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# NAVAL POSTGRADUATE SCHOOL
## Monterey, California

# THESIS

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# MICROPLANKTONIC ATP-BIOMASS AND GTP-PRODUCTIVITY ASSOCIATED WITH UPWELLING OFF PT. SUR, CALIFORNIA

by

10 Sherman Hughes/Bronsink

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Thesis Advisor: E. D. Traganza

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The measurement of productivity and "growth potential" using GTP and GTP/ATP ratios was found to be a valuable tool in examining rapidly changing upwelling features. Preliminary results obtained using the GTP technique suggest a relationship between the flux of nutrients across ocean fronts and planktonic productivity associated with frontogenic coastal upwelling systems.

# Microplanktonic ATP-Biomass and GTP-Productivity Associated with Upwelling off Pt. Sur, California

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# ABSTRACT

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# I. INTRODUCTION

This thesis examines the possibility that optimal growth conditions for microplankton occur near oceanic fronts as a result of horizontal nutrient fluxes. These fluxes may result from the sharp nutrient and thermal gradients that define such fronts. The research conducted here is part of a continuing study of the oceanic fronts and eddies formed by upwelling off Pt. Sur, California. During previous research [Traganza, Nestor, and McDonald, 1980a; Traganza, Conrad, and Breaker, 1980b], comparison of satellite thermal imagery to in situ biomass, nutrient, and thermal measurements showed large spatial variations in biomass concentrations. Microplanktonic blooms appeared greatest on the equatorward edge of the curl of "cyclonic upwelling systems" and adjacent to the sharp gradients in nutrients and temperature. There are several possible reasons for this distribution. The biomass may be advected into the area where it is found. It may be there initially, or it may appear as a preferential growth response to the newly formed front.

Preferential growth should be the result of optimal environmental conditions. Since large microplanktonic blooms (as measured by chlorophyll a and adenosine triphosphate (ATP)) appeared near sharp gradients of nutrients and temperature between upwelled, nutrient-rich, biochemically new water and nutrient depleted, biochemically old, oceanic water, a nutrient and thermal flux may provide the necessary growth conditions. A horizontal, outward flow from the upwelling system may maintain the gradients ("a natural chemostat") and simultaneously provide a mechanism for biological seeding of fronts with the newly upwelled organisms [Traganza, et al., 1980b].

## A. HORIZONTAL NUTRIENT FLUXES

Other studies have related phytoplankton production to horizontal and vertical nutrient gradients in Monterey Bay [Lasley, 1977] and to vertical fluxes of nutrients off Southern California [Eppley, Renger, Harrison, 1979].

Lasley [1977] computed the variations of phosphate, nitrate, and chlorophyll a using the distribution of variables equation [Sverdrup, et al., 1942]:

$$\frac{\partial C}{\partial t} = - u \frac{\partial C}{\partial x} - v \frac{\partial C}{\partial y} - w \frac{\partial C}{\partial z} + K \frac{\partial^2 C}{\partial x^2} + R \qquad 1)$$

where C represents the concentration of the variable (at 5m in Lasley's case), t is time, u, v, and w are water velocity in the x, y, and z directions (x defined as parallel to the coast, y perpendicular to the coast, and z as depth), K is the lateral eddy diffusion coefficient. R is a nonconservative term which represents uptake or assimilation of the given nutrient by phytoplankton.

From a knowledge of the lateral eddy diffusitivity coefficient for Monterey Bay, the surface circulation and the nutrient distributions within the bay, it was possible to compute the nutrient fluxes and compare them to the biomass. Measurements of the movement of isopleths of nutrients provided actual flux measurements for comparison. A study of a bay system has several advantages over the study of an exposed coastal upwelling feature interacting with a Western boundary current. The diffusivity coefficient (K) was already known for this area. Surface circulation and nutrient fluxes could be measured with relative ease, since the "feature" (the bay) was a fixed one. The peak in phytoplanktonic biomass (as measured by chlorophyll a) was found near Pt. Pinos where the gradients of nutrients (and presumably the fluxes) were greatest.

B. VERTICAL NUTRIENT FLUXES

Eppley [1979] postulated that carbon assimilation and therefore productivity could be directly related to vertical nitrate fluxes (dN/dz) following the equation:

$$\mu P(\text{production} \cdot m^{-3}) \sim \frac{K_z(dN/dz)}{z_o} \qquad 2)$$

where P is phytoplankton standing stock ($mg/m^3$), $\mu$ is its specific growth rate ($day^{-1}$) at depth $z_n$, and depth $z_o$(m) is the depth at which the nitrate concentration has increased to 1 μg - atom • liter$^{-1}$. The depth $z_o$ is arbitrary and could be chosen for another concentration if the coefficient $K_z$ were also changed.

## C. FRONTAL NUTRIENT FLUXES

In this study, biomass (ATP and chlorophyll a), nutrients (nitrates and phosphates), and sea surface temperature were collected on a developing upwelling feature detected by satellite (IR) imagery of the Central California coast on June 10-11, 1980. Productivity and growth potential (instantaneous productivity per unit biomass) were examined using the new method of guanosine triphosphate sampling [Karl, 1978].

Linear plots following the ship's track and surface maps of these parameters were constructed to show frontal locations (temperature and nutrients), concentrations of biomass (based on ATP and chlorophyll a), areas of high productivity (based on high ΔATP; see below), and areas of high growth potential (based on high ΔATP/ATP; see below).

## D. ASSAYING ATP AND GTP

The luciferin-luciferase assay principle for ATP [Holm-Hansen and Booth, 1966; Holm-Hansen and Karl, 1976] has been widely used in recent years. It involves measuring the light emission from the reaction

$$\text{ATP} + \text{LH}_2 + \text{O}_2 \xrightarrow{\text{FL}} \text{AMP} + \text{PP}_1 - \text{CO}_2 + \text{P} + h\nu \qquad 3)$$

[Holm-Hansen and Karl, 1978] where $LH_2$ is reduced luciferin, FL is firefly luciferase, $PP_1$ is inorganic pyrophosphate, P is product, and $h\nu$ is light energy.

It is relatively easy to extract ATP from "particulates" in sea water with the appropriate solvent. Once extracted, ATP can be measured and used to estimate living carbon biomass by application of a conversion factor representing the mean C/ATP ratio of the microbial (bacteria, algae, and microzooplankton) biomass [Holm-Hansen, 1969]. Even with the right solvent and appropriate analytical procedure there are problems associated with this assay method. The conversion factor is somewhat species dependant, and it is dependent on the energy charge (physiological state), and variation of the total adenylate pool, AMP + ADP + ATP [Traganza, 1979]. Diel and other effects have also been noted [Hunter, 1979].

Another problem area concerns the analytical interference of non-adenine nucleotide triphosphates (NTPs) in the assay [Rasmussen and Nielsen, 1968]. When the assay is conducted using crude firefly luciferase and integrated light readings (60 seconds or more of light emissions), Guanosine triphosphate (GTP), uridine triphosphate (UTP), and cystosine triphosphate (CTP) all alter the light emission characteristics. The effect is most pronounced when these NTPs are at or near the concentration of ATP. Crystaline luciferase enzyme is ATP specific [McElroy and Green, 1956]. Peak readings (reading the light emission over the first six seconds of the reaction instead of over 60 seconds) minimizes the interference, because ATP reacts much more rapidly with luciferin than other NTPs [Figure 1].

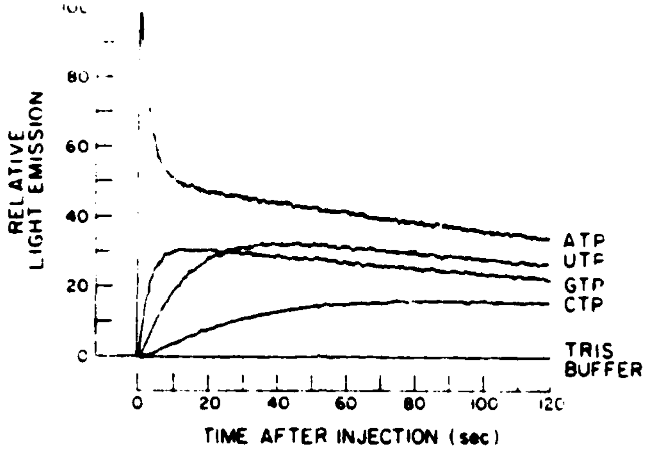


Figure 1. Kinetics of ATP, GTP, UTP, and CTP-dependent light emission using crude luciferase preparations. The concentration of each nucleotide was 4 x $10^{-8}$ M. [From Karl, 1978].

Measurements of ATP using crude extract and integrated readings result in an overestimation of the amount of ATP present because of the presence of other NTPs. This effect can be used to determine GTP levels which, in turn, may prove to be a measurement of productivity. Karl [1979] measured ATP in intertidal sediment extracts using both peak and integrated methods. The difference between these two values (ΔATP = ATP (integrated) - ATP (peak)) showed a high correlation (r = .96) to the measured amount of GTP present. The ΔATP values were poorly correlated to any other parameter in the experiment (ATP, location the sample was from, etc.). From this Karl concluded that ΔATP is useful as a relative measure of GTP, especially in intertidal extracts.

## E. GUANOSINE TRIPHOSPHATE

The ability to easily measure GTP is important to the study of mesocale ocean fronts because of its relation to productivity. GTP is known to be essential in the biosynthesis of protein. Specifically, it is necessary in the initiation of synthesis, the aminoacyl tRNA binding, and the translocation processes [Watson, 1977]. Since protein synthesis is a major factor in primary productivity, a correlation between GTP and primary productivity is expected. Studies have shown a high linear correlation between cellular growth rate and GTP concentration (when normalized to the amount of ATP present, i.e., GTP/ATP) for bacteria [Karl, 1978], algae [Iwamura, et al., 1963], protozoa [Echetebu and Plesner, 1977], and even fungi [Constantini et al., 1977]. The ratio of GTP to ATP may represent a "potential growth index" which would be invaluable because it would allow rapid assessment of productivity over large areas. This capability, combined with the rapid measurements of sea surface temperature (SST) and nutrients (nitrate and phosphate) may allow determination of the relation of productivity to fluxes in our rapidly developing systems.

# II. METHODS

Surface values of fluorescence (principally a measure of chlorophyll a), ATP, and ΔATP (as an index of relative GTP levels) were obtained off Pt. Sur, California during the development of a "cyclonic upwelling system" [Traganza *et al.*, 1980b]. Temperature and nutrients (nitrate and phosphate) were obtained by Hanson [1980] and used here for interpretation of these results.

Nutrients (nitrate and phosphate) were sampled at two minute intervals using a Technicon Autoanalyzer. Sea surface temperature (SST) was recorded continuously from an intake located at approximately 2.5 meters depth. Enhanced TIROS-N satellite images were obtained from the National Environmental Satellite Service (NESS) at Redwood City, California.

## A. CHLOROPHYLL a

Fluorescence was measured continuously during the cruises using a Turner Model III fluorometer and converted to pigment concentration (principally chlorophyll a) as described by Lorenzen [1966]. To calibrate the system, discrete 275 ml seawater samples were taken in triplicate every hour. These were filtered through Whatman 4.5 cm diameter G/FC (pore size ca 0.45 μm) glass fiber filters. The filters were folded, placed in polyethelene bags, frozen and analyzed within two weeks, using the methods of Strickland and Parsons [1968]. Chlorophyll a concentrations were determined from the fluorescence record at two minute intervals to correspond to the nutrient sampling rate. To generate an organic carbon equivalent for comparison with organic carbon derived from ATP, "chlorophyll a" concentrations were converted to carbon units (mg/l) by using the average C/chlorophyll conversion factor of 100 as proposed by Holm-Hansen [1969]. Eppley [1977] has recommended a conversion factor of 54 ± 17. The two will be compared in the discussion section.

## B. ATP AND ΔATP

ATP and ΔATP samples were taken at approximately 10 minute intervals. Fifty ml samples of sea water were filtered through a 200 μm nylon screen and then through a 2.5 cm (diameter) Reeve Angel 984-H (ca. 0.45 μm pore size) glass filter. The filter was then placed in 100°C Trizma (Tris (Hydroxymethyl) aminomethane and hydrochloride) buffer (pH 7.7) to extract the ATP and other nucleotides. The buffer was then frozen for later analysis. The modified ATP method of Holm-Hansen and Karl [1976] was used in the ATP analysis.

SAI photometers, Models 1000 and 3000 (SAI, 4060 Sorrento Valley Boulevard, San Diego, California, 92121) were used to determine ATP concentrations from peak height measurements of the light emitted from the samples with an extract of firefly luciferin and luciferase. Comparisons to standards (30, 15, 9, 6, and 3 ng/l) yielded ATP values in ng/l. These were converted to organic carbon biomass (mg/l) by using the average C/ATP conversion factor of 250 proposed by Holm-Hansen [1969] for the "microbial biomass" (bacteria, algae, and microzooplankton).

A relative measure of GTP present was computed using the "ΔATP" method of Karl [1978]. ATP values were determined using both peak (6 second) and integrated (15 second delay, 60 second assay) methods on an SAI ATP photometer. A strip chart was fitted to the photometer to record peak readings which were converted to ATP concentrations by comparison of peak heights to the peak height of the standards. Integrated readings were given by the photometer's digital readout and converted to ATP concentrations by comparison to the digital readouts of the known standards. The difference between these estimates of the ATP concentration in a given sample (ΔATP) was used as a relative measure of GTP in the sample. According to Karl, 40 to 50% of the ΔATP value is GTP (personal communication). The ΔATP values were normalized to the ATP by dividing by the amount of ATP present (ΔATP/ATP). This ratio provides an index of "potential growth" or an estimate of the instantaneous productivity per unit biomass.

## C. ΔATP GTP CORRELATION EXPERIMENT

As a test of the validity of using ΔATP as a measure of GTP on our instruments, a ΔATP vs. GTP correlation experiment was run using the SAI model 3000 photometer. Known concentrations of GTP and ATP were mixed in Trizma to represent varying percentages and absolute concentrations which may be found in sea water samples (Table I). "Peak" and "integrated" values were recorded on a strip chart interfaced to the photometer.

# TABLE I

## ΔATP AS A MEASURE OF GTP IN A BINUCLEOTIDE MIXTURE

| GTP (ng/1) | ATP (ng/1) | ΔATP (CPM*) | % GTP (by wt) |
|---|---|---|---|
| .3 | 5.7 | 7 | 5 |
| .6 | 5.4 | 8 | 10 |
| .9 | 8.1 | 11 | 10 |
| 1.5 | 4.5 | 6 | 25 |
| 1.5 | 13.5 | 30 | 10 |
| 1.5 | 28.5 | 49 | 5 |
| 2.25 | 6.75 | 21 | 25 |
| 3.0 | 3.0 | 2 | 50 |
| 3.0 | 27.0 | 76 | 10 |
| 3.75 | 11.25 | 66 | 25 |
| 4.5 | 4.5 | 31 | 50 |
| 7.5 | 22.5 | 182 | 25 |
| 7.5 | 7.5 | 123 | 50 |
| 9.0 | 0 | 0 | 100 |
| 11.25 | 4.75 | 137 | 75 |
| 15.0 | 15.0 | 269 | 50 |
| 15.0 | 0.0 | 79 | 100 |
| 22.5 | 7.5 | 329 | 75 |
| 30. | 0 | 286 | 100 |

*CPM = Counts Per Minute, proportional to the amount of light emitted in the reaction. Values shown are averages of up to four readings taken at each concentration.

# III. RESULTS

## A. ΔATP VS. GTP CORRELATION EXPERIMENT

A linear regression analysis was performed on values of ΔATP vs. GTP using a WANG Series 700 Advanced Programming Calculator.

When all concentrations of ATP and GTP were considered (66 data points), a correlation coefficient or r of .87 was obtained. Adenosine diphosphate (ADP), derived from ATP, is a necessary catalyst for GTP reaction, viz;

$$\text{ADP} + \text{GTP} \rightarrow \text{ATP} + \text{GDP} \qquad 4)$$

$$\text{ATP} \rightarrow \text{ADP} + \text{PP} + h\nu \qquad 5)$$

with no ATP present initially, the only source of ADP is the crude extract, which limits the reaction. If the values with no ATP present are excluded (leaving 57 data points), an r value of .92 was obtained. If mixtures with a very low ATP content yielding a ΔATP of less than 10 counts are also excluded (leaving 36 data points), an r value of .94 was obtained. (In the analysis of the June 10-11, 1980 cruise, only three data points of 189 had a ΔATP of less than 10 counts.)

## B. CRUISES

Linear plots of nutrients, temperature and biomass following the cruise tracks were computer constructed by an IBM 360. A VERSATEC plotter was used to construct surface contour maps of the parameters in the upwelling features studied. The contour maps were hand smoothed to minimize the effects of advection (the feature moved during the 40 hours that samples were taken which introduced structure into contour maps which did not exist in reality) and computer generated anomalies which occurred at the margins of the data field (the outside edges of the feature were distorted by the boundary conditions set into the computer). These tract plots and surface maps are presented in Figures 2 to 26.

### 1. September and November Cruises

Surface maps and linear track maps from the September 27-28, 1979 and November 29-30, 1979 cruises are presented for background (Figures 3 to 15). The November 29-30, 1979 cruise best illustrates the biomass patchiness that was encountered at the equatorward edge of a feature. The ATP measured biomass shows several "cells" (Figure 6). Biomass is highest along the equatorward front of the feature where it reaches over 400 ng ATP/1 (100 g C/1). Other, earlier cruises [Traganza, Conrad, and Greaker, 1980], also showed the highest concentrations of biomass along the equatorward edge of the upwelled feature. Without information on productivity (or "growth potential" analogous to assimilation

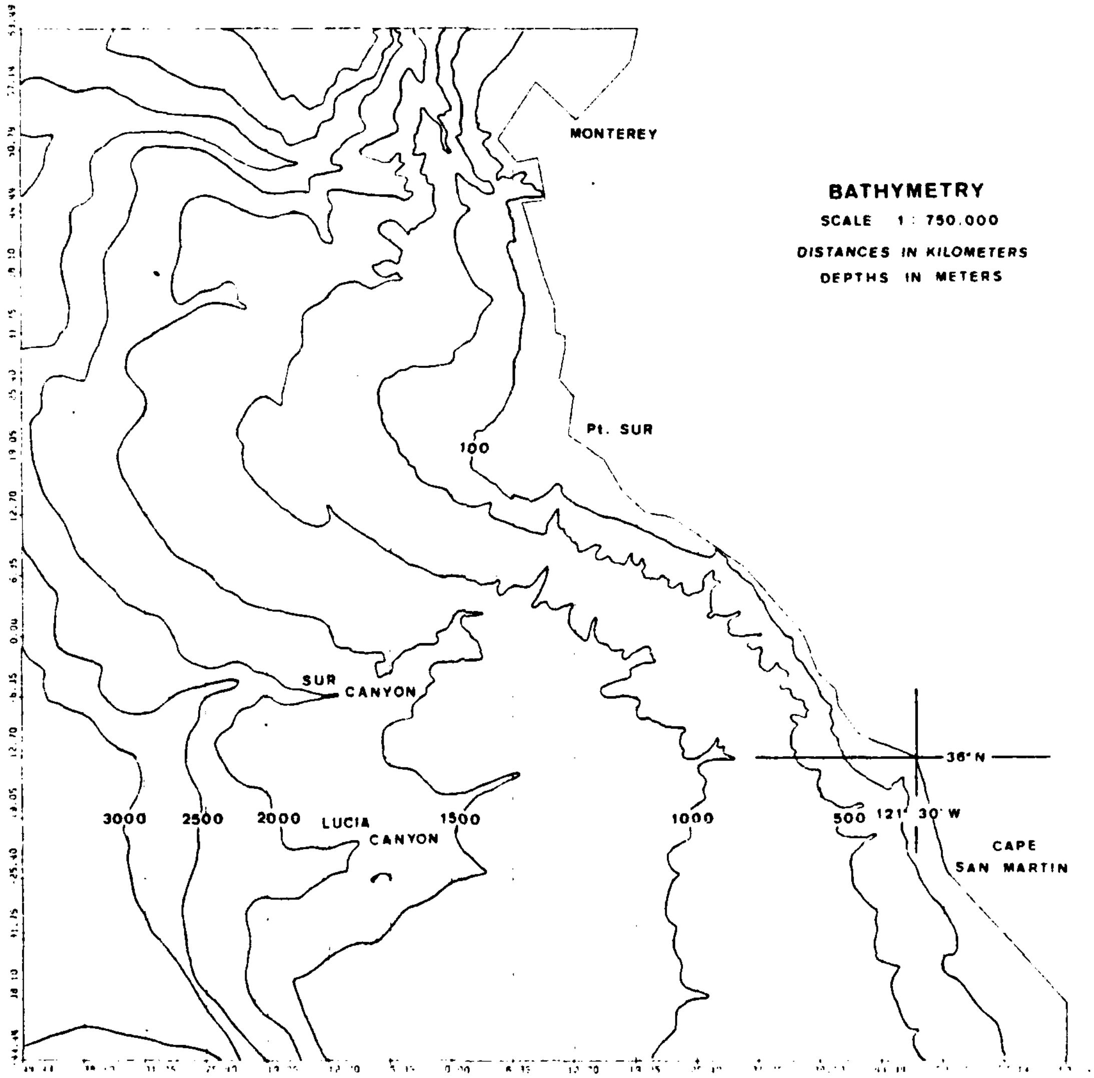


Figure 2. Bathymetry of the study area.

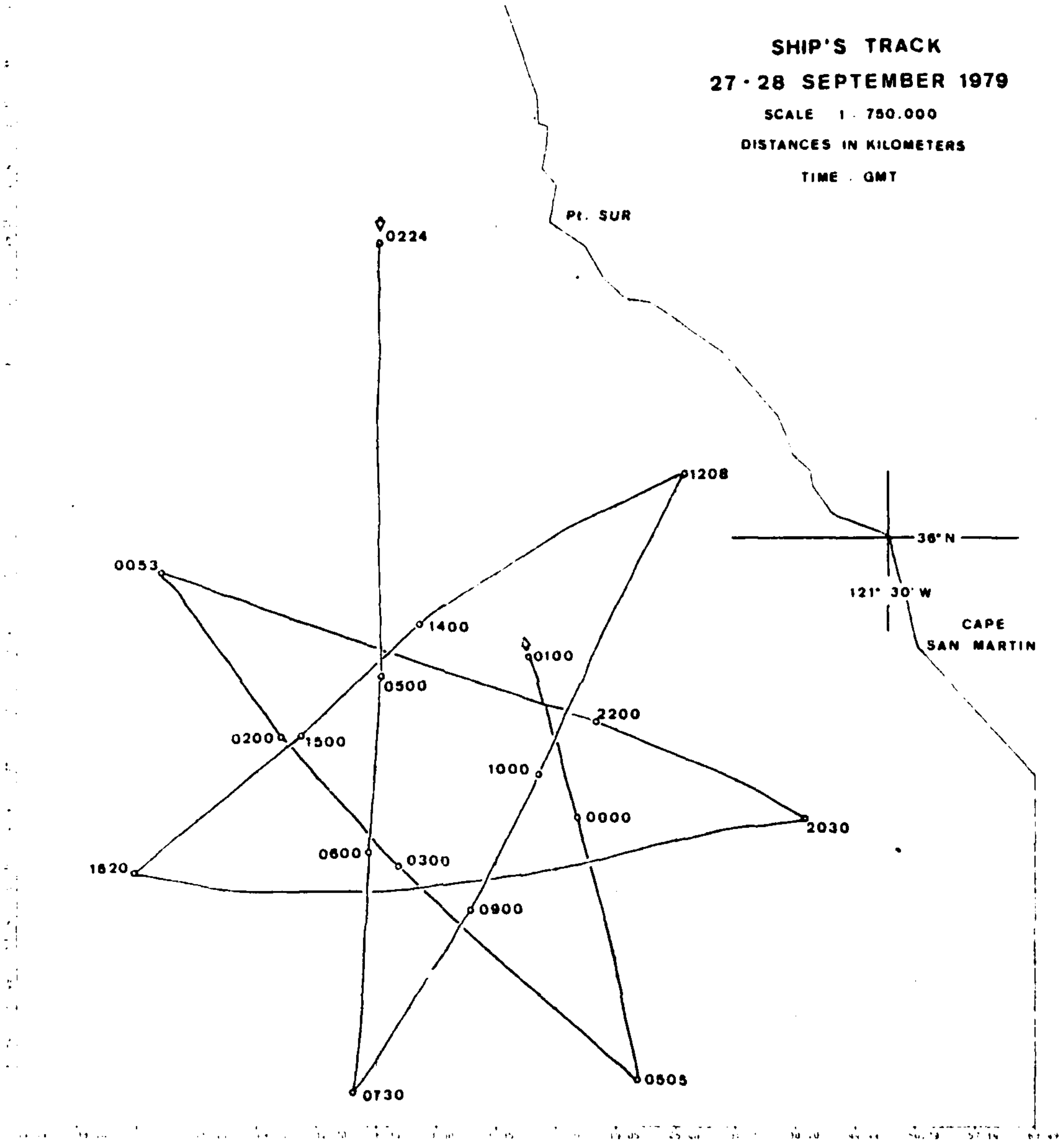


Figure 3. Cruise track for the September 1979 cruise.

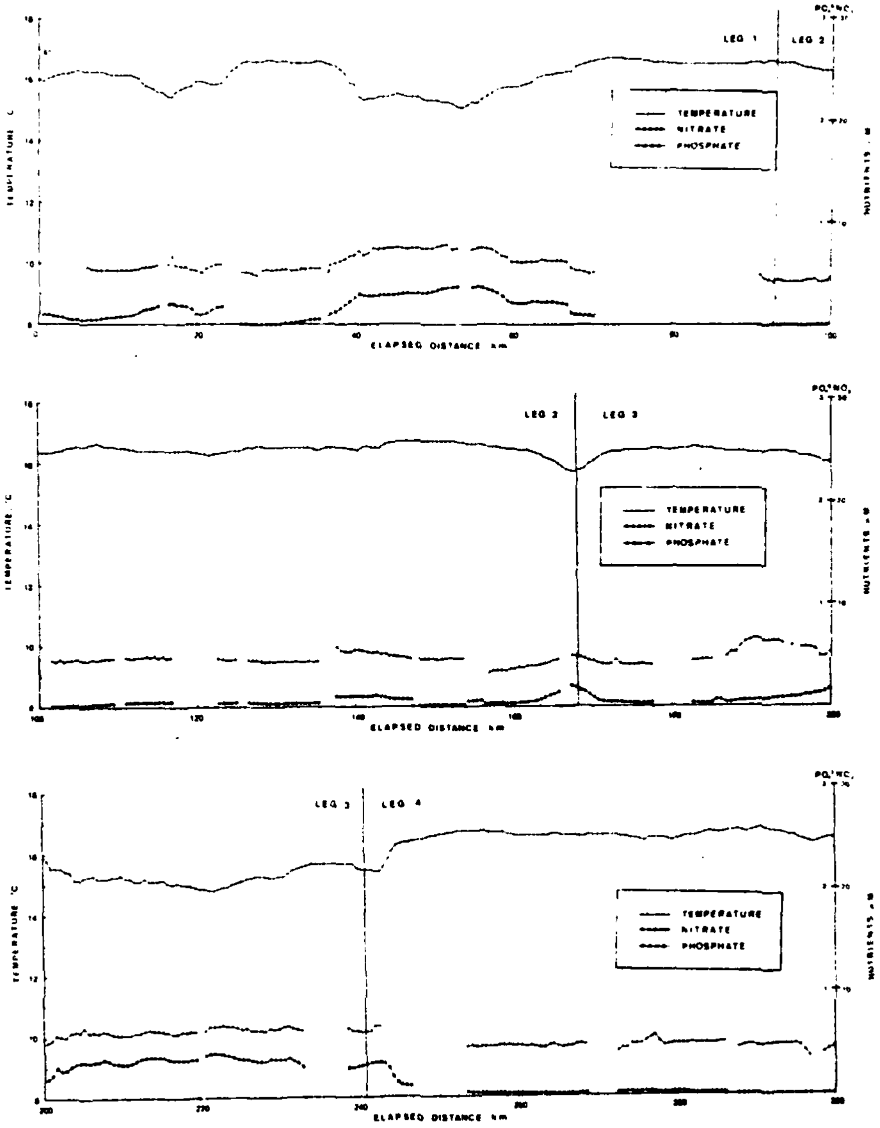


Figure 4. Nitrate, phosphate, and sea surface temperature versus elapsed distance along the track of the September 27-28, 1980 cruise.

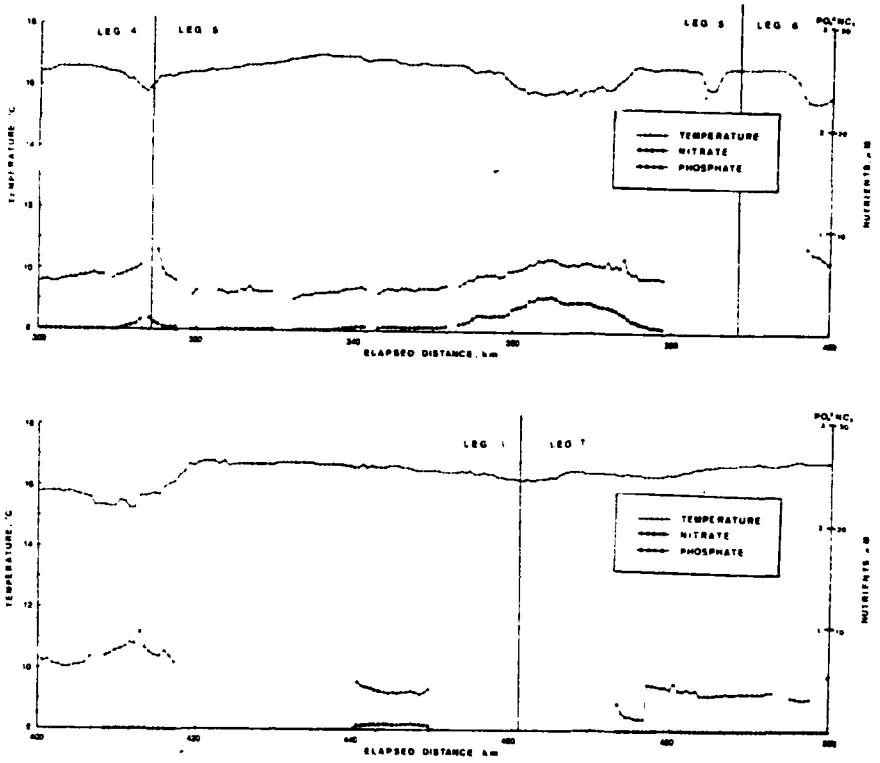


Figure 4. Continued.

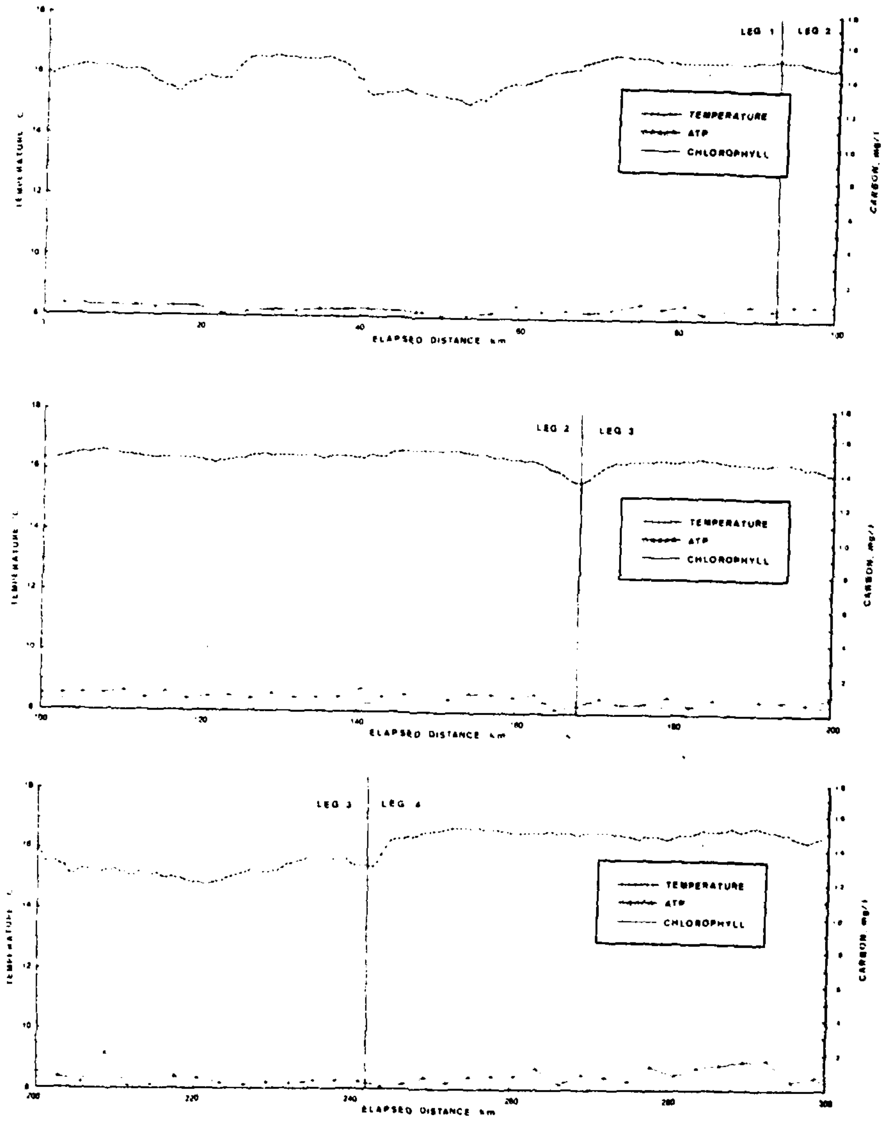
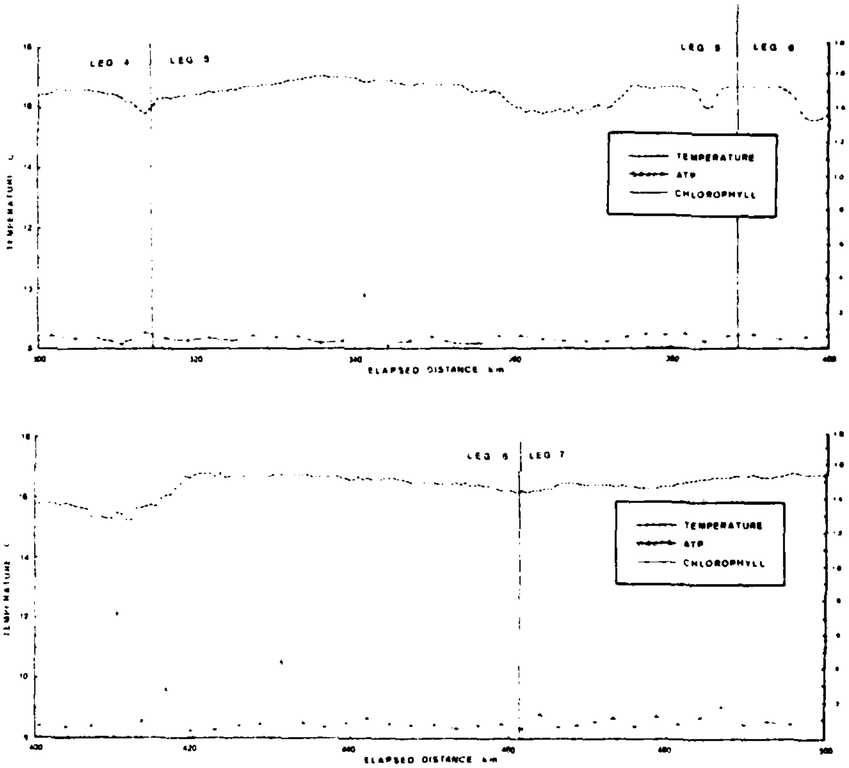


Figure 5. ATP, chlorophyll a, and sea surface temperature versus elapsed distance along the track of the September 27-28, 1980 cruise.



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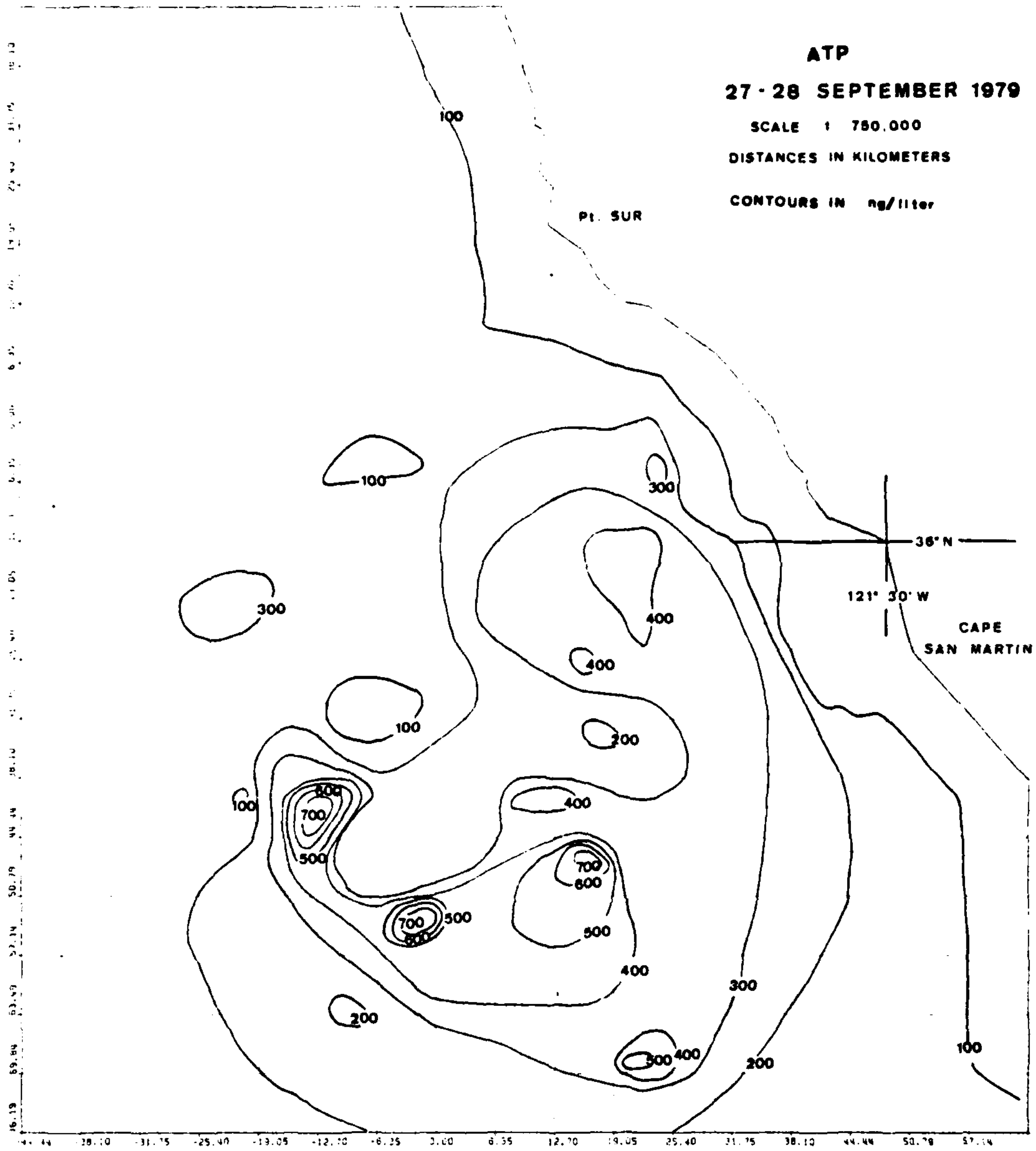

Figure 6. ATP distribution for the September 1979 cruise.

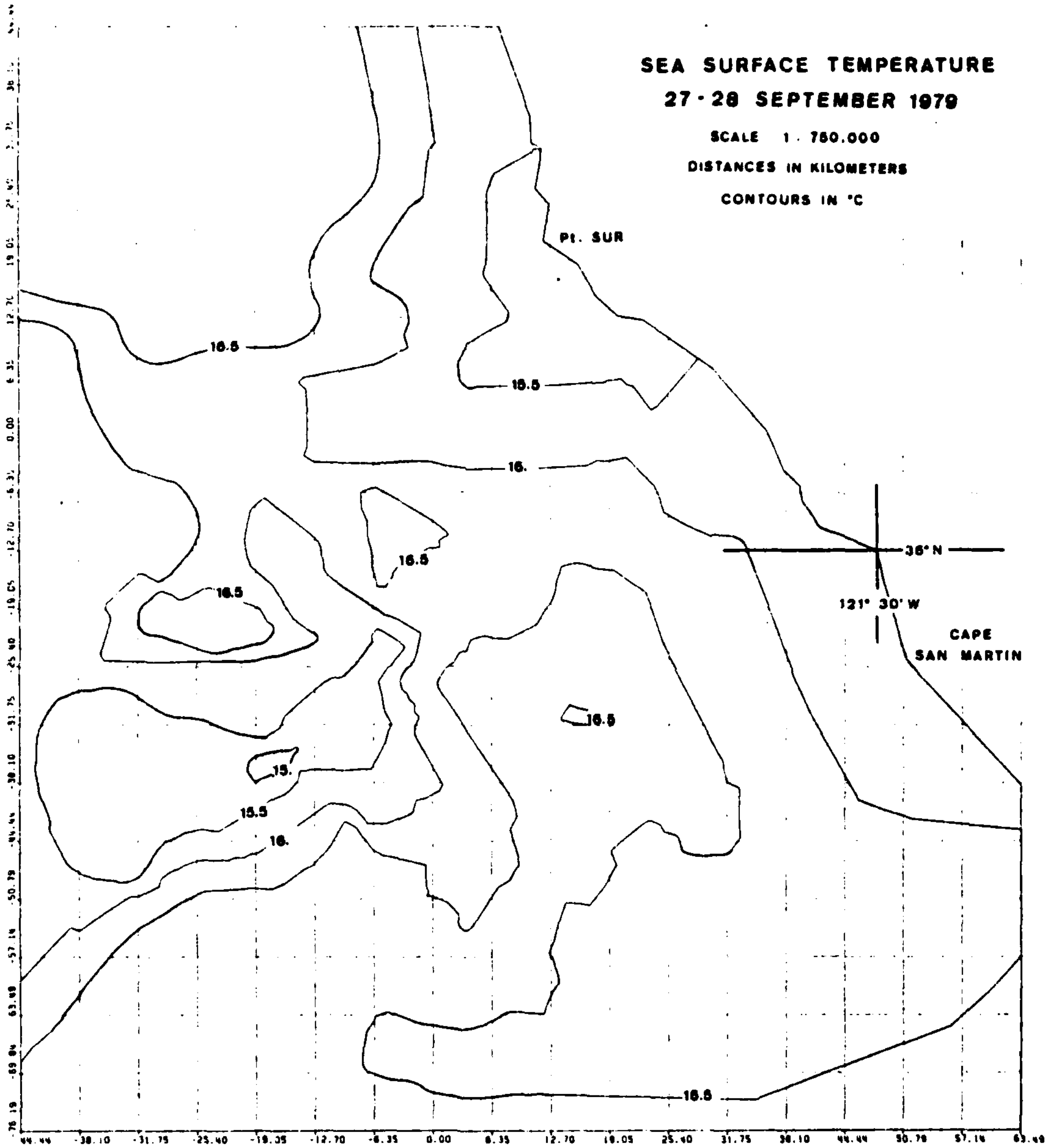

Figure 7. Sea surface temperature for the September 1979 cruise.

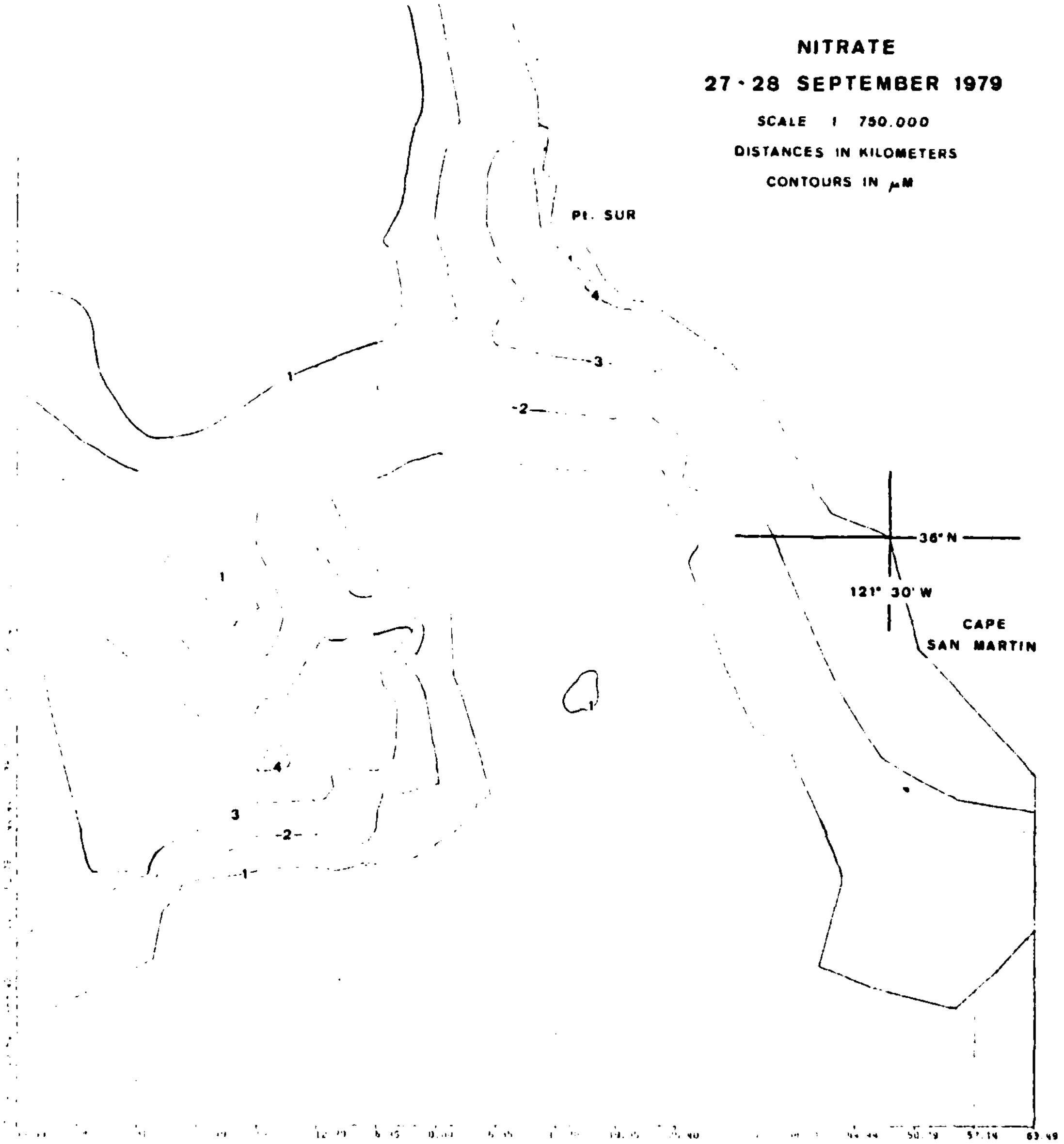

Figure 8. Nitrate distribution for the September 1979 cruise.

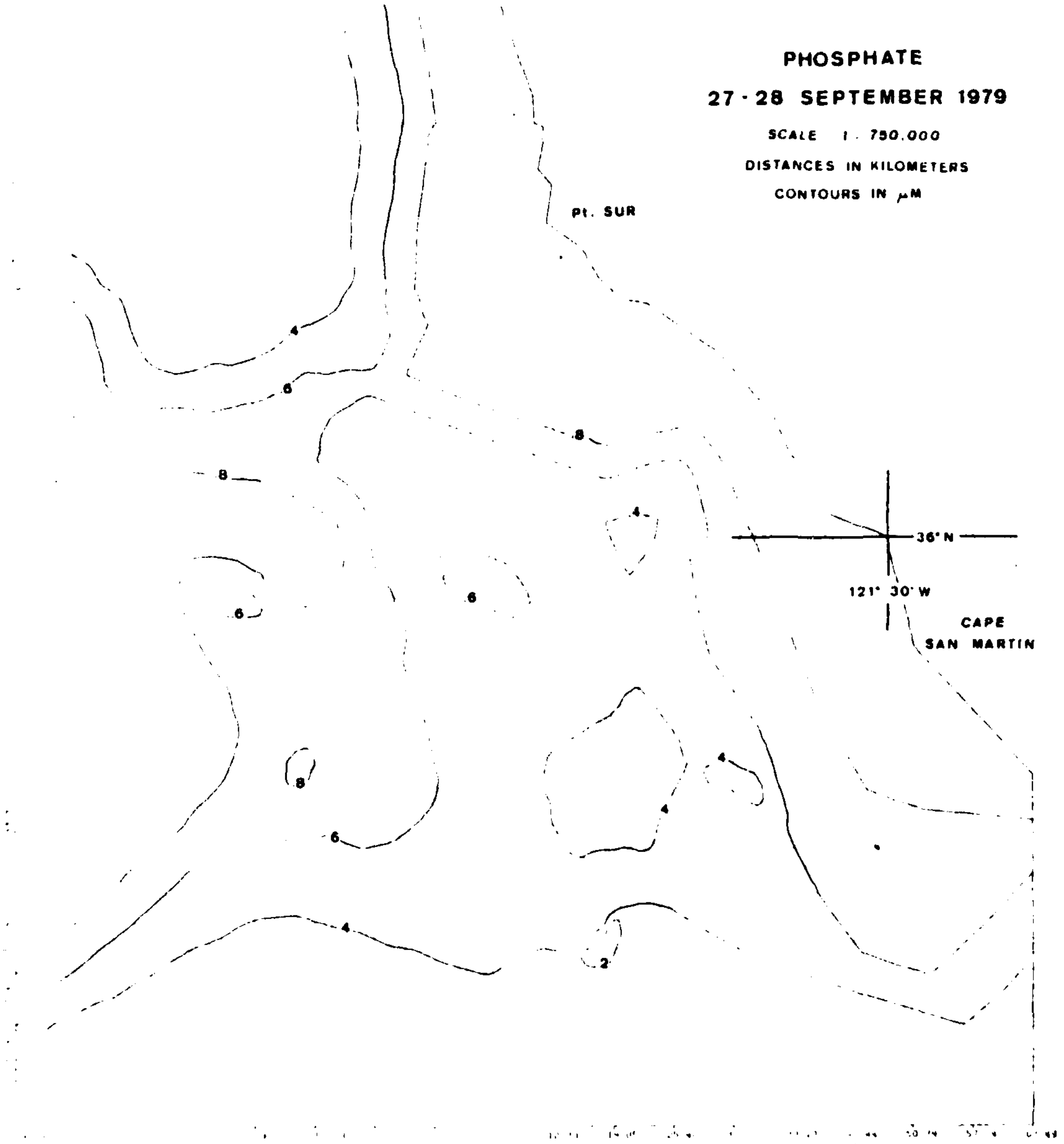

Figure 9. Phosphate distribution for the September 1979 cruise.

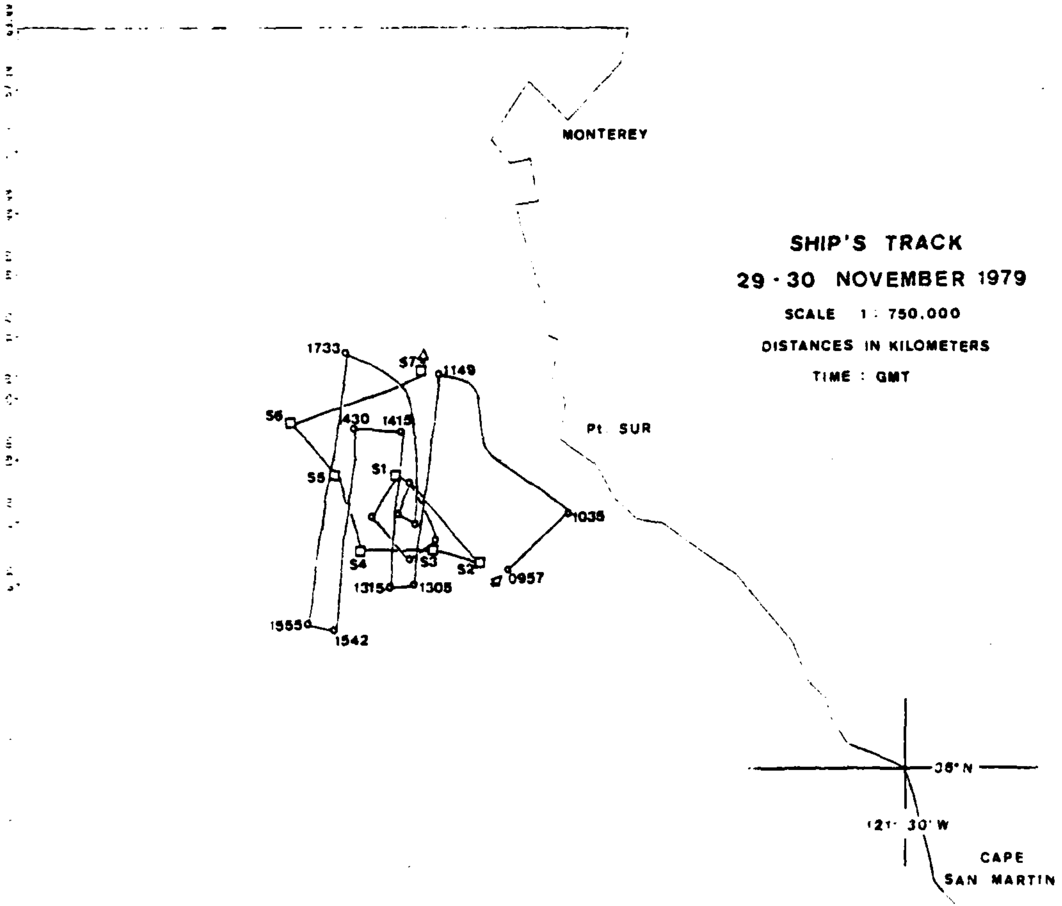

Figure 10. Cruise track for the November 1979 cruise. S represents a hydro station number.

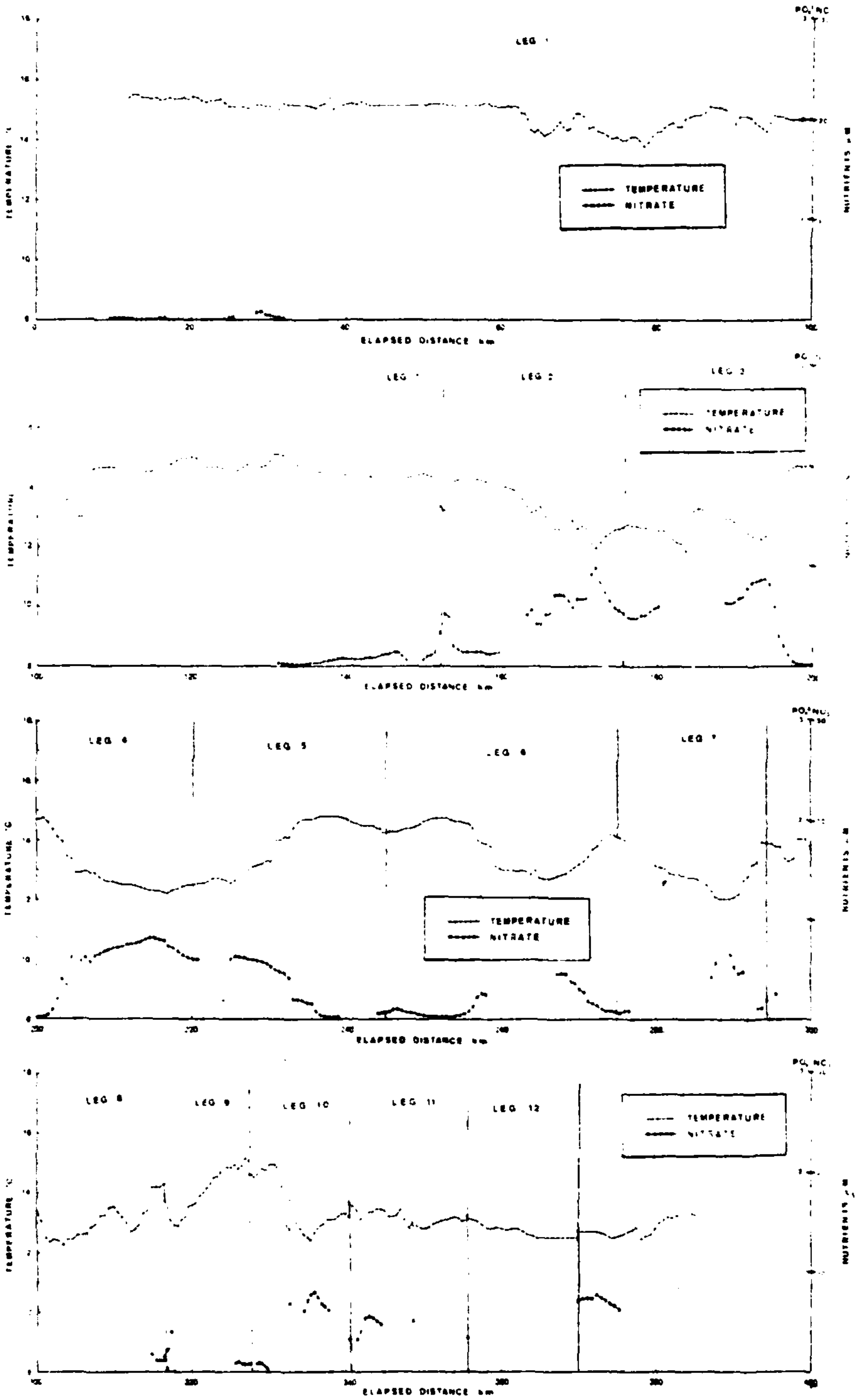

Figure 11. Nitrate and sea surface temperature versus elapsed distance along the track of the November 29-30, 1979 cruise.

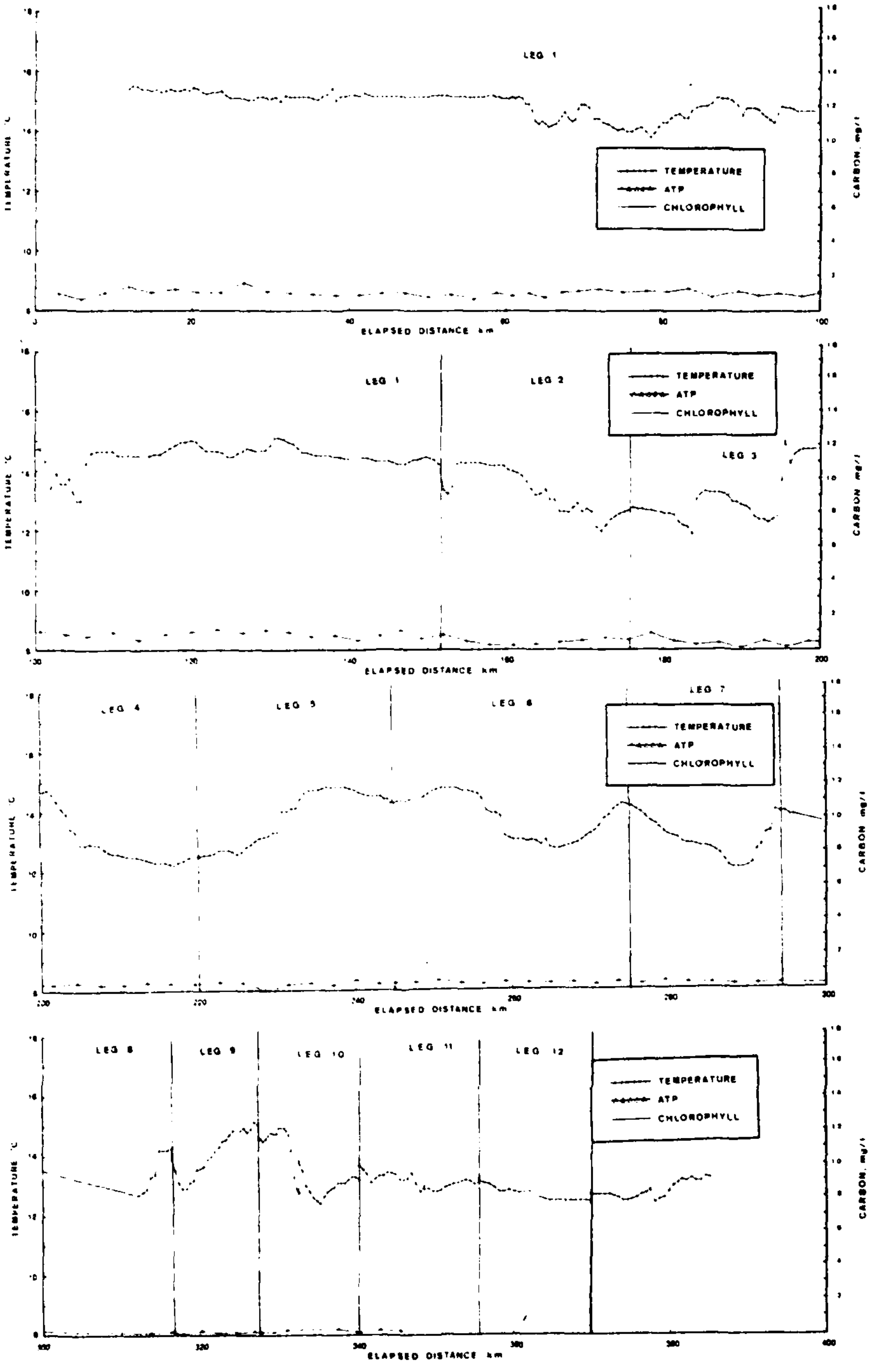

Figure 12. ATP, chlorophyll a, and sea surface temperature versus elapsed distance along the track of the November 29-30, 1979 cruise.

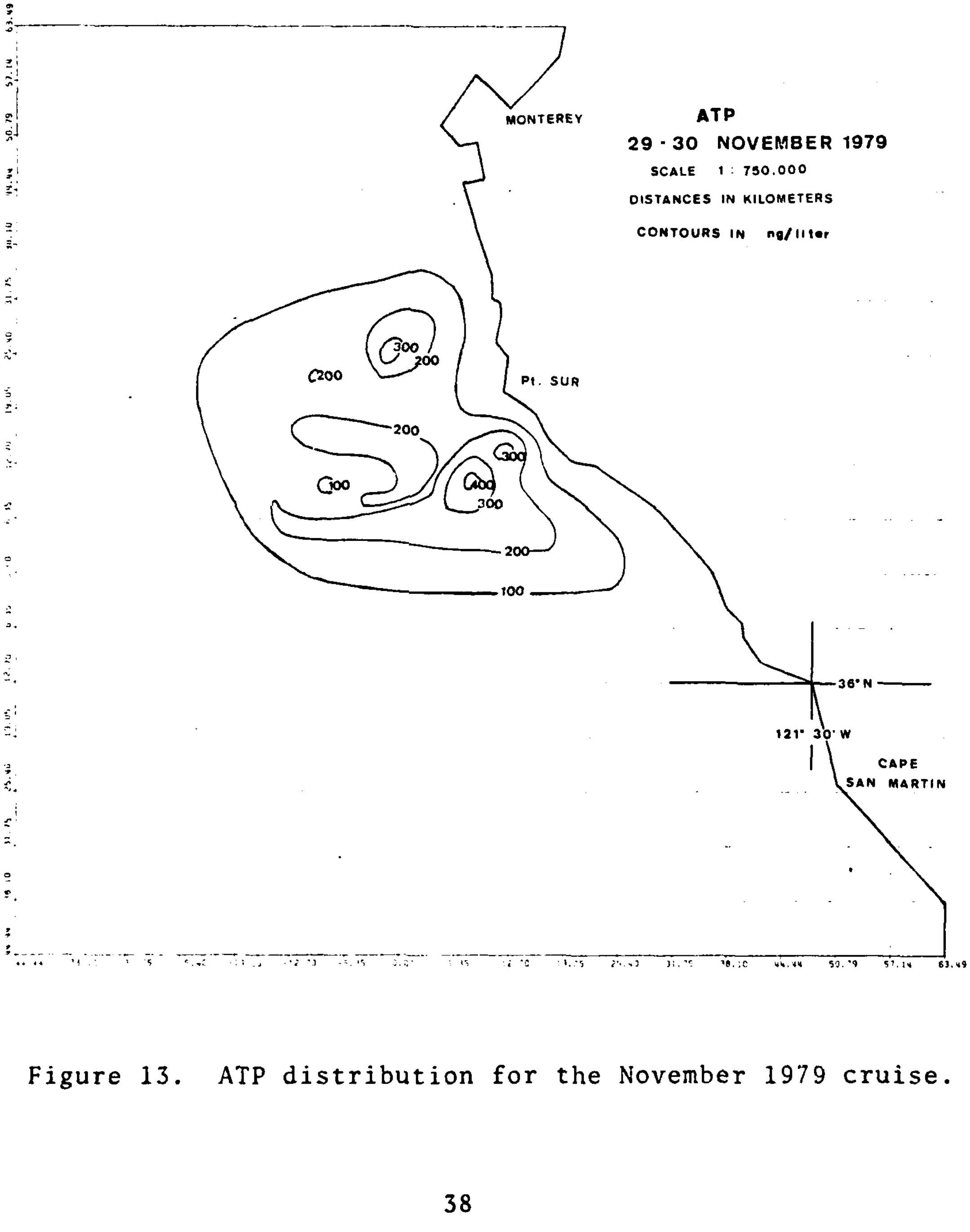

Figure 13. ATP distribution for the November 1979 cruise.

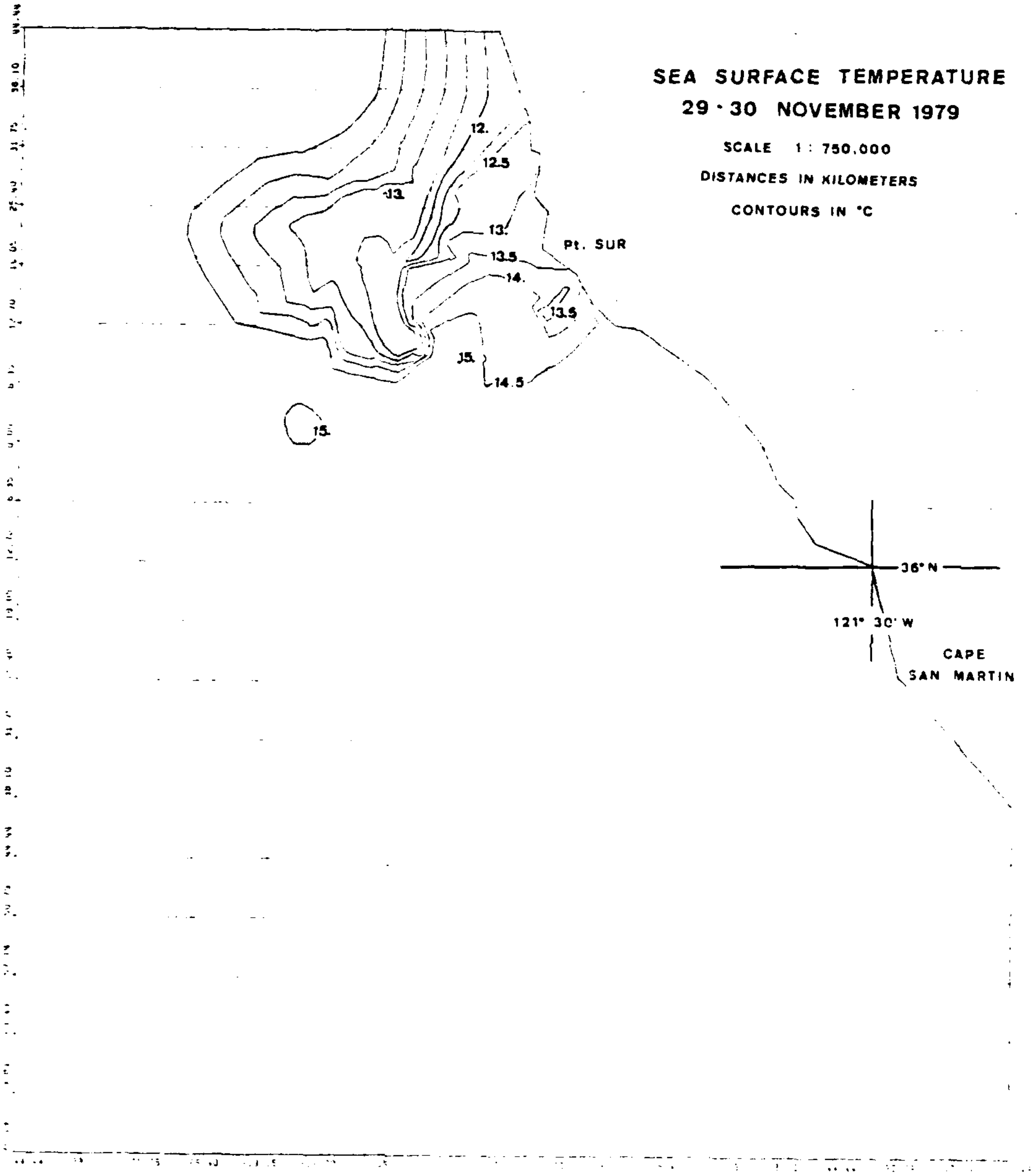

Figure 14. Sea surface temperature for the November 1979 cruise.

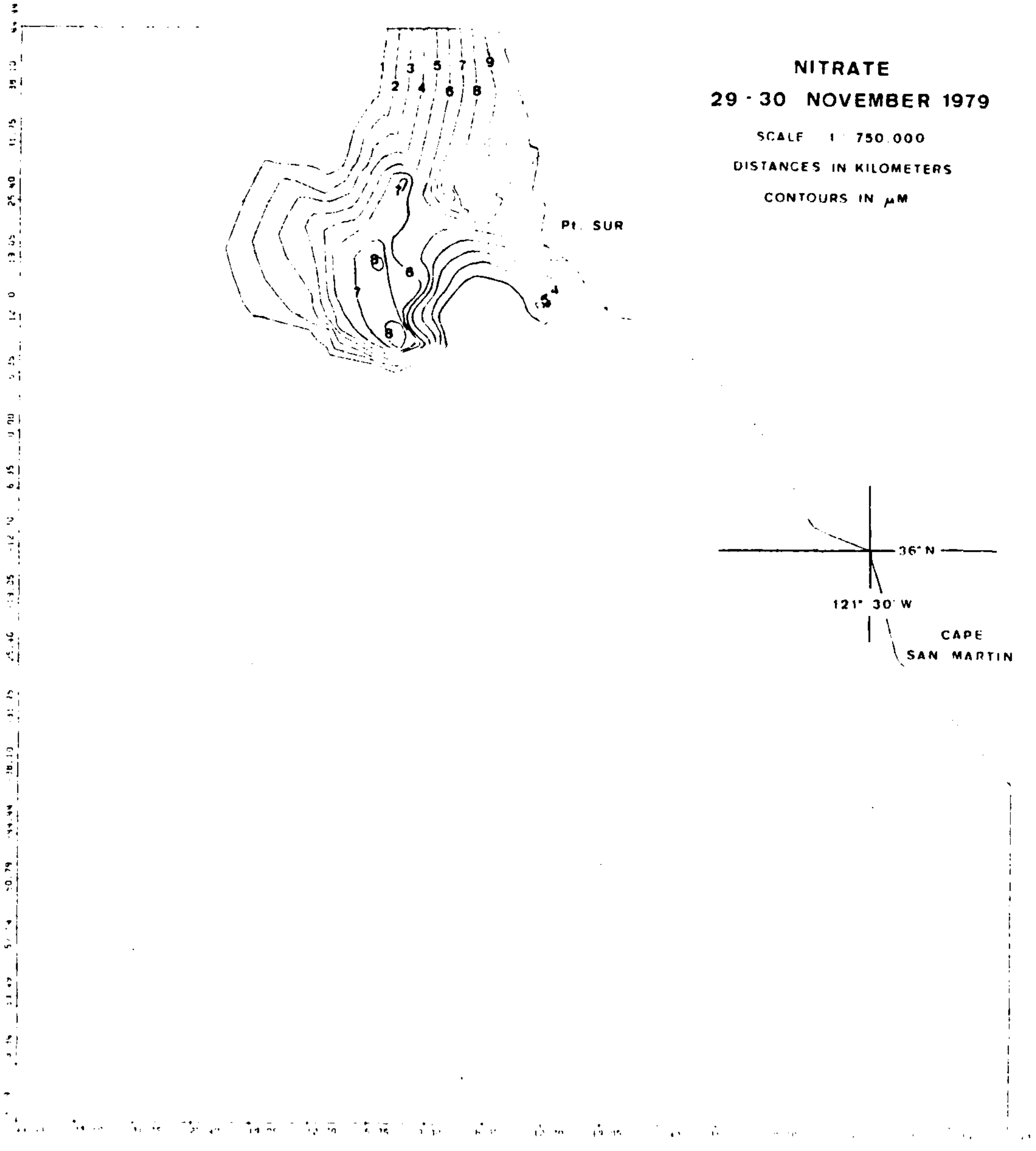

Figure 15. Nitrate distribution for the November 1979 cruise.

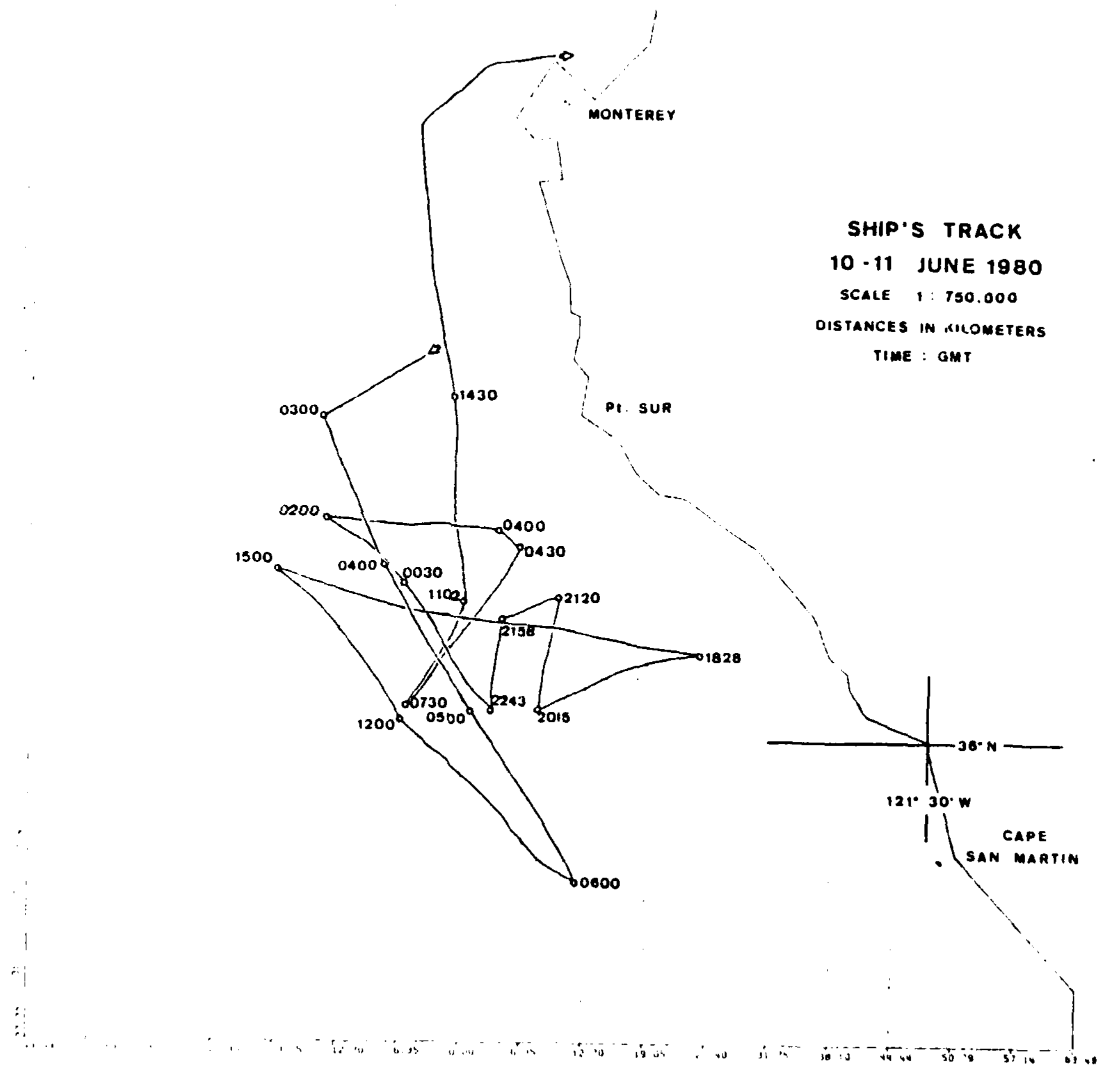

Figure 16. Cruise track for the June 1980 cruise.

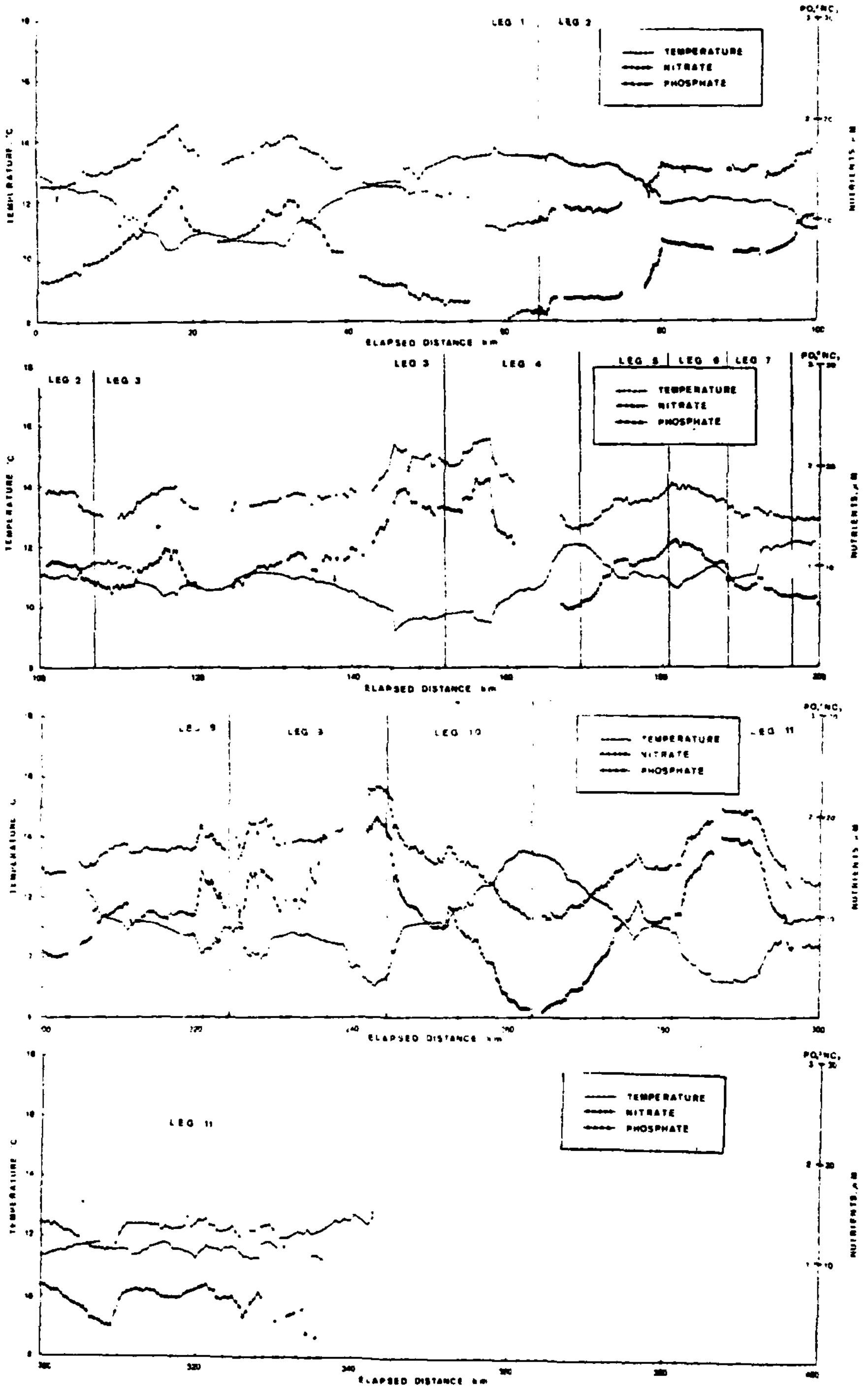

Figure 17. Nitrate, phosphate, and sea surface temperature versus elapsed distance along the track of the June 10-11, 1980 cruise.

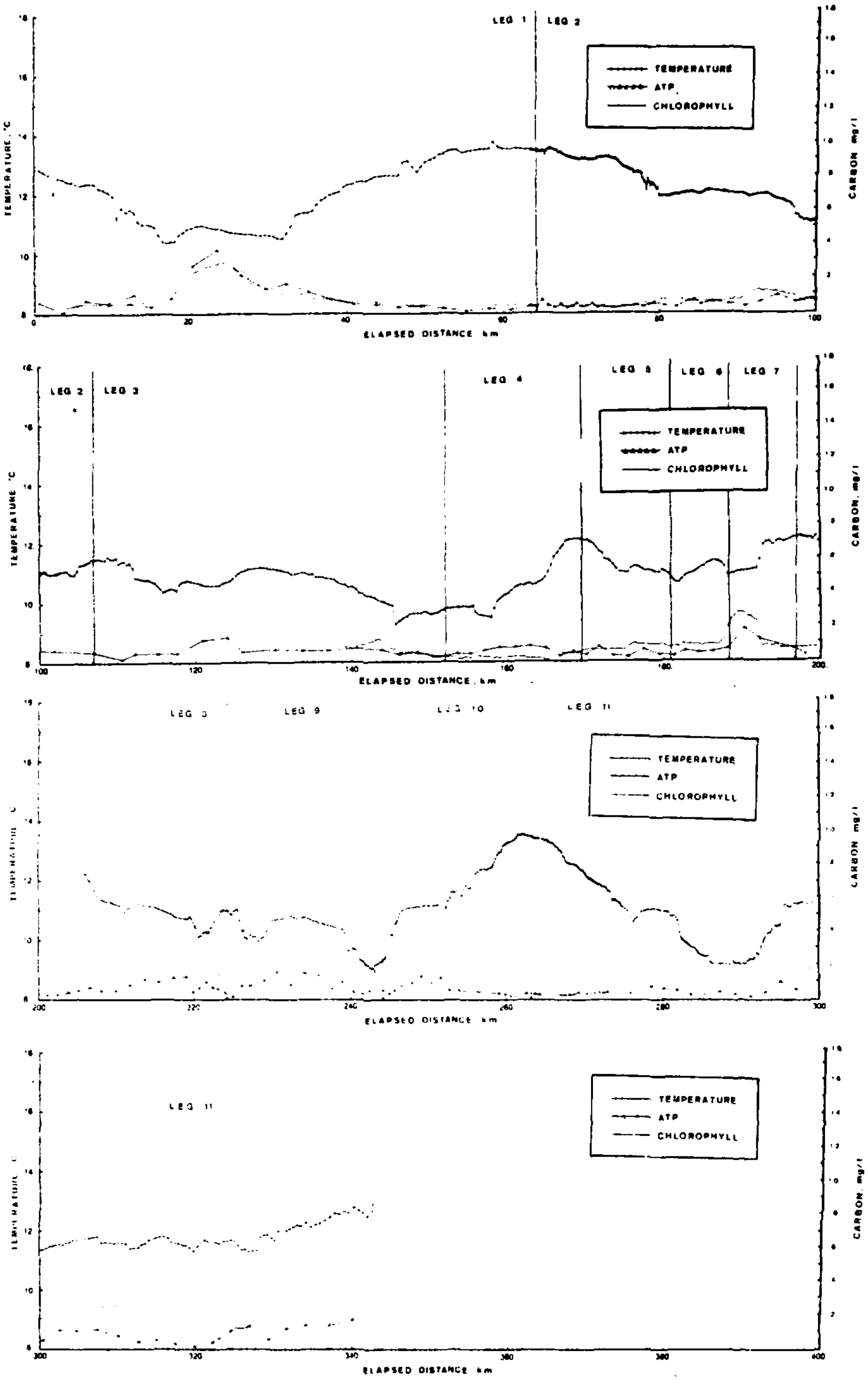

Figure 18. ATP, chlorophyll a, and sea surface temperature versus elapsed distance along the track of the June 10-11, 1980 cruise.

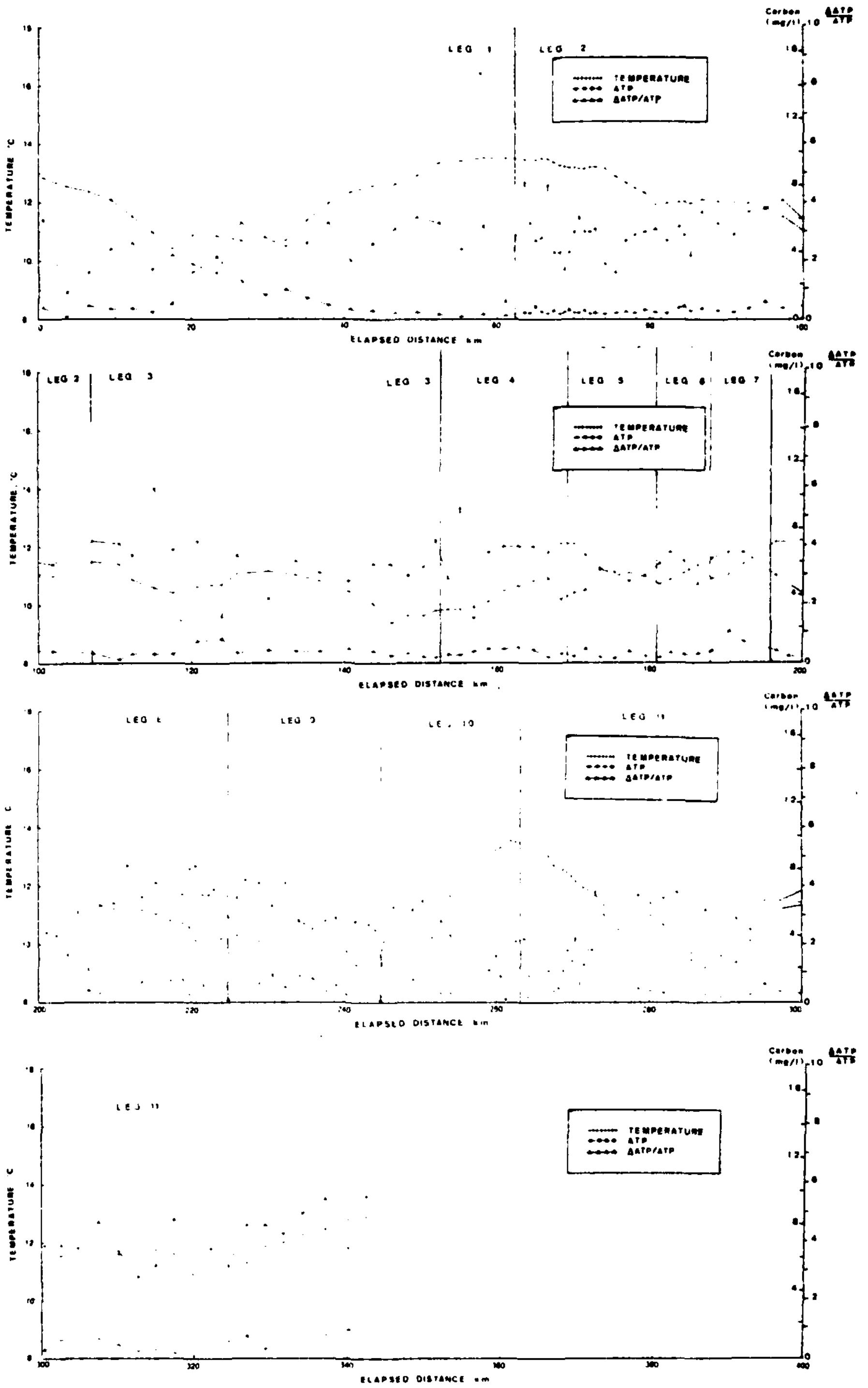

Figure 19. ATP, ΔATP/ATP ratio, and sea surface temperature versus elapsed distance along the track of the June 1980 cruise.

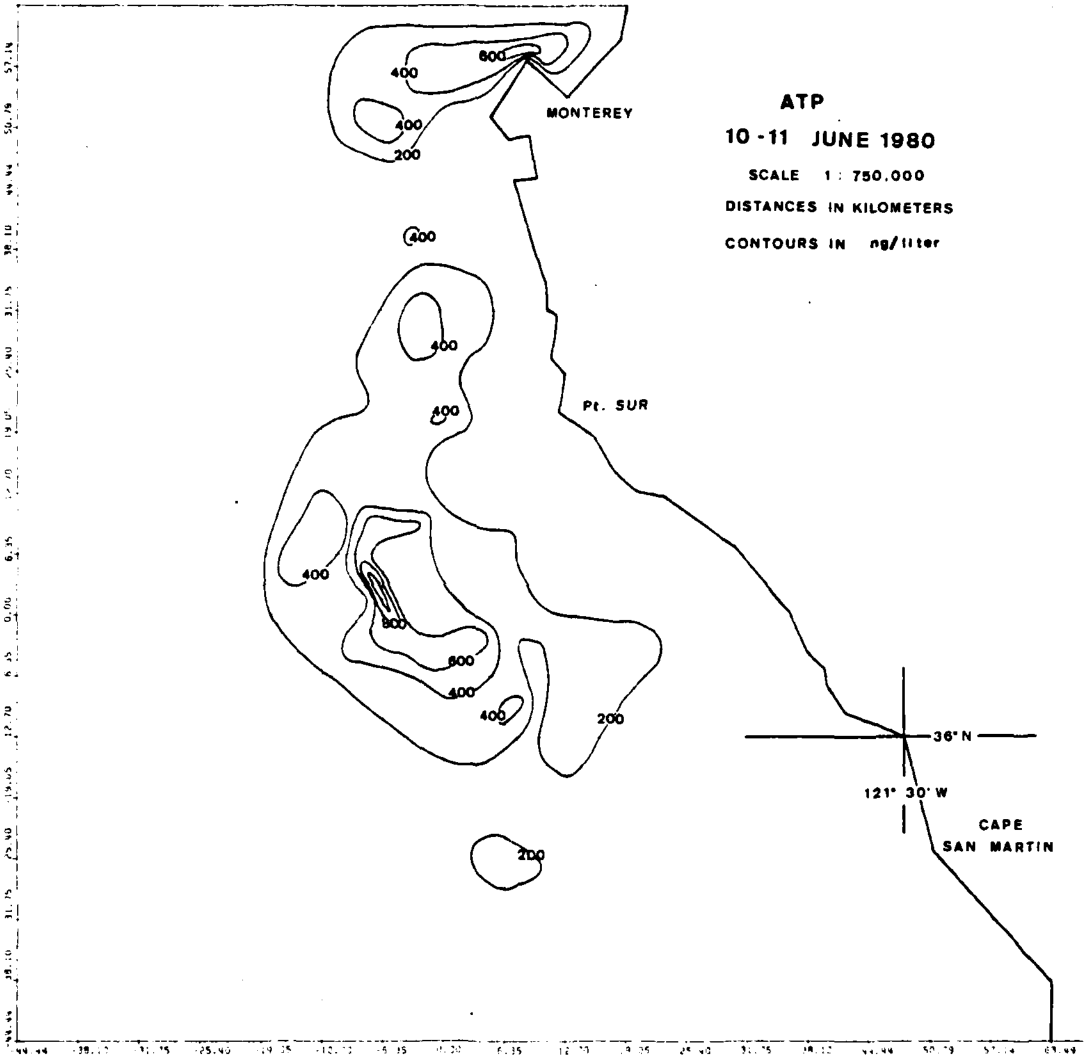

Figure 20. ATP distribution for the June 1980 cruise.

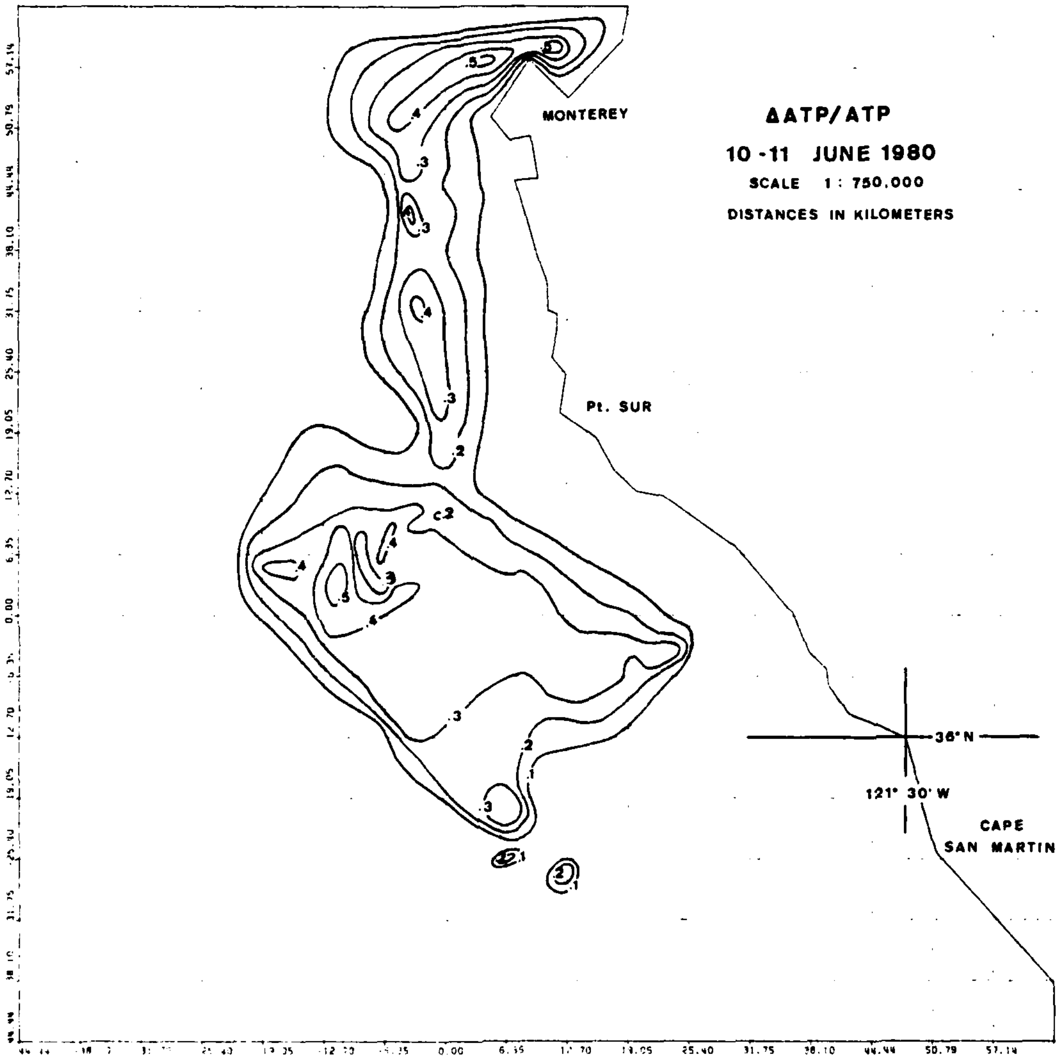

Figure 21. ΔATP/ATP ratio distribution for the June 1980 cruise.

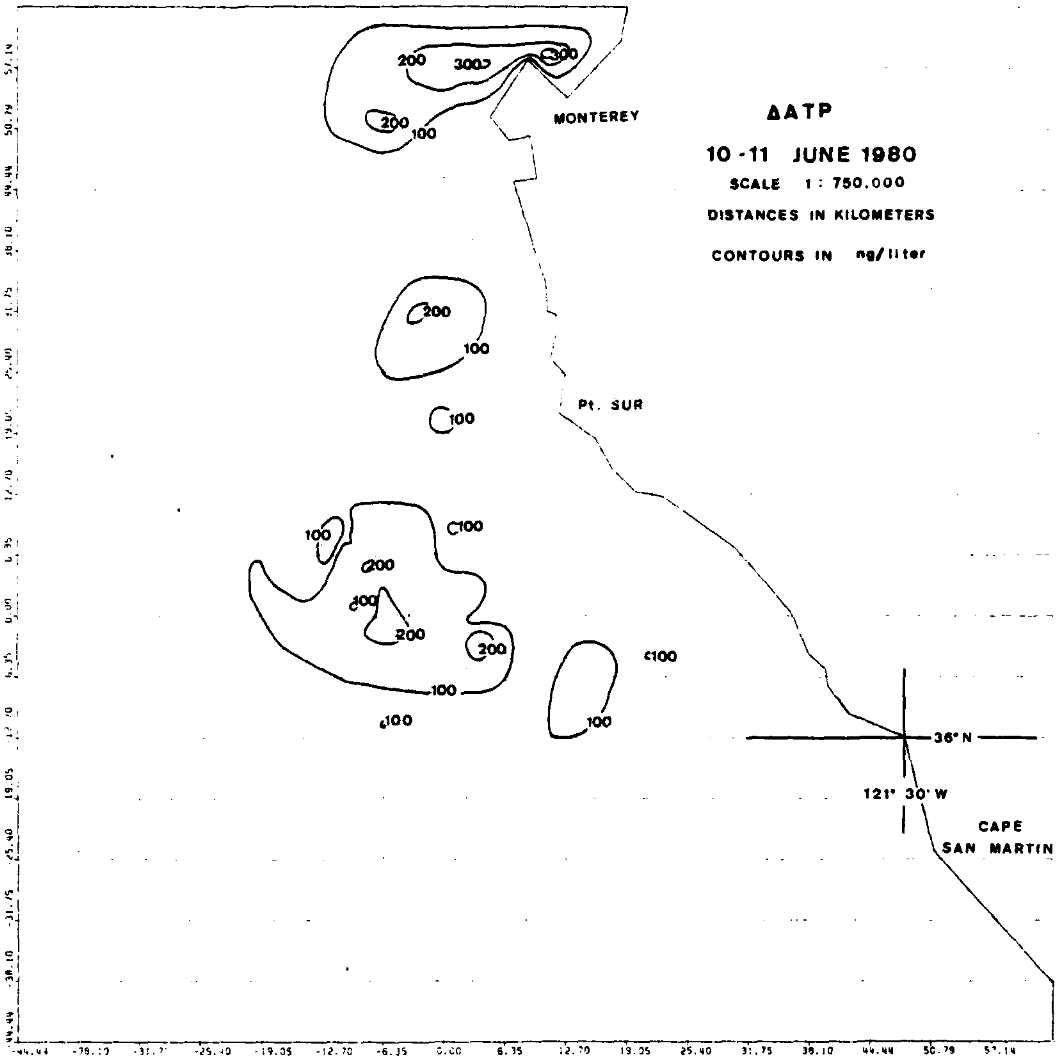

Figure 22. ΔATP distribution for the June 1980 cruise.

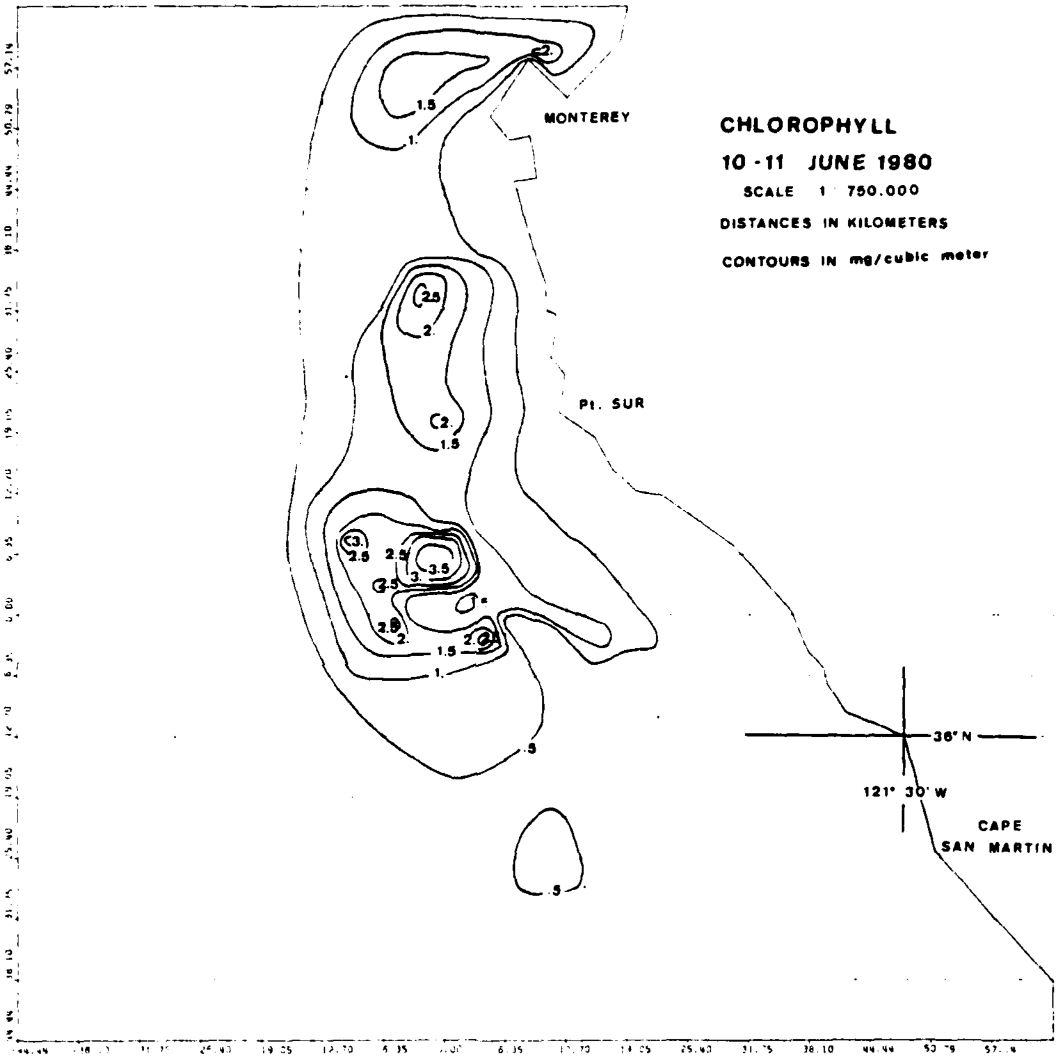

Figure 23. Chlorophyll distribution for the June 1980 cruise.

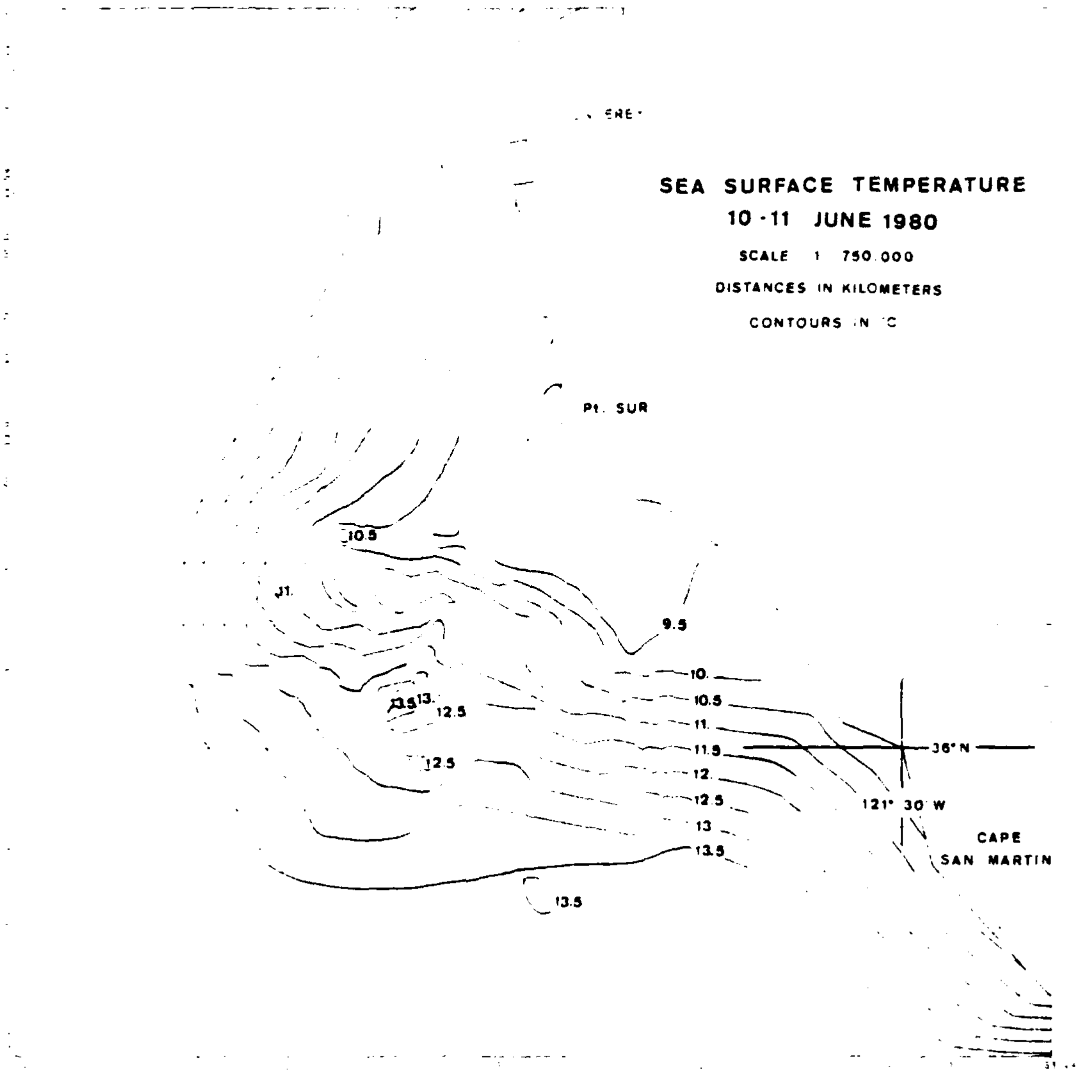

Figure 24. Sea surface temperature for the June 1980 cruise.

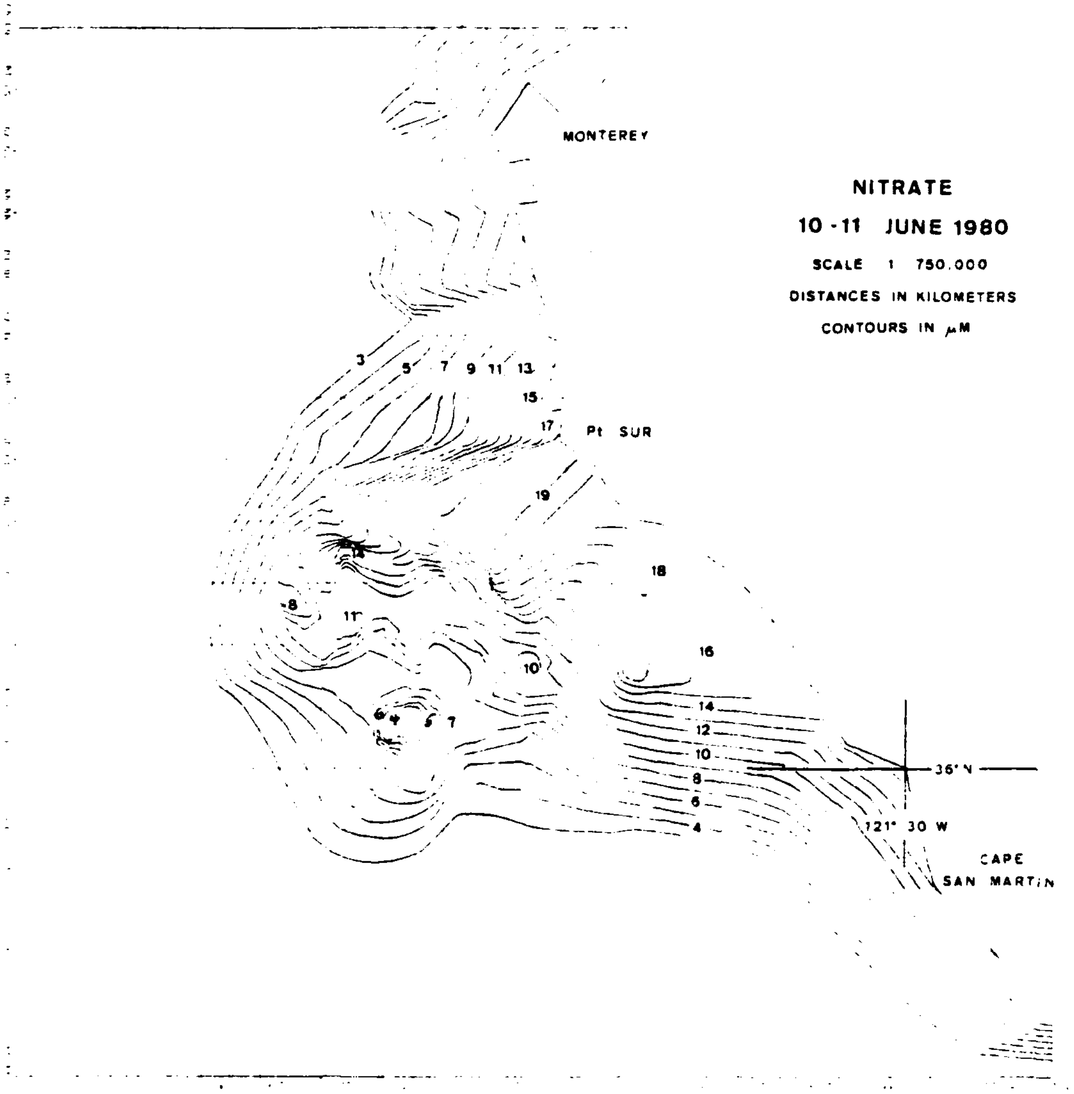

Figure 25. Nitrate distribution for the June 1980 cruise.

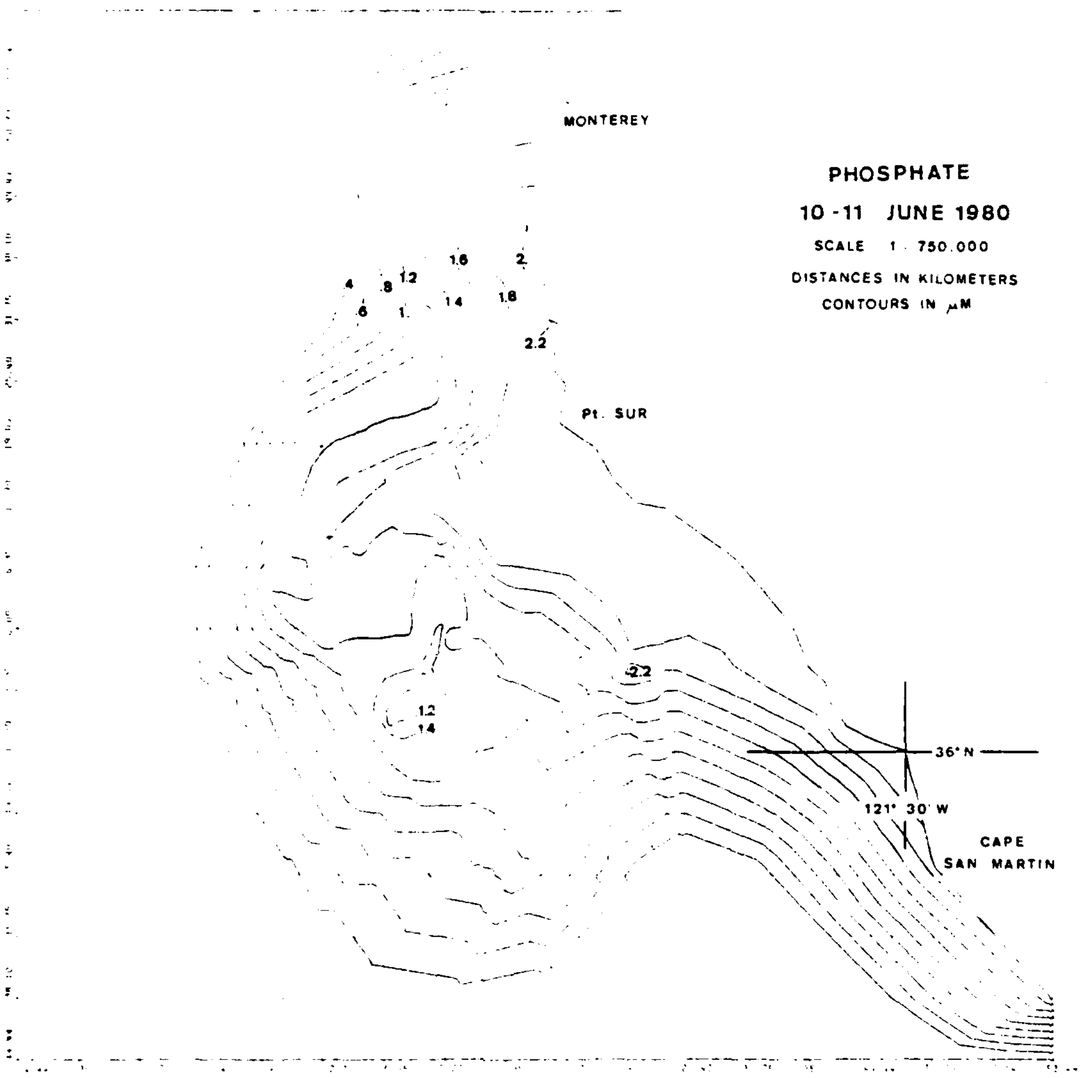

Figure 26. Phosphate distribution for the June 1980 cruise.

number - see comments below)) and surface circulation, the reason for this patchiness could not be considered.

### 2. The June Cruise

On June 10-11, 1980, in addition to temperature, nutrient, and ATP data, "chlorophyll a" data was collected and, for the first time, ΔATP and ΔATP/ATP values were computed. The range of these values, which were computed at approximately 10 minute intervals, are given in Table II along with chlorophyll a and ATP. There were 189 ATP, ΔATP, and ΔATP/ATP values on the June cruise.

## TABLE II

## RANGES OF ATP, ΔATP, ΔATP/ATP AND CHLOROPHYLL a FOR THE JUNE 11-12, 1980 CRUISE

| | high | low | mean | standard deviation |
|---|---|---|---|---|
| ATP (ng/l) | 1549 | 48 | 278 | ± 195 |
| ΔATP (ng/l) | 358 | .6 | 83 | ± 30 |
| ΔATP/ATP | .57 | -.01 | .30 | ± .11 |
| Chlorophyll a (mg/m ) | 5.59 | .17 | 1.11 | ± .83 |

Correlation coefficients for various parameters were computed and are summarized in Table III.

# TABLE III

## CORRELATION COEFFICIENTS BETWEEN ATP, ΔATP, ΔATP/ATP, CHLOROPHYLL *a*, AND TEMPERATURE FOR THE JUNE 1980 CRUISE

| Correlation of | Coefficient |
|---|---|
| ATP to CHL | .536 |
| ATP to ΔATP/ATP | .249 |
| ATP to ΔATP | .851 |
| ΔATP/ATP to CHL | .35 |
| ΔATP/ATP to TEMP | -.249 |
| ΔATP/ATP to ATP | .613 |
| ΔATP to TEMP | -.218 |
| ΔATP to CHL | .559 |

# IV. DISCUSSION

## A. ΔATP VS. GTP CORRELATION EXPERIMENT

The high correlation of ΔATP to GTP shows that in a binucleotid solution ΔATP may be taken as a measure of the relative amount of GTP present. In field samples there are other NTPs present (most importantly UTP) which enter into the reaction. Fortunately, for a given "system" (one with a relatively constant mix of microbial species) the percent of the ΔATP value which is GTP may be assumed to be constant [Karl, personal communication]. This constant, as mentioned previously, is on the order of 40 to 50% of the signal.

## B. THE JUNE CRUISE

The June cruise shows a feature in what appears to be the "initiation phase" [Conrad, 1980]. The thermal and nutrient gradients are strong and well defined, and there are strong correlations between nitrate and phosphate ($r = .96$), nitrate and temperature ($r = -.96$), and phosphate to temperature ($r = -.92$). These all point to "biochemically new" water [Traganza, et al., 1980] which has not had its initial conditions (temperature and nutrient concentrations) significantly altered by dynamical and biological processes. The satellite imagery (Plate 1) also shows a thermal pattern which has the appearance of an upwelling feature which is just forming and beginning to develop a cyclonic curl.

Plate 1. TIROS-N satellite IR image of the California coast, 9 June 1980.

ATP values are high (above 600 ng/l) in two areas (Fig. 20), the area of Monterey Bay off Pt. Pinos described by Lasley [1977] and discussed in the introduction, and in a narrow band along the seaward edge of the feature off Pt. Sur (stretching from about (5, -3) to (-3, 9) on the contour grid). This band closely follows the intermediate temperature band paralleling the peripheral margin of the satellite inferred feature and is in an area of water which is from 10.5 to 11.5 °Centigrade. This relation of the biomass to intermediate temperatures can also be seen in the linear plots (Figure 18). The maximum ATP concentrations are on the equatorward edge of the developing cyclonic curl (compare the SST figure and the ATP figure) which appears to be developing over the Sur Canyon. The nutrients are of intermediate concentration. Nitrates vary from 8 to 15 μM and phosphates from 1.2 to 1.8 μM in this area. The feature appears to be beginning a cyclonic spinup which would further concentrate and move this biomass along the equatorward edge of the feature.

Chlorophyll shows essentially the same distribution (Figure 23) with the exception of a large "cell" centered about (-1, 6) on the contour grid. Values here reach 3.5 $mg/m^3$. There are several possible explanations for this anomaly. ATP is subject to several variations that chlorophyll a is not. It is energy charge dependent and shows more diel variation than chlorophyll a does [Hunter, 1979].

In addition, the difference may come from sampling technique. The continuous flow of water through the fluorometer ("chlorophyll a" determination) is not prefiltered because this produces a clogging problem. This could result in phytoplankton (i.e., chain formers) larger than 200 microns being excluded from the ATP samples which are prefiltered, but not from the chlorophyll samples.

ΔATP (or "relative GTP") was highly correlated to ATP ($r = .85$). Since they are not measures of the same parameter (GTP $\sim$ instantaneous growth rate; ATP $\sim$ living biomass), it can be concluded that all of the biomass is in a relatively uniform productive state.

Cellular alkaline phosphatase may interfere with these field measurements. Alkaline phosphatase acts by selectively consuming ATP and GTP. ATP is consumed at a more rapid rate than GTP, destroying evidence of the initial relationship [Karl, 1980]. The results in our field measurements appeared to be too consistent with temperature and nutrient data to have been effected by this problem. However, a separate test as described by Karl [1980] has been conducted on our stored field samples by Dana Austin at the Naval Postgraduate School. There are no indications of alkaline phosphatase interference in six samples selected from representative locations.

The ΔATP/ATP ratio or "growth potential" provides information on the productivity state of the biomass. The "growth potential" is analogous to assimilation number (mg C uptake/mg Chl/hr). The standard deviation of the ΔATP/ATP ratio is only 37% of the mean value. This compares to a standard deviation of 70% of the mean for the ATP and 75% of the mean for chlorophyll. In other words, the "growth potential" varied very little and therefore the biomass adjacent to the fronts is in a relatively uniform productivity state. All of the biomass that is located adjacent to the nutrient fronts is present because of real growth. If the biomass were advected into the area, it should not remain at a high, uniform level. The only logical conclusion is that the biomass must be present as the result of real growth, i.e., presumably a preferential growth response to a horizontal nutrient flux across the sharp nutrient gradients.

The distribution of ΔATP/ATP is also of interest. The "growth potential" is high in the same area of Monterey Bay off Pt. Pinos described by Lasley [1977] and in the upwelling feature observed off Pt. Sur. In the feature, the "growth potential" is highest just seaward of the biomass peak. This suggests that the middle of the biomass peak is less active than the edges. This is not unexpected. Areas of high biomass are self-limiting in terms of growth, since they often encounter a growth limit such as light limiting or a nutrient shortage (although our data does not show a nutrient shortage). This also points to real growth in the system (at least in this early stage) because the distribution is as expected for a growing system.

The relationship of the biomass and growth potential to the front suggests that the gradients are an important part of the productivity. As mentioned previously, other authors [Lasley, 1977; Eppley, et al., 1979] have related biomass to gradients by considering the biomass and productivity to flux relationships. Both of these authors were able to infer the circulation to compute the flux from the gradients, something that we have been unable to do at this time. The dynamic features we are studying do not lend themselves to the techniques they employed. Lasley used a fixed feature (Monterey Bay) which had known circulation (from current studies and drifters). Eppley worked with vertical fluxes and was able to calculate the circulation by applying continuity equations. If the surface circulation were better known in upwelled features as described here, the possibility is strong that a relationship between nutrient fluxes and the productivity would be evident. The results would probably be similar to Lasley's, if the eddy diffusion term and the advection term parallel to the nutrient contours are negligible. This leaves a distribution of variables equation of:

$$\frac{\partial C}{\partial t} = - u \frac{\partial C}{\partial x} - w \frac{\partial C}{\partial z} + R \qquad 6)$$

This equation relates the changes in concentration of the parameter (nutrients in this case) directly to the fluxes associated with the vertical and horizontal gradients (with the exception, of course, of the biological term, R). If this equation is accepted as representing the behavior of the nutrients in the feature, there is a good qualitative agreement between the location of the biomass and productivity vs. the fluxes.

# V. CONCLUSIONS

1. The study of ΔATP and ΔATP/ATP ratios can provide valuable insight into productivity and growth potential. This method is especially valuable in studying dynamic features such as fronts and eddies, where a rapidly changing mesoscale environment and the need for large numbers of samples make more traditional methods unworkable.

2. Several conclusions about the initial or early phase of upwelling features can be drawn from the study of the June cruise.

a. Areas of high biomass are areas of high productivity. The biomass present appears to be there as the result of optimal growth conditions, not advection.

b. The highest growth is in the area surrounding the highest biomass, i.e., intermediate concentrations of biomass appear to be optimal. Even at this early stage in the feature, biomass is beginning to be limited in its growth by some factor.

c. Since both high biomass and high growth potential are found in the area of large nutrient and temperature gradients, the gradients must have a favorable impact on growth. A nutrient flux, as postulated earlier, may serve to connect the two. Unfortunately, until the surface circulation is better known, computation of surface fluxes is not possible.

If equation 6) is applicable to the June feature, however, the good correlation between productivity and fluxes is suggested qualitatively in the data if the velocities across the gradients are relatively constant.

d. With the exception of one chlorophyll *a* "cell" described earlier, the surface maps of ATP and chlorophyll *a* are essentially the same. A comparison of the surface maps and mean values suggests that the standard conversion ratios of C:ATP (250:1) and C:Chl (100:1) are not entirely accurate in this feature. If a C:Chl ratio of 60:1 were used instead of 100:1, the values would be in closer agreement, suggesting that the populations are largely phytoplankton. Eppley [1977] found the ratio of 54 ±17 for C:Chl in phytoplankton populations off Southern California which supports this suggestion. Without specific knowledge of C:Chl and C:ATP ratios in the populations under investigation, one cannot conclude that microzooplankton or bacterial populations are indicated rather than phytoplankton when ATP is larger than chlorophyll.

e. Satellite imagery may be used to infer potential biomass location and growth potential, at least in an initial stage of a feature's development but not all features may support biological activity. Studies of features in later stages of development may provide insight into the biomass and growth potential of older features. Applications of this technology may lead to the ability to remotely predict productive regions for fisheries and other applications. Such predictions would be dependent on the source water depth (a function of the feature's age, the season, and the recent wind history [Hanson, 1980]).

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