

Horizontal Transport and the Distribution of Nutrients in the Coastal Transition Zone off Northern California: Effects on Primary Production, Phytoplankton Biomass and Species Composition

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Conductivity-temperature-depth surveys during 1988 encountered strong baroclinic jets that were evident in acoustic Doppler current profiler and hydrographic data. During June and July 1988 a filament with high surface nitrate, high chlorophyll, abundant populations of neritic centric diatoms, and higher rates of primary production was evident perpendicular to the coast between Point Arena and Point Reyes. However, the high-nutrient and phytoplankton regions were not in the baroclinic jets but were south and inshore of them. Surface water transported offshore by the strong baroclinic jets was found to have relatively low nutrient content, suggesting that the jets themselves do not carry significant levels of coastally upwelled, high-nutrient water to the ocean interior. The low nutrient and salinity content of the jet suggests that the water originated several hundred kilometers upstream. Although the jets themselves do not appear to transport significant levels of nutrients directly from the coastal regime to the oceanic regime, dynamic processes associated with a meandering jet are likely responsible for high surface nutrients found several hundred kilometers offshore. Processes such as upwelling along the southern edge of the seaward jet result in significant enrichment of the coastal transition zone and in large blooms of neritic diatoms. During 1988 the high-nutrient, high-phytoplankton filament was present when the survey sequence began but then decayed after a month. The surface and subsurface nitrate fields were coherent with the dynamic topography field throughout the survey sequence; however, the surface and integrated chlorophyll fields were coherent only through the first two surveys. A decrease in phytoplankton biomass began during the third survey coincident with physical changes which occurred in that time frame: (1) an intensification of the undercurrent and (2) changes in the surface circulation from predominantly offshore to predominantly longshore. Understanding the processes responsible for the uncoupling between biology and physics is paramount for realistic biological models of this region.

INTRODUCTION

Eastern boundary current systems, and the strong coastal circulation patterns that are imbedded in them, are major oceanographic features that determine the physical, chemical, and biological character of a large portion of the global ocean [Ryther, 1969; Jahnke et al., 1990; Walsh, 1991]. An early view of the eastern boundary system was that they were broad, shallow, and slow currents [Wooster and Reid, 1963; Wooster, 1970] with a steady, slow, and uniform advective character. The concept of a slow and uniform current system began to change rapidly when satellite surveys clearly showed that the California and the Canary current systems consisted of a complex set of eddies and cross-stream jets [Bernstein et al., 1977]. Recently, a number of papers have provided documentation for the existence of energetic eddies and cross-stream jets as a dominant and persistent component of the dynamics of the eastern boundary current regions [Huyer, 1983; Mooers and Robinson, 1984; Huyer et al., 1984; Abbott and Zion, 1985; Davis, 1985; Flament et al., 1985; Rienecker et al., 1985; Kosro and Huyer, 1986]. The combination of traditional oceanography and satellite-borne surveys led to the coastal transition zone (CTZ) concept that jets and eddies determine the transition from the coastal processes to

the interior of the ocean beyond the continental margin. This concept of a highly energetic transition zone provided focus for the CTZ program in the form of well-defined questions on the origin, structure and consequences of these energetic processes.

The energetic jets and eddies of the coastal transition zone were originally identified on the basis of their temperature signature [Bernstein et al. 1977]. Later, ocean color [Abbott and Zion, 1985], dynamic height and velocity [Mooers and Robinson, 1984; Kosro and Huyer, 1986] were used to further describe these features. Before the CTZ work there was a preliminary physical and a partial biological description in terms of ocean color, but virtually no chemical description or studies on phytoplankton species distributions (see Traganza et al., [1983], for the only previous chemical description). Primary nutrient concentrations are useful for at least two reasons: (1) they provide an indication of the fertility of the region, and (2) they can be useful as tracers for deducing circulation and water mass structure [Tsuchiya, 1975, 1985; Chavez et al., 1985]. Nitrate, therefore, can provide an excellent means of describing the structure, source, and fate of the jets and eddies that complements that provided by temperature, salt, and ocean color.

The work described here used nitrate concentration and phytoplankton biomass and species composition in order to provide an improved resolution of the dynamic processes of the coastal transition zone and insight on how these processes determine the chemical and biological character of the adjacent ocean.

MATERIALS AND METHODS

A series of repeated conductivity-temperature-depth survey cruises were completed off northern California during 1988 (Table 1; Figure 1) as part of the Coastal Transition Zone (CTZ) program sponsored by the Office of Naval Research (ONR).

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Table 1. Cruises in the Northern California Coastal Transition Zone During 1988 With Individuals Responsible for the Different Measurements

Map	Ship	Date	Chief Scientist	Temperature, Salinity	ADCP	Nutrients	Chlorophyll
1	<i>Wecoma</i>	June 20-27, 1988	Kosro	Huyer	Kosro	Chavez	Chavez
2	<i>Point Sur</i>	July 5-12, 1988	Ramp	Ramp	Ramp	Chavez	Chavez
3	<i>Point Sur</i>	July 12 to July 18, 1988	Ramp	Ramp	Ramp	Chavez	Chavez
4	<i>Point Sur</i>	July 21-27, 1988	Stanton	Stanton	Stanton	Chavez	Chavez
5	<i>Wecoma</i>	July 29 to Aug. 4, 1988	Kosro	Huyer	Kosro	Chavez	Chavez

During each survey, surface nitrate was mapped with a horizontal resolution of 200 m yielding on the order of 10,000 observations per cruise. Continuous surface measurements of phytoplankton stimulated fluorescence were also collected. At the CTD stations (on the order of 75 per cruise) surface samples for chlorophyll *a* and phytoplankton species were collected from the ship's intake and from the surface Niskin bottle. Discrete water column samples to 500 m were collected with Niskin bottles on a rosette for the analysis of chlorophyll *a* and nutrients at stations 20 km apart. During 1987 [Kosro *et al.* this issue] size separations of chlorophyll *a* were performed using 1- and 5- μm Nuclepore filters [Chavez, 1989].

Continuous analysis of nitrate+nitrite was performed using reverse flow injection analyses [Johnson and Petty, 1983; Johnson *et al.*, 1985] with a Flow Injection Sciences model ATC-30005 on water collected from the ship's intake. Phytoplankton stimulated fluorescence was measured every 30 seconds using a Seatech fluorometer and a Seabird sealogger. The fluorometer

was immersed in a dark case through which water from the ship's intake flowed. The ship's intake was of the order of 5 m below the sea surface. Chlorophyll *a* concentration was measured on board ship with a Turner Designs model-10 fluorometer calibrated with commercial chlorophyll *a* (Sigma) [Chavez *et al.*, 1990]. The samples for determination of plant pigments are filtered onto 25-mm Whatman GF/F filters and extracted in acetone in a freezer for between 24 and 30 hours [Venrick and Hayward, 1984]. Other than the modification of the extraction procedure, the method used is the conventional fluorometric procedure of Holm-Hansen *et al.* [1965]. Nutrient samples collected from the CTD casts were frozen and returned to the Monterey Bay Aquarium Research Institute (MBARI), where they were analyzed on an Alpkem rapid flow analysis system for phosphate, silicate, nitrate, and nitrite using conventional wet chemistry [Sakamoto *et al.*, 1990]. Duplicate samples for phytoplankton species composition were preserved with cacodylate-buffered paraformaldehyde (pH of 7.4) and with

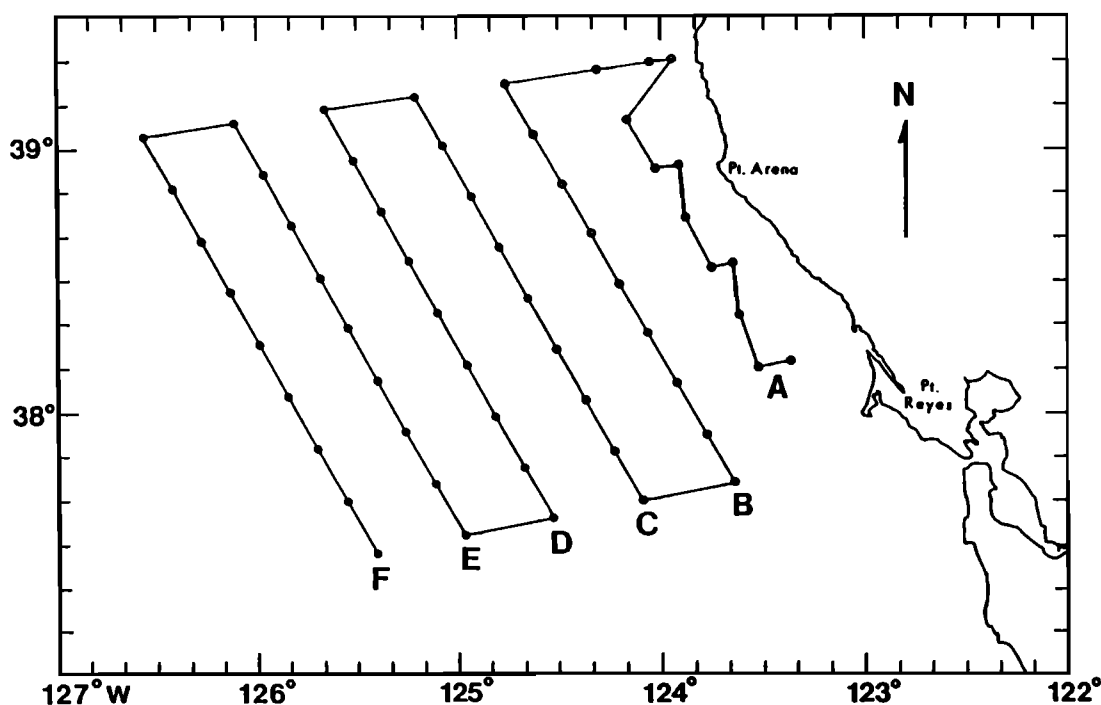


Fig. 1. Standard grid for the CTD surveys during 1988. Full completion of the grid required 1 week.

glutaraldehyde both to a final concentration of 2%. The paraformaldehyde samples were concentrated by gravity in settling chambers and counted using an inverted microscope [Utermöhl, 1958]. Settled volumes ranged from 25 to 50 mL depending on the chlorophyll concentration. Large organisms (i.e., netplankton) were counted over half the base of the settling chamber at 100x and small organisms (i.e., nanoplankton) were counted on transects, representing 2 mL of settled volume, at 400x. Organisms were identified to species whenever possible, however, when identification to species was not possible; as was the case with the small flagellates, individuals were assigned to a genus or group.

In view of the paucity of primary production measurements in the study area estimates were made using multiple regression models. Photosynthetically active radiation (PAR) was measured continuously on the two 1988 *Wecoma* cruises with a Biospherical 240l sensor. The PAR data were provided by C. Paulson of Oregon State University. PAR and surface chlorophyll were used to estimate primary production. The model relating chlorophyll, PAR and primary production was developed from observations in Monterey Bay (F.P. Chavez, unpublished data, 1990). In Monterey Bay, surface chlorophyll (plus phaeopigments) and PAR explain 70% of the variance in primary production (Figure 2).

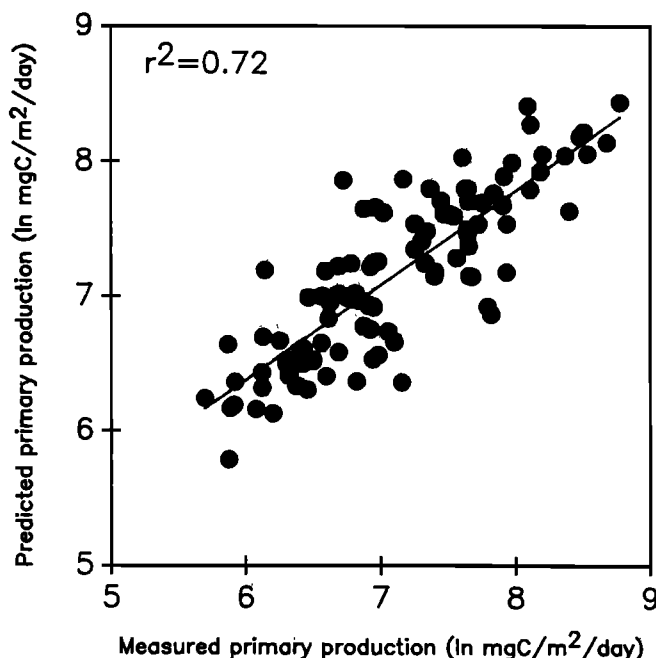


Figure 2. Scatter plot of measured euphotic zone depth integrated primary production against that predicted from surface pigments (chlorophyll+phaeopigments) and PAR (measured at the Monterey Bay Aquarium). The data were collected in Monterey Bay from April 1989 through April 1990. The model predicts slightly higher rates than those observed at lower levels and slightly lower levels than those observed at the higher levels. The regression equation is $\ln(\text{primary production (mgC/m}^2\text{/day)}) = 5.72 + 0.00029 \cdot \text{PAR } (\mu\text{E/cm}^2\text{/day, measured with a cosine sensor}) + 0.33 \cdot \ln(\text{surface chlorophyll } a + \text{phaeopigments (mg/m}^3\text{)})$

RESULTS

The surveys during 1988 focused on the the region off Point Arena and Point Reyes, where strong baroclinic jets were known to occur [Kosro and Huyer, 1986; Kosro et al., this issue]. The zone of interest, defined as the coastal transition zone, represents a transition between the narrow and productive coastal upwelling zone (about 25 km wide in the area of study) and the extensive oligotrophic central gyre. The surveys during 1988 also encountered strong baroclinic jets that were clearly visible in the acoustic Doppler current profiler (ADCP) and hydrographic data (Huyer et al., [this issue]; Figure 3).

The spatial distribution of biological and chemical properties showed that a filament with higher surface nitrate, higher chlorophyll, and abundant populations of neritic centric diatoms was evident off Point Arena and Point Reyes during late June and early July 1988 (Figures 3 and 4). The filament extended from the inner portion of the survey to the outer portion of the survey grid about 250 km from shore. The width of the feature, along the D line (Figure 1), was of the order of 75 km. The distinct mesoscale structure of the energetic eddies and cross-stream jets that are part of the California Current system was evident in the horizontal distribution of nitrate, chlorophyll, phytoplankton taxa, and dynamic topography (Figures 3 and 4).

The horizontal variability in surface nutrients and phytoplankton while coherent with the advective regime was not as expected. Visual inspection showed that the regions of strongest offshore flow were regions of relatively low levels of nutrients and phytoplankton. The higher surface nutrient and phytoplankton regions were primarily to the south (or inshore) and only partially imbedded in the regions of strong flow. Huyer et al. [this issue] showed that the strong baroclinic jets could be defined in terms of dynamic topography. Using the analysis of Huyer et al., it can be shown that off Point Arena, the strong offshore jets typically transport low nutrient and phytoplankton waters at the surface (Figure 5).

Continuous measurements of surface currents, nitrate, fluorescence, temperature and density show a clear offset between the location of the strong baroclinic jets and the maxima or minima in these properties (Figure 6). An exception to this pattern is salinity whose minima is coincident with the strongest flows. Huyer et al. [this issue] and Kosro et al. [this issue] have inferred from the low salinity, characteristic of northern waters, and other evidence that the strong baroclinic jets are part of a meandering California Current. The low nutrient levels found in the jets also suggests that these waters must have originated several hundreds of kilometers upstream rather than at the coast. The time scale of nutrient depletion in coastal upwelling systems is of the order of 5-10 days [MacIsaac et al., 1985] and the speed in the core of the jets was around 70 cm/s. If the water in the jet was of coastal upwelling origin it had to have travelled from 300-600 km prior to arrival at the D line (Figure 6). The D line, however, was only 150 km from shore, so it is likely that the water carried by the jets originated upstream of Point Arena.

The strong gradients in biological and chemical properties at the surface were also evident subsurface. Nitrate concentration at 100 m showed a strong gradient below the jet axis (Figures 3, 7, and 8) with the nitricline rising sharply on the south or inshore side of the jet (Figures 7 and 8). A strong and robust relationship was found between dynamic topography (or pycnocline depth) and nitrate concentration integrated to 100 m and confirms that

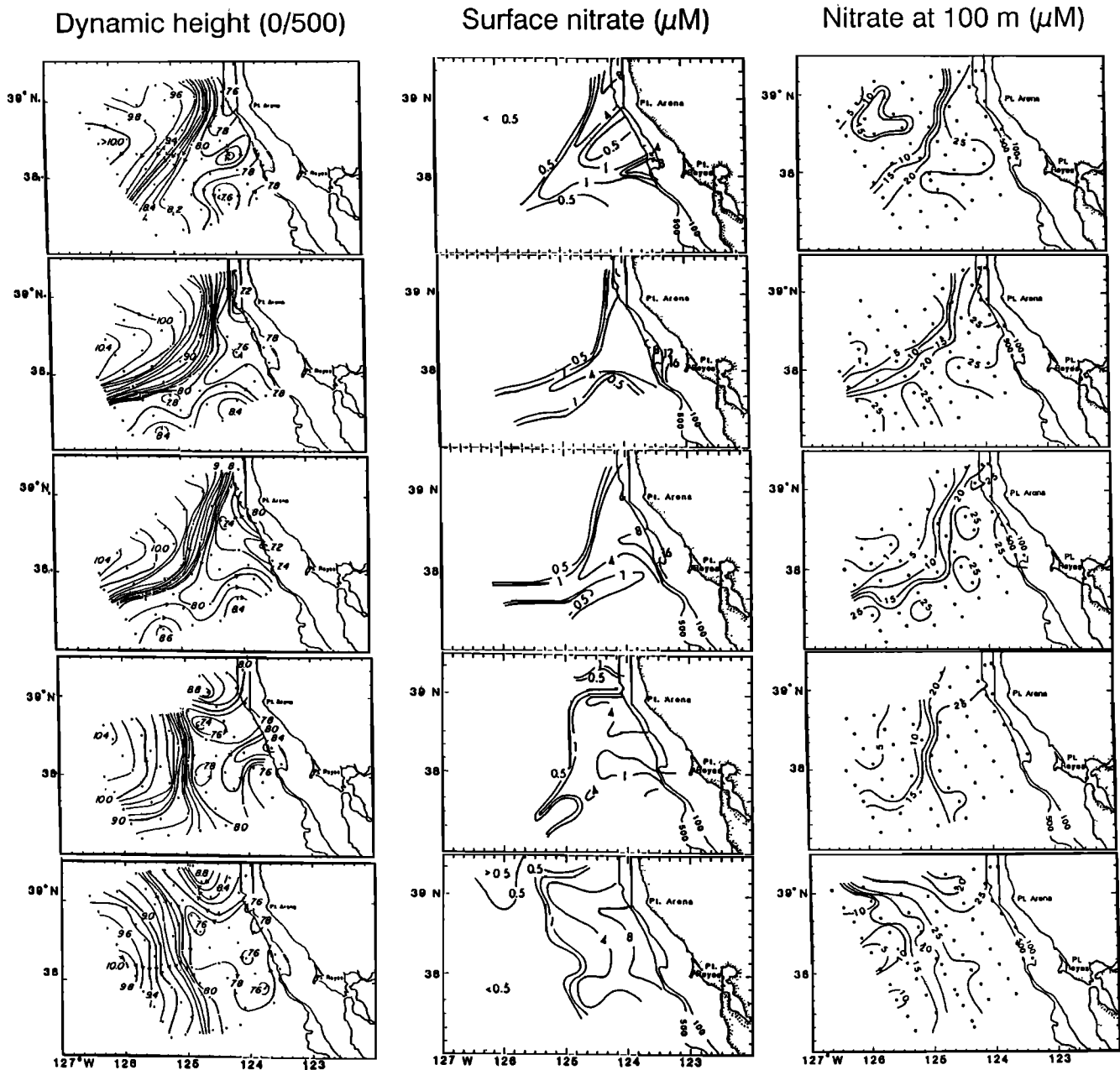


Fig. 3. Maps of geopotential anomaly (relative to 500 dbar), surface nitrate+nitrite (from continuous measurements), and nitrate at 100 m for the five surveys in Table 1.

the rise in the nutricline begins on the southern or inshore side of the jet (Figure 9). The doming of the nutricline, presumably as a result of dynamic processes associated with the jets, must be in part responsible for the increased nutrient levels at the surface but the exact mechanism for surface nutrient enrichment is yet to be fully resolved. Candidates include upwelling along the jet edges [Paduan and Niiler, 1990; Dewey and Moun, 1990] and vertical wind mixing on a shallow nutricline [Dewey and Moun, 1990]. The nutricline doming occurs over a larger scale than the surface enrichment, implying that vertical mixing is not the primary process at work. The distribution of properties suggests local upwelling at the southern edge of the jet (Figure 7; see also Figure 10 of Huyer *et al.*, [this issue]) and this mechanism seems

to be a strong candidate for supplying new nutrients to the coastal transition zone.

During 1988 the filament off Point Arena and Point Reyes was evident for close to a month and then decayed as flow became predominantly longshore. The surface and subsurface nitrate fields were coherent with the dynamic topography field throughout the survey sequence (Figures 3 and 9). The surface and integrated chlorophyll fields were well correlated with dynamic height (Figure 10) and coherent through the first two surveys (Figures 4 and 9). A decrease in phytoplankton biomass began during the third survey and may be related to physical changes which occurred in that time frame: (1) the undercurrent intensified [Huyer *et al.*, this issue] and (2) the circulation

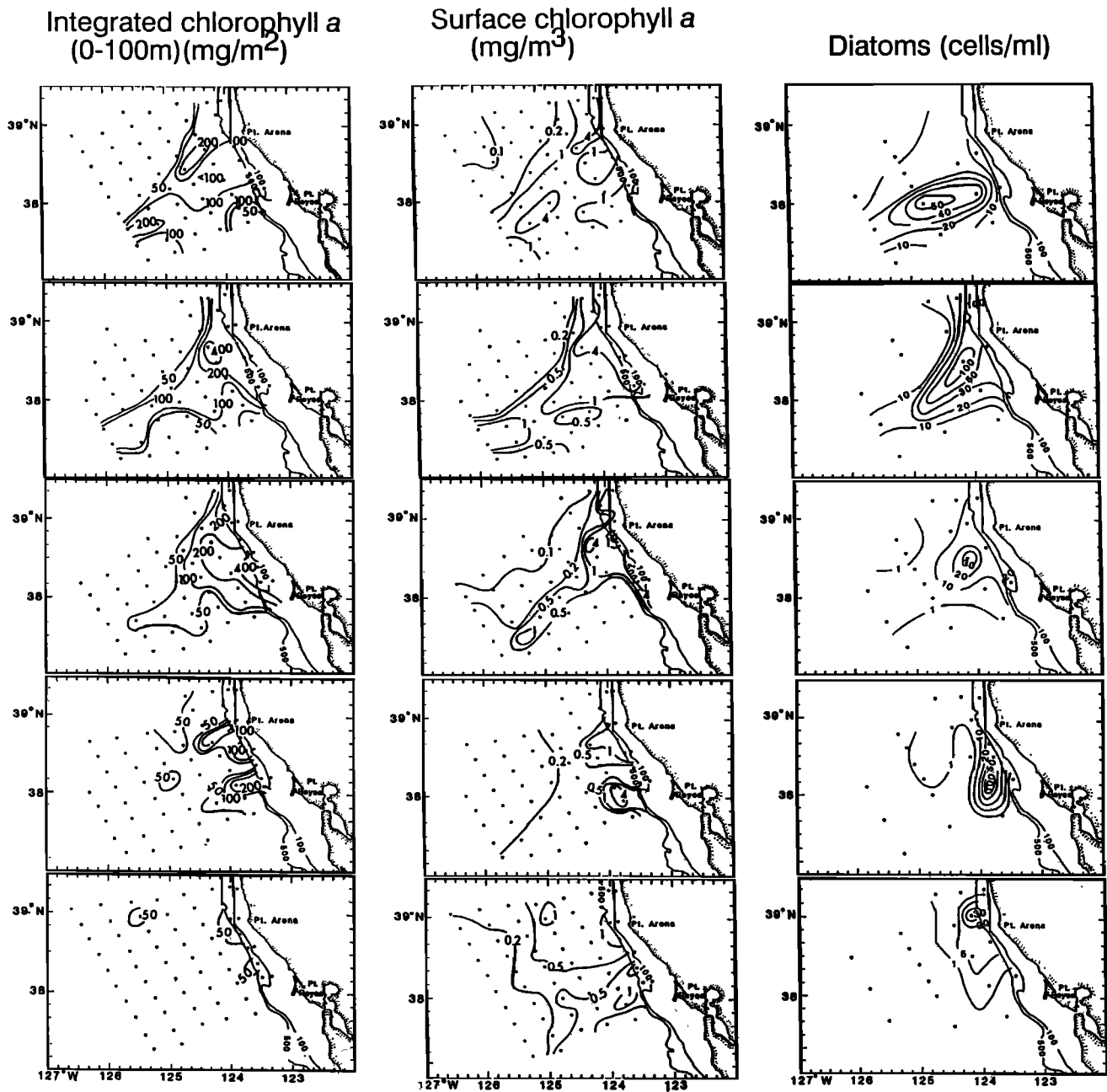


Fig. 4. Maps of integrated chlorophyll *a* (0-100 m), surface chlorophyll *a*, and surficial abundance of diatoms for the five surveys in Table 1.

changed from predominantly offshore to predominantly longshore (Figure 3). A time series of phytoplankton abundance along the D line (150 km offshore) shows the dramatic decrease in chlorophyll and neritic diatom populations (principally *Chaetoceros debilis*, *C. concavicornis*) from map 1 to map 5 (Figure 11), suggesting that the decrease in chlorophyll was related to a decrease in diatom abundance. The diatom bloom found during the first two surveys apparently resulted in a depletion of silicate with respect to nitrate over the course of the survey sequence (Figure 12). It is not clear why the phytoplankton populations decayed as flow became longshore or the undercurrent intensified, since nutrient levels remained high

and actually increased in many of the areas where phytoplankton levels diminished (Figures 3, 4, and 9).

The correlation between chlorophyll concentration and the abundance of diatoms was higher than with any other taxonomic group (Table 2) and diatoms dominated all samples where chlorophyll *a* (chl *a*) concentration exceeded 0.5 $\mu\text{g/L}$. Below this concentration the relative contribution of coccolithophorids and small flagellates to phytoplankton biomass increased. Dinoflagellates were never important contributors to phytoplankton biomass during the study period. Picoplankton populations could not be properly enumerated using settled samples but size separations during 1987 showed that on average

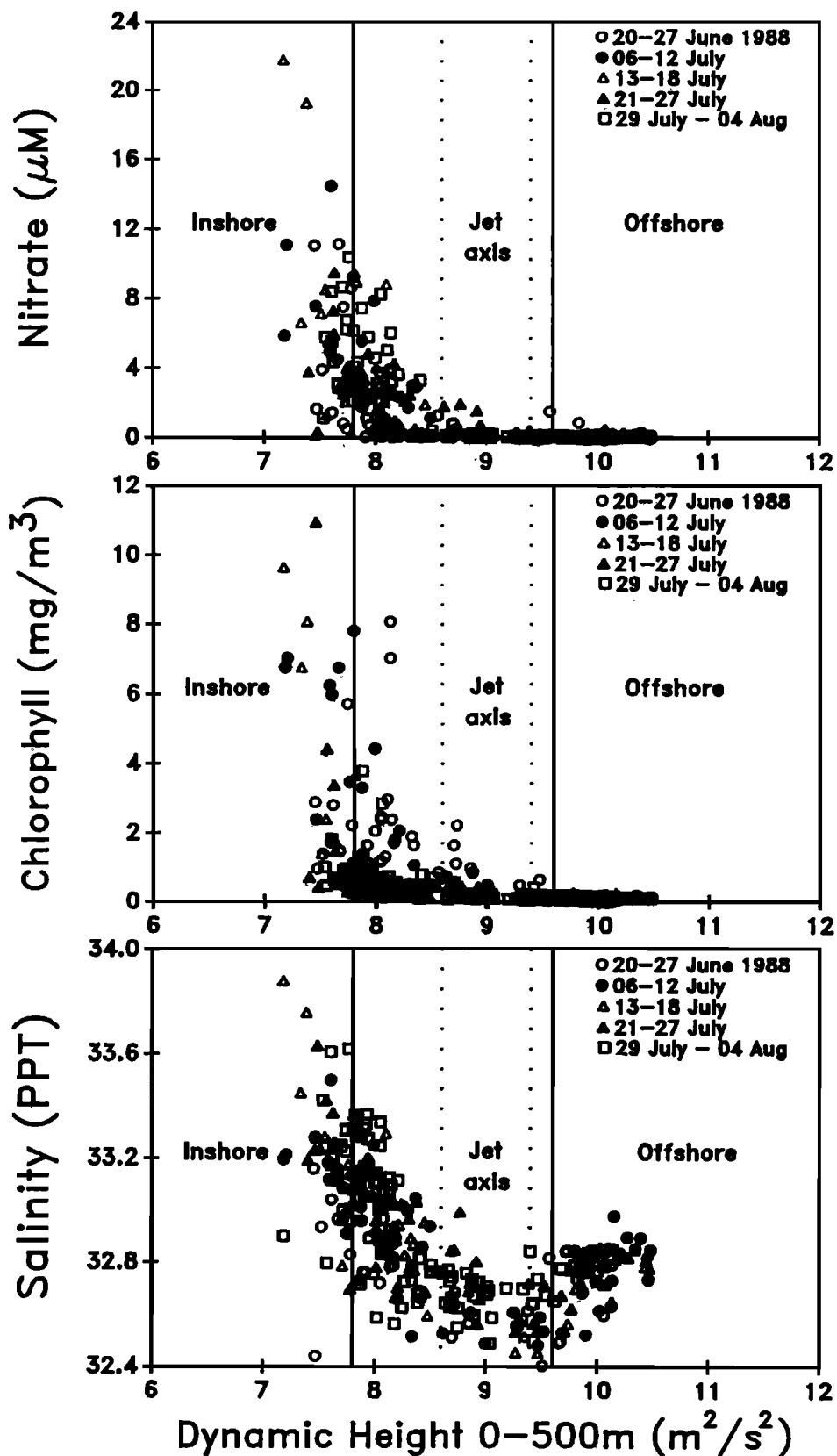
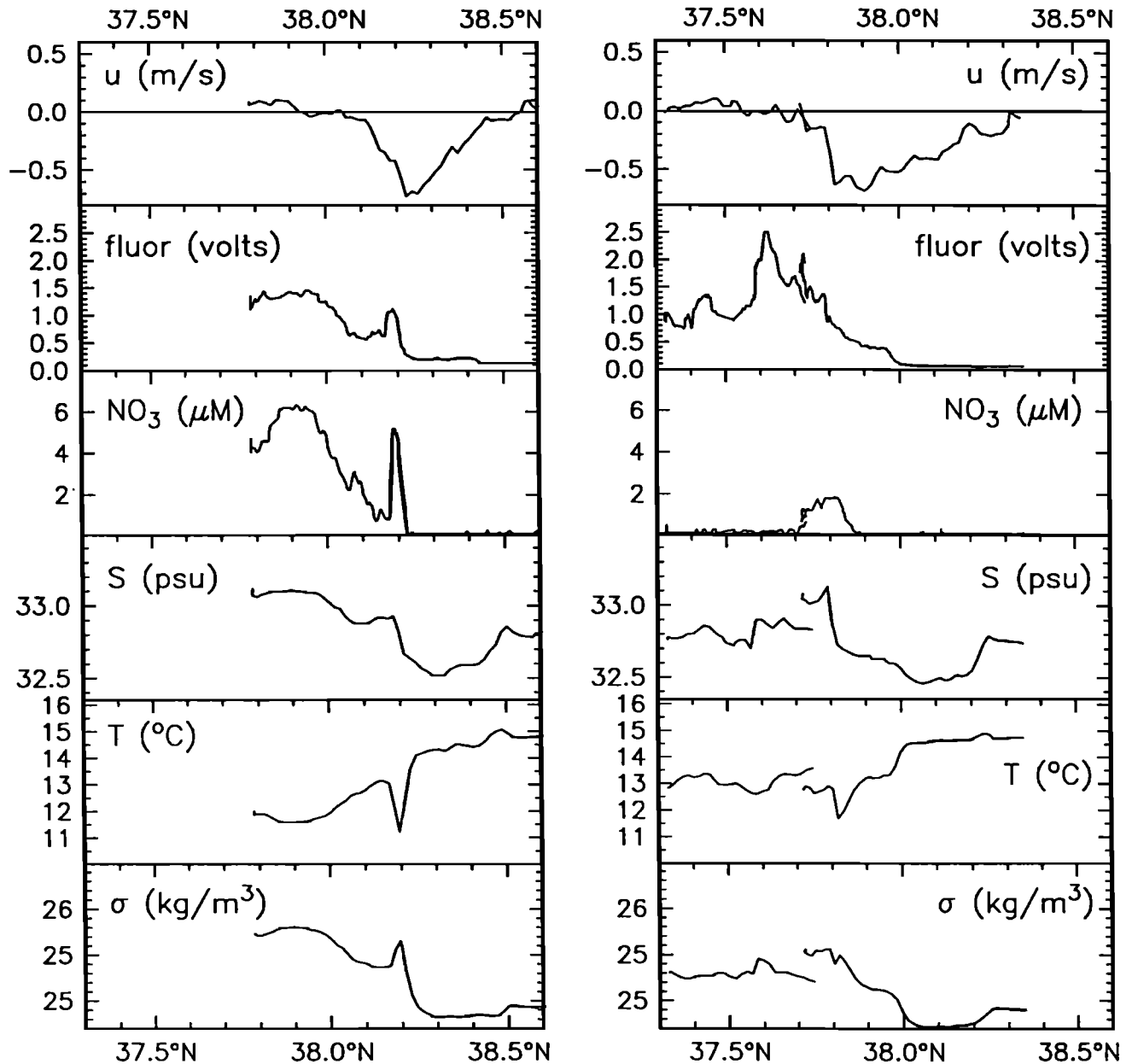


Fig. 5. Scatter diagrams of surface nitrate, surface chlorophyll and surface salinity against geopotential anomaly (relative to 500 dbar) for the five surveys in Table 1. The definition of the inshore, jet axis, and offshore portions of the coastal transition zone region is from *Huyer et al.* [this issue]. Clearly the areas of high nutrients, chlorophyll, and salinity are on the inshore (and southern) side of the jet.



D line, 6/26–6/27/88

E line, 6/25–6/26/88

Fig. 6. Values of near-surface variables along the D and E lines during the first survey cruise (normal component of the current, negative offshore (m/s), fluorescence (volts), nitrate+nitrite (mM), salinity (psu), temperature ($^{\circ}$ C), and density anomaly (kg/m^3). Fluorescence was well correlated with chlorophyll *a* ($r=0.91$), and the regression equation was chlorophyll = $-0.958 + 4.68 \cdot \text{fluorescence}$.

35% of the chlorophyll in the warm "eddy" found to the north of the Point Arena filament passed through a 1- μm Nuclepore filter. Recent work off Monterey Bay with epifluorescence microscopy [K.R. Buck and F.P. Chavez, unpublished data, 1990] shows that the warm eddy regions of the coastal transition zone are dominated by *Synechococcus*, prochlorophytes, and other very small (less than 5 μm) solitary phytoplankton. The size separations also showed that there is a relationship between chlorophyll concentration and the percentage of phytoplankton

retained by 5- μm Nuclepore filters (Figure 13); at levels over 2 $\mu\text{g chl } a/\text{L}$ almost all of the biomass, dominated by diatoms, was retained by the 5- μm filters. The vertical distribution of chlorophyll and nitrate show that in the oceanic (north or offshore) regions there is a deep chlorophyll maxima [Cullen and Eppley, 1981] coincident with the top of the nitracline and the depth of the 1% isolume (Figures 8 and 14).

The filament primary production rates predicted by the chlorophyll and light model (Figure 15) are similar to those found

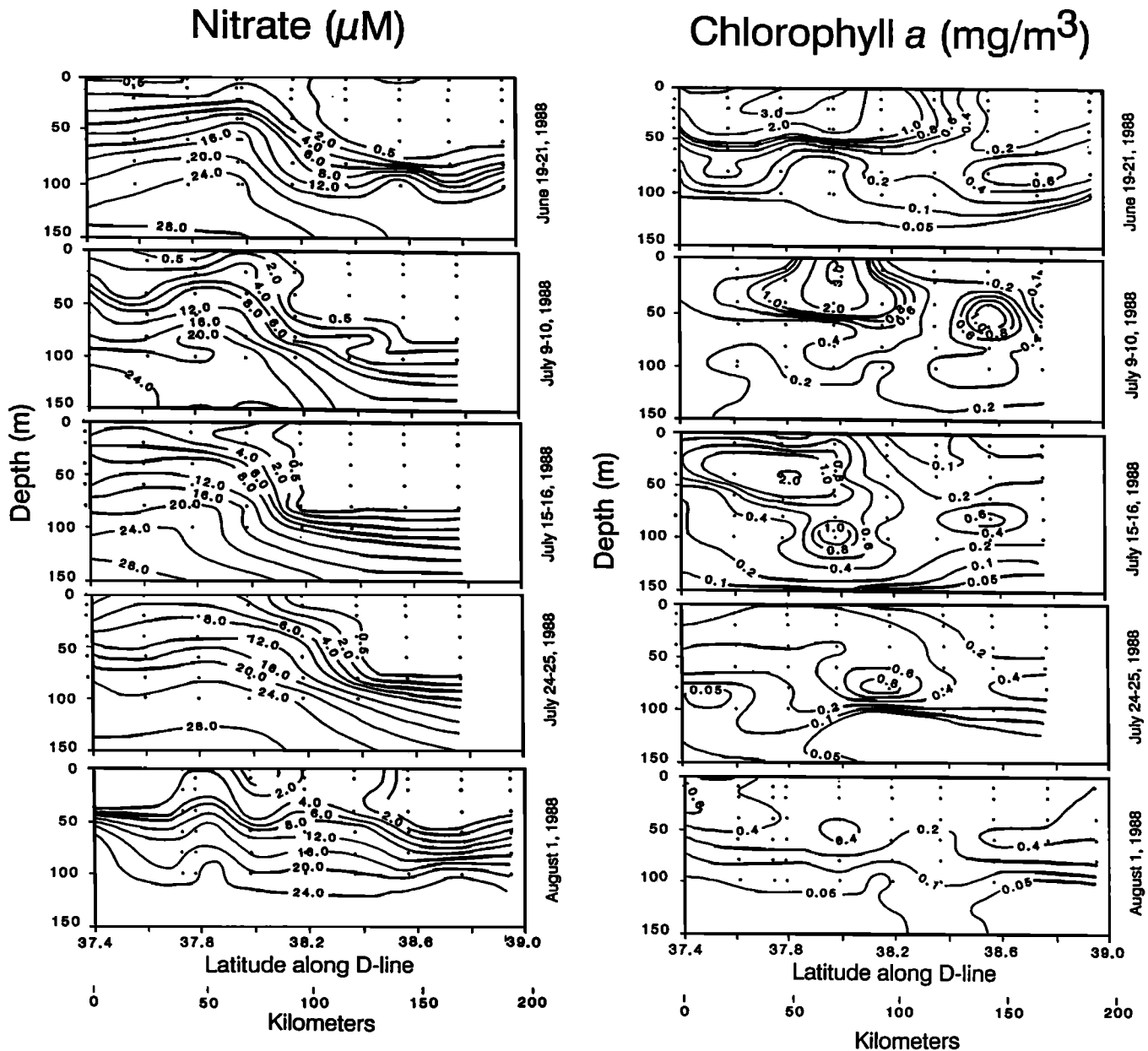


Fig. 7. Sections of nitrate and chlorophyll *a* along the D line (see Figure 1) for the five surveys in Table 1.

in other coastal upwelling environments [Chavez and Barber, 1987]. Primary production rates are close to 4 times higher in the filaments than in the warm oceanic eddies (Figure 15). The strong offshore baroclinic jets result in rates that are commonly found within the coastal upwelling domain (i.e., the Rossby radius of deformation) farther offshore. The mean production rates for the survey box were $1240 \text{ mgC/m}^2/\text{day}$ during the first survey, when abundant phytoplankton populations were found, and close to 50% lower ($740 \text{ mgC/m}^2/\text{day}$) during the last survey, when the offshore phytoplankton biomass was low.

DISCUSSION

Results from 1988 suggest that the strong baroclinic jets commonly found in the coastal transition zone [Kosro and Huyer, 1986] are not responsible for significant transport of coastally

upwelled, high-nutrient water to the ocean interior. The surface waters transported by the jets were found to have relatively low levels of nutrients (Figure 3). Waters of higher nutrient content were found several hundreds of kilometers from shore but they were typically to the south and inshore of the baroclinic jets. To the north and offshore of the jets the surface waters were warmer and had lower nutrient levels. Although the jets themselves do not appear to transport significant levels of nutrients directly from the coastal regime to the oceanic regime, dynamic processes associated with the jets are likely responsible for high surface nutrients found several hundred kilometers offshore. The high levels of surface nutrients offshore may be due to processes like upwelling along the southern edge of the seaward jet so that circulation patterns associated with the jets and eddies result in a contribution of new nutrients to the coastal transition zone.

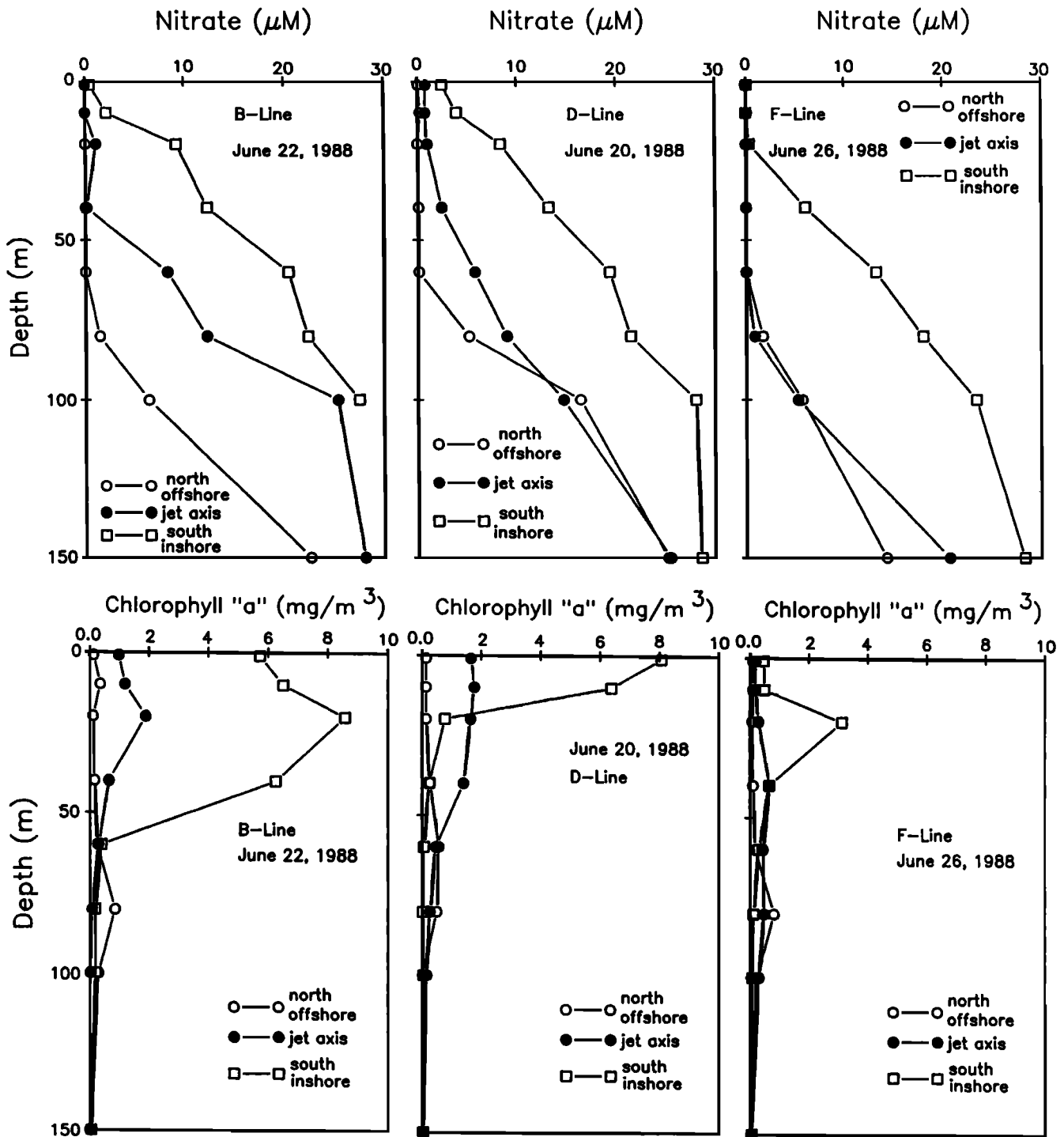


Fig. 8. Vertical profiles of nitrate and chlorophyll *a* made along the B, D, and F lines during the first survey in June 1988. The raised nutricline and enhanced phytoplankton populations are evident in all the inshore stations. The jet axis is intermediate between the inshore and offshore stations. The deep chlorophyll maxima in the north or offshore waters are at the same level as the 1% isolume and the top of the nutricline.

The strong correlation found in this study between dynamic height and upper ocean nutrient content (Figure 9) is similar in nature to the strong correlation found by Chavez [1987] and Chavez and Brusca [1991] for sea level and upper ocean nutrient content in the southeastern Pacific. Barber and Chavez [1986] argue that the basin-wide patterns in productivity of the tropical

Pacific are related to dynamic processes that regulate thermocline topography. The connection between thermocline topography and productivity is upper ocean nutrient content: when the thermocline and nutricline are deep (and dynamic height and sea level are high), the source of new nutrients is farther from the euphotic zone. Measurements of sea surface height from

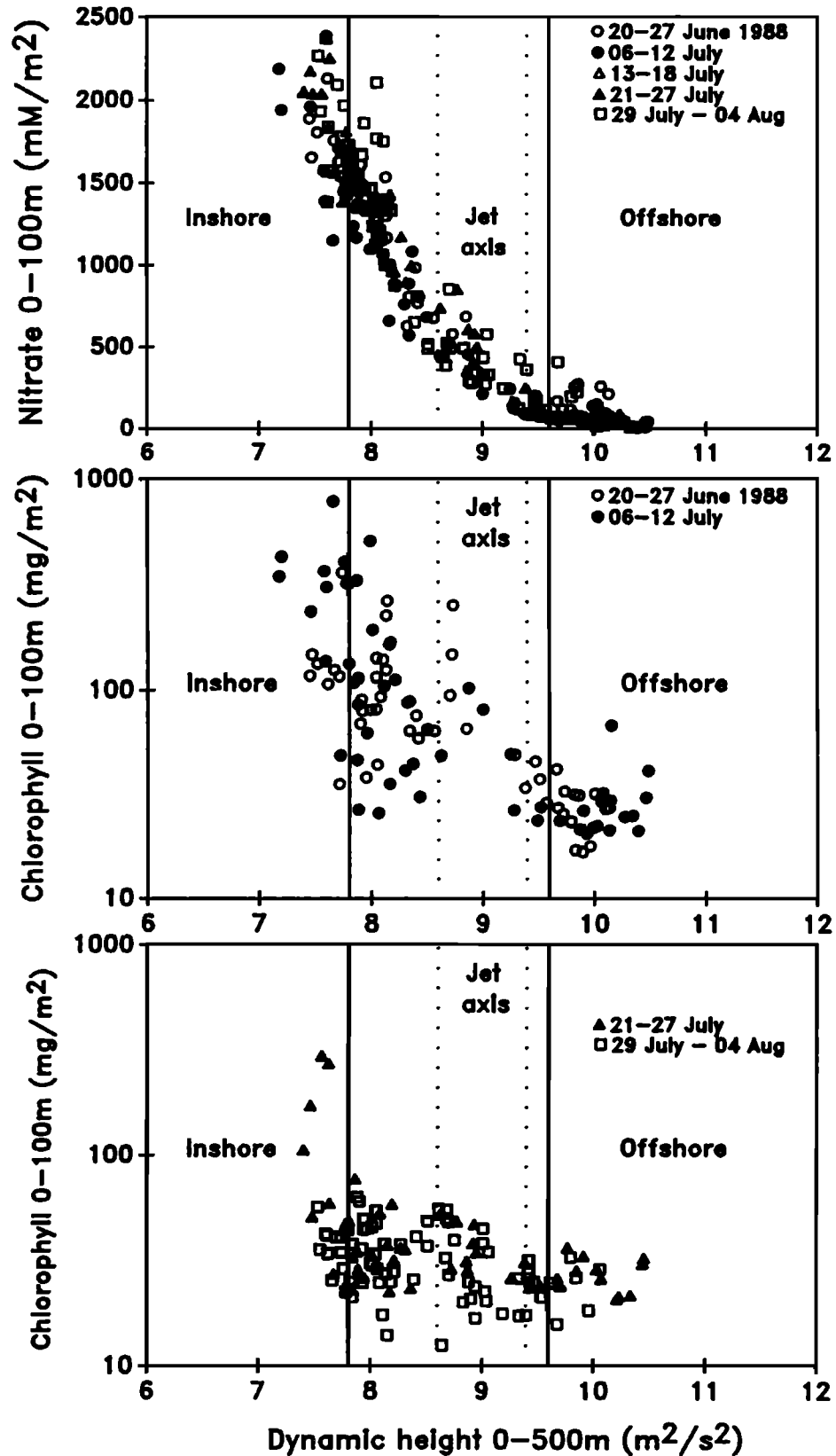


Fig. 9. Scatter diagrams of integrated nitrate and integrated chlorophyll *a* against geopotential anomaly (relative to 500 dbar) for the five surveys in Table 1. The definition of the inshore, jet axis and offshore portions of the coastal transition zone region is from *Huyer et al.* [this issue]. The relationship between dynamic height and nitrate is the same for all surveys, but the relationship changes for chlorophyll. Dynamic height explained 62% of the variance in integrated chlorophyll the first cruise, and the r^2 value decreased with each cruise until only 16% of the variance could be explained during the last cruise.

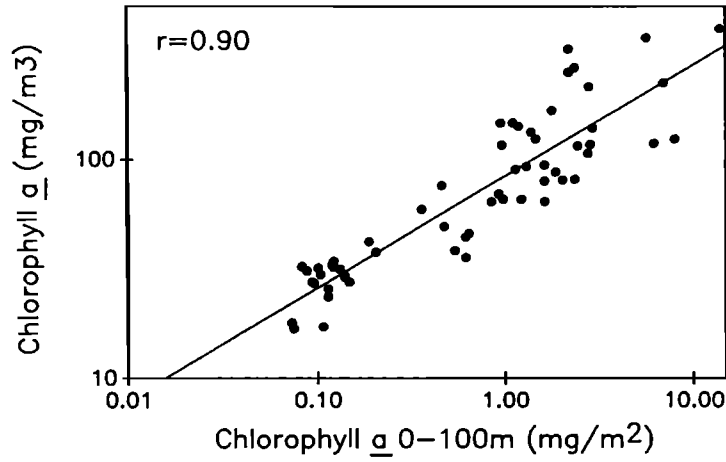


Fig. 10. Scatter plot of surface and integrated chlorophyll during the first cruise. The relationship was strong throughout the survey sequence with a correlation coefficient of 0.81 when all cruises were considered.

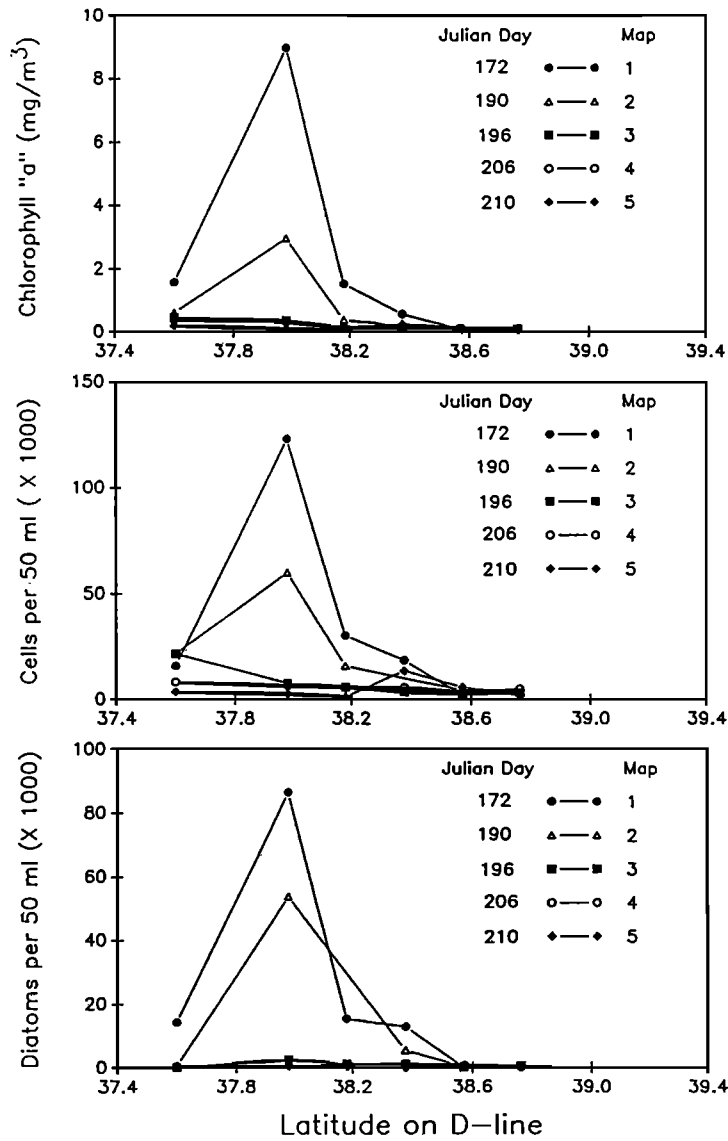


Fig. 11. Surface concentrations of chlorophyll *a*, phytoplankton cells, and diatoms along the D line (Figure 1) for the five surveys in Table 1. The decay in phytoplankton populations, primarily diatoms, from map 1 to map 5 is evident.

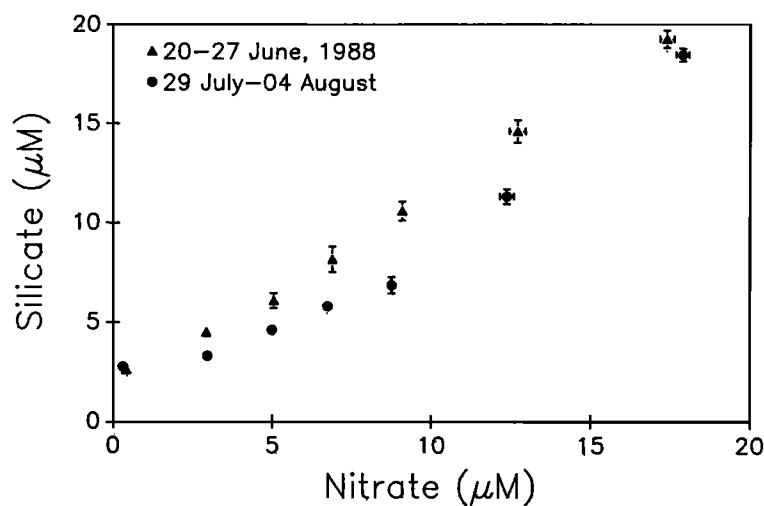


Fig. 12. Plot of nitrate against silicate showing a depletion of silicate with respect to nitrate between the first and the last survey. The data were binned and averaged on nitrate concentration (0-2, 2-4, 4-6, 6-8, 8-10, 10-15, 15-20). Also plotted are the standard error's of the means. Nitrate reaches very low levels before silicate (and phosphate) in this region.

satellites can likely be used to estimate upper ocean nutrient content in this region. More study is required, at least on the mesoscale, to better define the relationship between dynamic topography and phytoplankton biomass (Figure 9).

Two distinct phytoplankton communities were found in the coastal transition zone: (1) a coastal diatom-dominated community and (2) an oceanic small, solitary phytoplankton community. The spatial distribution of phytoplankton populations was similar to that observed for nutrients in that high-chlorophyll areas, dominated by neritic diatom communities, were found to the south and inshore of the jets and low chlorophyll areas, dominated by small solitary phytoplankton

characteristic of oceanic waters, were found to the north and offshore. The strong jets were partially imbedded in both systems and appear to act as a boundary between them [Hood *et al.*, 1990]. Not surprisingly, the species composition of zooplankton showed similar spatial structure [Mackas *et al.*, this issue]. It can be inferred from production rates and food web structure that vertical particulate flux resulting from the diatom-dominated communities should be several times the flux resulting from the small, solitary phytoplankton oceanic communities [Michaels and Silver, 1988].

The dramatic changes in phytoplankton populations observed during the survey sequence suggests that much of the week-to-

Table 2. Statistics and Correlation Coefficients of Phytoplankton groups vs. Chlorophyll Concentration for Samples Collected Along the D Line (Figure 1) During the Five Surveys (Table 1)

Variable	N	Mean	Standard Deviation	Maximum	Minimum	Correlation Coefficient
Chlorophyll, $\mu\text{g/L}$	32	0.81	1.68	8.98	0.05	
Phytoplankton, cells/50 mL	32	16297	24108	123190	1160	0.95*
Coccolithophorids, cells/50 mL	32	1876	1921	8425	200	0.43+
Diatoms, cells/50 mL	32	8587	18487	86415	9	0.79*
Centrics, cells/50mL	32	7548	16496	76640	9	0.75*
Pennates, cells/50mL	32	1019	2189	9775	0	0.86*
Dinoflagellates, cells/50 mL	32	343	482	2114	0	0.00
Silicoflagellates, cells/50 mL	32	12	49	275	0	0.56*
Monads, cells/50 mL	32	5498	6674	30350	300	0.64*

* Significant at the 99% confidence level.

+ Significant at the 95% confidence level.

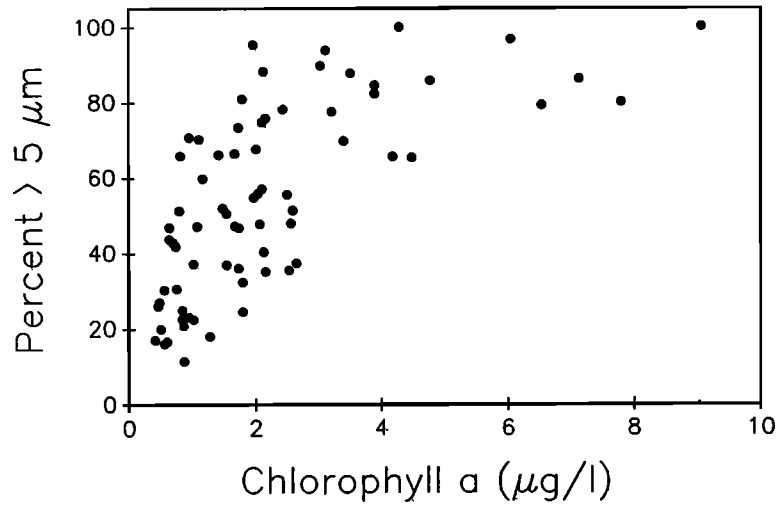


Fig. 13. Scatter plot of chlorophyll concentration against the percentage of chlorophyll retained by a $5\text{-}\mu\text{m}$ Nuclepore filter for the survey in May 1987 [see *Kosro et al.*, this issue].

month variability in phytoplankton biomass composition and production in this region can be related to the variability in the mesoscale circulation of the jets and eddies. Relationships between circulation, plankton, and nutrients in the California Current system derived from data collected quarterly [*Chelton et al.*, 1982] may need to be reinterpreted in light of these observations. The decrease in phytoplankton biomass and production, associated with the disappearance of diatom populations, about halfway through the sequence of surveys is extremely interesting even though we have yet to determine the reasons for the demise of the diatoms. The timing of the disappearance coincided with an intensification of the undercurrent [*Huyer et al.*, this issue] and a change in the circulation from a predominantly offshore pattern to predominantly longshore (Figures 3, 4, 6, 7, and 8). The observed changes may be related to seasonal variations in the California Current System. Just south of this region, Skosberg (1936) and Bolin and Abbott (1963), have described physical and biological changes that occur in July and August between the

upwelling period and the oceanic period when oceanic waters are observed closer to the coast. Episodic and dramatic decays in phytoplankton populations are probably important characteristics of this region and may contribute significantly to the removal of carbon (and silicate) from the surface to the deep sea and to the ecological character of the region [*Smetacek*, 1985; *Walsh*, 1983].

One interpretation for the decreases in phytoplankton populations is that the diatom-seeding mechanism (either upwelling to the south of the strong currents or offshore advection) disappeared after map 3. The uncoupling between the nutrient and phytoplankton fields which occurs after map 3 would then be a result of the lack of supply of neritic centric diatoms (the organisms generally responsible for high biomass in the ocean) to the offshore regions. A similar scenario has been proposed for the equatorial Pacific [*Chavez*, 1989]. *Martin and Gordon* [1988] found that the filaments of the coastal transition zone in northern California had relatively high levels of iron. *Martin* and his co-workers [*Martin*, 1990] suggest that iron is a particularly limiting nutrient in the ocean and conceivably the

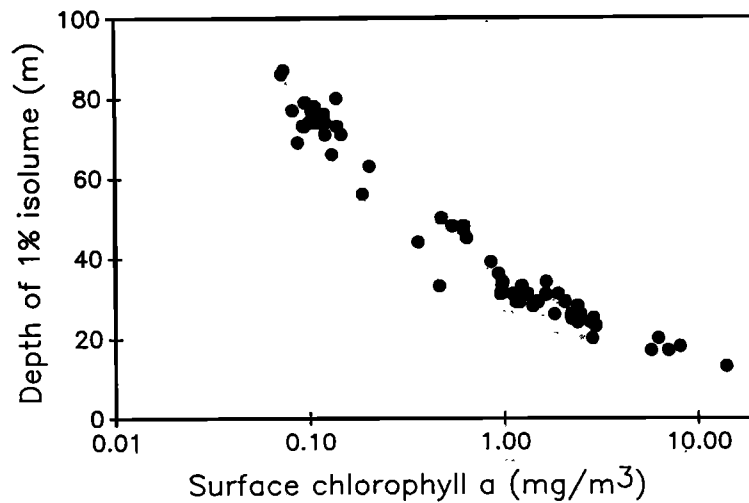


Fig. 14. Relationship between surface chlorophyll and the depth of the 1% isolume as estimated from an optical model [*Morel*, 1988] for stations of the first survey cruise.

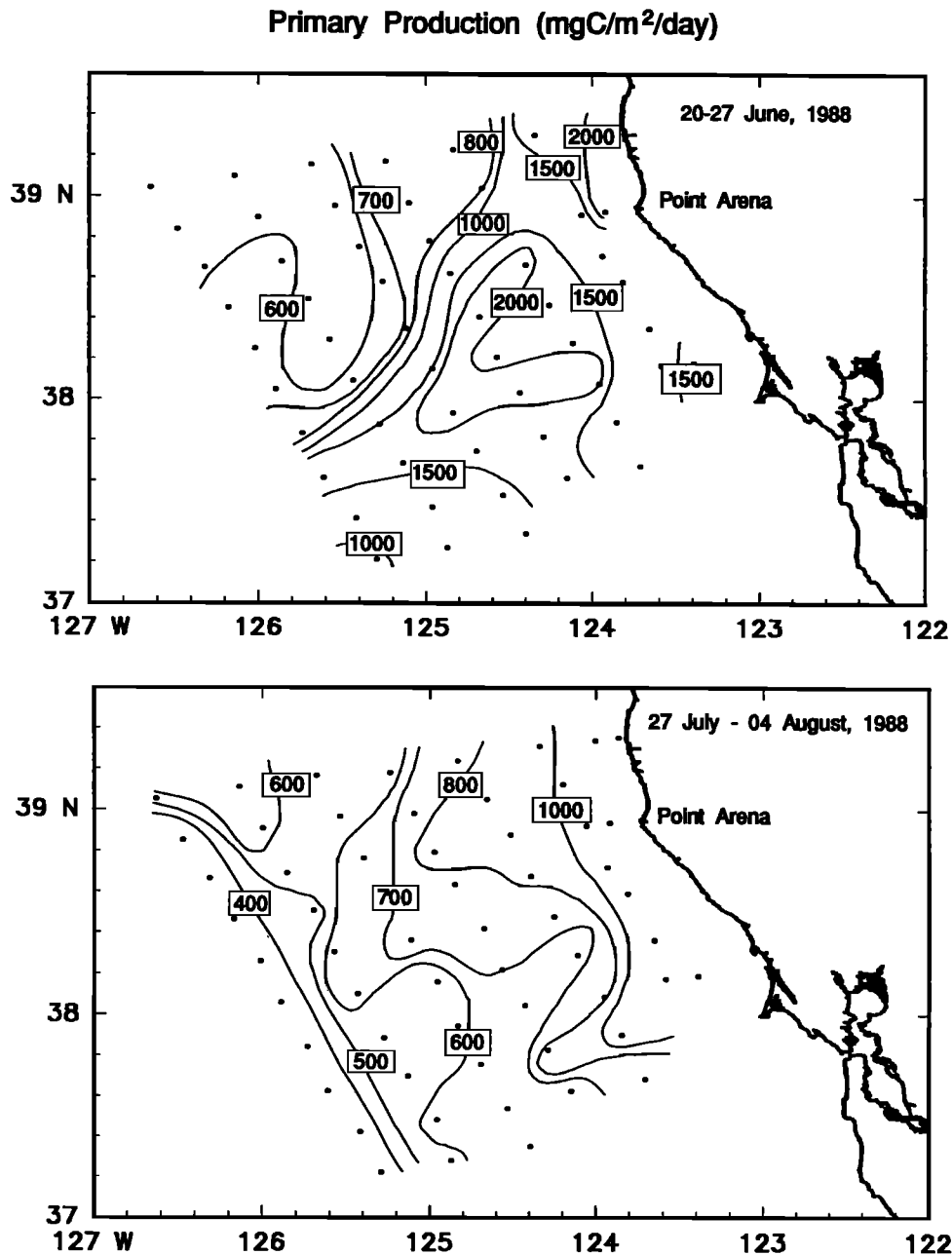


Fig. 15. Horizontal distribution of primary production during the first and the last cruises of 1988. Primary production was estimated from a multiple regression model that uses PAR and surface pigments (chlorophyll+phaeopigments)(see Figure 2).

decrease in phytoplankton standing stock may be associated with a decrease in the supply of iron. It may also be that vertical motion is a requirement for maintenance of nonmotile organisms such as diatoms in the euphotic zone and that vertical motion along the jet edge was relaxed when the undercurrent intensified or the jet changed direction. Grazing also needs to be considered; however, preliminary estimates suggest that macrozooplankton grazing was not sufficient to explain the dramatic changes (T.J. Cowles, personal communication, 1990). Understanding the processes responsible for high levels of phytoplankton biomass and production in the coastal transition zone and perhaps more importantly the rapid decreases in phytoplankton stocks is

required for development of realistic biological models of eastern boundary systems.

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REFERENCES

- Abbott, M., and P.M. Zion, Satellite observation of phytoplankton variability during an upwelling event, *Cont. Shelf Res.*, **4**, 661-680, 1985.
- Barber, R.T. and F.P. Chavez, Ocean variability in relation to living resources during the 1982-83 El Niño, *Nature*, **319**, 279-285, 1986.
- Bernstein, R.L., L. Breaker, and R. Whritner, California Current eddy formation: Ship, air and satellite results, *Science*, **195**, 353-359, 1977.
- Bolin R.L., and D.P. Abbott, Studies of the marine climate and phytoplankton of the central coastal area of California, 1954-1960, *California Cooperative Oceanic Fisheries Investigations Progress Report IX*, pp 23-25, 1963.
- Chavez, F.P., The annual cycle of SST along the coast of Peru, *Trop. Ocean-Atmos. Newsl.*, **37**, pp. 4-6, Cooperative Institute for Marine and Atmospheric Study, University of Miami, 1987.
- Chavez, F.P. and R.T. Barber, An estimate of new production in the equatorial Pacific, *Deep-Sea Research*, **34**, 1229-1243, 1987.
- Chavez, F.P., Size distribution of phytoplankton in the central and eastern tropical Pacific, *Global Biogeochem. Cycles*, **3**, 27-35, 1989.
- Chavez, F.P., K.R. Buck, and R.T. Barber, Phytoplankton taxa in relation to primary production in the equatorial Pacific, *Deep-Sea Res.*, **37**, 1733-1752, 1990.
- Chavez, F.P., and R. C. Brusca, The Galapagos Islands and their relation to oceanographic processes in the tropical Pacific, in *Galapagos Marine Invertebrates*, edited by M.J. James, Plenum, New York, in press, 1991.
- Chavez, F.P., R.T. Barber, and M.P. Sanderson, The slope of the temperature-nitrate relationship and the strength of the equatorial undercurrent, I, Cool conditions, *Trop. Ocean-Atmos. Newsl.*, **33**, Cooperative Institute for Marine and Atmospheric Study, University of Miami, pp. 8-10, 1987 1985.
- Chelton, D.B., P.A. Bernal, and J.A. McGowan, Large-scale interannual physical and biological interaction in the California Current, *J. Mar. Res.*, **40**, 1095-1125, 1982.
- Cullen, J.J., and R.W. Eppley, Chlorophyll maximum layers of the southern California Bight and possible mechanisms of their formation and maintenance. *Oceanol. Acta*, **4**, 23-32, 1981.
- Davis, R.E., Drifter observations of coastal surface currents during CODE: The method and descriptive view, *J. Geophys. Res.*, **90**, 4741-4755, 1985.
- Dewey, R.K., and J.N. Moum, Enhancement of fronts by vertical mixing, *J. Geophys. Res.*, **95**, 9433-9445, 1990.
- Flament, P., L. Armi, and L. Washburn, The evolving structure of an upwelling filament, *J. Geophys. Res.*, **90**, 11,765-11,778, 1985.
- Hickey, B.M., The California Current System -- Hypotheses and facts, *Prog. Oceanogr.*, **8**, 191-279, 1979.
- Holm-Hansen, O., C.J. Lorenzen, R. Holmes, and J.D. Strickland, Fluorometric determination of chlorophyll, *J. Cons. Perm. Int. Explor. Mer.*, **30**, 3-15, 1965.
- Hood, R.R., M.R. Abbott, A. Huyer, and P.M. Kosro, Surface patterns in temperature, flow, phytoplankton biomass and species composition in the coastal transition zone off northern California, *J. Geophys. Res.*, **95**, 18,081-18,094, 1990.
- Huyer, A., Coastal upwelling in the California Current system, *Prog. Oceanogr.*, **12**, 259-284, 1983.
- Huyer, A., R.L. Smith, and B.M. Hickey, Observations of a warm-core eddy off Oregon, January to March 1978, *Deep-Sea Res.*, **31**, 97-117, 1984.
- Huyer, A., P.M. Kosro, J. Fleischbein, S.R. Ramp, T. Stanton, L. Washburn, F.P. Chavez, T.J. Cowles, S.D. Pierce, and R.L. Smith, Currents and water masses of the coastal transition zone off northern California, June to August 1988, *J. Geophys. Res.*, [this issue].
- Johnson, K.S., and R.L. Petty, Determination of nitrate and nitrite in seawater by flow injection analysis, *Limnol. Oceanogr.*, **28**, 1260-1266, 1983.
- Johnson, K.S., R.L. Petty, and J. Thomsen, Flow injection analysis for seawater micronutrients, in *Mapping Strategies in Chemical Oceanography*, edited by A. Zirino, pp. 7-30, American Chemical Society, Washington, D.C., 1985.
- Kadko, D.C., L. Washburn and B. Jones, Evidence of subduction within cold filaments of the northern California coastal transition zone, *J. Geophys. Res.*, this issue.
- Kosro, P.M., and A. Huyer, CTD and velocity surveys of seaward jets off northern California, July 1981 and 1982, *J. Geophys. Res.*, **91**, 7680-7690, 1986.
- Kosro, P.M., A. Huyer, S.R. Ramp, L. Small, R.L. Smith, R. Barber, F.P. Chavez, T.J. Cowles, M.R. Abbot, P.T. Strub, R.T. Barber, P.F. Jessen, and L.F. Small, The structure of the transition zone between coastal waters and the open ocean off northern California, *J. Geophys. Res.*, this issue.
- Jahnke, R.A., C.E. Reimers, and D.B. Craven, Intensification of recycling of organic matter at the sea floor near ocean margins. *Nature*, **348**, 50-54, 1990.
- MacIsaac, J.J., R.C. Dugdale, R.T. Barber, D. Blasco, and T.T. Packard, Primary production in an upwelling center. *Deep-Sea Res.*, **32**, 503-529.
- Mackas, D.L., L. Washburn, and S.L., Smith, Zooplankton community pattern associated with a California Current cold filament, *J. Geophys. Res.*, this issue.
- Martin, J.H. and R.M. Gordon, Northeast Pacific iron distributions in relation to phytoplankton productivity, *Deep-Sea Res.*, **35**, 177-196, 1988.
- Martin, J.H., Glacial-interglacial CO₂ change: The iron hypothesis, *Paleoceanography*, **5**, 1-13, 1990.
- Michaels A.F. and M.W. Silver, Primary production, sinking fluxes and the microbial food web, *Deep-Sea Res.*, **35**, 473-490, 1988.
- Mooers, C.N.K., and A.R. Robinson, Turbulent jets and eddies in the California Current and inferred cross-shore transport, *Science*, **23**, 51-53, 1984.
- Morel, A., Optical modeling of the upper ocean in relation to its biogenous matter content (Case I Waters), *J. Geophys. Res.*, **93**, 10749-10768, 1988
- Paduan, J.D., and P.P. Niiler, A Lagrangian description of motion in northern California coastal transition filaments, *J. Geophys. Res.*, **90**, 18,095-18,109, 1990.
- Reinecker, M.M., C.N.K. Mooers, D.E. Hagan, and A.R. Robinson, A cool anomaly off northern California: An investigation using IR imagery, *J. Geophys. Res.*, **90**, 4807-4818, 1985.
- Ryther, J.H., Photosynthesis and fish production in the sea, *Science*, **166**, 72-76, 1969.
- Sakamoto, C., G.E. Friederich, and L.A. Codispoti, MBARI procedures for automated nutrient analyses using a modified Alpkem series 300 rapid flow analyzer, *MBARI Tech. Rept. 90-2*, Monterey Bay Aquarium Res. Inst., Pacific Grove, Calif., 1990.
- Skosberg, T., Hydrography of Monterey Bay, California, thermal conditions, *Transactions of the American Philosophical Society*, **29**, 152 p, 1936.
- Smetacek V.S., Role of sinking in diatom life history cycles: ecological, evolutionary and geological significance, *Mar. Biol.*, **84**, 234-251, 1985.
- Traganza, E.D., V.M. Silva, D.M. Austin, W.E. Hanson, and S.H. Bronsink, Nutrient mapping and recurrence of coastal upwelling centers by satellite remote sensing: Its implication to primary production and the sediment record, in *Coastal Upwelling: Its Sediment Record*, edited by E. Suess and J. Thiede, pp. 61-83, Plenum, New York, 1983.
- Tsuchiya, M., Subsurface countercurrents in the Pacific Ocean, *J. Mar. Res.*, **33**, (suppl.), 145-175, 1975.
- Tsuchiya M., The subthermocline phosphate distribution and circulation in the far eastern equatorial Pacific Ocean, *Deep-Sea Res.*, **32**, 299-315, 1985.
- Utermöhl, H., Zur Vervollkommnung der quantitativen Phytoplankton-Methodik, *Mitt. Int. Verein. Theor. Angew. Limnol.*, **9**, 1-38, 1958.
- Venrick, E.L. and T.L. Hayward, Determining chlorophyll on the 1984 Calcofi surveys. *Calcofi Rep.*, **25**, pp. 74-78, Calif. Coop. Oceanic Fish. Invest., La Jolla, 1984.
- Walsh, J.J., Death in the sea: Enigmatic phytoplankton losses, *Prog. in Oceanogr.*, **12**, 1-86, 1983.
- Walsh, J.J. Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen, *Nature*, **350**, 53-55, 1991.
- Whitledge, T.E., S.C. Malloy, C.J. Patton, and C.O. Wirick, Automated nutrient analysis of seawater in seawater, *Rep. 52398*, 216 pp., Brookhaven Natl. Lab., Upton, N.Y., 1981.
- Wooster, W.S., Eastern boundary currents in the South Pacific, in *Scientific Exploration of the South Pacific*, edited by W. Wooster, National Academy Press, 1970.
- Wooster, W.S., and J.L. Reid, Eastern boundary currents, in *The Sea, Vol 2*, edited by M.N. Hill, pp. 253-280, Interscience, New York, 1963.

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