervals and as a result of mixing events.

*c. Vertical profiles of chlorophyll fluorescence and temperature.* Every three hours over the four days, chlorophyll fluorescence and temperature were recorded as a function of depth using a configuration of pump, hose, fluorometer, and thermistor similar to that for continuous measurement, except that data were recorded on strip charts. The final three profiles were made using a Seamartech® submersible fluorometer fitted with a cowl to exclude excess ambient light. Our purpose was to establish the depth and shape of the subsurface chlorophyll maximum and its configuration relative to the vertical distribution of temperature. Samples for identification of phytoplankton species were also taken in these profiles, at 1 m depth and at the depth of maximum chlorophyll fluorescence. A full analysis of the species data will be reported later.

*d. Data processing.* Temperature, nitrate and fluorescence were recorded every 30 seconds over the four day period. The nitrate and fluorescence data were corrected for their respective lag times. The first estimates of lag times from the flow rate calculations were adjusted when necessary by checking for hysteresis in the plots of nitrate and fluorescence vs temperature during the passage of internal waves.

Some gaps in the data resulted when the fluorometer or the autoanalyzer was taken off-line for calibration. We were able to estimate the missing values by studying the relationships to temperature over short time period before and after the gap occurred.

Long- and cross-shore currents and temperature from the current meter string were recorded every 2 minutes. Temperature, nitrate and fluorescence series were block averaged to 2 minute intervals. The two sets of data were synchronized by adjusting for maximum coherence between the temperature records.

Spectral analyses were performed using an FFT routine on the Interdata 832. Time series were linearly detrended and cosine tapered. Power spectra have been band averaged for the plotting.

## 3. Results

*a. General features.* A vertical profile of temperature, chlorophyll, salinity, and nitrate concentration (Fig. 2) is a general representation of the conditions that prevailed during this study. The measurements were made on 18 August 1978, 4 days after the time series was completed; it is a typical summer profile. The general features include: (1) a montonic decrease of temperature over the water column; (2) essentially no nitrate in the surface waters, a sharp nitracline in the euphotic zone; and (3) a maximum in chlorophyll at mid-depth in the euphotic zone near the nitracline. Mean values at the chlorophyll maximum for the many profiles examined by

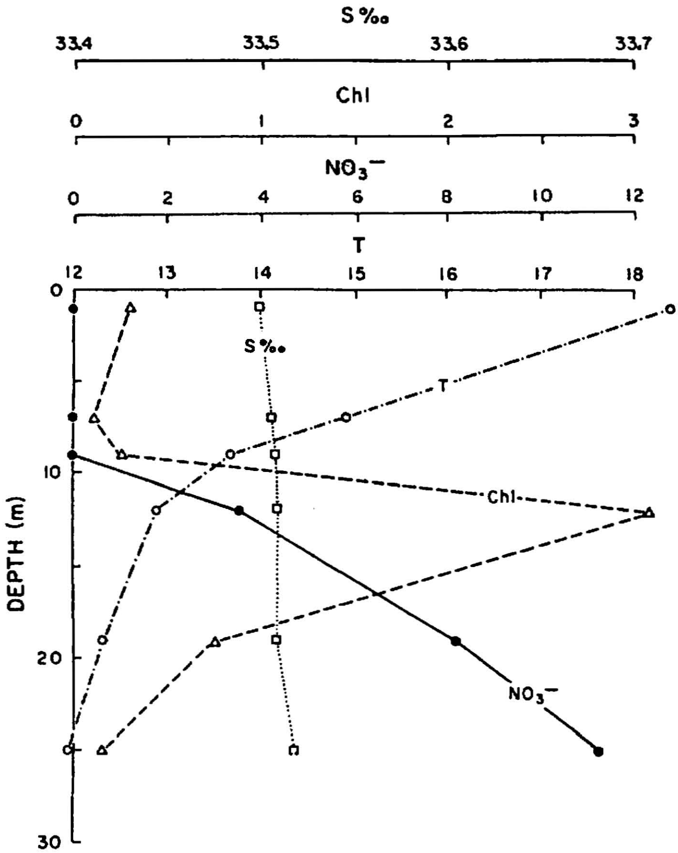


Figure 2. A typical vertical profile from the Southern California Bight, 3 km offshore of the study site, 18 August, 1978: open circles, temperature; triangles, chlorophyll; filled circles, nitrate; squares, salinity. The depth of 1% surface irradiance was 25 m.

Cullen and Eppley (1981) were: temperature 13.3°C, ambient light 6% of the surface values, growth rate 0.53 doublings of phytoplankton carbon per day.

*b. Currents and temperature.* Although we considered only a four days' record in this report, the variability in the temperature and current velocity fields on the shelf has been characterized for scales as long as months (Winant and Bratkovich, 1981). It is convenient to separate the variability of currents into three frequency bands: one associated with atmospheric motions with periods greater than a day, the tidal frequency (including all motion in the periods between a day and a few hours) and a frequency band associated with internal waves covering periods of a few hours or less. In the course of the observations described here, most of the variability is contained in the tidal and internal wave bands. The tidal motion has been described previously (Winant and Olson, 1976): longshore currents are barotropic, while on-

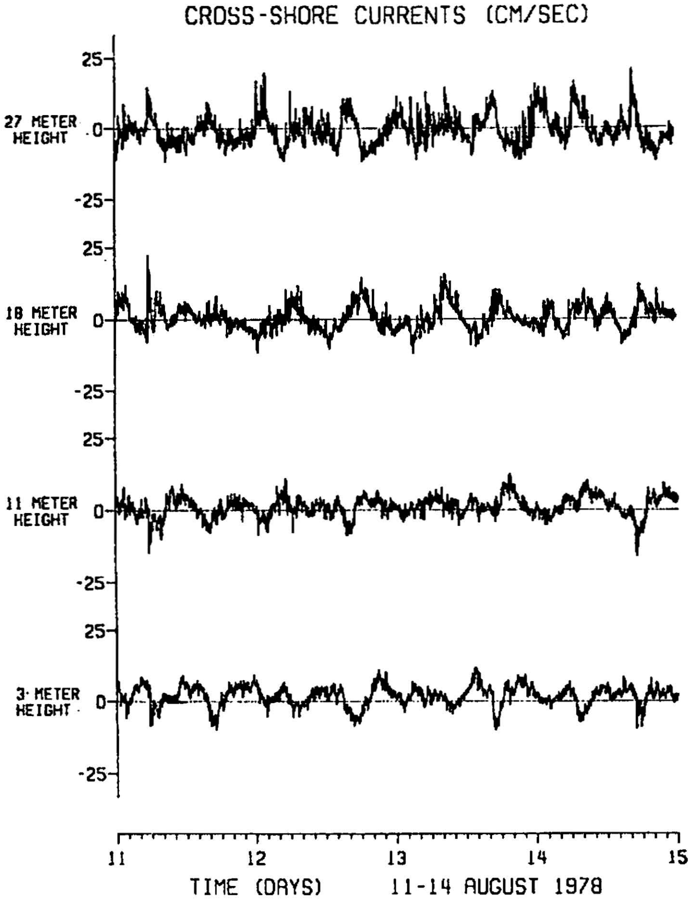


**Figure 3.** Time series of cross-shore current velocity, 11-14 August, 1978. Position of the current meter is designated by height above bottom. Assume a thirty-meter water column. Positive values indicate flow on shore.

shore currents, related to internal tides, are vertically sheared with a phase-shift of 180° across the water column. At internal wave frequencies, onshore currents are more energetic than longshore currents and retain the baroclinic phase relationships of the tidal band currents (Fig. 3). The measurements reported here are representative of the summer; variations in the current and temperature structure in other seasons are discussed by Winant and Bratkovich (1981).

Temperature increases monotonically from the bottom to the surface, and the gradient is more or less uniform. If we assume that the temperature field in the horizontal plane is homogeneous, temperature fluctuations observed at a given point can be directly related to vertical velocities. These in turn, because of the physical constraints imposed by the neighboring coast, may be directly related to the cross-

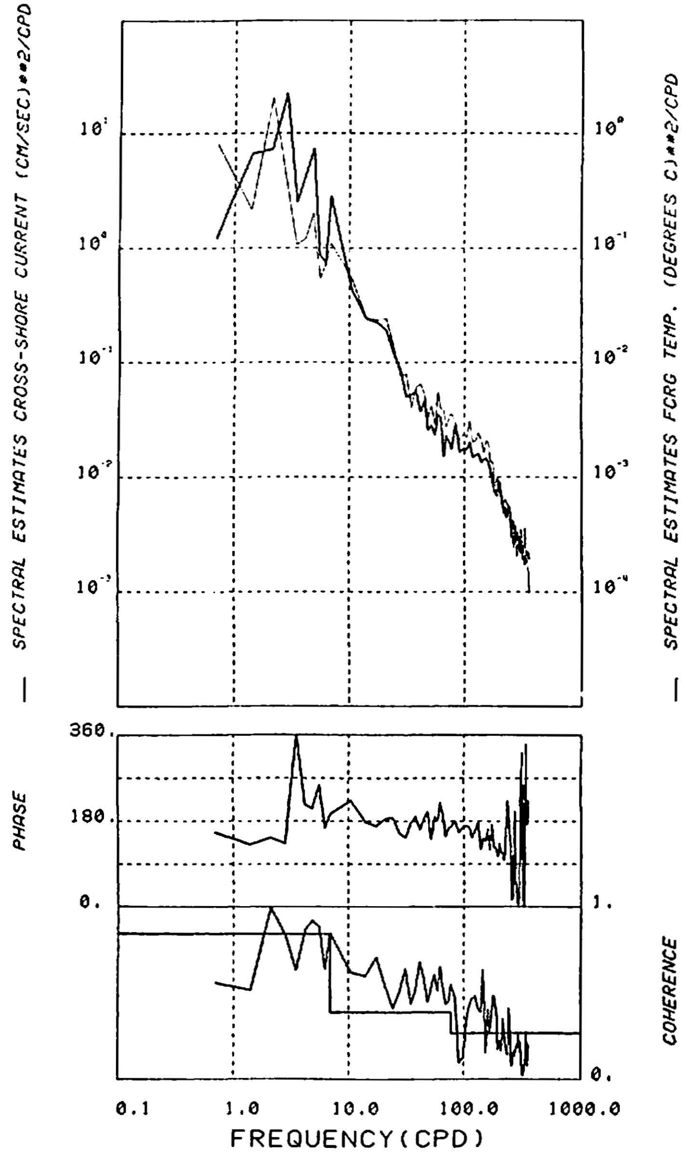
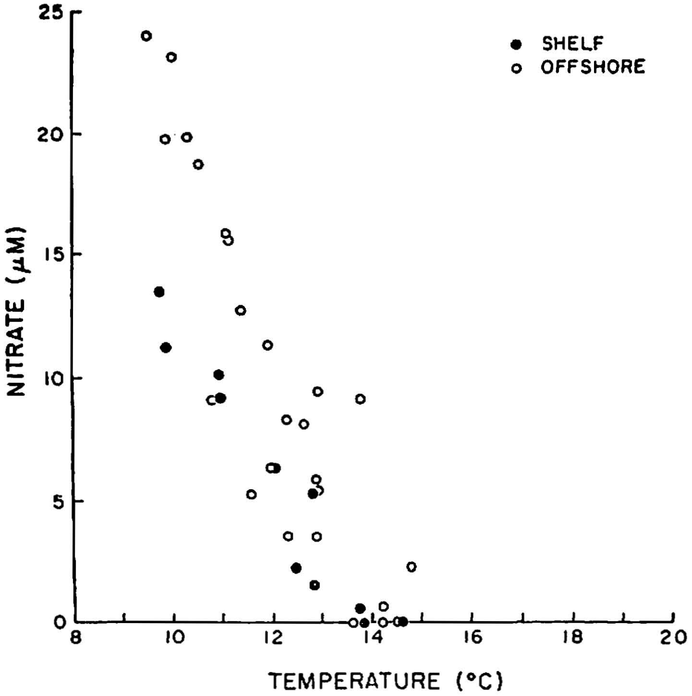
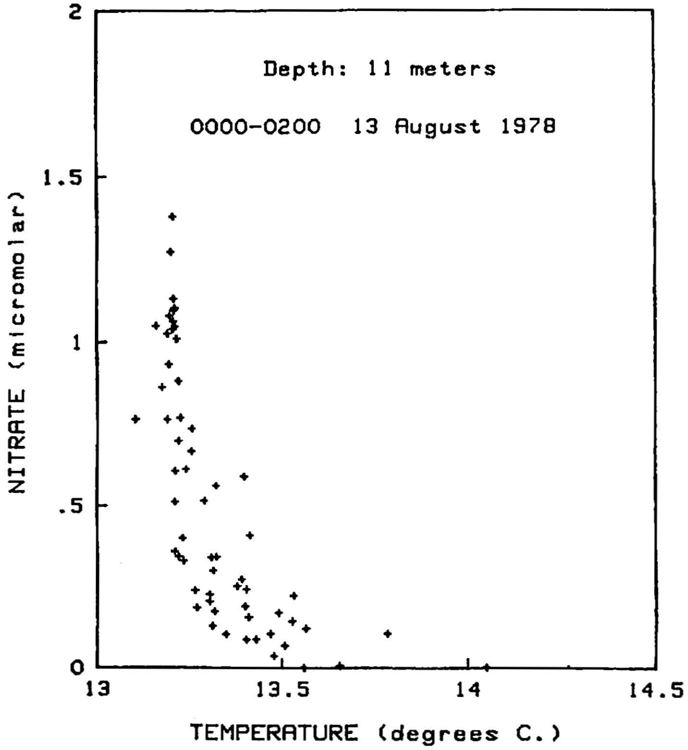


Figure 4. Spectral analysis of temperature and cross-shore current: Heavy line, current; light line, temperature.

shelf velocities, and if such is the case, one is led to expect a high degree of correlation between cross-shelf velocities and temperature. A spectral comparison (Fig. 4)

Figure 5. The relationship between nitrate concentration and temperature. (a) Measurements from bottle casts in the Southern California Bight, 18 to 23 August, 1978: filled circles, stations on the shelf (depth < 100 m); open circles, stations offshore. Values above 15° were zero and were not graphed. (b) Measurements from the time series, 0000 h to 0200 h on 13 August, 1978.


● SHELF
○ OFFSHORE
NITRATE (μM)
0
5
10
15
20
25
8
10
12
14
16
18
20
TEMPERATURE (°C)


Depth: 11 meters
0000-0200 13 August 1978
NITRATE (micromolar)
0
.5
1
1.5
2
13
13.5
14
14.5
TEMPERATURE (degrees C.)

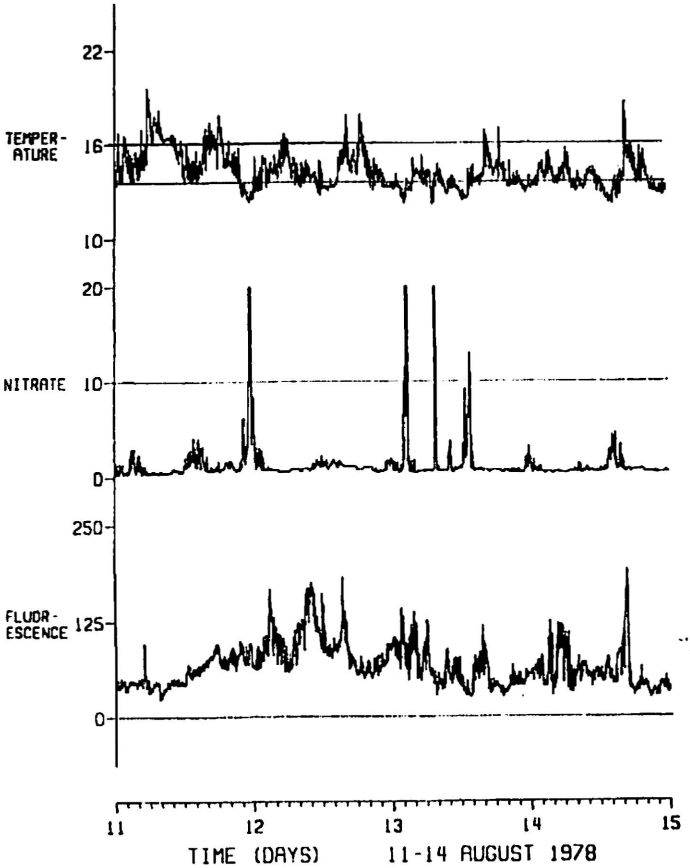


Figure 6. Time series of temperature, nitrate concentration, and fluorescence at 11 m depth 11-14 August, 1978. The line at 13.5° is drawn to illustrate that nitrate concentration rises above the background level when temperature dips below 13.5°.

confirms this inference and indicates that temperature can be considered as a conservative property of the physical environment when used for comparisons with nitrate and chlorophyll. Furthermore, a favorable comparison between estimates of the buoyancy frequency based on the mean temperature gradient and the buoyancy frequency cutoff observed in the spectra of temperature and horizontal currents also indicates that temperature adequately represents the density field (Winant and Bratkovich, 1981).

*c. The distribution of nitrate.* The relationship between nitrate and temperature in the Southern California Bight during August, 1978 was typical. Nitrate was absent when temperature exceeded 15°C (Fig. 5). The plots of nitrate vs temperature for bottle cast profiles from the Southern California Bight (Fig. 5a) are consistent with those obtained from the continuous measurements taken during this study (Fig. 5b);

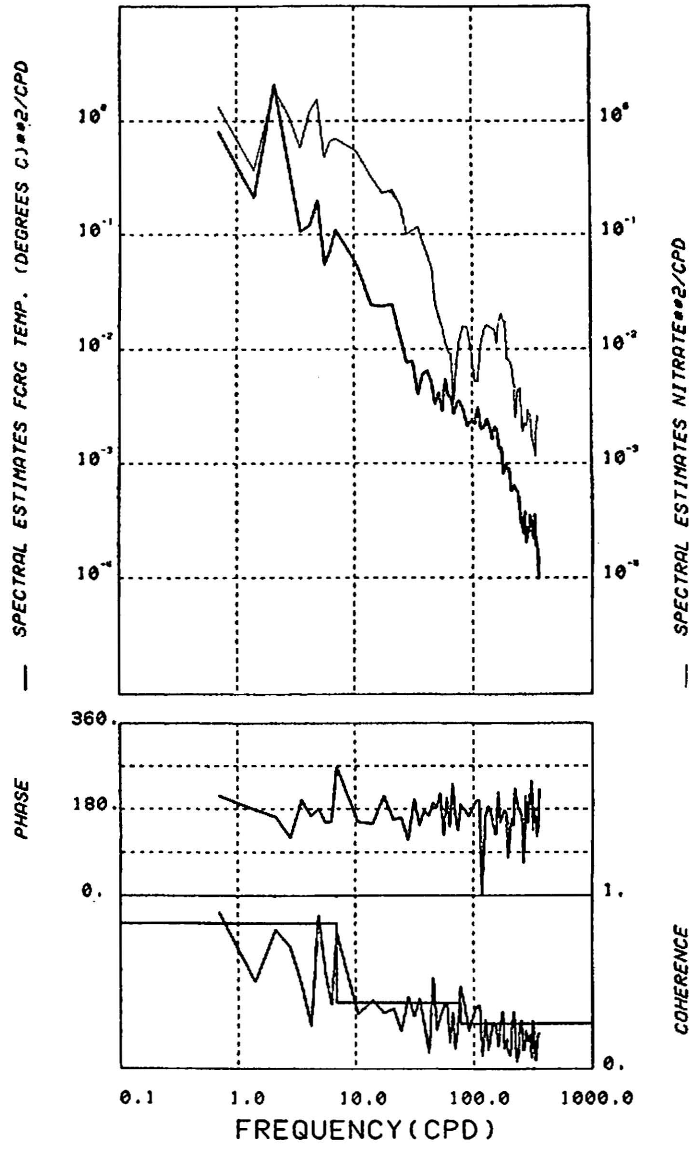


Figure 7. Spectral analysis of nitrate concentration and temperature at 11 m: Heavy line, temperature; light line, nitrate.

all are similar to those produced from historical data (Strickland, 1970; Zentara and Kamykowski, 1977). Note that the relationship between nitrate and temperature in Figure 5b is quite precise: similar plots were obtained for several periods over the course of the study.

For much of the four day record, the concentration of nitrate at 11 m was near

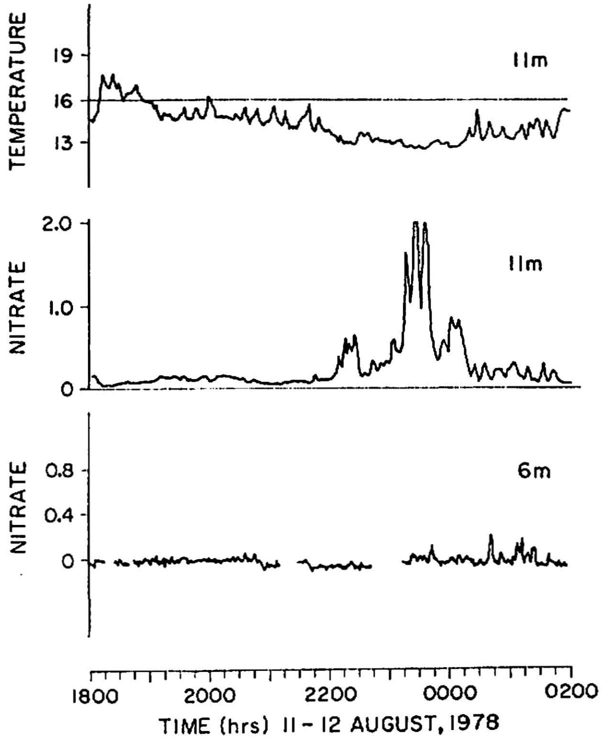


Figure 8. Time series of temperature and nitrate concentration at 11 m, and nitrate concentration at 6 m 2200 h, 11 August-0200 h, 12 August, 1978.

zero (Fig. 6) because the nitracline lay below the intake of the hose. Shoaling of the nitracline is evidenced by sharp increases of nitrate that were associated with minima of temperature, the correspondence expected from the typical profile in Figure 2.

The power spectrum of nitrate variation over time at 11 m shows peaks at frequencies corresponding to the semi-diurnal internal tide and its harmonics as well as to internal wave frequencies (Fig. 7). Temperature at 11 m also shows these features, suggesting that nitrate did not show modes of variation independent of temperature over the time scales of minutes to a day (cf. Denman and Platt, 1975).

Covariation of two simultaneously-measured variables as a function of scale can be examined explicitly with cross-spectral analysis (Platt and Denman, 1975; Jenkins and Watts, 1968). The output of the analysis is a plot of coherence$^2$ vs frequency and the associated phase angle (the lag between the peaks of periodic covariation, expressed in degrees). The technique is appropriate for variables that are related by a linear function, and it is fairly accurate even when random noise is added to the data. However, when cross-spectral analysis is applied to variables that show monotonic but nonlinear relationships, sensitivity is lost. When two vari-

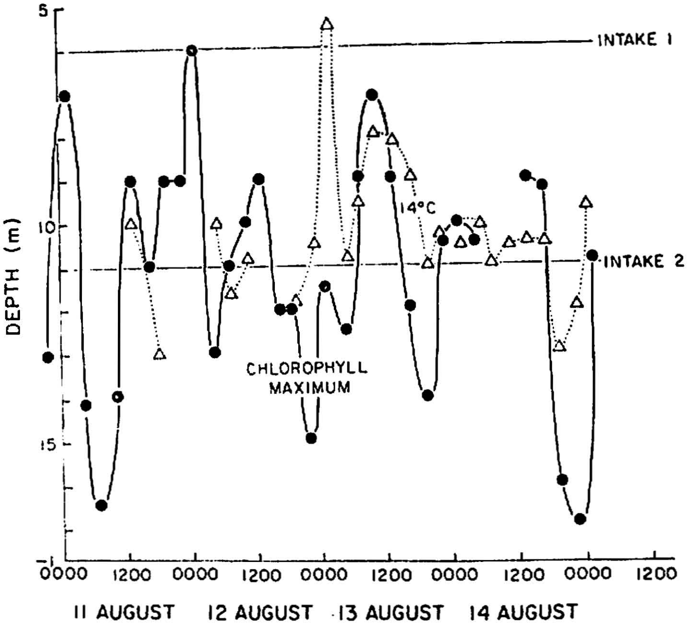


**Figure 9.** Position of the fluorescence maximum (filled circles), and 14°C isotherm (triangles) determined from vertical profiles, 11-14 August, 1978. When two maxima were found, the depth of the upper peak was recorded.

ables are related by a nonmonotonic function, even exact common variation can be invisible to cross-spectral analysis (Star and Cullen, 1981). Thus, given the nonlinear relationship between nitrate and temperature at 11 m (Fig. 5b), cross-spectral analysis (Fig. 7) suggested what was subjectively obvious from our examination of nitrate-temperature plots similar to Figure 5b: nitrate was a function of temperature at all frequencies. The negative covariation of nitrate and temperature was reflected in the 180° phase shift in Figure 7.

The record of nitrate concentration at 6 m depth showed only one example of nitrate concentration above the blank value. It occurred between about 2300 h and 0200 h on the night of 11-12 August. The beginning of the event at 6 m was coincident with temperature minima and nitrate spikes at 11 m depth (Fig. 8). However, elevated levels of nitrate were detected at 6 m until about 0200 h, about 1.5 h after nitrate concentration at 11 m had decreased sharply. The chlorophyll maximum shoaled to its minimum depth in the four-day record at about this time (Fig. 9). It is not immediately clear whether the nitrate burst was due only to the shoaling of the nitracline to nearly 6 m depth or whether turbulent mixing also played a role. The current meter records were used to examine this question further; i.e., to calculate shear between the upper two current meters (about 3 and 11 m below the surface) and from this to approximate a Richardson's number. At the time when

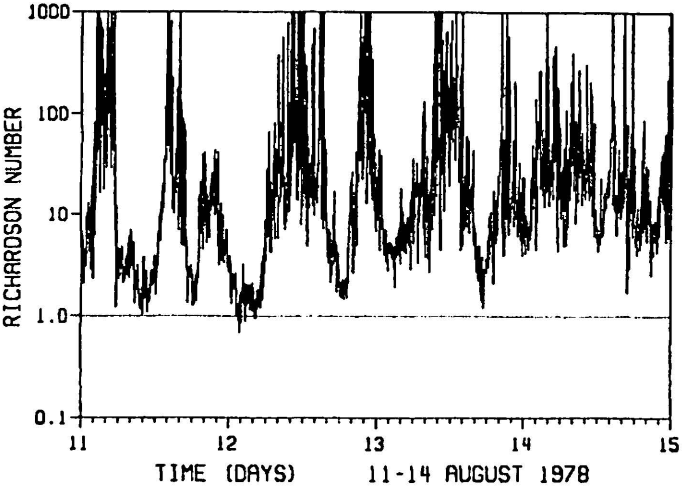


Figure 10. Time series of the Richardson number calculated for the depth interval between 3 and 12 m, 11-14 August, 1978.

nitrate was measured at 6 m depth, the Richardson's number (Fig. 10) was the minimum for the four-day record, indicating the maximum likelihood of vertical mixing (Turner, 1973).

*d. The distribution of chlorophyll.* A plot of depth of the chlorophyll maximum and depth of the 14° isotherm (Fig. 9) shows that to some extent, vertical motions of the chlorophyll maximum were associated with movements of the isotherms, hence vertical motions of the water and thus cross-shelf currents. However, the peak of chlorophyll fluorescence also moved independently from the temperature structure: maximum distances between the chlorophyll maximum and the 14° isotherm were found at night, when the chlorophyll peak was as much as 5 m deeper than the 14° isotherm (cf. Dandonneau, 1977).

If the variation of fluorescence was determined primarily by the vertical advection of a typical profile (Fig. 2) past the sampling port with the passage of internal waves, one would expect to see maxima of fluorescence immediately preceding and following nitrate spikes and temperature minima. Furthermore, the power spectrum of fluorescence should show the same general features as that of temperature, except that the fluctuations of fluorescence might produce peaks in the power spectrum at twice the frequency of peaks in the temperature spectrum because the unimodal fluorescence distribution would exhibit two maxima per large-amplitude vertical cycle while the monotonic temperature distribution would exhibit only one.

Our data are roughly consistent with these expectations. The time series of fluorescence (Fig. 6) seems to reflect in large part the vertical excursions of the chlorophyll maximum in concert with the thermocline and nitracline, but the record

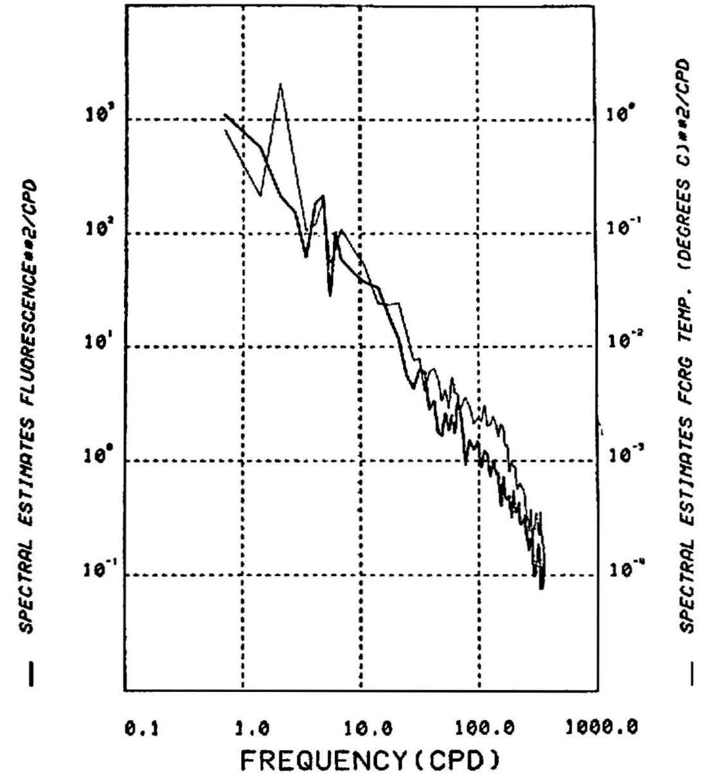


Figure 11. Spectral analysis of fluorescence and temperature at 11 m: Heavy line, fluorescence; light line, temperature.

is very difficult to interpret rigorously. The power spectrum of fluorescence at 11 m (Fig. 11) shows maxima at the frequencies of the harmonics of the semi-diurnal internal tide, as well as a "shoulder" of relatively high variance at internal wave frequencies, matching well with the power spectrum of temperature when the expected frequency shift is taken into consideration. The coherence spectrum for fluorescence and temperature is not reported because the analysis is not designed to deal with nonmonotonic covariation (Star and Cullen, 1981).

A better understanding of the nature of the variability in fluorescence came from examination of temperature-fluorescence plots. Short-term stability of chlorophyll distributions in relation to the density field was indicated by the good correspondence between fluorescence and temperature for periods of a few hours or less (Fig. 12). However, many of these short-term relationships differed from each other. These relationships differed for two reasons: (1) the hose intake, at fixed depth, sampled different segments of the chlorophyll profile; (2) the chlorophyll profile changed independently from the temperature profile (Fig. 9). When data for periods longer than several hours are plotted, an amorphous cloud of points results, reflecting a

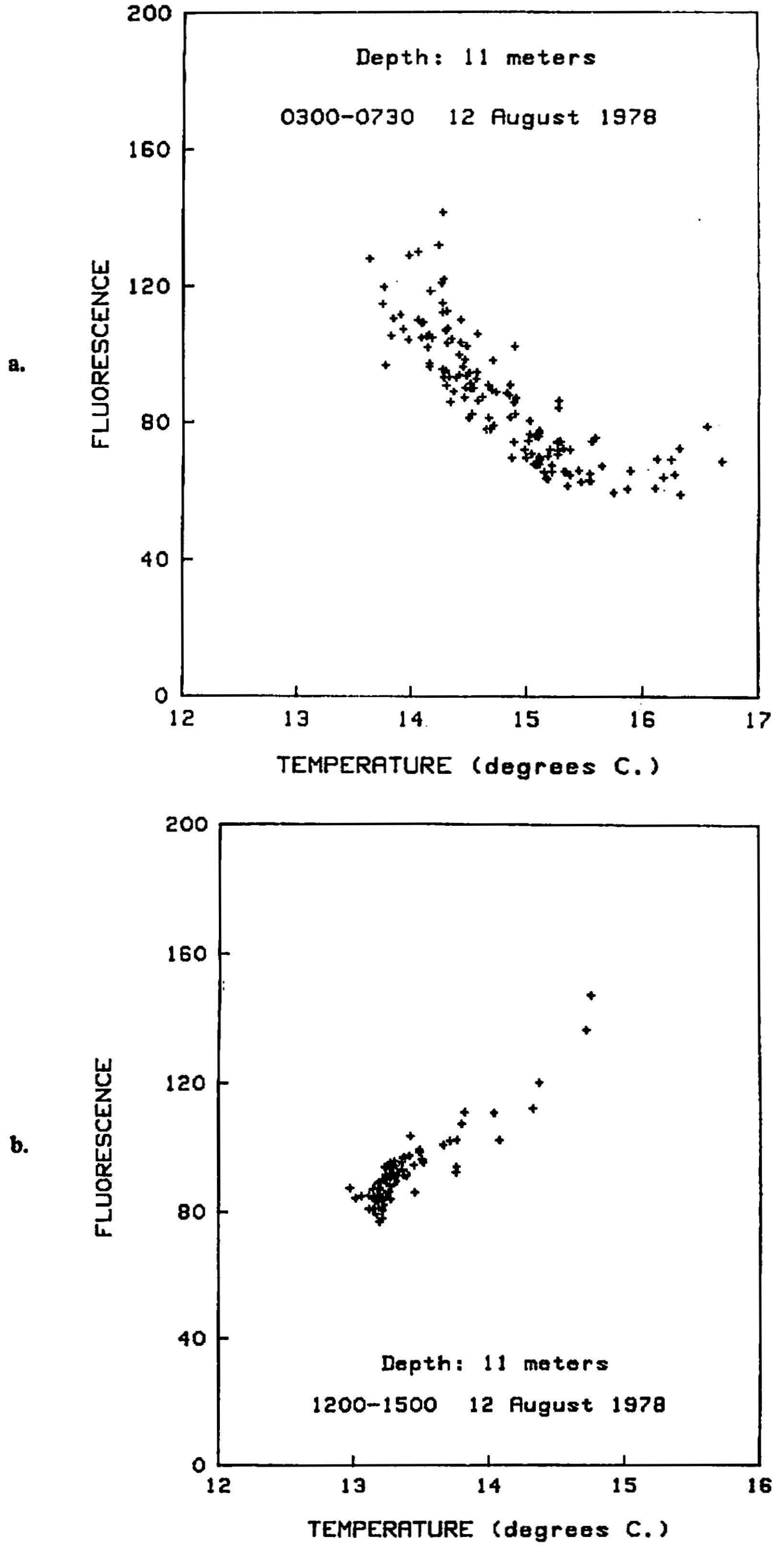
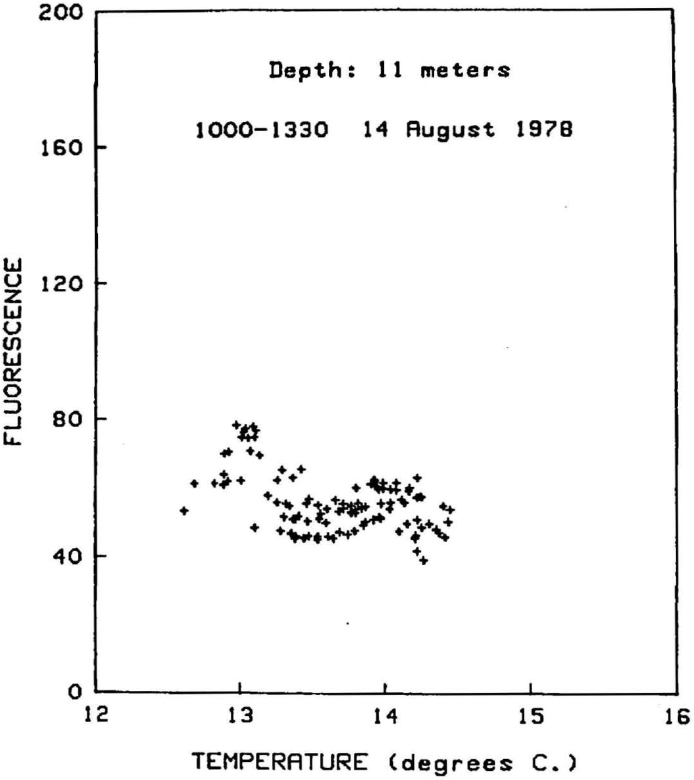
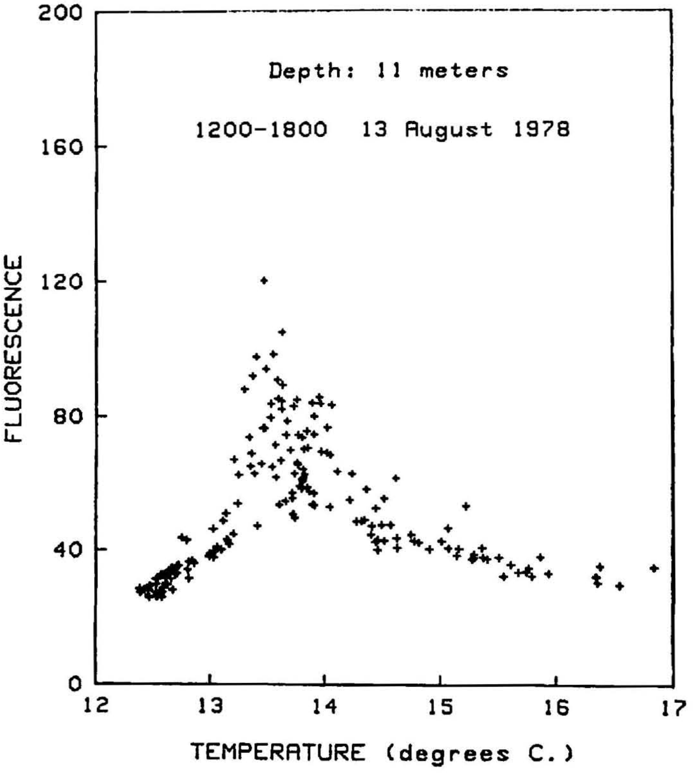


Figure 12. The relationship between fluorescence and temperature at 11 m depth during discrete intervals over the study period. (a) 0300-0730, 12 August; (b) 1200-1500, 12 August; (c) 1000-1330, 14 August; (d) 1200-1800, 13 August.

c.


Depth: 11 meters
1000-1330 14 August 1978
FLUORESCENCE
200
160
120
80
40
0
12
13
14
15
16
TEMPERATURE (degrees C.)

d.


Depth: 11 meters
1200-1800 13 August 1978
FLUORESCENCE
200
160
120
80
40
0
12
13
14
15
16
17
TEMPERATURE (degrees C.)

lack of long-term stability in the distribution of chlorophyll relative to density.

One reason for the de-coupling of the vertical motion of the phytoplankton from that of the water over scales greater than a few hours could be the swimming behavior of motile phytoplankton. The enumerations of phytoplankton from the study indicated that the chief organisms found in the chlorophyll maximum layer were motile dinoflagellates: *Prorocentrum micans, Ceratium furca* and *Ceratium tripos* on 11 August and *C. tripos* thereafter. These dinoflagellates were also recorded in the surface (1 m) samples, primarily in the day, with peak abundances near noon. Concentrations at the surface were not high enough to make visible patches, however.

Since diatoms are not likely to move independently of water motion, save for sinking, we used the concentration of diatoms as a biological reference and calculated the ratios of abundances of *Ceratium spp.* to diatoms at 1 m and at the chlorophyll maximum for each sampling expecting that the migration of dinoflagellates into and out of these strata would be reflected in the abundance of dinoflagellates relative to diatoms. At 1 m, this ratio was a maximum at mid-day each of the four days of the study. In the chlorophyll maximum, the ratio assumed a minimum value at 1300 h for three of the four days. Clear maxima in the ratio were found at 0400 on two nights in the chlorophyll maximum layer.

These results suggest a vertical migration of a part of the dinoflagellate populations out of the chlorophyll maximum layer in the day and back at night. Such a pattern was indicated also in the fluorescence vs depth profiles: dual peaks were seen between 1600 h and 0100 h on two days when a downward migration would be expected (Eppley *et al.*, 1968). A portion of the population was at $\geqslant$ 10 m depth every night regardless of water motion and shoaling thermocline. From the vertical profiles of fluorescence and from the species counts it was clear, however, that only a fraction of the dinoflagellate cells, perhaps one half, were involved in these migrations.

## 4. Discussion

*a. The distribution of nitrate.* Nitrate is not found in measurable quantities in the upper 10 m (Fig. 2) and more generally, where the temperature is greater than about 13.5°C (Fig. 5). Beneath the 13.5°C isotherm, the concentration of nitrate increases with depth as temperature decreases. These features can account for the differences between the temperature and nitrate time series at 11 m (Fig. 6): temperature fluctuates regularly throughout the record, reflecting water motions, while nitrate remains steady near zero during much of the time, showing strong variation inverse to temperature only when the temperature drops below about 13.5°C. The fact that the temperature below which nitrate became measurable remained nearly constant during the study indicates that the nitrate gradient neither advanced nor receded much in relation to the density field during the study. The close relationships between nitrate and temperature for the short records (cf. Fig. 5b) suggest that there is little irregularity in the distribution of nitrate on the scale of hours. Although the nature of the data imposed limitations on the usefulness of cross-spectral analysis of nitrate and temperature, the coherence spectrum showed a phase difference between nitrate and temperature of about 180°C at all frequencies (Fig. 7), indicating also that in spite of differences from the time series of temperature, the fluctuations in nitrate can be explained by advection.

Spectral analysis of the record of nitrate confirms the observation of Armstrong and LaFond (1968) that changes in the vertical distribution of nitrate are related to the passage of internal waves. The present data extend the relationship to tidal frequencies (Fig. 7).

*b. Nitrate pulse at 6 m depth.* Nitrate was measurable at 6 m depth only between about 2300 h and 0200 h on the night of 11-12 August (Fig. 8). A simple explanation of the phenomenon would be a shoaling of the nitracline. However nitrate at 11 m was a maximum at the beginning of the event and had fallen to much lower concentrations by the time maximum nitrate was found at 6 m. Temperature at 11 m was climbing after 0000 h, suggesting that the nitracline was not at its minimum depth when relatively high values for nitrate were measured at 6 m. A sharp peak in cross-shore current shear was found about 0000 h and a second peak at about 0100 h (not shown). The minimum Richardson's number was found a short time later, about 0130 h (Fig. 10), corresponding to peak shear in the longshore direction and maximum combined shear. The dominant period of fluctuation of both fluorescence (not shown) and nitrate at 6 m during the event was about 10-15 • $h^{-1}$ (Fig. 8), and maxima of nitrate corresponded to minima of fluorescence. The frequency was typical of internal waves, but was about twice that at 11 m. These observations are consistent with perturbed (modal) vertical distributions near 6 m reflecting upward mixing of water with low fluorescence and high nitrate. Thus we propose that the event, at least in its later stages (2345 h to 0200 h) can be explained as follows: the shoaling of the nitracline and the thermocline to near 6 m depth and the high current shear set the stage for observing shear instabilities associated with internal waves and it is likely that the nitrate pulse at 6 m was a manifestation of vertical mixing as a result of such a mechanism.

If so, the mixing may have been spatially localized. Herman and Denman (1979) discussed vertical mixing at subsurface boundaries from a similar point of view. They also observed 8-10 m vertical excursions of chlorophyll maximum layer, in this case at the shelf/slope water boundary south of Nova Scotia. As in the present study, nitrate above the discontinuity was low and concentrations within the chlorophyll maximum were about 2 μM and higher below.

*c. The distribution of chlorophyll.* The nature of the vertical distribution of chlorophyll was such that the results of spectral analysis required cautious interpretation. Nonetheless, the spectral analysis provides no justification for rejecting the null hypothesis that during the study, the distribution of chlorophyll is determined by water motions over the time scales studied. However, the degree to which the hypothesis holds cannot be unambiguously assessed by comparing the spectra in Figure 11, and the more appropriate cross-spectral analysis cannot be validly applied to the fluorescence time series. Other manipulations of the data do suggest that causes other than advection are responsible, at least in part, for the observed fluctuations in fluorescence: (1) the chlorophyll maximum moved independently from isotherms (Fig. 9), (2) the magnitude of maximum chlorophyll changed, (3) temperature-fluorescence relationships differed on scales of hours or more (Fig. 12), and (4) part of the phytoplankton (dinoflagellates) were shown to migrate vertically.

*d. Characteristic scales.* When the nitracline is poised at a particular isopycnal, the supply of nitrate to the euphotic zone from vertical mixing is balanced by the uptake of nitrate by the phytoplankton. Vertical movements in the water column can affect the balance between biological uptake and diffusive supply; upward motion brings nitrate-rich water to better-lighted depths, allowing an increase of biological demand (MacIsaac and Dugdale, 1972); conversely, descending motions lead to a decrease in the capacity for biological uptake near the nitracline. However, there are limitations to the response of the nitracline to changing conditions: even in the absence of biological uptake, the nitracline can advance (relative to an isopycnal) no faster than the diffusive time scale $t_D$ [the vertical mixing time scale $t_D = L^2 \cdot K_z^{-1}$ where $L$ is the characteristic distance (m) and $K_z$ is the coefficient of vertical eddy diffusion ($m^2 \cdot d^{-1}$)]; even in the absence of diffusion, biological uptake can erode the nitracline only as fast as the turnover time for nitrate, $t_N$ [$t_N = NO_3^-$ ($\mu$g—at $\cdot$ $1^{-1}$) $\div$ nitrate consumption rate ($\mu$g—at $NO_3^- \cdot 1^{-1} \cdot d^{-1}$)]. Thus, the shape of the nitracline, relative to density (temperature) will not change in direct response to fluctuations more rapid than the characteristic biological and diffusive time scales.

Using a reasonable value for $K_z$, 10 $m^2 \cdot d^{-1}$ (Eppley *et al.*, 1979) and a length scale of 10 m for the nitracline, a diffusive time of 10 d is calculated. The turnover time of nitrate within the nitracline can be roughly approximated by assuming average concentrations of 5 $\mu$g—at $\cdot$ $1^{-1}$ particulate nitrogen in the phytoplankton and an algal growth rate of 0.5 doublings $\cdot$ $d^{-1}$ (nitrate consumption rate = 1 $\mu$g—at $\cdot$ $1^{-1} \cdot d^{-1}$), leading to a $t_N$ of 5 d. If our reasoning is correct, the nitracline should have a stable relationship with density over periods of several days, being unaffected by the influence of internal waves, internal tides, and the diurnal cycle of irradiance. During this study, such a stable relationship was evident. Because this study was performed at a fixed site, the horizontal scale of change in the shape of the nitracline is inextricably related to the measured temporal rate of change: the integrated velocity difference (net displacement) between 3 m and 12 m depth was about 20 km (not shown) during this study. Nonetheless, the nitrate-temperature relationship was stable most of the time, indicating longshore horizontal homogeneity in the vertical distribution of nitrate.

The invariant nature of nitrate profiles (plotted versus temperature), even in the face of horizontal advection demonstrates that nitrate profiles reflected conditions averaged over relatively long temporal and spatial scales. The variable nature of chlorophyll distributions (Fig. 9) even when plotted versus temperature (Fig. 12), suggests that the characteristic scales for variability in the vertical distributions of the phytoplankton are shorter than those for nitrate. This is possible because the distribution of chlorophyll in the vertical dimension can be influenced by motility (Kamykowski, 1980; Eppley *et al.*, 1968) sinking (Steele and Yentsch, 1960; Bienfang, 1981) and changes of the chlorophyll content (Cullen, 1982) of phytoplankton in addition to growth and diffusion. Thus, the characteristic temporal scale for change of vertical profiles of chlorophyll need not be so long as that for nitrate, which is determined by growth and diffusion alone. Our data (Figs. 9, 12) show clearly that the features of the chlorophyll distribution changed over intervals of several hours. The changes in the position of the chlorophyll maximum relative to the 14° isotherm (Fig. 9) and in the proportions of dinoflagellates to diatoms in the surface and chlorophyll maximum were consistent with the inference that a portion of the phytoplankton migrated vertically. Given a swimming speed of 1-2 $m \cdot h^{-1}$ for dinoflagellates (Kiefer and Lasker, 1975) and a thickness of about 6 m for the chlorophyll maximum layer, the characteristic time scale of change of chlorophyll profiles due to the behavior of phytoplankton is 3-6 h. Thus, dinoflagellates may exert some control over vertical displacements by internal tides, but they are not able to overcome the motions of short-period internal waves (cf. Kamykowski, 1974).

The comparison between relevant time scales of change for nitrate and chlorophyll leads to a better understanding of causality in the close association between the subsurface chlorophyll maximum and the nitracline (cf. Dandonneau, 1977; Herbland and Voituriez, 1979; Cullen and Eppley, 1981). Although in some regions the nitracline may be in effect determined and maintained by the phytoplankton distribution in the sense that the subsurface chlorophyll maximum acts as a sink for nutrients (Anderson, 1969), during this study the distribution of nitrate was stable and determined on relatively long time scales while the distribution of chlorophyll reflected the behavior of phytoplankters which moved somewhat independently from the physical and chemical environment but still retained some association with the nitracline. Thus, if causality for the relationship between the nitracline and chlorophyll maximum could be ascribed, it would be attributed to the influence of the vertical distribution of nitrate on the behavior of phytoplankton. Such a causal mechanism has been demonstrated in the laboratory (Heaney and Eppley, 1981; Cullen and Horrigan, 1981).

## 5. Conclusion

Water circulation on the Southern California Shelf is closely associated with vertical motions in the water column and these motions exert strong effects on the phytoplankton, primarily by modifying irradiance and the supply of nutrients. The depth of the nitracline is indicative of the nutrient supply; it is determined by the balance of vertical mixing of nitrate from below and the uptake of nitrate by phytoplankton in the euphotic zone. Our results indicate that the balance represents average conditions over a few days or more, thus important modes of water movement (internal waves, internal tides) and environmental change (day/night) have little proximate influence on the vertical distribution of nitrate in relation to conservative properties; i.e., nitrate is a passive contaminant on temporal scales of days or less. In general, the phytoplankton act as a passive contaminant also, but the motile component (dinoflagellates) can respond behaviorally to environmental change in time scales of hours and hence moves somewhat independently from circulation patterns such as internal tides. The control that some phytoplankton have over environmental conditions in the face of large fluctuations in the physical field is undoubtedly of selective advantage to them, especially near the coast where internal tides can expose the plankton to large fluctuations in irradiance. Comparison of variation and covariation of water movements, nutrients, and phytoplankton during this study has led to a better understanding of the interactions between phytoplankton and the environment on the Southern California Shelf. Similar studies in other environments and during different seasons would yield different, but equally useful, results.

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