

Phytoplankton and Photosynthetic Light Response in the Coastal Transition Zone off Northern California in June 1987

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In June 1987 the geostrophic flow in the coastal transition zone off northern California (between 50 and 150 km off the coast from Point Reyes to just north of Cape Mendocino) was dominated by a well-defined, southward-meandering current. Three vertical sections are presented that show the hydrographic structure of the current down to 100 m and its relationship to the distribution of phytoplankton biomass. The sections show that the geostrophic adjustment brought cold, saline, deep water up to the surface on the low steric height, or cold side of the flow, and that this upwelled water supported a relatively large diatom biomass (chlorophyll-*a* concentrations between 1 and 10 mg m⁻³). We present particle size spectra and photomicrographs of the phytoplankton that show that the diatom biomass was dominated by chain-forming species (e.g., *Skeletonema costatum*, *Chaetoceros* spp., *Thalassiosira* spp., and *Rhizosolenia alata*, but also a single-celled *Actinocyclus* sp.). Photosynthetic light response measurements reveal that these diatom communities were capable of high photosynthetic rates (P_{max} between 5 and 25 mg C mg Chl *a*⁻¹ h⁻¹). Although most of the diatoms were located in cold, slow-moving water on the low side of the current, some were being carried downstream. High chlorophyll concentrations were observed at depths > 75 m in and along the cold edge of the flow in all of our sections; we show evidence that in two out of three cases this was the result of water mass subduction.

INTRODUCTION

Cold filaments appear off northern California when upwelled coastal water is advected offshore in seaward-flowing jets in the California Current system [Mooers and Robinson, 1984; Flament *et al.*, 1985; Rienecker *et al.*, 1985; Kosro and Huyer, 1986; Rienecker and Mooers, 1989] (see also results summarized by Strub *et al.* [this issue]). Cold coastal water is carried seaward along the low steric height side of these jets [Strub *et al.*, this issue], and there is evidence that it is subducted down and under the current as it moves offshore [Flament *et al.*, 1985; Washburn *et al.*, this issue; Kadko *et al.*, this issue]. The total volume transport in the seaward-flowing jets off northern California is at least 1 to 2 Sv [Mooers and Robinson, 1984; Kosro and Huyer, 1986; Huyer *et al.*, this issue]. Thus they represent a sizable fraction (> 20%) of the climatological mean California Current [Mooers and Robinson, 1984]. However, the volume transport of upwelled coastal water in these jets (i.e., in filaments) is probably less than half of the total seaward transport.

Cold filaments usually have relatively high pigment concentrations associated with them [Abbott and Zion, 1985, 1987; Strub *et al.*, 1990; Abbott and Barksdale, this issue]. Thus it appears that they advect both coastal water and coastal phytoplankton biomass offshore, and it has been assumed that they carry nutrients seaward as well. These observations have led to speculation that filaments are an important mechanism for enrichment of the offshore (> 200 km) regions of the California Current system [Mooers and Robinson, 1984; Rienecker *et al.*, 1985]. These speculations

challenge the traditional view, which holds that production offshore in the California Current system is supported by nutrients and biomass advected southward from higher latitudes [Smith, 1971; Chelton *et al.*, 1982].

The data presented in this paper were collected off northern California in June (9-18) 1987. This survey is one of three that sampled a station grid between 50 and 150 km off the coast from Point Reyes to just north of Cape Mendocino (Figure 1). The grid covered much of the coastal transition zone (CTZ) between cold, freshly upwelled water near the coast, and warm, oceanic water offshore. The 1987 surveys show that a seaward jet often seen off Point Arena during the upwelling season (which usually has a filament associated with it) is part of a large-scale, meandering, southward flow in the California Current system [Hood *et al.*, 1990; Kosro *et al.*, this issue]. In this paper we examine the subsurface hydrographic structure along this meandering flow, and its relationship to distributions of phytoplankton biomass and species composition in the upper 100 m of the water column. We also present photosynthetic light response data which provide information about the physiological characteristics of the phytoplankton communities in the study area.

METHODS

Conductivity, temperature, and depth (CTD) observations were made with a Neil Brown Mark IIIb CTD system. The probe was calibrated for pressure, temperature, and conductivity by the manufacturer, and the temperature and conductivity data were checked against in situ calibration samples. Salinity, density (σ_θ), and the geopotential anomaly (dynamic height) were calculated using standard algorithms [Schramm *et al.*, 1988].

The satellite thermal (advanced very high resolution radiometer, or AVHRR) image was collected at the Scripps Satellite Oceanography Facility. The data were geographically corrected, calibrated to infrared brightness tempera-

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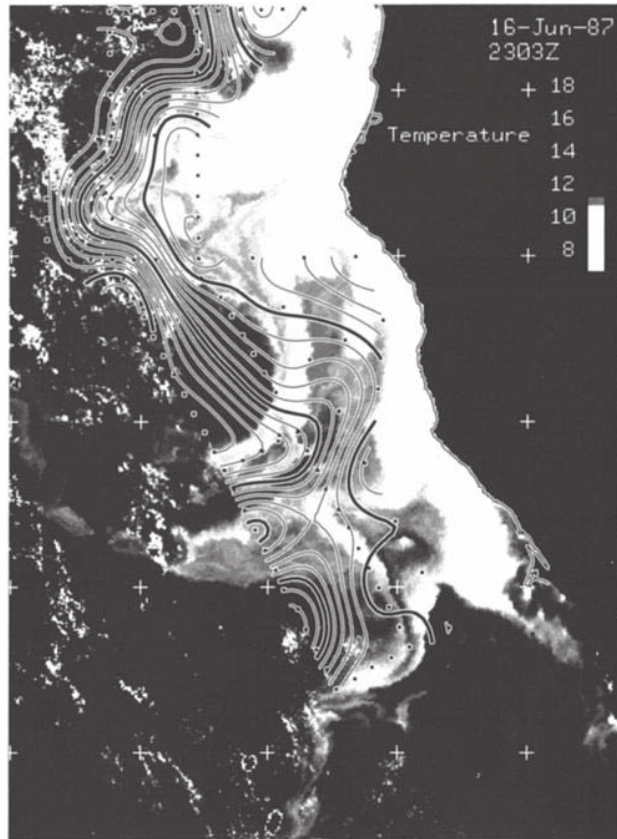


Fig. 1. A satellite AVHRR thermal image of northern California coastal waters collected on June 16, 1987 with steric height (5/500) contours superimposed [from Kosro *et al.*, this issue]. The light grey shades represent cold water.

ture, and linearly mapped to grey shades using Miami DSP software to give relative values of surface temperature.

A rosette sampler equipped with 5-L Niskin bottles was used to collect water for biological analyses. The bottles used to collect samples for ^{14}C productivity measurements were acid washed (10% HCL) and thoroughly rinsed in Milligie-filtered fresh water at the beginning of the cruise, and their neoprene closures and O-rings were replaced with silicon ones. Chlorophyll-*a* samples were filtered (Whatman GF/F), frozen, and stored in darkness for subsequent shore-based laboratory analysis. They were analyzed within 2 months of collection, and concentration was determined fluorometrically after 24-hour dark extraction in 90% acetone [Venrick and Hayward, 1984]. Particle size spectra (total particle volume per unit volume of sample plotted as a function of particle diameter) between 4 and 100 μm equivalent spherical diameter (E.S.D.) were generated at sea using a Coulter Electronics particle analyzer (model TA II) equipped with a 280- μm aperture. Each spectrum represents an average of three 200-mL replicate samples that were refrigerated in darkness and analyzed within 2 hours of collection. Each sample was prefiltered through 295- μm mesh nitex to prevent aperture clogging. Phytoplankton samples were preserved in 2% buffered formalin and stored for microscopic analysis. In the laboratory, 50-mL aliquots were settled, stained with rose bengal, and examined to identify the

dominant phytoplankters, but the samples were not counted. Representative fields were selected and photographed to give a visual impression of both species composition and relative species density.

The photosynthetic light response of the phytoplankton (production (P) versus irradiance (I) curves) was measured at sea with two modified, temperature controlled photosynthetrons [Lewis and Smith, 1983]. Seawater samples (250-mL) were inoculated with 250 μCi $\text{H}^{14}\text{CO}_3^-$, and 5-mL aliquots were incubated for 1 hour in blue light (tungsten/halogen source filtered through blue Plexiglas) at intensities between 0 and 3000 $\mu\text{E m}^2 \text{ s}^{-1}$. The incubations were terminated with the addition of formalin (approximately 2% final concentration), tightly sealed, and then stored for subsequent shore-based analysis. In the laboratory, samples were agitated for 2 hours after addition of 0.5 mL of 1.5 *N* HCL to drive off excess radiolabel. Then 10 mL of Aquasol (NEN products) was added to each sample, and the activity of the resulting gel was determined using a Beckman LS1800 liquid scintillation counter. All samples were analyzed within 9 months of collection.

The chlorophyll-specific P versus I curve parameters α , P_{max} , and β were estimated by fitting the following empirical three parameter equation of Platt *et al.* [1980] to the data:

$$P = P_s(1 - e^{-a})e^{-b} \quad (1)$$

where P is the production rate, $a = \alpha I/P_s$, $b = \beta I/P_s$, and I is irradiance. P_s is a parameter whose relationship to P_{max} will be defined below. This equation was fit to our data using a nonlinear, least squares grid search technique [Bevington, 1969].

We define the relationship between the parameters P_s and P_{max} following Platt *et al.* [1980]. First, we calculate the derivative of equation (1) with respect to light:

$$\frac{\partial P}{\partial I} = (\alpha + \beta)e^{-(\alpha + \beta)I} - \beta e^{-\beta I} \quad (2)$$

Setting $\partial P/\partial I = 0$ specifies the point I_{max} where photosynthesis is maximum,

$$I_{\text{max}} = \frac{P_s}{\alpha} \log_e \left(\frac{\alpha + \beta}{\beta} \right) \quad (3)$$

Substituting this value of I in equation (1) gives the maximum production rate:

$$P_{\text{max}} = P_s \left(\frac{\alpha}{\alpha + \beta} \right) \left(\frac{\beta}{\alpha + \beta} \right)^{\beta/\alpha} \quad (4)$$

Equation (1) describes the light response of phytoplankton over the entire range of intensities encountered in the ocean, including those which cause photoinhibition. The shape of the curve is dependent upon the parameters α , P_{max} , and β , where α determines the slope of the curve at low light intensities, P_{max} determines the maximum chlorophyll-specific photosynthetic rate, and β determines the degree of photoinhibition at high light intensities.

RESULTS

Surface Patterns in Temperature, Flow, and Phytoplankton Biomass

The surface patterns in temperature, flow, and phytoplankton biomass during the June 1987 R/V *Wecoma* CTZ

cruise are described in detail elsewhere [Hood *et al.*, 1990; Kosro *et al.*, this issue]. Here we briefly review some of these results.

Coastal winds were generally upwelling favorable in April, May, and June 1987 off northern California, which resulted in a decreased coastal sea level and a persistent cold surface thermal signature along the northern California coast prior to and during the June cruise [Kosro *et al.*, this issue]. Figure 1 shows the surface temperature patterns in the study area on June 16, 1987 (which was toward the end of the cruise), and their relationship to dynamic height (5/500) contours determined from shipboard hydrographic observations. The light grey shades in Figure 1 show a heterogeneous cold region all along the coast from the California-Oregon border (42°N) to Point Reyes (38°N). A broad tongue of cold water extended seaward about 150 km off Cape Mendocino, and two cold filaments extended seaward more than 200 km off Point Arena and Point Reyes.

The boundary between cold coastal water and warm offshore water was associated with a well-defined meandering southward flow in the California Current system (Figure 1). This current flowed southward into the study area north of Cape Mendocino and then took an abrupt seaward turn. It meandered seaward directly off Cape Mendocino and then shoreward again south of Cape Mendocino. Off Point Arena, the flow turned sharply seaward once again and intensified to form a jet which flowed out of the study area. An onshore flow was present farther south that turned seaward again off Point Reyes. In the seaward flows north of Cape Mendocino and off Point Arena the surface velocities exceeded 50 cm s⁻¹ [Kosro *et al.*, this issue].

The distribution of chlorophyll-*a* at the sea surface (Figure 2) was similar to the distribution of cold water observed in the AVHRR image (Figure 1). The chlorophyll concentrations were generally higher (> 1 mg m⁻³) and more patchy in the cold water nearshore, and lower (< 1 mg m⁻³) and more homogeneous in the warm water offshore. Very high chlorophyll concentrations (> 6 mg m⁻³) were observed toward shore on the northernmost zonal station line, and there was a seaward extension of moderately high values (> 1 mg m⁻³) off Cape Mendocino. High chlorophyll concentrations were also associated with the cold water that extended seaward off Point Arena (> 1 mg m⁻³) and Point Reyes (> 6 mg m⁻³).

Vertical Sections Through the Frontal Zone

Line A. The vertical sections along station line A (the northernmost zonal line in Figures 1 and 2) are shown in the left column of Figure 3. This line crossed a sharp density front that outcropped at the sea surface between stations 121 and 123 about 100 km offshore (the inshore edge of the station line was approximately 50 km from the coast). Only the seasonal pycnocline extended all the way up to the surface at this front. The deep, permanent pycnocline, which we have indicated with the grey-shaded region between the 25.6 and 25.9 σ_θ contours, leveled off between about 25 and 50 m depth, though it may have outcropped farther inshore. The frontal region separated a warm, less saline, and less dense water mass in the upper 75 m of the water column offshore from a cold more saline and more dense water mass that extended up toward the surface nearshore. A salinity minimum was present on the seaward side of the front near the surface between stations 89 and 122.

The core of the southward-meandering current crossed line A between stations 121 and 123 in the frontal region. The highest southward velocities (> 70 cm s⁻¹ relative to a 500 m reference level) were at the surface between stations 122 and 123. If we define the current by the -10 cm s⁻¹ velocity contour it was about 50 km wide and over 100 m deep. The southward flow was coincident with the boundary between chlorophyll-poor water offshore and chlorophyll-rich water nearshore. The -30 cm s⁻¹ contour grades from about 0.2 mg m⁻³ on the seaward side to about 3.0 mg m⁻³ on the landward side. Most of the chlorophyll (concentrations > 3.2 mg m⁻³) was located in the slow-moving, dense water landward of the southward flow. A deep patch of chlorophyll-rich water was present below 75 m at station 122 (kilometer 55). This patch was in a 10 cm s⁻¹ southward flow. Farther offshore, a deep chlorophyll maximum was present, defined by the 0.4 mg m⁻³ contours between 50 and 75 m depth.

Line C. Vertical sections through line C, which was oriented zonally along 40°N just south of Cape Mendocino (see Figures 1 and 2), are shown in the center column of Figure 3. Along this line the seasonal pycnocline outcropped between stations 48 and 50 over 150 km from shore, and the deep, permanent pycnocline (indicated by the grey-shaded region) shoaled up toward the surface in a stepped manner and outcropped about 50 km from shore. Here, too, a warm, less saline water mass dominated the upper 75 m of the water column offshore, and a cold, more saline water mass extended up toward the surface nearshore.

In the line C section, the core of the southward-flowing current was located about 150 km from shore where the seasonal pycnocline outcropped at the surface. As in the northern line A, the boundary between chlorophyll-poor water offshore and chlorophyll-rich water nearshore was coincident with the southward flowing current. The -30 cm s⁻¹ contour grades from about 0.2 mg m⁻³ on the seaward side to about 1.0 mg m⁻³ on the landward side. Moderately high chlorophyll values (> 0.8 mg m⁻³) extended deeper than 75 m in the high velocity-region. As in the northern section (line A) the highest chlorophyll values were associated with the slower-moving water in the upper 50 m of the water column landward of the current. The chlorophyll concentrations were generally lower in this section than in line A.

Line II. Station line II was oriented approximately parallel to the coast between 80 and 110 km from shore, and it obliquely intersected the meandering current where it turned seaward off Point Arena (see Figures 1 and 2). Vertical sections along this line are shown in the right hand column of Figure 3. The temperature and salinity contours bow upward toward the surface south of station 36, but the salt doming was shifted south relative to temperature. Also, the 10° and 11°C temperature contours diverge markedly between stations 31 and 35. The combined temperature and salt effect on density resulted in an upward doming of isopycnals south of station 36. The deep, permanent pycnocline (indicated by the grey-shaded region) outcropped at the surface between stations 29 and 30. The seaward flow off Point Arena is apparent in the geostrophic velocity section between stations 33 and 37. The core of this flow, as indicated by the -30 cm s⁻¹ contour, was located between stations 34 and 35, north of where the permanent pycnocline outcropped. A meander in the southward flow (see Figure 2)

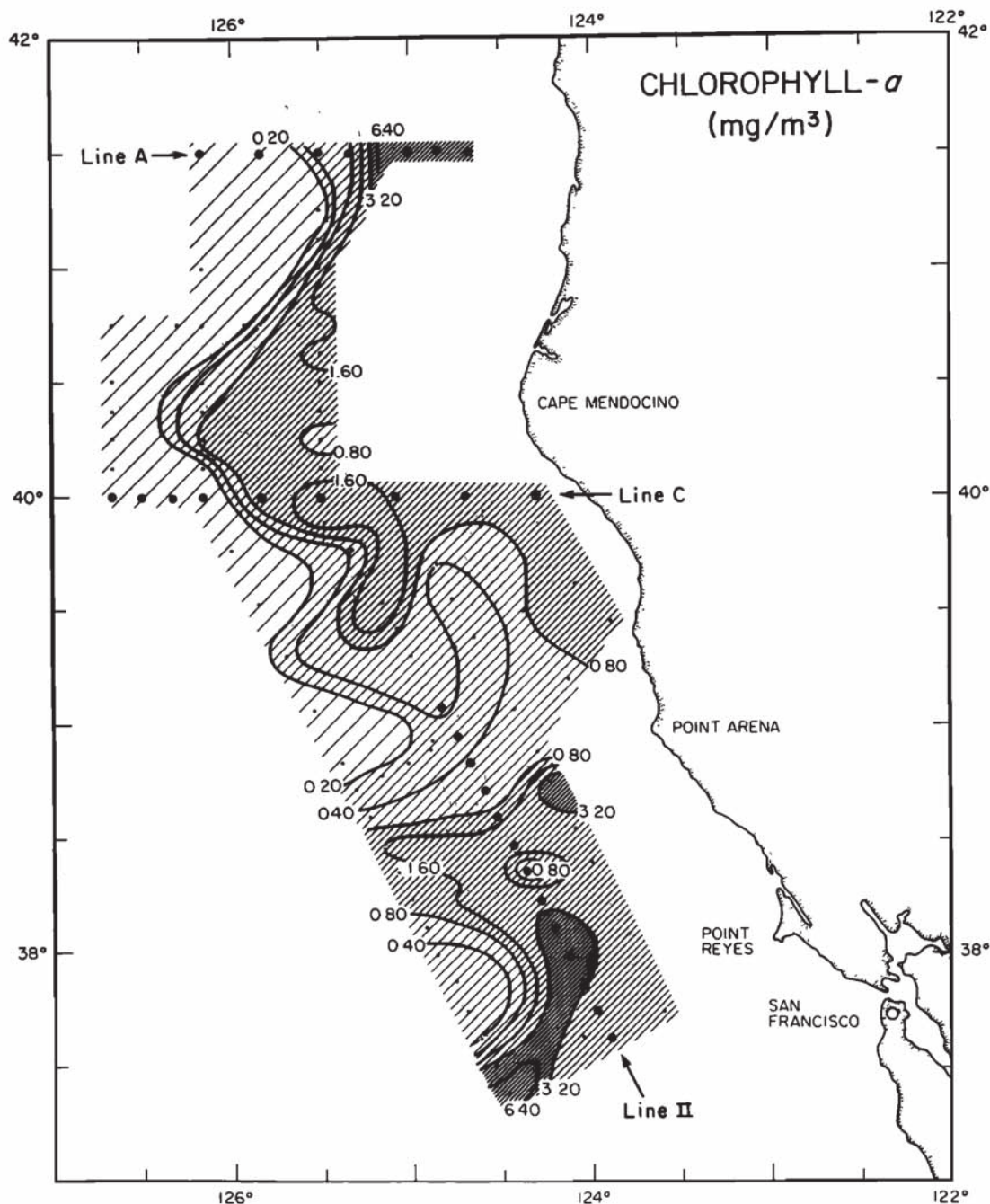


Fig. 2. The near-surface (5 m) chlorophyll-*a* concentration off northern California during the June cruise.

was sampled south of station 31, where a 10 cm s^{-1} flow moved seaward between stations 29 and 31 and then landward once again between stations 28 and 29.

The chlorophyll concentrations along this line increased dramatically south of the seaward flow off Point Arena (south of station 35). They increased from 0.4 mg m^{-3} on the northern side of the flow to more than 1.6 mg m^{-3} on the southern side of the flow. The highest chlorophyll values were associated with the slower-meandering flow south of station 31. Concentrations exceeded 6 mg m^{-3} between 25 and 50 m in the 10 cm s^{-1} seaward flow between stations 29 and 31. Between stations 28 and 35, relatively high chlorophyll concentrations ($> 1.6 \text{ mg m}^{-3}$) extended below the maximum depth that we sampled (75 m).

Particle Size Spectra, Photomicrographs, and Light Response Curves of the Phytoplankton

Line A. Figure 4 shows particle size spectra at four points in the line A chlorophyll section. These data reveal that where the chlorophyll concentrations were high nearshore in the upper 50 m of the water column, there was also a large volume of relatively large particles (Figure 4, top). At the surface at station 123 and at 20 m at station 125 the spectra represent mixed diatom assemblages dominated by chain-forming species (e.g., *Skeletonema costatum*, *Chaetoceros* spp., and *Thalassiosira* spp.; Figure 5, top). Chain-forming diatoms were detected at 75 m at station 122 also, but their volume was less (Figures 4 and 5, bottom right).

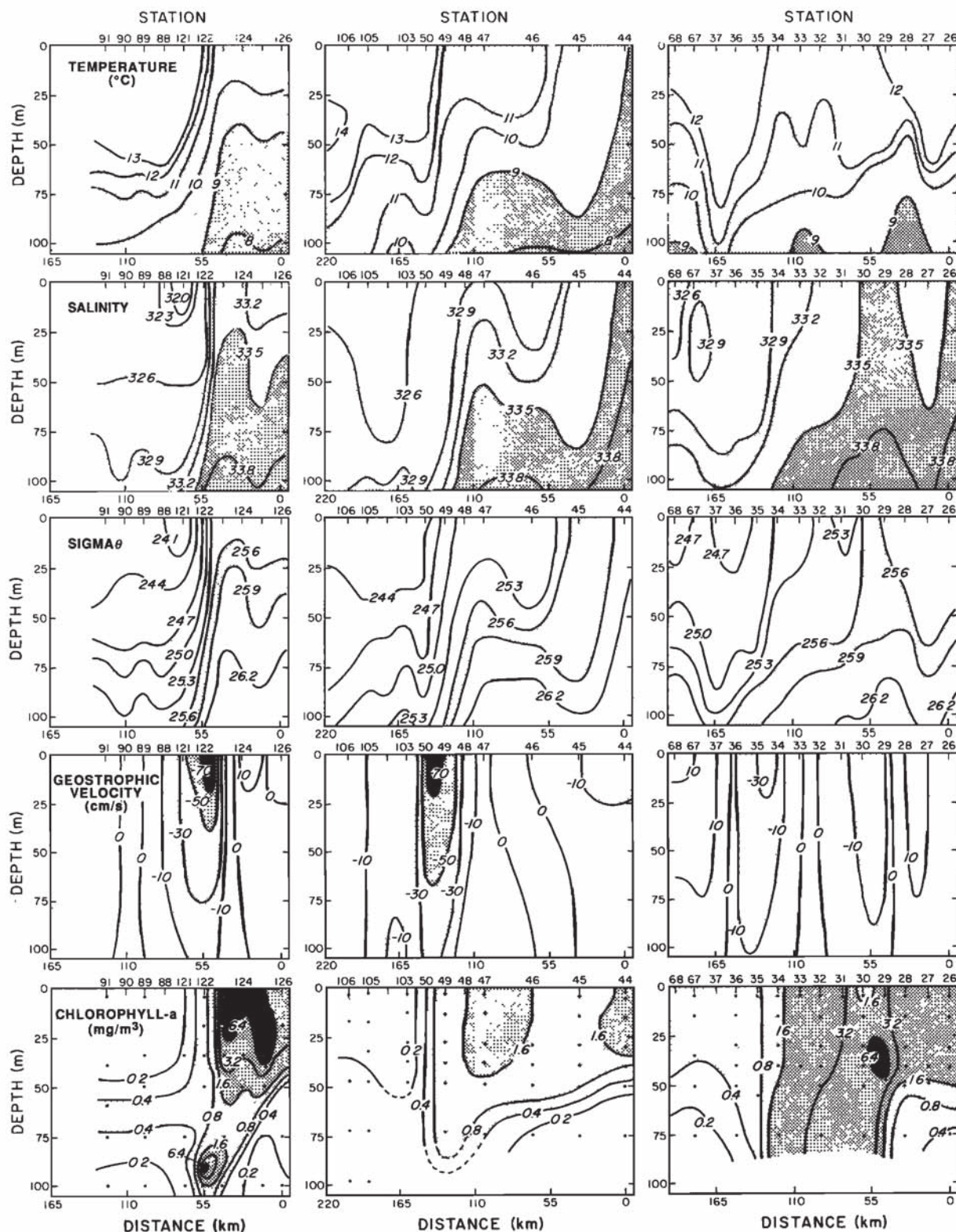


Fig. 3. Vertical sections of temperature, salinity (psu), density (σ_θ), geostrophic velocity (relative to a 500 m reference level), and chlorophyll-a concentration along station lines A (left), C (middle), and II (right).

In the deep chlorophyll maximum offshore at station 91, the chain-forming diatoms were largely absent, and smaller single-celled phytoplankters dominated the flora (Figures 4 and 5, bottom left).

In Figure 6 we have superimposed light response curves on the line A chlorophyll section. The highest P_{max} and α values were measured near the surface at station 123 where the diatom volume was large (Figure 6, top left); 20 m below

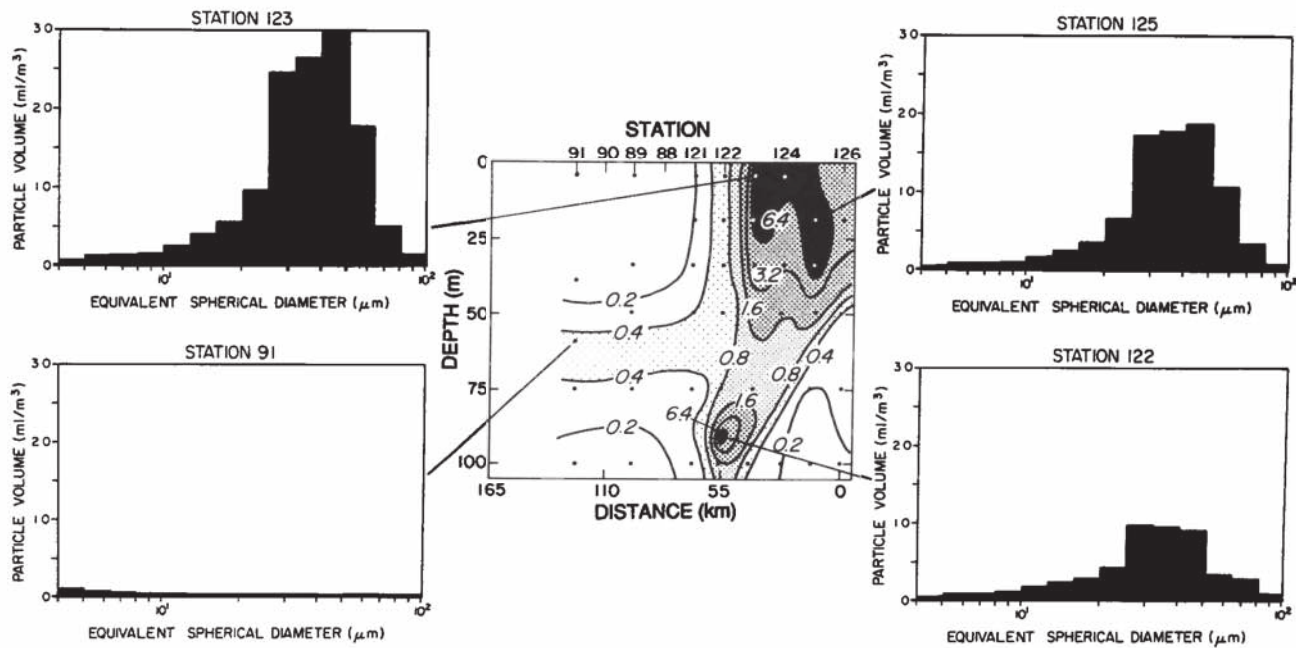


Fig. 4. The line A chlorophyll section with particle size spectra.

the surface at station 125 both P_{max} and α were markedly lower (Figure 6, top right), but this may reflect the differences in the time of day of the measurements (diel variability in light response). The P_{max} and α values were lower still in the deep patch of chlorophyll at station 122 (Figure 6, bottom right), and they were lowest in the deep chlorophyll maximum offshore (Figure 6, bottom left). The latter probably reflected diel variability in light response to some extent also.

Line C. Diatoms were detected in line C, where the chlorophyll concentrations were above 0.8 mg m^{-3} (Figures 7 and

8). Compared with line A their volumes were lower by a factor of about 3 (note expanded y axis scales in Figure 7). The size structure of the diatom communities at the surface at stations 44 and 47 were different (Figure 7, top). The particles were smaller nearshore where short chains of *Chaetoceros debilis* dominated the flora (Figures 7 and 8, top right), and larger offshore where the phytoplankton community was more diverse (Figures 7 and 8, top left). At station 49 the total particle volume was lower at 40 m, but diatoms were detected (Figures 7 and 8, bottom right). As in line A, the diatoms were largely absent in the deep water offshore

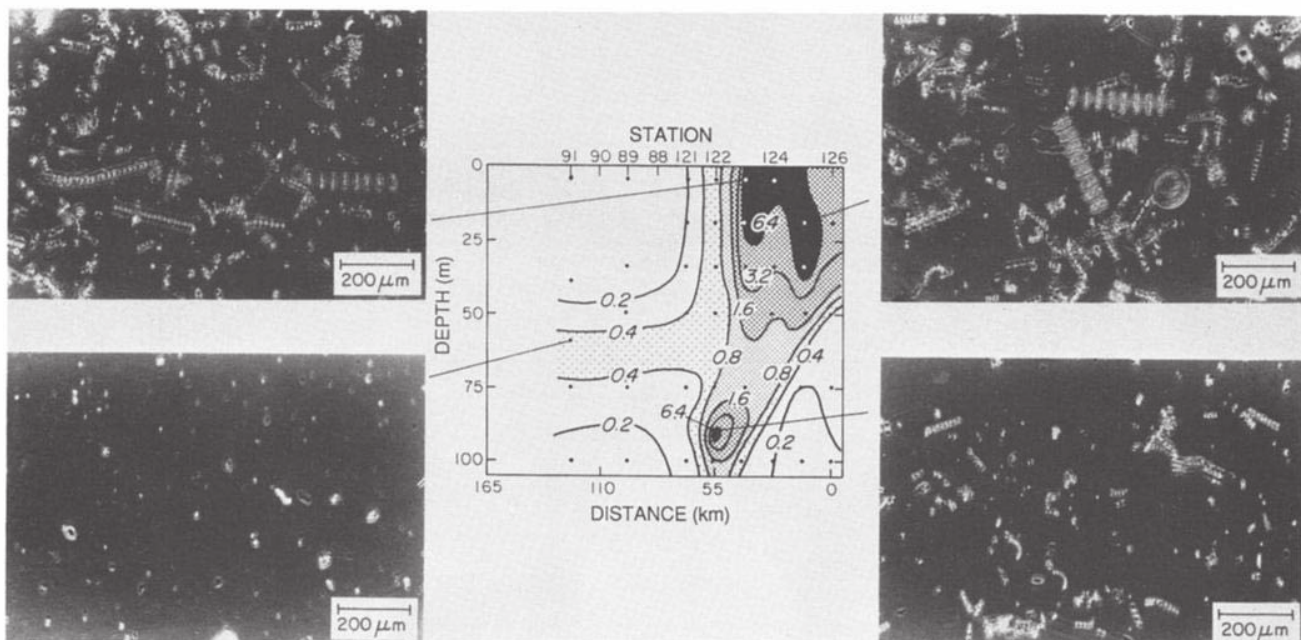


Fig. 5. The line A chlorophyll section with photomicrographs of phytoplankton.

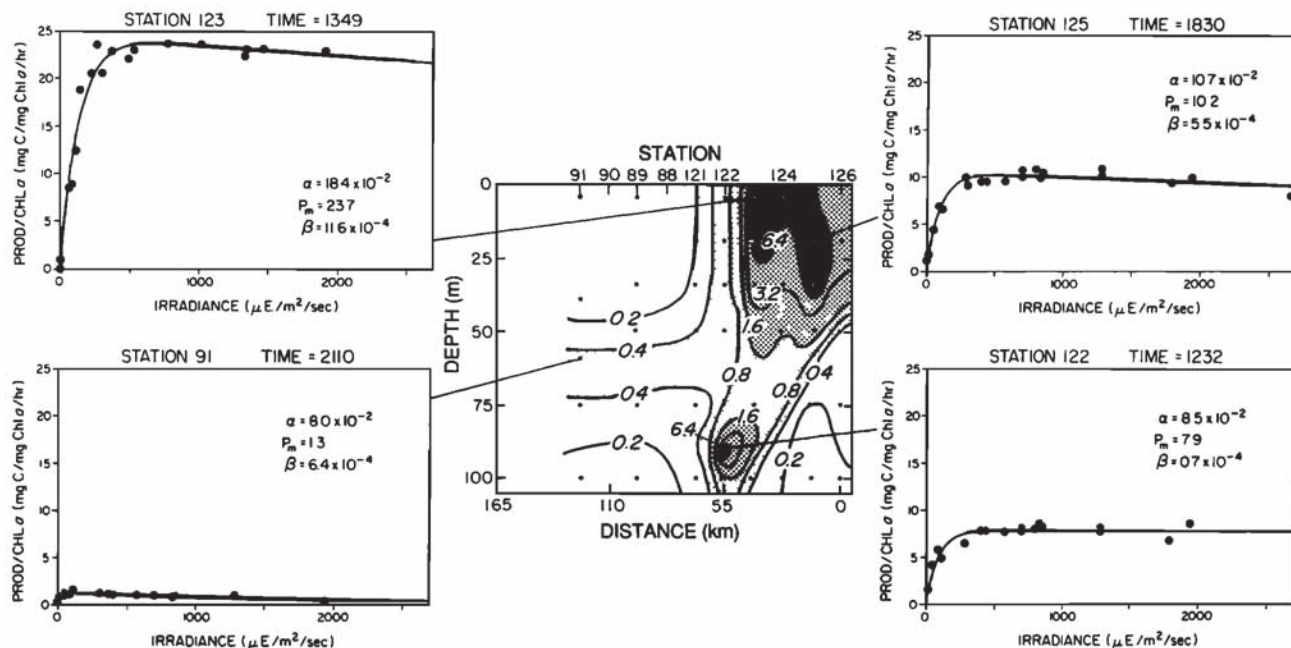


Fig. 6. The line A chlorophyll section with photosynthetic light response curves. The units of P_{max} are $\text{mg C mg Chl a}^{-1} \text{ h}^{-1}$, and the units of α and β are $\text{mg C mg Chl a}^{-1} \text{ h}^{-1} (\mu\text{E m}^{-2} \text{ s}^{-1})^{-1}$. The times are local, and they show when each 1-hour incubation was started.

(50 m at station 105) where small, single-celled phytoplankton dominated the flora (Figures 7 and 8, bottom left).

In line C the P_{max} and α values were higher near the surface where the chlorophyll concentrations were higher and diatoms were more abundant (Figure 9, top). The light response curves of the diatom communities at stations 47 and 44 were markedly different (note smaller α and larger β at the latter), but this may largely reflect the differences in the time of day of the incubations. At depth at stations 49 and 105 offshore, where the chlorophyll concentrations were lower, the P_{max} and α values were lower (Figure 9, bottom),

especially at station 105, where diatoms were absent. Photoinhibition was marked at 40 m at station 49 (Figure 9, bottom right).

Line II. Figure 10 shows particle size spectra at four points along station line II. At both depths at station 33, the particle volumes were large and the size distributions were narrow (top left and bottom right). The narrow peaks were caused by a large, discoid, single-celled *Actinocyclus* sp. (Figure 11, top left and bottom right). *Rhizosolenia alata* was also present at both depths at station 33. To the south in the subsurface chlorophyll maximum at station

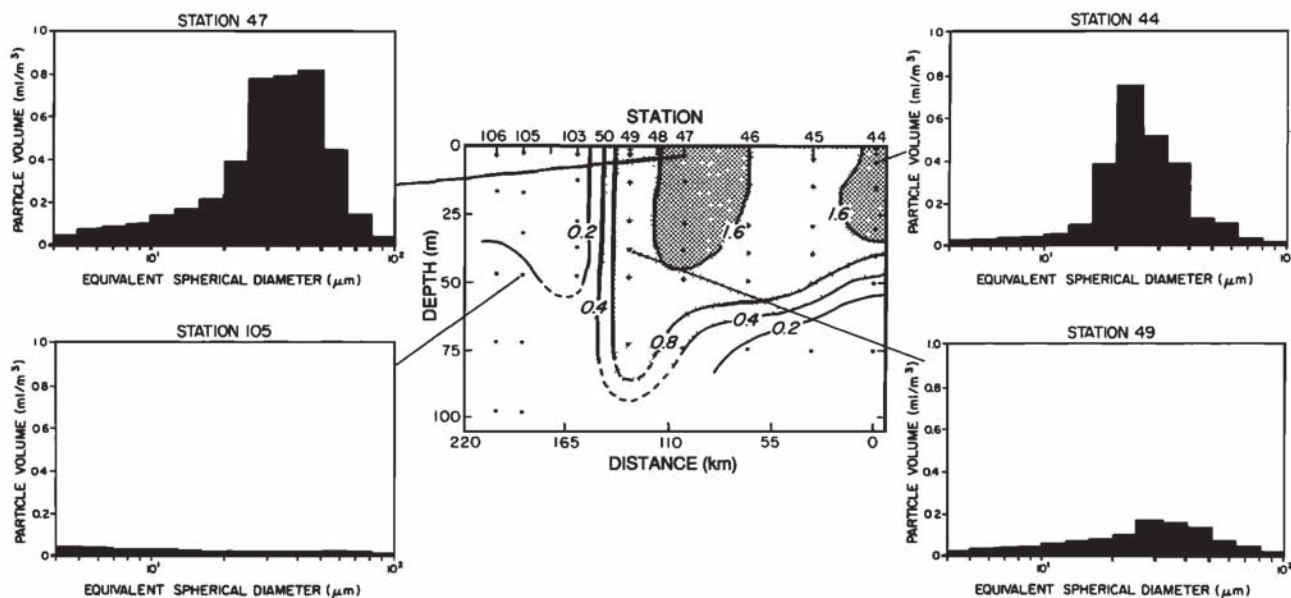


Fig. 7. The line C chlorophyll section with particle size spectra.

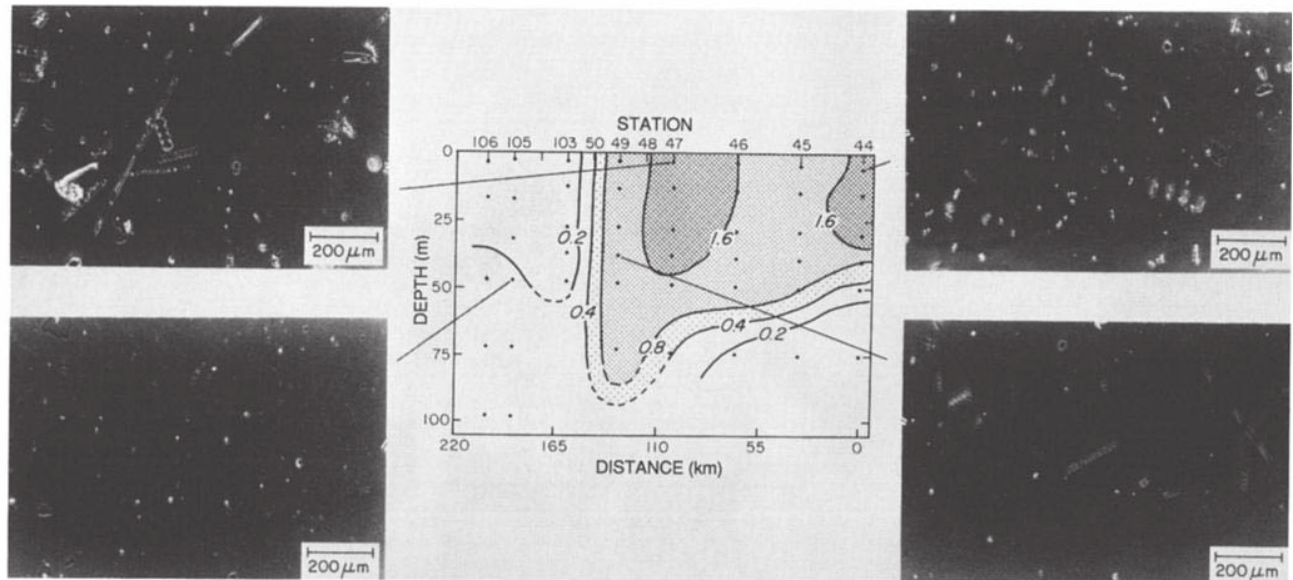


Fig. 8. The line C chlorophyll section with photomicrographs of phytoplankton.

29, the particle size distribution was much broader and the peak was shifted left (Figure 10, top right). This reflects the presence of several smaller chain-forming diatom species (e.g., *Chaetoceros* spp., *Skeletonema costatum*, *Thalassiosira* spp., *Nitzschia* spp., and *Thalassionema* sp.; Figure 11, top right). Where the chlorophyll concentrations were low to the north at station 35 diatoms were largely absent (Figures 10 and 11, bottom left).

The light response curves measured at station 33, where the diatoms *Actinocyclus* sp. and *Rhizosolenia alata* were abundant (Figure 12, top left and bottom right), and at 55 m at station 35, where diatoms were largely absent (Figure 12, bottom left), were all similar. In each case, P_{max} was relatively low and photoinhibition was evident (relatively large β values). The α values were slightly higher for the

two deep samples. The light response of the mixed diatom assemblage at station 29 to the south was distinctly different (Figure 12, top right). These cells had a much higher P_{max} , they exhibited less photoinhibition at high light levels (small β values), and α was large. The curves for stations 29 and 33 were measured at night, so the α and P_{max} values were probably lowered as a result of diel variations in light response.

DISCUSSION

Evidence of Upwelling, Entrainment, and Subduction

The distribution of cold, chlorophyll-rich surface water in the study area was clearly related to the position of the southward-meandering current that dominated the

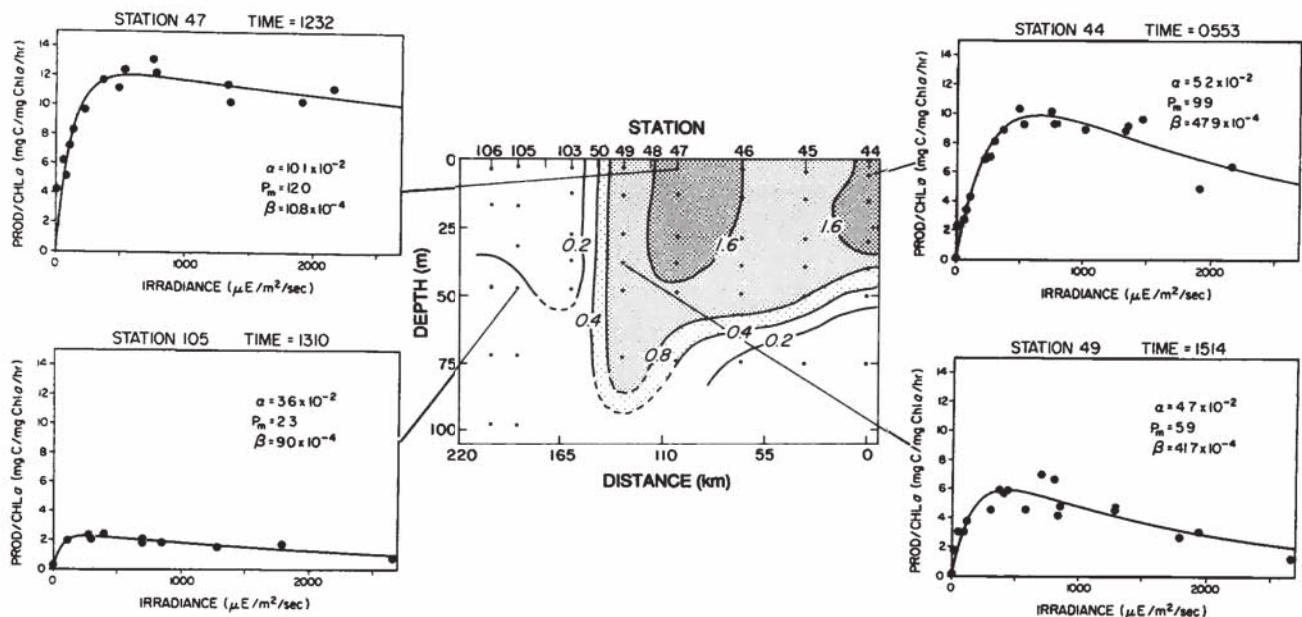


Fig. 9. As in Figure 6 for line C.

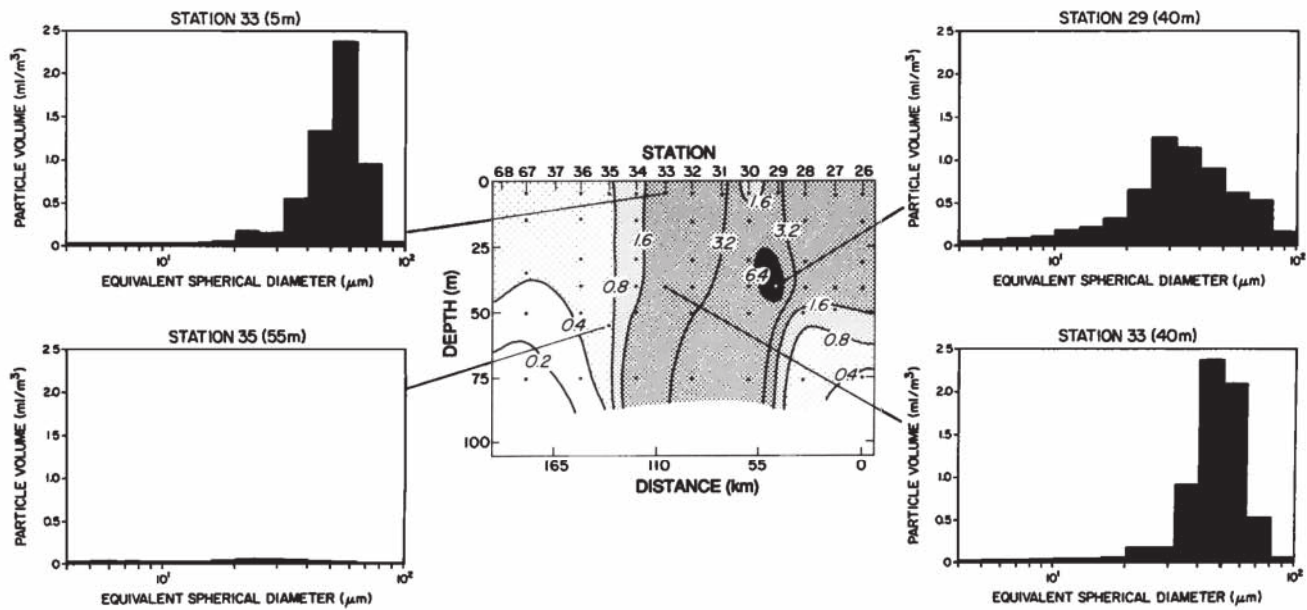


Fig. 10. The line II chlorophyll section with particle size spectra.

geostrophic flow (Figures 1 and 2). This current generally separated a more eutrophic region nearshore from a more oligotrophic region offshore. The broad tongue of cold, chlorophyll-rich water that extended seaward off Cape Mendocino was bounded by the flow, and the cold, chlorophyll-rich filament that extended seaward off Point Arena was bounded to the north by an offshore flow, and to the south by an onshore flow (see Hood *et al.* [1990] for a more detailed discussion of the surface patterns). Since most of the phytoplankton biomass in the study area was located in relatively slow-moving, cold water on the low steric height side of the meandering current, and not in the current itself, Hood *et al.* [1990] speculated that the geostrophic adjustment associated with the flow brought cold, nutrient-rich, deep water

up into the euphotic zone and that this stimulated diatom production adjacent to it. The vertical sections presented in this paper (Figure 3) (and by Kosro *et al.* [this issue]) are consistent with this view. All three sections in Figure 3 show a cold, saline, dense water mass that extended up toward the surface on the low side of the current. Surface nutrient data presented by Kosro *et al.* [this issue] show that this water was enriched with nitrate. Figures 4 through 12 show that it supported a high biomass of various diatom species that were capable of high photosynthetic rates. Hayward and Mantyla [1990] and Chavez *et al.* [this issue] similarly argue that the geostrophic adjustment associated with a meandering current off northern California brought nutrient-rich, deep water up into the euphotic zone, and that this stimu-

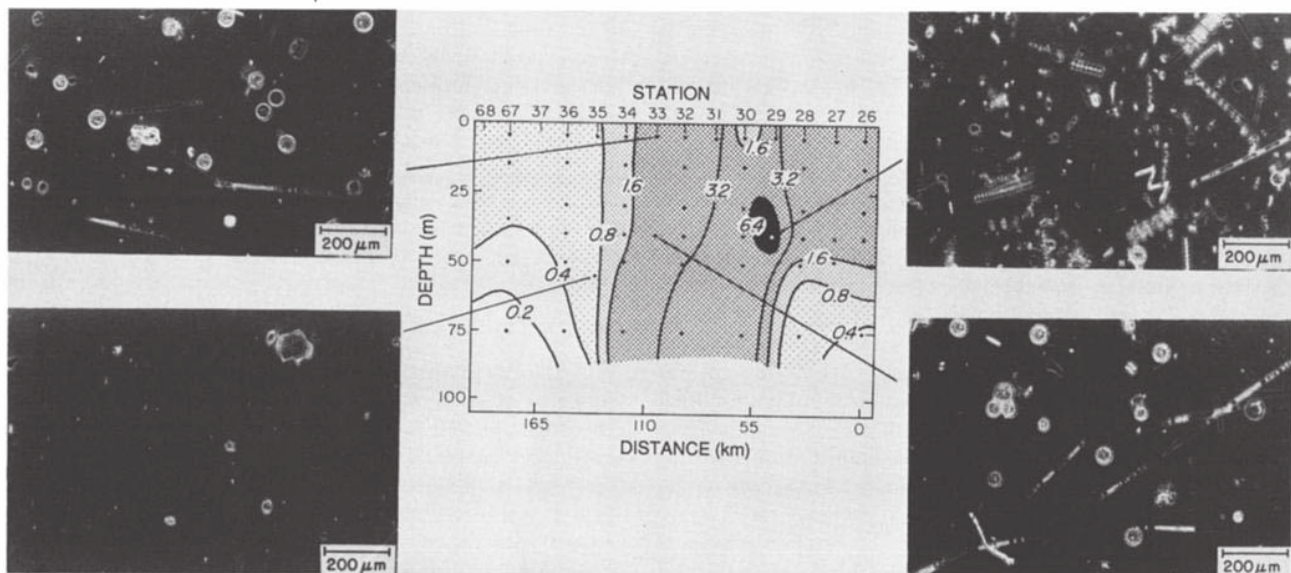


Fig. 11. The line II chlorophyll section with photomicrographs of phytoplankton.

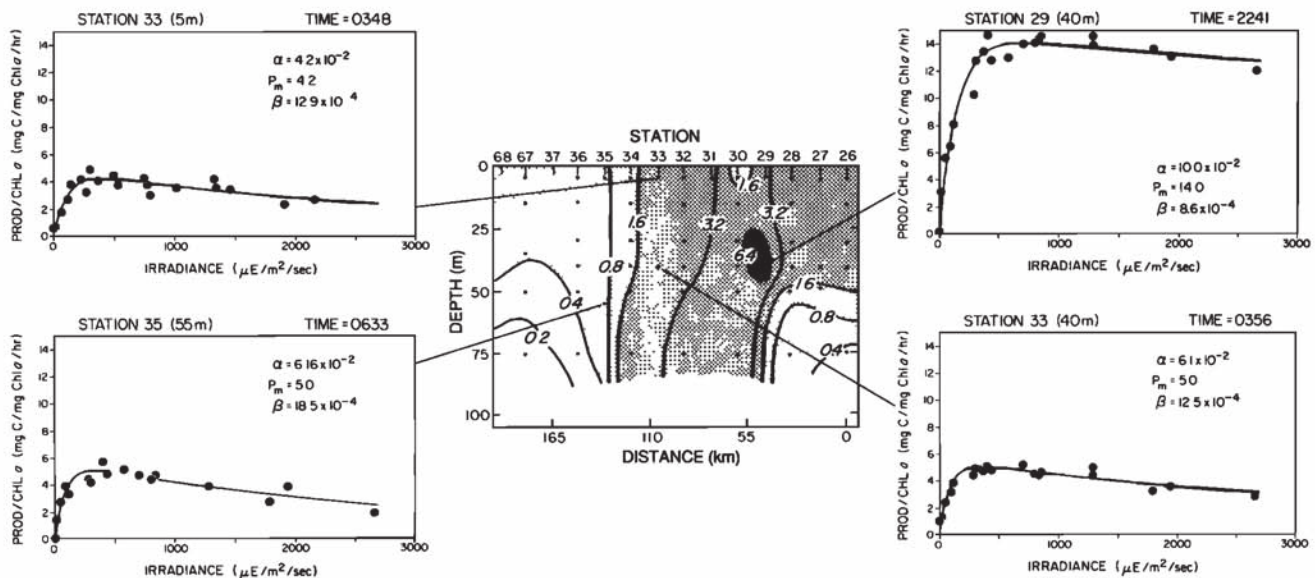


Fig. 12. As in Figure 6 for line II.

lated phytoplankton growth. However, *Chavez et al.* [this issue] also show a survey where this process apparently did not result in an increase in phytoplankton growth and/or biomass accumulation.

Some of the diatom biomass in our study area was being advected downstream in the current. In the northernmost section (line A) chain-forming diatoms were being carried south at the surface along the inshore edge of the flow (station 123, Figures 3, 4, and 5), and the diatoms in the deep patch of chlorophyll below 75 m were embedded in the southward flow (station 122, Figures 3, 4, and 5). Chlorophyll concentrations were about 1 mg m^{-3} in the current on its low side where it crossed southeastward through line C (Figure 3), and diatoms were detected there also (Figures 7 and 8). In the southern portion of the study area (line II) the chlorophyll concentrations in the seaward flow off Point Arena were of the order of 1 mg m^{-3} on its southern side (Figure 3), and the dense mixed diatom population below the surface farther south was moving seaward at about 10 cm s^{-1} and also southward (Figures 3, 10, and 11). *Strub et al.* [this issue] emphasize that there is similar evidence in other CTZ surveys that cold, nutrient-rich, and chlorophyll-rich water is advected downstream and offshore in seaward-flowing jets off Cape Mendocino and Point Arena. They point out that chlorophyll maxima are sometimes found in the core of these flows, and that some fraction of this biomass is probably advected back toward shore in meanders.

There is evidence that downward transport was occurring in the frontal zone at the low or cold edge of the current in all of our sections. The deep patch of chlorophyll-rich water that was embedded in the southward flow below 75 m in line A (Figure 3) was composed of chain-forming diatoms like those at the surface inshore (Figures 4 and 5). Given the high chlorophyll concentrations in the water column above this deep patch, we can assume that the euphotic zone was considerably shallower than 75 m (probably less than 30 m). Thus the diatoms in the deep patch could not have grown there, and we conclude that they must have grown nearer to

the surface somewhere upstream and were then transported downward. *Washburn et al.* [this issue] show similar evidence in a 1988 CTZ survey that phytoplankton biomass (chlorophyll) was being subducted below the euphotic zone in a seaward flow off Point Arena, and they suggest that it occurs along isopycnal surfaces. If this was the pathway in line A, then the diatoms at depth would have been transported along the deep pycnocline (grey-shaded area in σ_θ in Figure 3) at the inshore edge of the southward flow.

We interpret the chlorophyll and phytoplankton distributions in line C similarly. Moderately high chlorophyll concentrations ($> 0.8 \text{ mg m}^{-3}$) extended below 75 m in the current (Figure 3), and chain-forming diatoms were detected at 40 m in the flow (Figures 7 and 8) similar to those at the surface inshore. Thus it appears that diatoms from the surface were being carried downstream and transported downward. Relatively high chlorophyll concentrations extended below 75 m in line II (Figure 3) also. As in the northern section, we assume that this chlorophyll was well below the euphotic zone and therefore could not have grown there, but it appears that mixing was at least partly responsible for the downward transport. This is indicated in the hydrographic data in Figure 3 (and in the light response data; see discussion below), which show that density was vertically uniform in the upper 50 m of the water column south of the seaward flow off Point Arena (between stations 30 and 35).

Interpretation of the Light Response Curves

The light response curves, and the magnitudes of the fitted parameters α , P_{max} , and β (in Figures 6, 9, and 12) reflect at least four natural sources of variability in the phytoplankton populations. These are taxonomic composition, light history, viability (physiological condition), and the diel cycle in photosynthesis [*Richardson et al.*, 1983]. We are primarily interested in the degree to which the curves reflect the first three of these sources of variability, but diel oscillations in the photoresponse of natural assemblages of marine phytoplankton cannot be ignored. Productive di-

atom assemblages can exhibit ten-fold diel changes in P_{\max} [Harding et al., 1982] that can overshadow the other effects. Many studies have demonstrated and characterized diel variability in both α and P_{\max} [e.g., MacCaull and Platt, 1977; Prézélin and Ley, 1980; Harding et al., 1982; Prézélin et al., 1987], and it probably occurs in β also. Diel oscillations in P_{\max} and α covary and have daily maxima in the light period (usually midday or early afternoon) and minima in the dark period [Harding et al., 1982; Prézélin et al., 1987], and the amplitude of the oscillations in P_{\max} are usually more pronounced (e.g., four-fold and two-fold variations in P_{\max} and α , respectively, for diatoms [Prézélin et al., 1987]).

The diel variability in the light response curves in Figures 6, 9, and 12 complicates their interpretation, but since we know in general the timing and the amplitude of the effect, we can distinguish other sources of variability. In all of the sections where the volume of chain-forming diatoms (e.g. *Chaetoceros* spp., *Skeletonema costatum*, and *Thalassiosira* spp.) was large, P_{\max} was relatively high ($> 5 \text{ mg C mg Chla}^{-1} \text{ h}^{-1}$), regardless of the depth from which the sample was taken or the time of day of the incubation. Where chain-forming diatoms were absent, P_{\max} was relatively low ($< 5 \text{ mg C mg Chla}^{-1} \text{ h}^{-1}$). This apparent positive correlation between diatom volume and P_{\max} is statistically significant [Hood, 1990], and it has been observed in the field before [e.g., Curl and Small, 1965; Malone, 1971; Pearl and Mackenzie, 1977; Harding et al., 1982; Prézélin et al., 1987]. The P_{\max} of the diatom community at the surface at station 123 in line A (Figure 6) is close to the theoretical maximum assimilation number (chlorophyll-specific production rate) of $25 \text{ mg C mg Chla}^{-1} \text{ h}^{-1}$ predicted by Falkowski [1981], and the P_{\max} of the chain-forming diatoms below the surface at station 29 in line II (Figure 12) was also quite high ($14 \text{ mg C mg Chla}^{-1} \text{ h}^{-1}$), considering that it was measured at night on a sample from 40 m depth.

We can also distinguish differences in the light response curves for different depths that appear to be related to photoadaptation. This provides information about rates of vertical mixing [Lewis et al., 1984; Cullen and Lewis, 1988]. Phytoplankton in a uniformly mixed water column that is turning over rapidly (within a few hours) will have similar light response characteristics everywhere in the mixed layer because the cells do not reside at any one light level long enough to adjust to it. Since the time-course of photoadaptive changes in P_{\max} is of the order of several hours [Lewis et al., 1984], large differences in P_{\max} (e.g., a factor of 2) between surface (high light) and deep (low light) phytoplankton populations that have been collected and incubated at the same of time of day indicate that the cells have experienced different light conditions for at least several hours.

In line II at station 33 (just south of the seaward flow off Point Arena; see Figure 3) the light response of the diatoms at the surface and at 40 m depth was similar, which indicates that the upper 50 m of the water column was turning over in less than a few hours. Thus the light response data are consistent with the hydrographic data in Figure 3, which suggest that mixing was at least partly responsible for the high chlorophyll concentrations that extended below 75 m in line II.

We have argued that the diatoms in the deep patch of chlorophyll at station 122 in line A were subducted below the euphotic zone. The P_{\max} of this community was lower than that of the surface diatoms at station 123 by a factor of

3. This suggests that the cells at depth had been under low- or no-light conditions for at least several hours and that they were not transported to 75 m by rapid mixing processes. These diatoms may have been in low-light conditions for much more than several hours. Kadko et al. [this issue] estimate a subduction rate of 25 m d^{-1} in the frontal zone of a seaward flow off Point Arena. At this rate it would have taken 3.6 days for the diatoms at station 122 to arrive at 90 m depth if they were transported directly down from the surface, and they would have been at the surface at least 30 km upstream (assuming an average horizontal speed of 10 cm s^{-1}). Thus the lower P_{\max} of the diatom community at depth at station 122 may indicate some degree of cell senescence and also taxonomic differences, but the cells were clearly viable ($P_{\max} = 7.9 \text{ mg C mg Chla}^{-1} \text{ h}^{-1}$).

SUMMARY AND CONCLUSIONS

The evidence of entrainment and downstream advection in our data supports the interpretations of cold filaments in Rienecker et al. [1985], Rienecker and Mooers [1989], and Strub et al. [this issue], and the evidence of subduction in our data supports the interpretations of Flament et al. [1985], Kadko et al. [this issue], and Washburn et al. [this issue]. Diatoms were being carried downstream in the southward-meandering current, and it appears that viable cells had been subducted along the cold edge of the flow. The data presented in this paper also support the interpretations of Hayward and Mantyla [1990], and Chavez et al. [this issue]. Although diatoms were being carried downstream in the southward-meandering current, most of their biomass was located in relatively slow-moving water on the low steric height side of the flow where upwelling was occurring. These diatom communities were capable of high photosynthetic rates (P_{\max} between 5 and $25 \text{ mg C mg Chla}^{-1} \text{ h}^{-1}$), which suggests that they were healthy, growing populations. We reiterate the basic conclusion of Hood et al. [1990] that vertical, as well as horizontal transport associated with the southward-meandering current was responsible for the phytoplankton distributions in the study area. Cells were being advected downstream and subducted down and under the meandering current, and it appears that upwelling associated with the geostrophic adjustment brought deep water up to the surface and stimulated phytoplankton growth adjacent to the flow.

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