Submitted to Deep Sea Research

LBL-11277
Preprint

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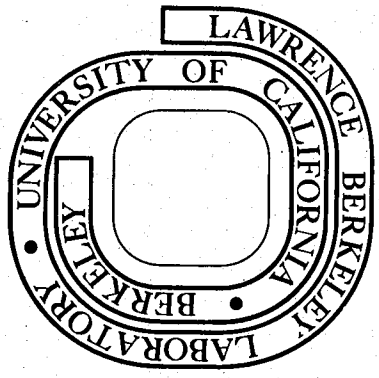
July 1980

Prepared for the U.S. Department of Energy
under Contract W-7405-ENG-48



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Phytoplankton dynamics in oceanic waters off Ke-ahole Point, Hawaii[1,2]

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1 Oceanic Institute Contribution No. 163
2 Lawrence Berkeley Laboratory Contribution No.

Abstract

Phytoplankton activity in an oligotrophic environment was studied on six cruises over a 14-month period. Phytoplankton biomass and productivity displayed considerable temporal variability despite the relative constancy of the physical and chemical environment. No evidence of seasonality or diurnal variability in phytoplankton biomass was observed.

Annual average ($\pm$ s.d.) depth-integrated values (0-260 m) for chlorophyll *a*, phaeopigment, ATP, and primary productivity were 24.55 ± 10.31 mg$\cdot$m^{-2}, 11.81 ± 7.20 mg$\cdot$m^{-2}, 3.00 ± 1.78 mg$\cdot$m^{-2}, and 8.79 ± 7.82 mg C$\cdot$m^{-2},h^{-1}, respectively; over the year these parameters were seen to vary over ranges of 3X, 6X, 10X, and 26X, respectively. The mean depths of the chlorophyll and phaeopigment maxima were 85 ± 9 m and 95 ± 11 m, respectively; the pheopigment maximum was always located at or below that of chlorophyll. Size fractionation studies showed that at this oceanic station about 80% of the phytoplankton biomass occurred in the $< 5\ \mu$m fraction.

Low ambient nutrient levels were typical at the depth of the chlorophyll maximum, indicating that nutrient assimilation was actively occurring in that layer. Elevated nutrient levels were typical at the deeper phaeopigment maximum layer. The results of sinking rate and size fractionation experiments, together with evidence of physiological viability in this layer suggest that phytoplankton sinking and possibly its association with the nutrient regime influence the accumulation of biomass in this region.

Productivity biomass ratios (mg carbon· mg chlorophyll $\underline{a}^{-1} \cdot h^{-1}$) were consistently low and indicative of strong nutrient limitation. Variations in phytoplankton biomass did not account ($p > 0.10$) for the high variability in photosynthetic activity among the six site visits; neither did the slopes or upper depth limits of the nitrate or phosphate gradients (as indicators of the supply rate of new nutrients) show any correlation ($p > 0.10$) with the observed primary productivity. There were significant correlations ($p < 0.01$) between depth-integrated phaeopigment stocks and integrated primary production ($r = 0.92$), and between integrated phaeopigments and integrated ammonium levels ($r = 0.80$). It is postulated that variations in the supply of regenerated nutrients via grazing (indexed by phaeopigments) were primarily responsible for the observed temporal variability in photosynthesis. Indications of a close coupling between grazing and phytoplankton activity in these waters is supportive evidence for the commonly held belief that animal excretion products are significant sources of nutrients for phytoplankton in oligotrophic systems. The observed relationship between phaeopigments and primary production may be related in part to the predominance of small cells in this phytoplankton community since the latter are probably grazed by small filter feeders which produce amorphous, slow-sinking, rather than encapsulated, fast-sinking fecal material.

Introduction

Because the warm, oligotrophic regions of the open sea are subject to less severe seasonal temperature cycles than are the temperate waters, and because these warm regions are permanently underlain by a strong pycnocline, they are regarded as the least variable surface waters of the sea in biological terms.

There are relatively few studies addressing temporal variation in subtropical latitudes; the subject has been reviewed by Sournia (1969) and Owen and Zeitzschel (1970). While there have been several intensive field studies of phytoplankton dynamics within the subtropical central gyre of the North Pacific (e.g. Thomas, 1970a,b; Venrick, 1971; Eppley, Renger, Venrick and Mullin, 1973; Venrick, McGowan and Mantyla, 1973; Perry, 1976), there appears to be little information concerning temporal variability in the open Pacific other than the seasonality study of Owen and Zeitzschel (1970) in the eastern Pacific. The annual range of primary production in subtropical oceans has been shown to vary by factors of about three (Owen and Zeitzschel, 1970, eastern tropical Pacific; Jitts, 1969, Indian Ocean) to nearly 17 (Menzel and Ryther, 1960, Sargasso Sea). These studies and others based on assessments made during single site visits to Pacific oceanic locales (e.g. Eppley et al., 1973; Gilmartin and Revelante, 1974; Gundersen, Corbin, Hanson, Hanson, Hanson, Russell, Stollar, and Yamada, 1976; Bienfang and Gundersen, 1977), yield estimates of daily water column production ranging from about 80 to 400 mg $C \cdot m^{-2} \cdot l^{-1}$ in subtropical oceanic areas.

The two-layer model of production in warm oceanic surface waters overlying a strong pycnocline (Dugdale and Goering, 1967) postulates that dissolved inorganic nitrogen as the limiting nutrient is supplied to phytoplankton by in situ regeneration and by slow upward diffusion from deep water. Variations in the supply of nutrients by these two processes would naturally be difficult to observe, especially considering the scarcity of seasonal surveys in lower latitudes. Little is known of the speed at which "normal" conditions return after transient atmospheric or hydrographic phenomena (storms or passing eddy systems). Neither are regenerative processes, such as zooplankton excretion, and their variation well enough documented to explain observed annual ranges in phytoplankton stock and production. The study of Eppley et al. (1973) indicates some diel and spatial variation of excretory regeneration in the North Pacific gyre, but did not address longer-term changes.

We present here the results of a 14-month survey at a deep and hydrographically "oceanic" station (19°55' N, 156°10' W). The station, located about 12 miles off Ke-ahole Point on the western coast of the island of Hawaii, has a bottom depth of about 1300 meters, and is one of the projected sites for an OTEC-1 pilot project by the U.S. Department of Energy. On six 2-day occupations of the site, the water column was sampled for temperature, salinity, dissolved oxygen, nutrients, plant pigments, ATP, and primary productivity. The six site visits, hereafter discussed as cruises #1 through #6, took place in October 1978 and April, June, August, October and December of 1979. The means and temporal variations in phytoplankton biomss

and productivity are discussed with respect to analytical error and diurnal, vertical, and seasonal variability, together with a description of the size composition of the phytoplankton assemblages and the contributing causes for temporal variations in the biological community in this subtropical environment.

Methods

On each of the six occupations of the station, hydrocasts were taken near noon, dusk, midnight, and dawn. Twelve depths were sampled on each cast: the noon and midnight casts sampled a target-depth range of 0 to 1000 m, the dusk and dawn casts covered the range of 0 to 300 m. Target depths were corrected with reversing-thermometer observations; true depths sampled in the two types of hydrocasts ranged to about 900 and 260 m, respectively. Subsamples were drawn from the 10-liter Niskin samplers through mesh screens of 202 μm pore size to remove larger phytoplankton.

Salinity determinations for all casts and depths were made ashore with a Bissett-Berman inductive salinometer. Samples were stored in screw-top plastic bottles for transport. Typical standard deviations of triplicate analyses of a sample were 0 to 0.001 ‰. Dissolved oxygen was analyzed for all casts and depths by the Winkler titration method as described by Strickland and Parsons (1972). The samples, drawn from the Niskin bottles before any other water, were fixed aboard ship with the manganous sulfate and alkaline iodide reagents, and transported to shore for analysis in 300 ml BOD bottles. Typical standard deviations of triplicate titrations on a sample were 0 to 0.05 $ml \cdot l^{-1}$

(0 to 1 drop from the titration burette). Subsamples for nutrient analyses were taken from the Niskin samplers into clean 60 ml, amber, polyethylene, screw-top bottles, then promptly filtered through prewashed Whatman GF/C or Gelman A-E glass fiber filters and immediately frozen. Samples remained frozen until just before analyses which took place at the laboratory (see Carpenter and McCarthy, 1975; Eppley, Sharp, Renger, Perry and Harrison, 1977; McCarthy and Goldman, 1979). All nutrient analyses were performed on a Technicon AutoAnalyzer II system according to the methods of Strickland and Parsons (1972) and Technicon (1977) for nitrate-nitrite, phosphate, and silicate; Solórzano (1969) for ammonium; and Demanche, Curl and Coughenower (1973) for urea.

Plant pigments were measured using a Turner 111 fluorometer, according to the procedures of Yentsch and Menzel (1963) and Holm-Hansen, Lorenzen, Holmes and Strickland (1965) for extracted samples--except that 0.45 μm pore cellulose acetate (Gelman GN-6), rather than glass fiber, filters were used. Triplicate 100 ml subsamples from each Niskin bottle on the dawn and dusk (0 to 300 m) hydrocasts were filtered at a differential pressure of $\leq$ 1/3 atmosphere. Filters were placed into foil-wrapped centrifuge tubes containing 5 ml of 90% spectral quality acetone, spun in a tube-mixer to disintegrate the filters, and stored at sub-zero temperatures for several days prior to analysis at the laboratory. Before analysis all samples were vigorously agitated again to remix the contents and then centrifuged to separate the residual filter material from the extracted pigments. Typical coefficients of variation for the triplicate analysis of chlorophyll a and phaeopigments were about 10% and 20%, respectively.

Determinations of ATP were done, like the pigment analyses, on triplicate subsamples of waters obtained from the dawn and dusk hydrocasts. The 1-liter subsamples were filtered onto the membrane filters described above; filters were plunged immediately into tubes containing 5 ml boiling TRIS buffer (0.05M), and extracted for 10 minutes before storage in a freezer. Extracts were analyzed according to the methods described by Karl and LaRock (1975) and Karl (1978), which involve measurement of the fluorescence of firefly-lantern extract in an ATP Photometer (SIA Corp.). Typical coefficients of variation were about 20%.

Carbon-fixation rates were determined by ^{14}C-uptake experiments (Steemann Nielsen, 1952) as described in Strickland and Parsons (1972). Triplicate samples were drawn from the upper nine Niskin samplers (0-150 m target depth) of the dawn hydrocast; samples were placed in 300 ml BOD bottles and injected with about 40 μCi of $NaH^{14}CO_3$ in basic (pH = 9) salt solution. Samples were attached to a line and incubated <u>in situ</u> at the depths of sample origins; the incubation rig was bottom weighted and set free of the ship to drift under a buoy. All samples were prepared and deployed shortly before dawn to avoid exposure of deep samples to surface light intensities (Goldman, Mason and Wood, 1963; Steemann Nielsen, 1964; Holm-Hansen, 1974). <u>In situ</u> incubations took place from dawn to late afternoon; for all cruises the incubation periods ranged from 10.0 to 11.5 hours. Upon recovery, samples were injected with 10^{-7}M DCMU (Bishop, 1958; Ensor, 1964; Eppley and Renger, 1974) to halt photosynthesis uniformly, and immediately filtered through Gelman GN-6 filters

(0.45 μm pore size). Introduction of DCMU takes a short time relative to the filtration time, and was employed to optimize the comparability of samples first and last filtered. The filters were placed into plastic LSC vials containing 0.5 ml of 10% HCl to drive off residual ^{14}C in solution (Lean and Burnison, 1979). In the laboratory ashore, the vials were flushed with air before addition of 10 ml of LSC cocktail (Aquasol-2) and counted on a Searle Delta 300 Liquid Scintillation Counter which was calibrated to yield counting efficiency from the external standard ratio for the conversion of cpm to dpm. Correction for the presence of particulate ^{14}C due to nonphotosynthetic processes was attempted using both the dark bottle and zero-time blank methods. Dark bottle counts in these waters, however, were high and highly variable, and frequently exceeded light bottle counts. Zero-time blanks (Berman and Williams, 1972) were prepared by filling the BOD bottles with sample, adding ^{14}C solution and immediately filtering the contents; such blank values, which account for both impurities in the ^{14}C stocks and the efficiency of removing residual dissolved ^{14}C from the filter, were low and highly reproducible. In view of the uncertainty concerning the exact meaning of dark bottle values (Williams, Berman and Holm-Hansen, 1972; Eppley and Sharp, 1975; Taguchi and Platt, 1977; and others) to the measurement of photoautotrophic synthesis of carbon by ^{14}C uptake, and the low rates of ^{14}C uptake being measured (Steemann Nielsen and Al Kholy, 1956), correction of ^{14}C samples was made using zero-time blank values. Standardization of the total ^{14}C activity injected into samples was performed for each cruise by a serial dilution method. Five serial dilutions of

the working ^{14}C stock were made using pH=9 buffered distilled water; aliquots of the diluted stock were added to vials containing phenethylamine (Iversen, Bittaker and Myers, 1976) and subsequently admixed with LSC cocktail. Linear regression analysis of dpm versus dilution factor was then performed to give the working activity used for the samples; correlation coefficients from this regression were typically $r = 0.99$.

Vertical profiles of scalar (nondirectional) irradiance were taken six times during each of the carbon-fixation experiments on cruises #4 and #5. Measurements were made with a profiling quantum scalar irradiance meter (Biospherical Instruments, Inc.) in units of quanta$\cdot cm^{-2} \cdot s^{-1}$. The instrument is designed to be sensitive to photosynthetically-active radiation (PAR) in the wavelengths 400-700 mm. Extinction coefficients were calculated from each profile, as the slope of the regression of log (I_z/I_o) on depth, where I_z is the measured irradiance at each depth.

Results

Physico-chemical Data

Composite plots (Fig. 1a-d) of all salinity, temperature, σ_t, and dissolved oxygen observations made during this survey indicate conditions typical of the subtropical Pacific. Salinity data show: (1) a surface layer (70 to 80 m deep) subject to effects of rainfall and evaporation, where salinity ranged from about 34.15 to 34.80‰; (2) a salinity maximum between 100 and 150 m (reflecting the North Pacific Central Water) where salinity sometimes

exceeded 35.10‰; (3) declining salinities until a minimum is reached at 300 to 400 m (reflecting the North Pacific Intermediate Water) with values ranging between 34.00 and 34.34 ‰; and finally, (4) slowly increasing salinity with depth (representing the Pacific Deep Water). Mixed-layer temperatures were between 24.2 and 28.0°C; the oceanic thermocline and pycnoclines are evident between about 70 m and 400 m in Figures 1c and 1d; dissolved oxygen (Fig. 1b) is at or above saturation (4.8 - 6.1 $ml \cdot l^{-1}$) in the photic zone, with concentrations declining to about 1 $ml \cdot l^{-1}$ in the deep water, reflecting oxygen utilization by organisms. The profiles were not made with sufficient detail to indicate a depth for the oxygen minimum.

Composite plots of dissolved plant nutrients show patterns typical of open ocean waters (Fig. 2). Phosphate and oxidized nitrogen ($NO_2^- + NO_3^-$) were present in low and uniform concentrations, usually less than 0.2 μM, in the mixed layer, increasing sharply at about 90 m where the pycnocline begins. Nitrate-nitrite and phosphate in the photic zone (from 0-125 m corrected depths) had mean concentrations of 0.27 and 0.16 μM, respectively. Ammonium had low and uniform concentrations (mean = 0.25 μM) throughout the photic zone, and showed no increase through the pycnocline. Urea appeared to decrease slowly with depth, from the surface values near 1 μM through the photic zone, with no apparent association with the pycnocline. The mean urea concentration was 0.74 μM. Silicate was usually at concentrations of 1 to 3 μM (mean = 2.11 μM) in the photic zone, with higher levels appearing at greater depths.

Phytoplankton Data

On all six site visits the vertical profiles of chlorophyll a and phaeopigments (Figs. 3 and 4) were similar in shape for both substances. Concentrations were low and uniform within the upper 40 to 60 m mixed layer; layers of maxima occurred between 60 and 120 m, and below this depth concentrations declined rapidly to low and uniform values. This is a common pattern in the waters around Hawaii (Bienfang, 1977; Bienfang and Gundersen, 1977) and in many regions of the oceans (Lorenzen, 1965; Saijo, Iizuka and Asaoka, 1969; Hobson and Lorenzen, 1972; Venrick, et al., 1973; Jeffrey, 1976). There were, however, detailed differences between the vertical distributions of chlorophyll a and phaeopigments, and large differences in the concentrations of each among the six site visits. Properties of the pigment distributions and their variability are quantified and summarized in Table 1.

In the mixed (0-60 m) layer, chlorophyll levels were generally low ($\bar{x}$ = 0.11 mg·m^{-3}); depth-integrated values for this layer averaged 5.38 mg·m^{-2}, accounted for about 20% of the total chlorophyll, and displayed a five-fold variation over the year. Total depth-integrated chlorophyll over the 0-260 m layer ranged from 13.77 to 45.13 mg·m^{-2} and averaged 24.55 mg·m^{-2} (Table 2). The depth of the subsurface maximum ranged from 62 to 94 m and chlorophyll values in this region ranged from 0.17 to 0.64 mg·m^{-3} ($\bar{x}$ = 0.31 mg·m^{-3}).

Phaeopigment concentrations were generally lower and more variable temporally than chlorophyll; this was true both for the surface regions and

within the subsurface maxima. In the mixed layer, phaeopigments were usually near the limits of detection (Table 1). Near the maxima, phaeopigment levels ($\bar{x} \pm$ s.d. = 0.15 $\pm$ 0.12 mg$\cdot$ m^{-3}) were about one-half those of chlorophyll and were more variable, having a coefficient of variation about twice that for chlorophyll. The depth of the phaeopigment maximum always occurred at or below that of chlorophyll. The mean ($\pm$ s.d.) depth of the phaeopigment maximum was 94 $\pm$ 11 m, and ranged from 76-111 m throughout the study. Similar differences in the vertical locations of the pigment maxima have been observed by Yentsch (1965) and Lorenzen (1967). Depth-integrated phaeopigment values over the 0-60 m and 0-260 m regions averaged 1.23 and 11.81 mg$\cdot$ m^{-3} (Table 2), respectively. Using ratios of concentration (mg$\cdot$ m^{-3}) data, the mean phaeopigment:chlorophyll ratio (P/C) was 0.29 within the 0-60 m layer and 0.45 over the 0-260 m region. Comparison of the vertically integrated values yields similar P/C ratio estimates (0.29 and 0.55, respectively). A greater percentage of the total water column chlorophyll (20.4%) was found in the mixed layer than was evident for phaeopigments (10.4%).

The data were also examined for diurnal differences in the standing stocks of chlorophyll and phaeopigments (Fig. 5). Differences between integrated chlorophyll *a* stocks (0 to 260 m) estimated from dawn and dusk hydrocasts were small and not statistically significant (t-test, $p > 0.10$). This is also qualitatively apparent from Figures 3 and 4. In most cases the dawn and dusk profiles for either chlorophyll or phaeopigments could not be distinguished from one another (given the analytical variation); they were very

similar compared to the differences between sampling dates. No pronounced seasonal trend was apparent from the data taken over the 14-month period (Fig. 5).

The distribution of phytoplankton biomass between two size classes ($< 5\ \mu m$, $> 5\mu m$) was examined over the 0–243 m depth range during the October 1978 cruise (#1). Pigment samples, collected on 5.0 μm pore size filters (Nuclepore polycarbonate membranes) under low (< 2 cm Hg) vacuum, were compared with samples collected on 0.45 μm filters. To investigate the size distribution of primary productivity, parallel carbon-fixation experiments were performed similarly over the 0–107 m region by filtration of ^{14}C samples through 0.45 μm and 5.0 μm filters after incubation. Defining the total phytoplankton biomass as that collected on 0.45 μm filters, percentages in the fraction $> 5\ \mu m$ were calculated (Table 3). Throughout the photic zone most of the phytoplankton biomass was found to occur in the $< 5.0\ \mu m$ size fraction; over the upper 123 m only $26 \pm 12\%$ of the chlorophyll occurred in the $> 5\ \mu m$ fraction. Overall, the chlorophyll contained in particulates $> 5\ \mu m$ ranged from 4.2 - 75% ($\bar{x} \pm$ s.d. $= 29.7 \pm 14.0\%$); values greater than 40% were confined to depths $\geq$ 123 m, i.e., below the photic zone. There appeared a tendency for phytoplankton populations in the layer of the pigment maxima (58–91 m) to have lower percentages in the larger fraction than was true for other parts of the profiles. Similar but somewhat lower fractions of phaeopigment occurred in the $> 5\ \mu m$ fraction. Over the 0–123 m region the amount of phaeopigment in the $> 5\mu m$ fraction ($\bar{x} \pm$ s.d. $= 13.2 \pm 4.2\%$) was roughly

half that of chlorophyll; below 123 m, the phaeopigment in fractions > 5μm increased along with chlorophyll values. For all depths where comparisons were made, the percentage of carbon fixation activity in the >5 μm fraction ($\bar{x} \pm$ s.d. = 12.9 $\pm$ 8.3%) was lower than the percentage of chlorophyll biomass in that fraction. Thus the carbon fixation attributable to the particle fraction >5μm took place at lower rates per unit biomass than the carbon-fixation in the smaller size fraction.

During the October 1979 cruise (#5), the distributions of chlorophyll *a* and phaeopigment in the <5 μm and > 5μm fractions were examined closely at closely spaced intervals over the region (48-133 m) of the pigment maxima (Fig. 6). Distinguishable differences are apparent in the vertical patterns and the depths of the maxima of these two pigments. The chlorophyll maximum was fairly pronounced from 60 to 100 m and centered near 85-90 m, while the phaeopigment maximum was evident between 85 and 130 m and centered at about 100 m. The appearance of the phaeopigment maximum about 10 m below that for chlorophyll in these closely spaced samples is consistent with the findings from the study as a whole (Figs. 3 and 4). The percentage of chlorophyll in the > 5 μm fraction ranged from 8-27% within this 48-133 m region and is similar to values observed earlier (Table 3). Near the center of the chlorophyll maximum (63-94 m), values for the > 5 μm contribution were somewhat lower than those outside this range. Phaeopigment in the > 5 μm fraction ranged from 11.3 - 26.7% of the total within this layer (48-133 m) of the subsurface maximum. The different vertical patterns of these two pigments

evident in these closely spaced samplings (Fig. 6) were attributable mainly to variations in the $< 5\ \mu m$ fraction. The size fraction studies showed that well over half of the phytoplankton biomass and productivity in this environment, often 80-90%, was found in organisms that pass through $5.0\ \mu m$ Nuclepore filters.

Vertical distributions of ATP concentrations (Fig. 7) are characterized by generally high and variable values in the mixed layer, followed by declining concentrations below 100 m. The subsurface concentration maximum seen in pigment profiles is not apparent in the ATP data. High variability in mixed-layer concentrations, which cannot be entirely accounted for by analytical variation, creates an appearance of one or more minor subsurface maxima in some ATP profiles. Such peaks are not generally found at similar depths as the pigment maxima. ATP concentrations in the upper 100 m ranged from 2.37 to 52.75 $\mu g \cdot m^{-3}$, with a mean of 20.60 $\mu g \cdot m^{-3}$ (s.d. = 11.82 $\mu g \cdot m^{-3}$, n = 91). Below 100 m, the overall mean was 7.30 $\mu g \cdot m^{-3}$ (s.d. = 5.23 $\mu g \cdot m^{-3}$, n = 51). Vertically integrated (0-260 m) ATP values ranged from 0.56 -5.72 $mg \cdot m^{-2}$ over the twelve hydrocasts; the mean ($\pm$ s.d.) integrated ATP value was $3.00 \pm 1.78\ mg \cdot m^{-2}$ (Table 2). As for the chlorophyll data, there was no apparent diurnal variation in ATP standing stocks. The tenfold range in integrated ATP values over the year was rather more than the three to fivefold ranges of the plant pigments; this may be due to the covariation of components other than phytoplankton which are measured in the ATP assessment. The ratio of integrated chlorophyll to integrated ATP (0 to 260 m) over the year ranged from 4.4 - 17.2 and showed a mean ($\pm$ s.d.) of 10.1 ± 4.5.

Chlorophyll:ATP ratios, from the quotients of concentration data, averaged 4.0 (n = 60) within the upper 60 m, and 5.9 over the entire 260 m range (n = 144).

Rates of primary production had vertical distributions (Fig. 8) that were highly variable with time, both in shape and in the rates of carbon fixation. The profiles do not indicate photoinhibition of fixation near the surface, nor do they show distinct subsurface maxima. There is a general uniformity through the mixed layer and down to 80 to 100 m, below which carbon fixation drops to low and at times undetectable levels. The six integrated production estimates ranged from 0.72 to 18.70 mg $C \cdot m^{-2} \cdot h^{-1}$ and a mean of 8.79 mg $C \cdot m^{-2} \cdot h^{-1}$ (Table 2). The coefficient of variation was equal to 89%; thus, the estimate of yearly production carries with it a similarly large uncertainty. Multiplying the mean fixation rate of 8.79 mg $C \cdot m^{-2} \cdot h^{-1}$ by 12 $h \cdot d^{-1}$ x 365 $d \cdot yr^{-1}$ yields a point estimate of 38.5 g $C \cdot m^{-2} \cdot yr^{-1}$ and a range of 4.0 - 72.6 g $C \cdot m^{-2} \cdot yr^{-1}$ for the site. An integration of the six individual production estimates over time, taking account of the varying intervals between cruises, yields a yearly production estimate only about 4% higher than the figure derived from the simple mean.

The depth-integrated (0 to 125 m) primary production rates under a square meter of sea surface were not significantly correlated (Table 4) with the integrated stocks of either chlorophyll a or of ATP ($p > 0.05$). Neither were there significant correlations between integral production rates and the depth of the upper boundaries or the slopes of the NO_3^- and $PO_4^{\equiv}$ gradients. There was also no correlation ($p > 0.05$) between production and the integrated

levels of NH_4^+, NO_3^- or $PO_4^{\equiv}$ (Table 4). The 26-fold variation among the production values for the six site visits is far in excess of the variation in either of the biomass indicators (pigments and ATP), which showed extremes of three to tenfold. Further, the production variation cannot be explained by variation in light levels; differences in percent cloud cover among the samplings were not related in any systematic way to carbon-fixation estimates.

Profiles of production-to-biomass ratios (P/B), expressed in the units mg C·mg chlorophyll $\underline{a}^{-1}\cdot h^{-1}$, sometimes showed rapidly declining values with increasing depth (Fig. 9), indicating some relationship to the light extinction with depth, but sometimes had very different shapes. The P/B ratios at the surface ranged from 0.11 to 8.35 mg C·mg chlorophyll $\underline{a}^{-1}\cdot h^{-1}$ during the six cruises; carbon fixation was undetectable in the deepest samples (150 m target depth) on three of six cruises, and otherwise it was low. For all cruises, the calculated P/B values within the light-saturated layer were low enough to indicate strong nutrient limitation in these waters (Curl and Small, 1965; Thomas, 1970a; Thomas and Dodson, 1972; Eppley et al., 1973; Laborde and Minas, 1974; Malone, 1977).

The scalar irradiance measurements, made in units of quanta·$cm^{-2}\cdot s^{-1}$, were used to calculate extinction coefficients for the photic zone, and to estimate the total irradiance received by the ^{14}C-fixation experiments at each depth during the incubation periods. The six extinction coefficients obtained on cruise #4 were quite uniform throughout the day, having a mean of 0.033 m^{-1} (s.d. = 0.005 m^{-1}). On cruise #5 they were lower and slightly

more variable: $0.027 \pm 0.008\ m^{-1}$. These coefficients are typical of open ocean waters of high clarity. Irradiance totals for the incubation periods were derived by integrating the irradiance values through the day for each depth. The irradiance levels at 1 m depth for the 10-hour incubation periods on cruises #4 and #5 were 26.2×10^{20} and 11.4×10^{20} quanta$\cdot cm^{-2}$ ($= 43.5$ and $18.9\ E \cdot m^{-2}$).

Discussion

A noteworthy feature of these results is the large temporal variation observed in both the standing stocks and productivity rates of the phytoplankton community in this subtropical environment. This variation was not mirrored to any significant degree by changes in the physico-chemical parameters or ambient concentrations of essential plant nutrients. Variations in microbial biomass levels were not restricted to the surface layer but rather were observed to extend throughout at least the upper 150 m. It is often implied that the absence of pronounced climatic variation in subtropical environments connotes temporal stability in the phytoplankton communities of subtropical waters. The variability of depth-integrated values (0-260 m) for chlorophyll a (3x), phaeopigment (6x), ATP (10x), and primary production (26x) portray highly variable biological conditions in waters that were similar from cruise to cruise chemically and physically. This is worthy of attention, whether the variability is due to spatial heterogeneity (e.g. Platt and Filion, 1973) or temporal changes in a single ecosystem. Inspection of the phytoplankton

data (Table 2) does not suggest that this variation should be interpreted as seasonality. The survey site is subject to considerable advective exchange of water via vigorous currents and eddy systems which regularly traverse the area (Patzert, 1969; Wyrtki, Graefe and Patzert, 1969). Patzert (1969) showed that the volume transports in these eddies can be as large as $8 \cdot 10^6 \cdot m^3 \cdot s^{-1}$ and that most of the horizontal flow is concentrated in the upper 150 m. Generated and driven by strong local winds blowing through the Aleinuihaha Channel. between the islands of Maui and Hawaii, these eddies typically move away from the island of Hawaii in a westerly or northwesterly direction. These eddies have formation times of 2-6 weeks and are believed to develop whenever strong trade winds prevail. The potential water exchange suggested by such advective processes is of the order to be influential to the measured temporal variations in microbial biomass, and it seems reasonable that the generation and movement of these wind-driven eddies are important to the phytoplankton activity in this area.

A subsurface chlorophyll maximum layer appeared as a characteristic of this environment and the repeated examination of this layer provides data regarding characteristics of its temporal variation at a single station. Despite the concomitant variability of microbial biomass indices, this feature appeared in all 12 hydrocasts, displayed considerable consistency in its vertical position, accounted for a majority of the chlorophyll in the photic zone, and showed less temporal variation than concentrations in the overlying waters. The coefficients of variation (s.d./$\overline{x}$) for the observed depths of

the chlorophyll ($\bar{z}$ = 85 m) and phaeopigment ($\bar{z}$ = 95 m) maxima were 0.11 and 0.12, respectively, and were among the lowest such values attained for the various parameters considered. Chlorophyll concentrations at the maximum ranged from 0.17 to 0.64 $mg \cdot m^{-3}$, were roughly triple the average values for the upper 60 m, and displayed coefficients of variation which were about 70% that of the overlying waters (Table 1). Phaeopigment maxima were in all cases found at or below the depth of the chlorophyll maxima, and the increased levels of both pigments at the maxima were shown on two separate occasions to be due primarily to biomass which passed through a 5 μm filter. These results indicate that the deep chlorophyll maximum is a comparatively stable feature of this otherwise highly variable system, and suggest stability in the mechanism(s) responsible for its maintenance.

Investigations showing that the deep chlorophyll maximum is an ubiquitous feature of various oceanic environments (Menzel and Ryther, 1960; Steele, 1964; Yentsch, 1965; Lorenzen, 1965; Anderson, 1969; Saijo et al., 1969; Hobson and Lorenzen, 1972; Venrick et al., 1973; Jeffrey, 1974; Keifer, Olson and Holm-Hansen, 1976; Bienfang and Gundersen, 1977; Reid, Stewart, Eppley and Goodman, 1978; Shulenberger, 1978; Herbland and Voiturez, 1979; and others) have also prompted a number of hypotheses concerning the functional processes responsible for its development. These include the mechanisms of 1) cell sinking (Steele and Yentsch, 1960) and its interrelation with either the prevailing density structure (e.g. Anderson, 1969; Saijo et al., 1969; Goering, Wallen and Nauman, 1970) or physiological responses to the low light/high nutrient

environment leading to decreased sinking rates (Steele and Yentsch, 1960; Eppley, Holmes and Strickland, 1967); 2) differential zooplankton grazing (Lorenzen, 1965); 3) in situ production (Anderson, 1969); 4) adaptive changes in the chlorophyll/carbon (Steele, 1964) or chlorophyll/cell ratio (Keifer, Holm-Hansen, Goldman, Richards and Berman, 1972; Keifer et al., 1976); and 5) combinations of these four mechanisms. There are two pieces of information which indicate that maintenance of the deep chlorophyll maximum at this oceanic station involves the process of cell sinking. Bienfang (in press) showed that the sinking rates of populations taken from just above the chlorophyll maximum were significantly ($p < 0.01$) lower than those measured for populations taken from the overlying waters, and studies on light-limited, steady-state cultures of the nannoplankton Thalassiosira fluviatilis also showed reduced sinking rates at low light levels approximating those prevailing at the deep chlorophyll maxima in these waters (Bienfang, in preparation). Secondly, the ambient nitrate and phosphate concentrations at the depth of the chlorophyll maximum were found to be similar to those of the overlying waters, i.e. nutrient assimilation is actively occurring in that layer, as evidenced by the maintenance of low ambient nutrient levels. The sinking rate data together with the evidence of physiological viability suggest that biomass settling, and possibly its association with the nutrient regime near the maximum, affect the accumulation of biomass in these waters. This conclusion is in agreement with that of Venrick et al. (1973), and does not necessarily preclude concomitant changes in chlorophyll/cell.

The depth-integrated ATP values from the six cruises were not significantly correlated with the integrated chlorophyll or primary productivity ($p > 0.05$). As an indicator of planktonic biomass, ATP differs from chlorophyll in that ATP is not restricted to photoautotrophs. Our ATP determinations included organisms which were small enough to pass the 202 μm prescreen and large enough to be collected on the 0.45 μm pore filters, thus some bacteria and microzooplankton were undoubtedly captured and analyzed. The temporal variation in ATP stocks (Table 2) was greater than that observed for chlorophyll. Considering all samples collected in the upper 260 m (n=144), ATP values ranged from 0.01 - 52.7 $\mu g \cdot m^{-3}$ ($\bar{x}$ = 15.8 $\mu g \cdot m^{-3}$). The vertical distributions of ATP did not show a subsurface maximum as continuously evident for both chlorophyll and phaeopigment profiles. The coefficients of variation (s.d./$\bar{x}$) for the ATP data from the six site visits were similar to those of the plant pigments. Ratios of chlorophyll:ATP were highly variable, but in general were lower within the photic zone than below it. By comparison of the concentration data from all hydrocasts (n=144), the average ($\pm$ s.d.) chlorophyll:ATP ratio was 5.9 $\pm$ 5.2, and by comparison of the depth-integrated values (n=12) the average chlorophyll:ATP ratio was 8.3 $\pm$ 4.2. It is possible that some or all of our ATP values may underestimate true values, because ATP analysis done in TRIS buffer can be subject to some ATP destruction by alkaline phosphatase activity in the extracts (D. Karl, pers. comm.).

Data from the six site visits did not reveal any correlation ($p > 0.10$) between primary productivity values and the prevailing standing stocks (indexed by either chlorophyll or ATP), indicating that variation in phytoplankton biomass did not account for the variations in photosynthetic activity. Since observed P/B ratios were indicative of pronounced nutrient limitation (Curl and Small, 1965; Thomas, 1970a), attention was directed toward examination of factors which might influence the specific rates of metabolic activity via changes in the supply rate of nutrients to this nutrient-limited environment. Ambient nutrient levels were in all cases low and relatively invariant, reflecting phytoplankton demand at or above nutrient supply rates. Evidence that variations in the vertical supply rate of "new" nutrients, derived from oxidized forms of nitrogen and/or phosphorus from the aphotic zone (e.g., Eppley, Renger and Harrison, 1979; Herbland and Voiturez, 1979), was examined for association with this variable productivity; this was done by analysis of the nutrient profiles (not presented) and production data from each cruise. Neither the slope nor the upper depth limit of the nitrate or phosphate gradients were correlated ($p > 0.10$) with the observed variations in primary productivity. (Table 4). These findings at this subtropical location are different from those of Herbland and Voiturez (1979) in the eastern tropical Atlantic.

It is likely that changes in the supply rate of nutrients derived from regenerative processes were responsible for the observed temporal variations in primary productivity at this subtropical station. The relative importance of regenerated nutrients to the phytoplankton activity in oligotrophic systems

has been addressed in several works (Dugdale and Goering, 1967; Thomas, 1970b; Thomas and Owen, 1971; MacIsaac and Dugdale, 1972; McCarthy, 1972; Eppley et al., 1973; Perry, 1976). Such studies have suggested a close coupling between levels of phytoplankton activity and the grazing-excretion processes of zooplankton. We note that the fluorometric techniques employed here to determine phaeopigments do not allow for a more detailed delineation of decomposition products, e.g. chlorophyllide a, phaeophorbide a, and phaeophytin a (Jeffrey, 1974). We found a significant ($p < 0.01$) correlation between the depth-integrated phaeopigment and ammonium levels (Fig. 10); and no such correlation existed between phaeopigments and either nitrate or phosphate. We also found a significant correlation ($r = 0.92$; $p < 0.01$) between the six depth-integrated primary production estimates and the depth-integrated phaeopigment levels prevailing at the time (Table 4, Fig. 11). We believe that in this environment the phaeopigment levels can be taken as an indicator of grazing, and thus representative of the regenerative nutrient supply. The tenability of a causal relationship between phaeopigment (as an indicator of nutrient regeneration) and primary production is supported by the low P/B ratios which are indicative of strong nutrient limitation. The regression analysis indicates that about 84% of the variation in production per square meter of sea surface was associated with variations in the integrated phaeopigment stocks. The P/B data (mg C · mg chlorophyll $a^{-1} \cdot h^{-1}$) were similarly correlated with the phaeopigment levels ($r = 0.85$; $p < 0.05$). High phaeopigment concentrations have been observed to be associated with the stocks of small

zooplankton (Lorenzen, 1965; Glooschenko, Moore and Vollenweider, 1972; Jeffrey, 1974; Shuman and Lorenzen, 1975). Because in this environment most of the phytoplankton biomass occurs in the < 5 μm fraction (Fig. 6, Table 3), it is likely that a substantial share of the grazing is by small zooplankton; many of these do not encapsulate their solid waste into pellets (Shuman and Lorenzen, 1975). Thus the phaeopigment, produced by digestive acidification of chlorophyll, remains among the suspended particulate material of the photic zone rather than sinking rapidly in pellets. Since small zooplankton regenerate nitrogen and phosphorus more rapidly per unit of biomass than larger plankters (Johannes, 1964; Hargrave and Geen, 1968; Mullin, Perry, Renger and Evans, 1975), and are generally more abundant (Johannes, 1964; Beers and Stewart, 1969; Mullin et al., 1975; Hirota and Szyper, 1976), they are expected to be the major agents of excretory regeneration. Assessment of the activity of the smaller animals, however, requires special techniques (McCarthy, Taylor and Loftus, 1974; Caperon, Schell, Hirota and Laws, 1979); thus most estimates of excretory regeneration in nature are made for larger, less influential animals (e.g. Corner and Davies, 1971; Mullin et al., 1975; Szyper, Hirota, Caperon and Ziemann, 1976; Smith and Whitledge, 1977). These studies and others (e.g., Martin, 1968; Jawed, 1973; Smith, 1978), though restricted to large zooplankton, yield estimates of contributions to plant uptake ranging from 0 to 100 percent. Caperon et al. (1979) found that excretion closely balanced plant uptake (in a coastal embayment) when organisms of all sizes, including those passing through 35 μm mesh, were considered.

The evidence of an active interface between grazing and phytoplankton activity at this subtropical station supports the hypothesis (Dugdale and Goering, 1967; McCarthy and Goldman, 1979) that animal excretion products, e.g. ammonium and/or urea, are significant sources of nitrogenous nutrients supporting phytoplankton growth in oligotrophic waters (Figs. 10, 11). In this environment, as elsewhere in the open sea, nutrient control of phytoplankton activity is difficult to observe with sample-to-sample correspondence between nutrient concentration and carbon fixation. Reasons for this difficulty include a) small-scale temporal and spatial variation in regenerative nutrient inputs, b) rapid uptake capabilities of phytoplankton, and c) limitations on limits of detection of existing analytical methods for dissolved nutrients. Nevertheless, we were able to recognize a coupling between a parameter of nutrient input (grazer-produced phaeopigments) and primary production by examining parameters integrated over the photic zone and sampled with a period of about two months. By illustrating the effects of storm activity on food chain dynamics, Walsh (1976) and Walsh, Whitledge, Barnevik, Wirick, Howe, Esaias and Scott (1978) make a good case for the importance of changes in the dominant frequencies of variability in physical habitat by defining the relative importance of grazing pressures to nutrient utilization patterns. If, as postulated (Walsh, 1976; Walsh et al.,1978), low-frequency variability characterizes the oligotrophic waters of the central gyres, herbivory is expected to be of pronounced importance to the nutrient cycles in these waters. It may well be that the characteristically low dominant frequency of physical variability in the system allowed for the recognition of what we

believe to be phytoplankton responses to local eddies; the generation and subsequent movement of eddy systems through the study area (Patzert, 1969) represent potentially important variability in the physical habitat in this otherwise low-variability system. The temporal and spatial scales of habitat variability indicated by the eddy processes, together with these phytoplankton results (Table 2, Fig. 10, 11) suggest that the variability in phytoplankton activity was coupled to variation in the supply of regenerated nutrients which in turn was influenced by variability in the physical system.

In addition to lending support to the phaeopigment-primary production hypothesis, the results of the two size-fractionation studies (Table 3, Fig. 6) indicate several interesting features about the phytoplankton community in this environment. Both trials (from different cruises) revealed a high percentage (about 80%) of the total plant pigment to be contained in small organisms. On cruise #1, the mean percent ($\pm$ s.d.) of total chlorophyll found in the $> 5\ \mu m$ fraction was $23.6 \pm 10.8\%$ over the depth range of 0.107 m; on cruise 4 that fraction was $10.4 \pm 2.9\%$. The importance of nannoplankton to the standing stocks of oceanic systems has been shown also by Malone (1971) and Taguchi (1980); near the subsurface maximum at several tropical North Pacific stations, Taguchi (1980) found almost 96% of the chlorophyll to be in the $<20\ \mu m$ fraction; unfortunately no tests were made with filters having smaller pore sizes like those used in this study. There are also apparent differences in the vertical distributions of phaeopigments between the two size fractions. On both cruises when these trials were done, the region of a

phaeopigment maximum began at similar depths for both size fractions (i.e. 80-90 m); however, the maximum for larger particles extended much deeper (to about 200 m on cruise #1, and to the deepest sampled depth, 133 m, on cruise #4) than the maximum of the smaller particles. For chlorophyll a, the two size fractions exhibited profiles with very similar shapes, and having no indication of such an effect. The phaeopigment maxima of both the small and larger (> 5 μm) fraction were found deeper than their respective chlorophyll maxima.

The occurrence of the phaeopigment maximum at depth greater than that of the chlorophyll maximum may be related to both the light-lability of phaeopigments (Lorenzen, 1965; Yentsch, 1965; Jeffrey, 1974, Shuman, 1978) and a co-occurring sinking phenomenon. At depths above the chlorophyll maximum, phaeopigments may be degraded by light, thus partially reducing the prevailing levels. It is also plausible that particles with higher P/C ratios may sink more rapidly than particles with little phaeopigment. Dead or moribund particles, such as those having passed through grazers' digestive tracts and subject to acidification, would have higher P/C ratios than particles not subjected to grazing. Physiological buoyancy-maintaining mechanisms could be rendered inoperative in such cells; higher sinking rates have been shown to coincide with senescence and/or cell damage of various sorts (Steele and Yentsch, 1960; Smayda and Boleyn, 1965, 1966a,b; Eppley et al., 1967; Smayda, 1970). The involvement of sinking processes in this observation is consistent with our finding that a chlorophyll maximum was found at similar

depths for both large and small size fractions, but the phaeopigment maximum was deeper and less well defined for larger particles, i.e., cells having disrupted physiological activity are sinking at rates determined primarily by hydrodynamic principles, resulting in larger particles sinking more rapidly. We also noted that ambient NO_3^- and $PO_4^{\equiv}$ levels at the depth of the phaeopigment maxima were almost always higher than levels in the overlying waters. This evidence that nutrient assimilation in the phaeopigment maximum layer was not sufficient to maintain low nutrient levels in that layer is different from the situation found at the slightly more shallow chlorophyll maximum; this is evidence that impaired and/or more strongly limited metabolic activity was typically associated with the layer of the phaeopigment maximum at this oceanic station.

In summary, we observed large variations in the biomass and productivity of phytoplankton in a relatively constant physical and chemical environment. It is plausible, in fact, that we did not observe the absolute extremes of temporal variation in any of the parameters measured, since the survey was relatively short. Few such sets of estimates for the temporal variation in stocks and production of phytoplankton are available for warm, oligotrophic environments. Only by attention to a fairly subtle relationship, namely that between phaeopigment stocks (as an index of nutrient regeneration by microzooplankton) and production, were we able to account for a significant portion of the variation in phytoplankton activity. Such a relationship may not hold, however, in environments where most of the phaeopigments are produced

by the grazing activity of larger zooplankton which encapsulate their fecal material into fast-sinking pellets. The relationship between phaeopigments and production might well be examined wherever a large portion of the plant pigments reside in very small particles.

Acknowledgments

This work was performed under Subcontract #498392 between the University of Hawaii and Lawrence Berkeley Laboratory. Support funds were also provided by National Science Foundation Grant #OCE78-19234 P. Bienfang. We thank Dr. E. Noda for the temperature and σ_t data, Dr. D. Ziemann for the nutrient data, and Dr. D. Karl for helpful discussions concerning ATP analysis. This study is done in memory of our friends and colleagues lost aboard the M/V Holoholo in December 1978; we thank all those who assisted in the search efforts, and especially Marine Affairs Coordinator Dr. John P. Craven for his tenacity in support of the search. This work was partially supported by the U.S. Department of Energy under Contract No. W-7405-ENG-48.

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Table 1. Summary of the chlorophyll a and phaeopigment properties in the water column off Ke-ahole Point, Hawaii. Data from twelve hydrocasts are compiled to show the means ($\bar{x}$) and ranges of synoptic pigment parameters, the number of determinations (n), and the coefficient of variation (s.d./$\bar{x}$) for each.

Parameter	Units	Mean	Range	n	s.d./$\bar{x}$
I. Chlorophyll a (C)					
A. Concentrations					
1. Upper 60 m	$mg \cdot m^{-3}$	0.11	0.02-0.26	66	0.57
2. At the deep maximum	$mg \cdot m^{-3}$	0.31	0.17-0.64	12	0.39
B. Depth-Integrated Values					
1. 0-60 m range	$mg \cdot m^{-2}$	5.38	1.93-10.30	12	0.52
2. 0-260 m range	$mg \cdot m^{-2}$	24.55	13.77-45.13	12	0.42
3. % in layer above 60 m	%	20.4	12-30	12	0.32
C. Depth of Deep Maximum	m	85	62-94	12	0.11
II. Phaeopigments (P)					
A. Concentrations					
1. Upper 60 m	$mg \cdot m^{-3}$	0.03	0.00-0.09	66	0.66
2. At the deep maximum	$mg \cdot m^{-3}$	0.15	0.04-0.15	12	0.78
B. Depth-Integrated Values					
1. 0-60 m range	$mg \cdot m^{-2}$	1.23	0.07-2.20	12	0.63
2. 0-260 m range	$mg \cdot m^{-2}$	11.81	3.67-22.53	12	0.61
3. % in layer above 60 m	%	10.4			
C. Depth of Deep Maximum	m	94	76-111	12	0.12
III. P/C Ratios					
A. Ratios of Concentrations					
1. Upper 60 m	No units	0.29	0.0-1.80	66	1.00
2. All samples	No units	0.45	0.0-2.00	144	0.98
B. Ratios of Integrated Values					
1. 0-60 m range	No units	0.29	0.01-0.59	12	0.62
2. 0-260 m range	No units	0.55	0.081-1.186	12	0.64

Table 2. Depth-integrated values describing phytoplankton parameters on six site visits to the oceanic station off Ke-ahole Point, Hawaii. Chlorophyll a, ATP, and phaeopigments were integrated to 250 m and have units of $mg \cdot m^{-2}$; values reflect the means of dawn and dusk hydrocasts. Primary productivity ($mg\ C \cdot m^{-2} \cdot h^{-1}$) was determined on the dawn casts only and reflect integration to approximately 120 m.

Parameter	Cruise 1 October 1978	Cruise 2 April 1979	Cruise 3 June 1979	Cruise 4 August 1979	Cruise 5 October 1979	Cruise 6 December 1979
Chlorophyll a	17.40	14.64	22.24	23.90	24.70	44.45
ATP	1.38	0.84	2.58	3.32	5.58	4.27
Phaeopigments	17.47	4.92	16.50	9.80	18.07	4.07
Primary productivity	18.70	3.12	10.01	2.86	17.32	0.72

Table 3. Percentages of chlorophyll a, phaeopigments, and carbon fixation found in the particle size fraction > 5 μm off Ke-ahole Point, Hawaii, on cruise #1 (October 1978). Percentages were calculated from the means of duplicate determinations for both the total stocks and the larger size fraction.

Depth (m)	Percent in > 5 μm Fraction		
	Chlorophyll a	Phaeopigments	Carbon fixation
0	14.3	16.7	10.3
5	37.5	16.7	24.6
23	33.3	10.0	13.9
41	37.5	12.5	26.1
58	18.2	7.1	5.0
74	14.3	16.7	4.2
91	12.0	7.1	11.6
107	21.4	16.7	7.7
123	42.9	15.4	-
163	25.0	25.0	-
202	50.0	75.0	-
243	50.0	50.0	-

Table 4. Correlations among depth-integrated water column parameters at the survey site. All parameters except primary production were integrated to 250 m, and means of the dawn and dusk hydrocasts were used in the analysis. Production, determined on dawn casts only, was integrated to approximately 120 m. Only the phaeopigment production correlation (*) is significant (n=6, $p < 0.05$).

	parameter #	1	2	3	4	5	6
primary production mg C · m	1						
phaeopigments mg · m^{-2}	2	0.915*					
chlorophyll a mg · m^{-2}	3	-0.422	-0.401				
ATP mg · m^{-2}	4	0.080	0.165	0.636			
ammonium mg-at · m^{-2}	5	0.565	0.687	0.196	0.790		
nitrate + nitrite mg-at · m^{-2}	6	-0.677	-0.404	0.303	0.308	0.103	
phosphate mg-at · m^{-2}	7	0.154	0.331	-0.731	-0.463	0.010	0.274

FIGURE CAPTIONS

Figure No.

1 Composite plots of physico-chemical parameters (a) salinity, (b) dissolved oxygen, (c) temperature (d) σ_t in the water column at the survey site (19° 55' N, 156° 10' W). Plots include data from 24 hydrocasts taken over a 14-month period.

2 Composite plots of dissolved nutrient concentrations (μM) in the upper 200 m at an oceanic station off Ke-ahole Point, Hawaii. Plots include data from 12 hydrocasts over a 14-month period.

3 Vertical profiles of chlorophyll a concentrations ($mg \cdot m^{-3}$) at the survey site. Data from dawn and dusk hydrocasts are represented by dashed- and solid-line plots, respectively. Horizontal bars indicate the s.d. about the means of triplicate analyses.

4 Vertical profiles of phaeopigment concentrations ($mg \cdot m^{-3}$) at the survey site. Data from dawn and dusk hydrocasts are represented by dashed- and solid-line plots, respectively. Horizontal bars indicate the s.d. about the means of triplicate analyses.

5 Depth-integrated standing stocks of chlorophyll a ($mg \cdot m^{-2}$) from dusk and dawn hydrocasts, a. from the entire water column sampled (0-260 m), and b. for the 0-60 m layer above the chlorophyll maximum.

6 Distributions of chlorophyll a and phaeopigments in two size fractions ($< 5\ \mu m$, $\geq 5\mu m$) within the region of the subsurface maxima. Samples were taken from an additional hydrocast during cruise #5 and data reflect the means of duplicate analyses for each depth and filter type.

7 Vertical profiles of ATP concentrations ($\mu g \cdot m^{-3}$) at the survey site. Data from dawn and dusk hydrocasts are represented by dashed- and solid-line plots, respectively. Horizontal bars indicate the s.d. about the means of triplicate analyses.

8 Vertical profiles of primary productivity rates (mg $C \cdot m^{-3} \cdot h^{-1}$) at the survey site. Horizontal bars indicate the s.d. about the means of triplicate analyses.

9 Vertical profiles of productivity:biomass (P/B) ratios (mg C · mg chlorophyll $a^{-1} \cdot h^{-1}$) at the survey site.

10 Relationship between integrated levels of phaeopigments and ammonium under a square meter of sea surface at the survey site. The correlation is significant at the $p < 0.01$ level ($r = 0.80$, $n = 12$).

11 Relationship between primary production and phaeopigment under a square meter of sea surface during this survey. Depths of integration are specified in Table 2. The correlation is significant at $p < 0.01$ (d.f. = 4).

Figure 1

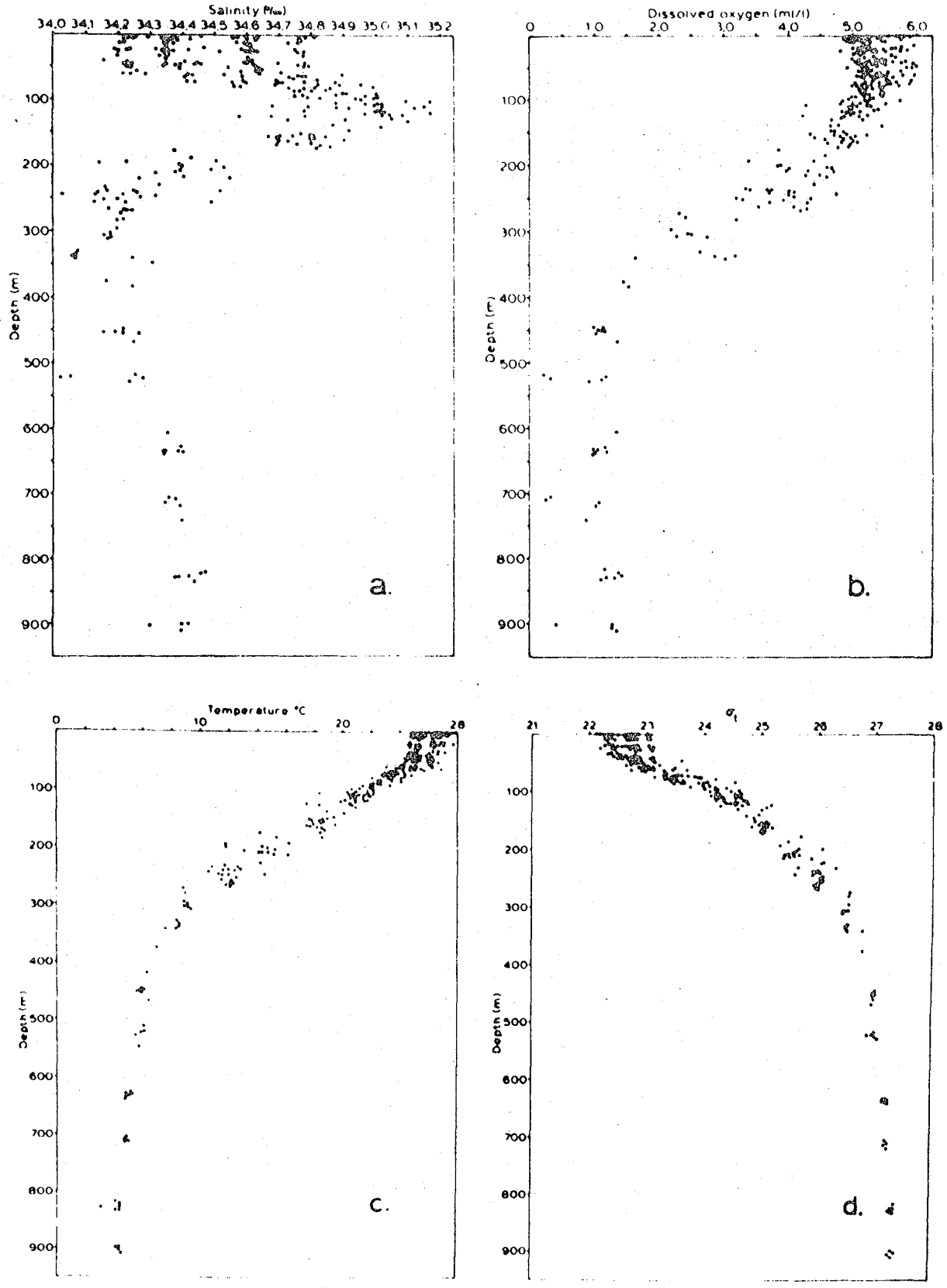

Salinity (‰)
34.0 34.1 34.2 34.3 34.4 34.5 34.6 34.7 34.8 34.9 35.0 35.1 35.2
Depth (m)
100 200 300 400 500 600 700 800 900
a.
Dissolved oxygen (ml/l)
0 1.0 2.0 3.0 4.0 5.0 6.0
b.
Temperature °C
0 10 20 28
c.
σ_t
21 22 23 24 25 26 27 28
d.

Figure 2

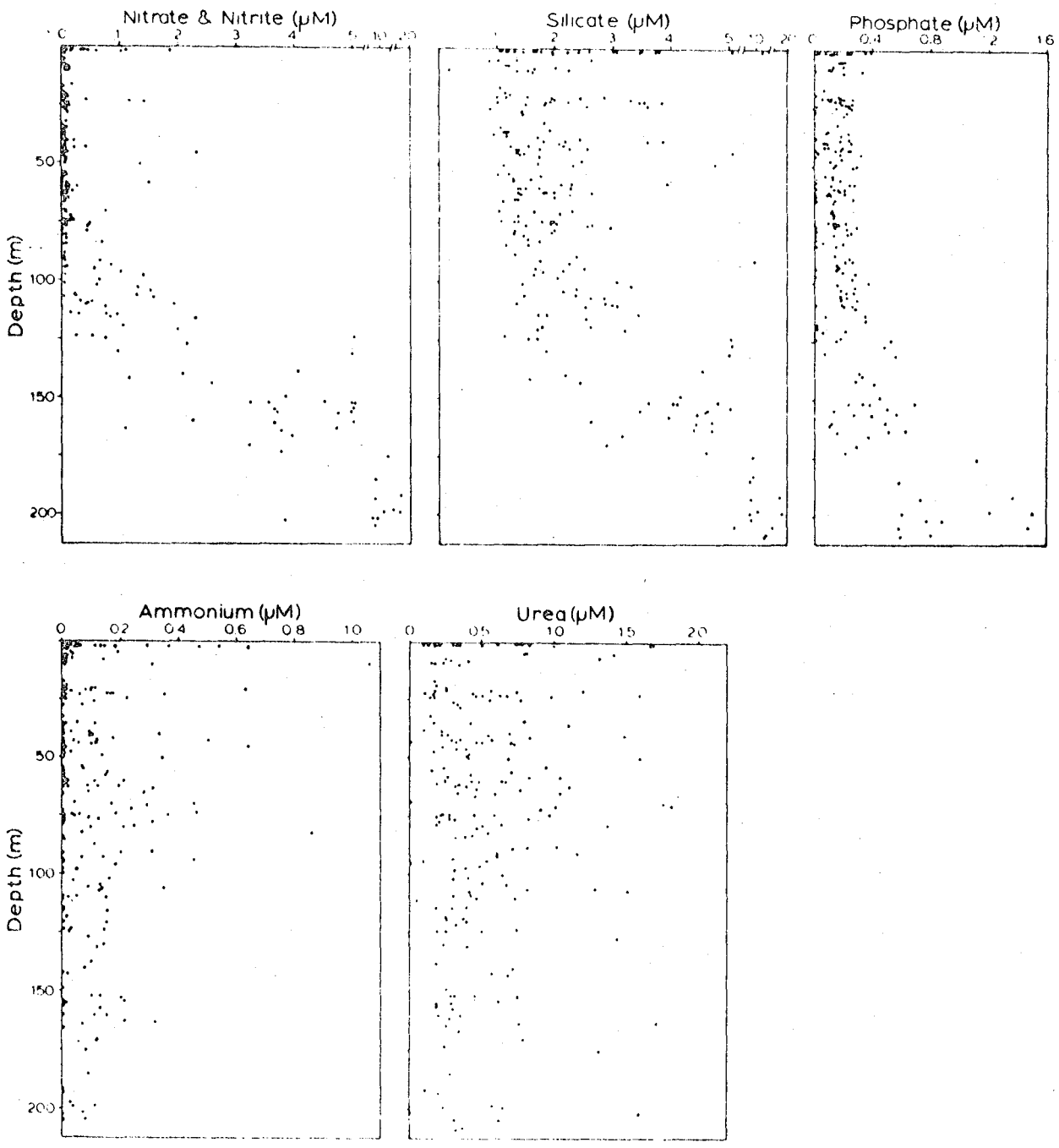
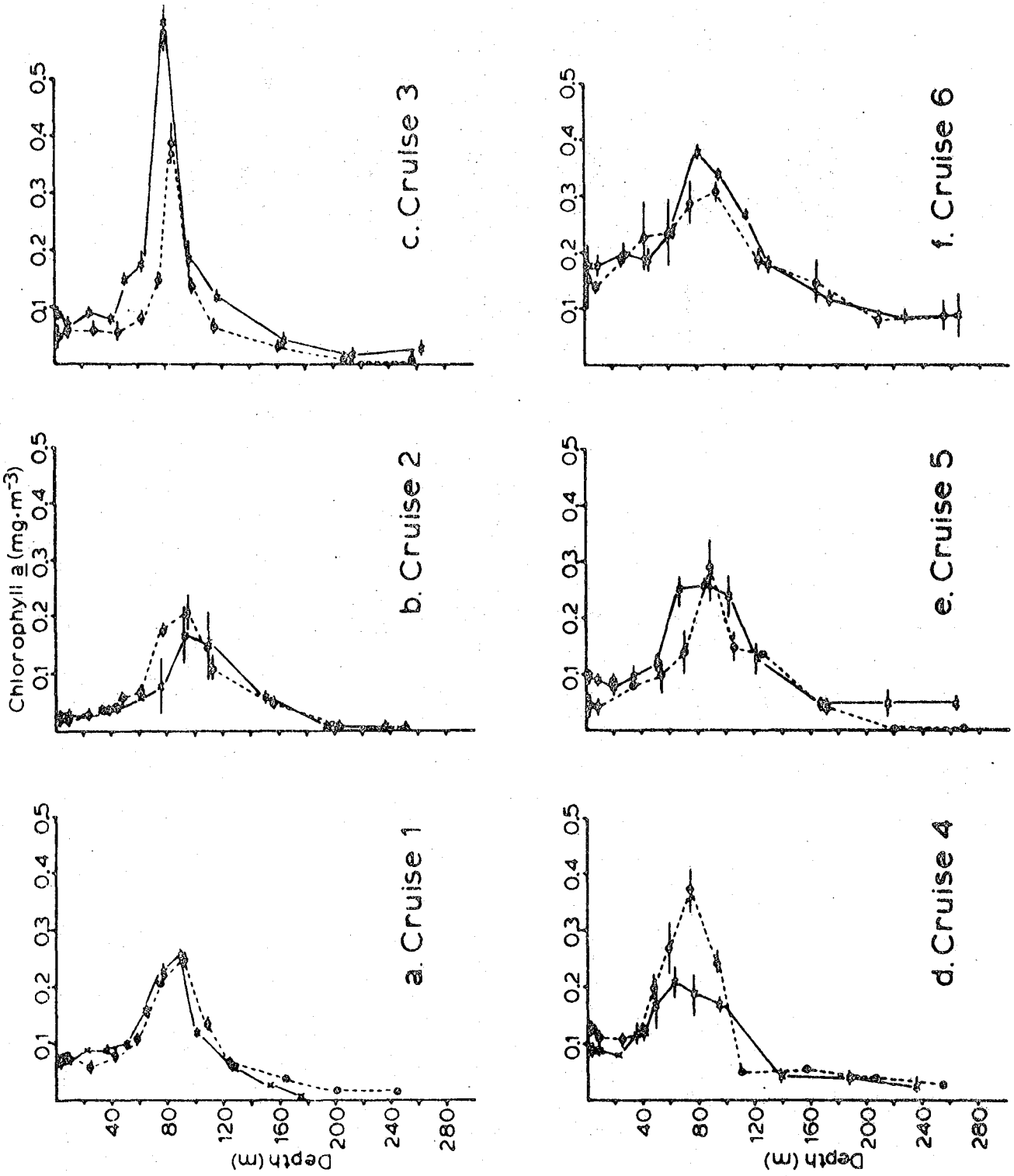

Nitrate & Nitrite (μM)
Silicate (μM)
Phosphate (μM)
Ammonium (μM)
Urea (μM)
Depth (m)
50
100
150
200

Figure 3


Chlorophyll a (mg·m-3)
0.1
0.2
0.3
0.4
0.5
a. Cruise 1
b. Cruise 2
c. Cruise 3
d. Cruise 4
e. Cruise 5
f. Cruise 6
40
80
120
160
200
240
280
Depth (m)

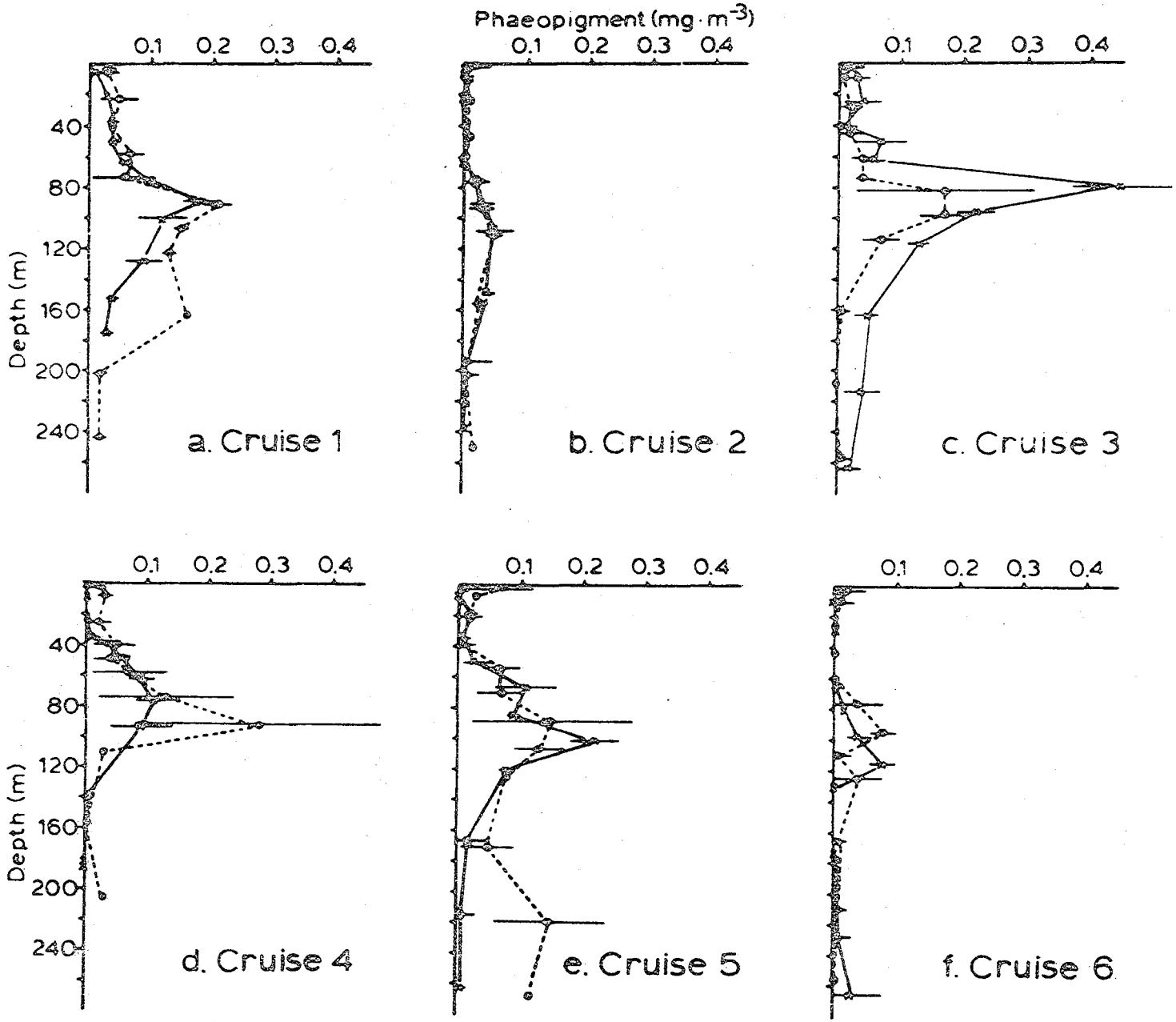

Phaeopigment (mg·m⁻³)
0.1 0.2 0.3 0.4
Depth (m)
40
80
120
160
200
240
a. Cruise 1
b. Cruise 2
c. Cruise 3
d. Cruise 4
e. Cruise 5
f. Cruise 6

Figure 4

Figure 5

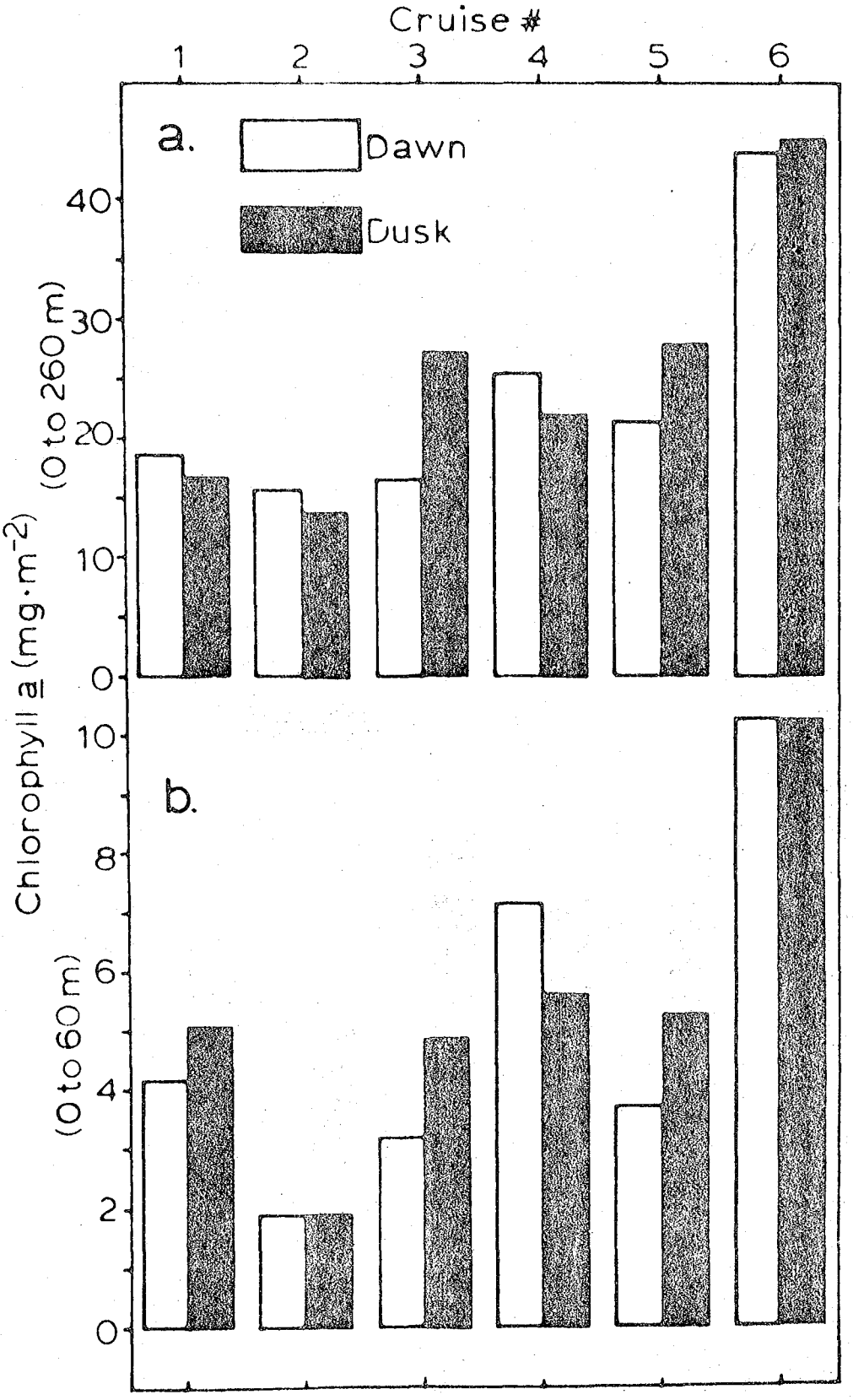
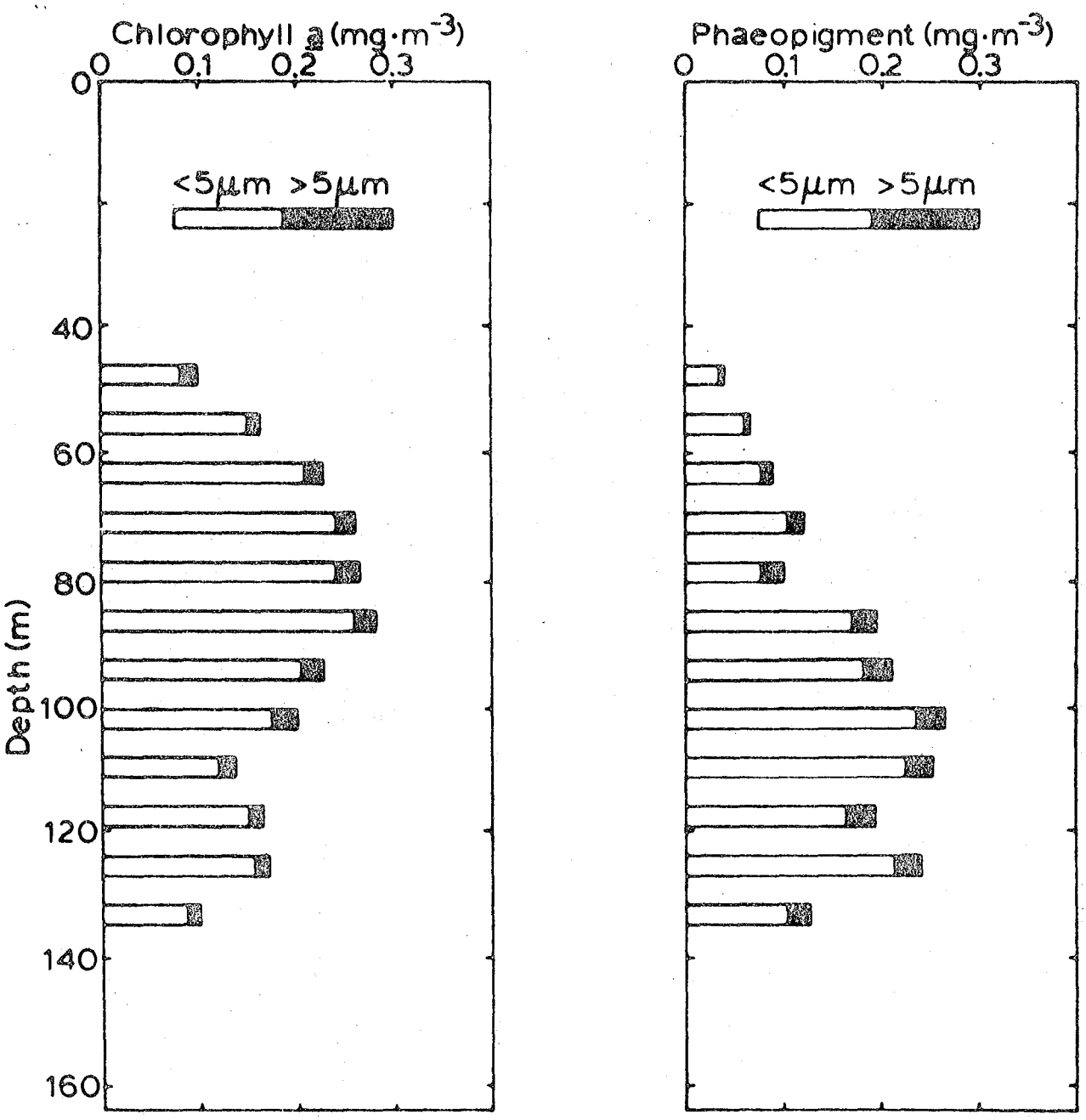

Cruise #
1
2
3
4
5
6
a.
Dawn
Dusk
40
30
20
10
0
(0 to 260 m)
Chlorophyll a (mg·m⁻²)
b.
10
8
6
4
2
0
(0 to 60 m)

Figure 6


Chlorophyll a (mg·m-3)
0 0.1 0.2 0.3
<5µm >5µm
Phaeopigment (mg·m-3)
0 0.1 0.2 0.3
<5µm >5µm
Depth (m)
0
40
60
80
100
120
140
160

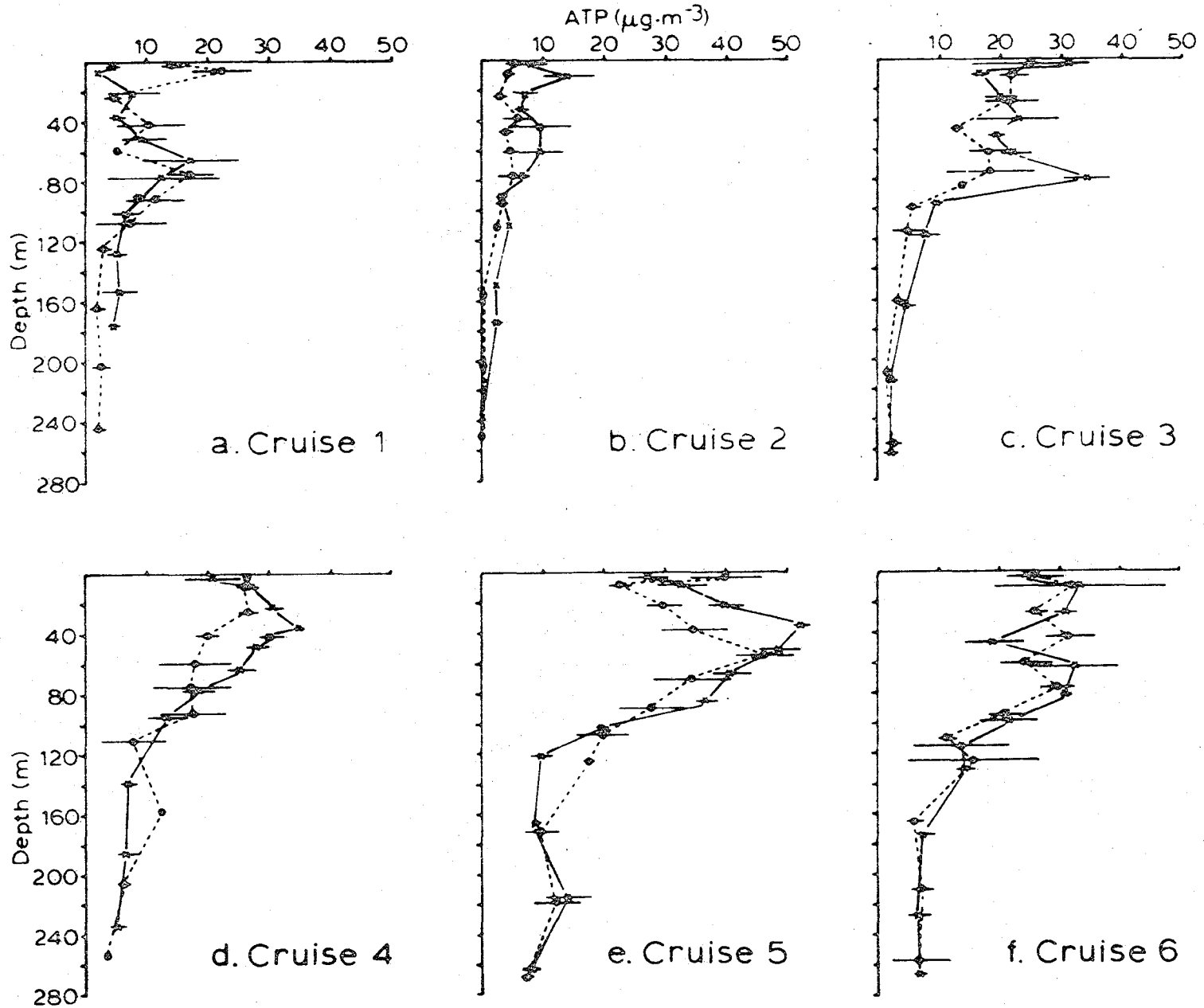

ATP (μg·m⁻³)
10 20 30 40 50
Depth (m)
40
80
120
160
200
240
280
a. Cruise 1
b. Cruise 2
c. Cruise 3
d. Cruise 4
e. Cruise 5
f. Cruise 6

Figure 7

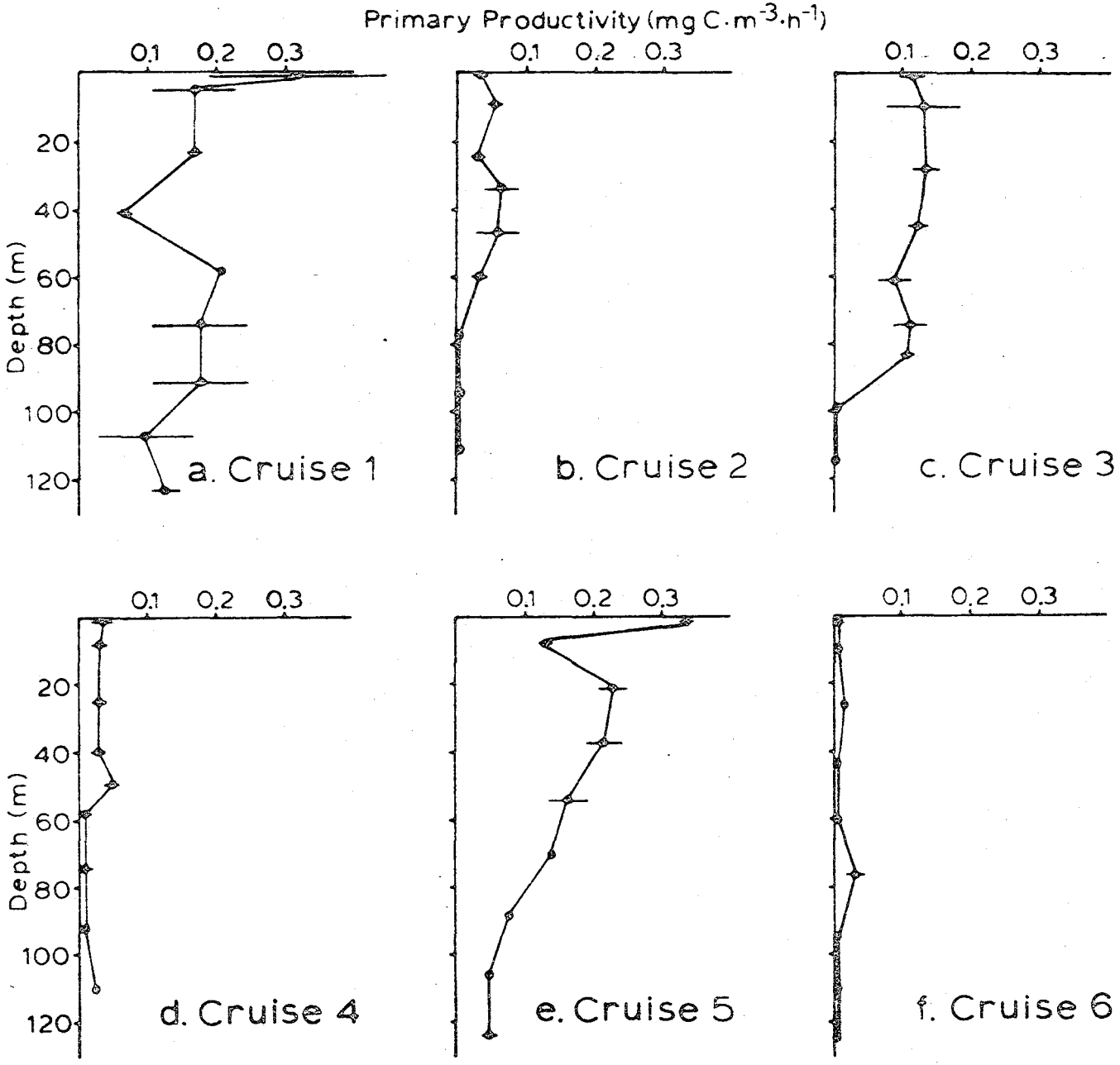

Primary Productivity (mg C·m⁻³·h⁻¹)
0.1
0.2
0.3
Depth (m)
20
40
60
80
100
120
a. Cruise 1
b. Cruise 2
c. Cruise 3
d. Cruise 4
e. Cruise 5
f. Cruise 6

Figure 8

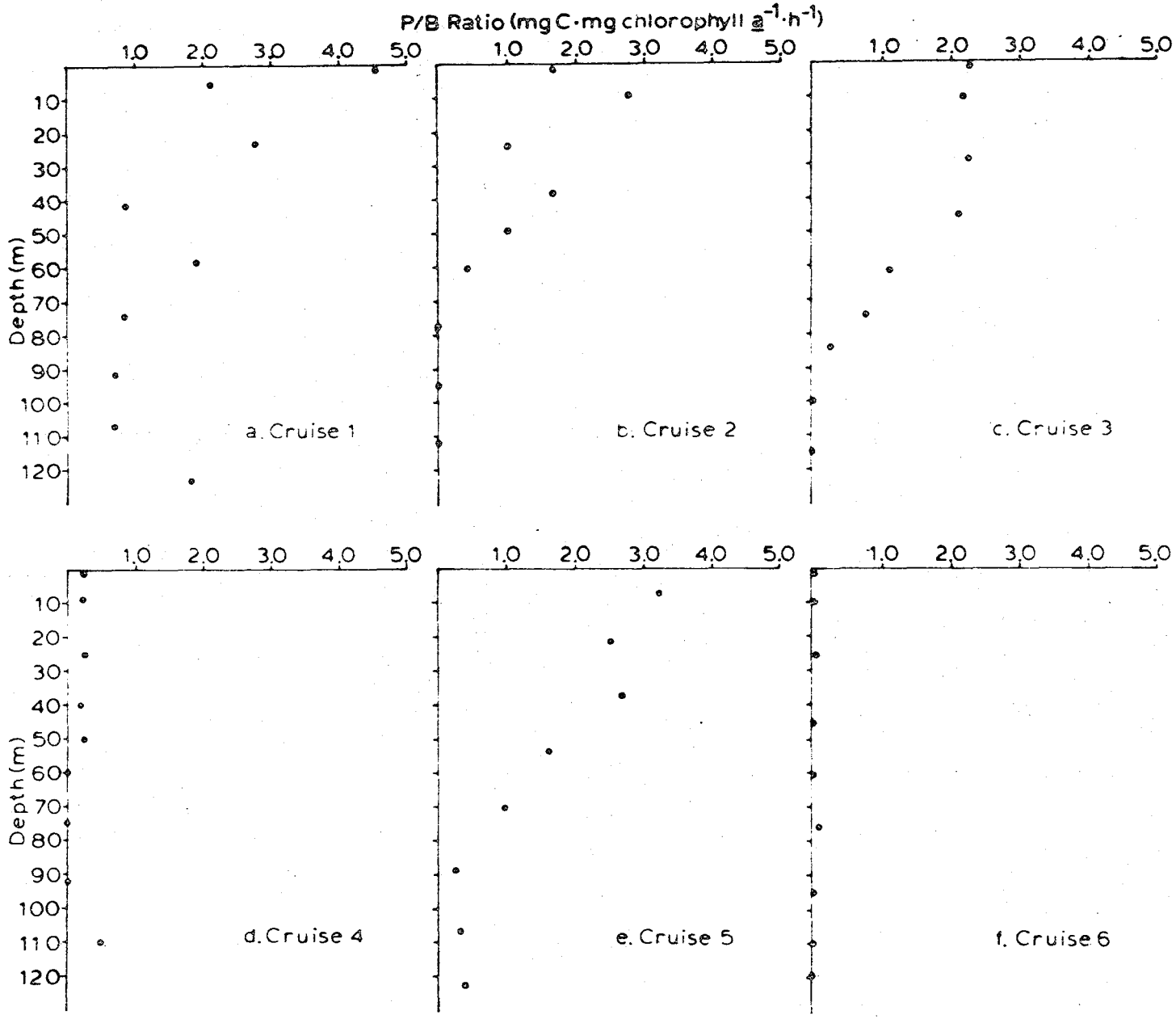

P/B Ratio (mg C·mg chlorophyll a^{-1}·h^{-1})
1.0 2.0 3.0 4.0 5.0
Depth (m)
10 20 30 40 50 60 70 80 90 100 110 120
a. Cruise 1
b. Cruise 2
c. Cruise 3
d. Cruise 4
e. Cruise 5
f. Cruise 6

Figure 9

Figure 10

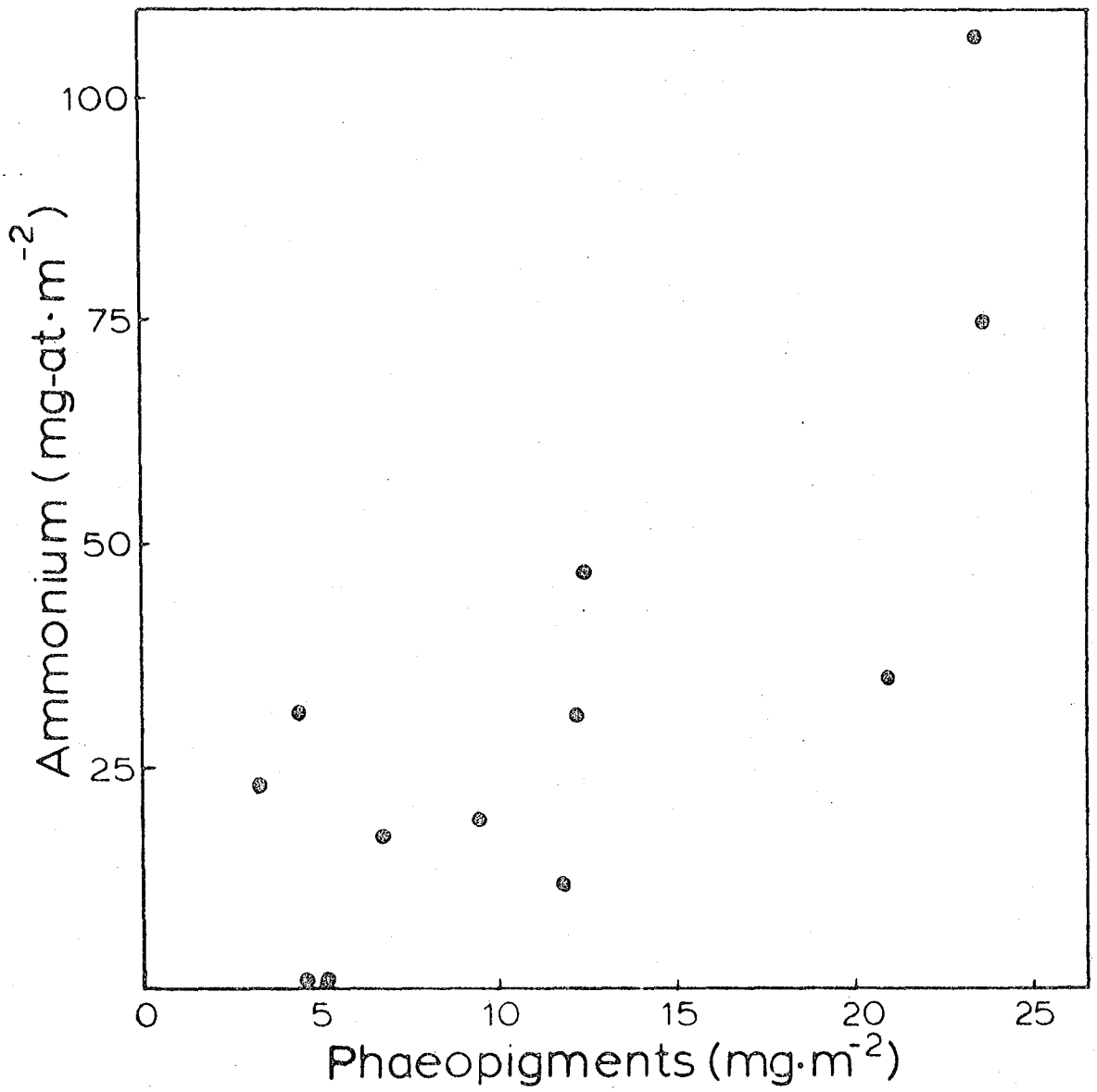
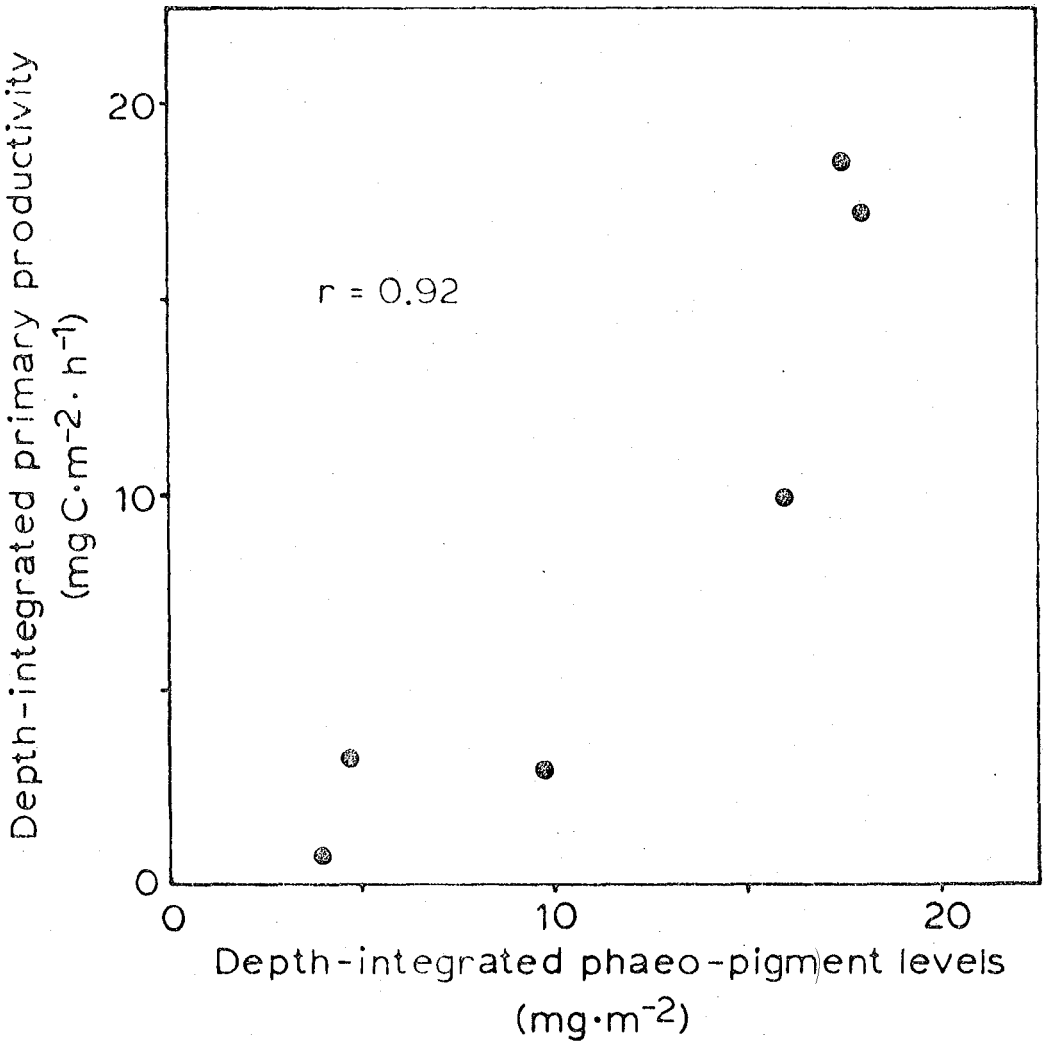

Ammonium (mg-at·m^{-2})
100
75
50
25
0
5
10
15
20
25
Phaeopigments (mg·m^{-2})

Figure 11


Depth-integrated primary productivity
(mg C·m⁻²·h⁻¹)
20
10
0
r = 0.92
0
10
20
Depth-integrated phaeo-pigment levels
(mg·m⁻²)

This report was done with support from the United States Energy Research and Development Administration. Any conclusions or opinions expressed in this report represent solely those of the author(s) and not necessarily those of The Regents of the University of California, the Lawrence Berkeley Laboratory or the United States Energy Research and Development Administration.