

# UC San Diego

## UC San Diego Previously Published Works

### Title

A multivariate analysis of planktonic interactions in the eastern tropical North Pacific

### Permalink

<https://escholarship.org/uc/item/1cn5225t>

### Journal

Deep Sea Research Part A Oceanographic Research Papers, 29(12)

### ISSN

0198-0149

### Authors

Ohman, Mark D  
Anderson, George C  
Ozturgut, Erdogan

### Publication Date

1982-12-01

### DOI

10.1016/0198-0149(82)90036-x

Peer reviewed

## A multivariate analysis of planktonic interactions in the eastern tropical North Pacific\*

MARK D. OHMAN,† GEORGE C. ANDERSON† and ERDOGAN OZTURGUT‡

(Received 4 May 1981; in revised form 31 March 1982; accepted 1 July 1982)

**Abstract**—Biological and hydrographic properties were sampled in the eastern tropical North Pacific (DOMES region) in two seasons, late summer (29 August to 13 October) 1975 and winter (18 February to 13 March) 1976. Differences between cruises and spatial patterns were summarized with factor analysis and non-metric multidimensional scaling and then analyzed in detail by other statistical techniques.

Significant between-cruise differences were detected in the concentrations of nitrate and suspended particulate matter in the surface mixed layer and in vertically integrated standing stocks of microzooplankton and day macrozooplankton. Integrated chlorophyll *a* also increased in winter, but the productivity: chlorophyll *a* ratio decreased. The near-surface phytoplankton community appears to be more shade-adapted in winter.

Pronounced differences in correlation patterns were observed in 1975 and 1976. In winter 1976, integrated primary production rates varied inversely with the nitracline depth and positively with mixed-layer nitrate concentration, sea-surface irradiance (PAR), and integrated chlorophyll *a*, while zooplankton standing stock covaried with mixed-layer nitrate concentration ( $P \leq 0.05$ ). In contrast, none of the correlations was significant in summer 1975 ( $P > 0.10$ ). In 1975, short-term (30 to 60 h) variations in surface chemical properties and in integrated chlorophyll *a* were greater than in 1976. The weaker correlations observed in 1975 may have been influenced by the apparent increase in variability. The vertical supply of nitrate, phytoplankton growth, and zooplankton grazing appear to have been more closely coupled in winter 1976 than in summer 1975.

### INTRODUCTION

INVESTIGATIONS of the biological dynamics of tropical open-ocean regions remain few in number and limited in duration (but see BLACKBURN, LAURS, OWEN and ZEITZSCHEL, 1970; VINOGRADOV, GITELZON and SOROKIN, 1970; TRANTER, 1973; LONGHURST, 1976; VINOGRADOV, 1977; BAARS, ZIJLSTRA and TIJSEN, 1979; HERBLAND and VOITURIEZ, 1979), in contrast to the more intensively studied subtropical ocean regions. Studies of subtropical systems suggest a close coupling between rates of phytoplankton growth and zooplankton grazing and excretion (e.g., EPPLEY, RENGER, VENRICK and MULLIN, 1973; MCCARTHY and GOLDMAN, 1979; JACKSON, 1980; SHARP, PERRY, RENGER and EPPLEY, 1980; BIENFANG and SZYPER, 1981). As biological processes in tropical ocean areas are forced differently from those in subtropical regions, due to pronounced meridional gradients in wind stress and currents, strong vertical current shear, and vertical advection of limiting nutrients in divergence zones, it seems less likely that such a close coupling would be a persistent

---

\* Contribution No. 1283 from the School of Oceanography, University of Washington.

† School of Oceanography, WB-10, University of Washington, Seattle, WA 98195, U.S.A.

‡ P.O. Box 55373, Seattle, WA 98155, U.S.A.

characteristic of tropical regions. In addition to the activities of grazers, vertical advection or minor nutrient limitation may also regulate phytoplankton growth in the tropical ocean (THOMAS, 1979).

We have investigated interrelationships of properties of biological interest in the eastern tropical North Pacific at two different times of year. We summarize spatial patterns and between-cruise differences with factor analysis and multidimensional scaling. The suggested trends are explored further with other statistical methods, and comparisons are made between the strengths of correlations observed during the two cruise periods.

The data originate from the 1975 and 1976 cruises of the DOMES (Deep Ocean Mining Environmental Study) project (see OZTURGUT *et al.*, 1978). The region (bounded by approximately 5°30' to 18°N, 126° to 151°W) is free of influence by coastal processes, in contrast to parts of the EASTROPAC area directly to the east. Presentations and analysis of the original data can be found in BISCHOFF and PIPER (1979) and HIROTA (1977a, b, zooplankton and micronekton).

#### MATERIALS AND METHODS

##### *Sampling*

Sampling was from the R.V. *Oceanographer* along three meridional transects at 150°45'W, 138°22'W, and 126°00'W (Fig. 1). Seven stations, separated by approximately 1° intervals of latitude, were occupied on each transect between 29 August and 13 October 1975 (hereafter termed late summer), and five stations, separated by approximately 1.5° intervals, were occupied on each transect between 18 February and 13 March 1976 (winter). Discrete samples were taken with 5 to 30-l Niskin bottles on a rosette sampler at depths corresponding to 100, 50, 25, 12, 6, 1, 0.1, and 0.01% of the irradiance at 0.5 m, as determined by submarine photometer. Three additional depths were sampled between 200 and 400 m. Samples deeper than 400 m are not considered here. A detailed account of analytical methodology and a listing of the data used in this analysis may be found in the publications listed in the introduction.

Mixed-layer depths were determined from vertical profiles of the Brunt-Väisälä frequency, averaged from 1 to 10 CTD casts at each station. The nitracline depth is defined as the depth where the nitrate concentration first exceeds 0.3  $\mu\text{M}$ , to permit comparison with other results (HERBLAND and VOITURIEZ, 1979).

Primary production rates were determined by *in situ*  $^{14}\text{C}$  incubations (EL-SAYED and TAGUCHI, 1979). Water samples were incubated in 125-ml bottles between local apparent noon and local sunset at the light depths indicated above. Vertically integrated values were determined using the trapezoidal rule from the surface to the 0.1% light depth. Because of the uncertainty of preservation of flagellates and monads, vertical integrations of phytoplankton abundance were made using only the counts of diatoms, coccolithophorids, and dino-flagellates from FRYXELL, TAGUCHI and EL-SAYED (1979).

Microzooplankton (35 to 183  $\mu\text{m}$ ) was collected in pump casts made over 25-m intervals from 0 to 150 m; macrozooplankton was sampled with 70-cm diameter, 183- $\mu\text{m}$  mesh bongo nets (HIROTA, 1977b).

##### *Statistical methods*

Multivariate methods were used with those properties measured at each depth and station. First, the best variance-stabilizing transformation was applied to each variable based on the

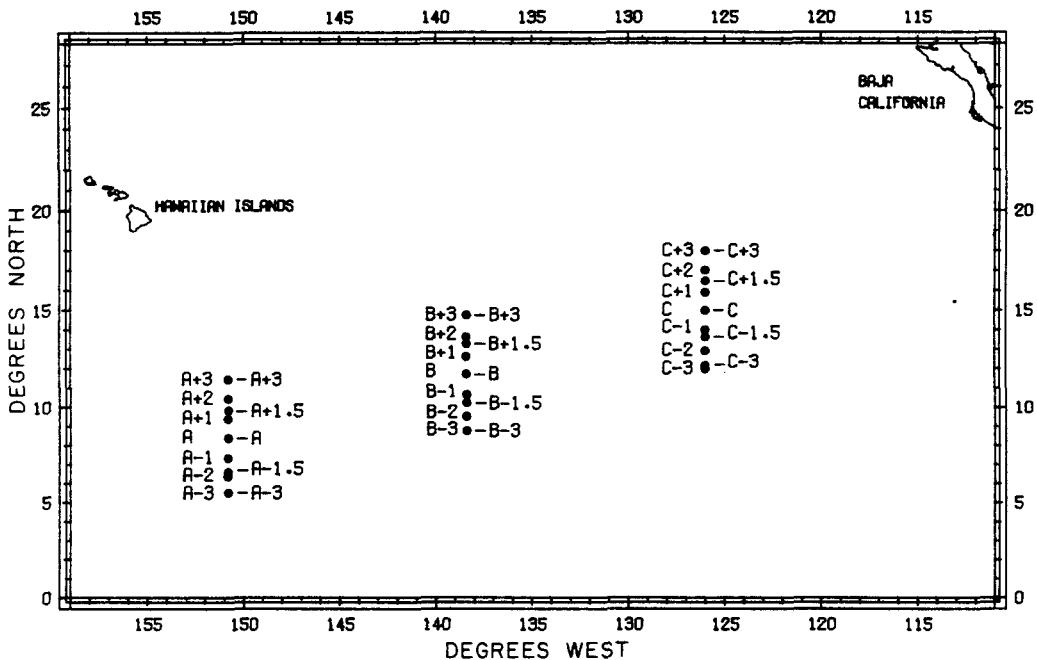


Fig. 1. Stations occupied in September and October 1975 (labeled to the left of station positions) and in February and March 1976 (dashed line and label to the right of station positions).

results of a Kolmogorov–Smirnov test of departure from a normal distribution: temperature,  $\sqrt{x}$ ; salinity, n.t.; sigma- $t$ , n.t.; dissolved oxygen,  $\sqrt{x}$ ; nitrate,  $\sqrt{x}$ ; phosphate,  $\sqrt{x}$ ; silicate,  $\log(x + 1)$ ; electron transport system activity, n.t.; adenosine triphosphate,  $\log(x)$ ; primary production,  $\sqrt{x}$ ; chlorophyll  $a$ ,  $\sqrt{x}$ ; phaeopigments,  $\sqrt{x}$ ; n.t. = no transformation. Each variable was then standardized to have a mean of 0 and unit variance.

Factor analysis (FA) is chosen over principal components analysis (PCA) because the FA model allows for both experimental error and for determination of some covariance patterns by unmeasured variables. In contrast, with PCA a derived axis is an exact mathematical transformation of the input data, and one therefore assumes that all measurements have been made without error and that no unmeasured causes for covariance exist (HARMAN, 1976). Tests for the suitability of a correlation matrix for factor analysis can be found in DZIUBAN and SHIRKEY (1974), who suggested that factor analysis of a correlation matrix is appropriate when Bartlett's test is rejected, when the proportion of off-diagonal elements of the anti-image covariance matrix  $>0$  is close to 0%, and when the Kaiser–Meyer–Olkin measure is large ( $>0.80 = \text{'meritorious'}$ ).

Factor analysis, like PCA, assumes that there is a linear relationship between measured variables and derived axes. Numerous studies have demonstrated departures from this assumption and illustrate the problem of distortion of interpoint distances that frequently occurs in a PCA solution (e.g., FASHAM, 1977; GAUCH, WHITTAKER and WENTWORTH, 1977) or an FA solution (WESTMAN, 1975). For this reason an alternative ordination method, non-metric multidimensional scaling (MDS), was used for close analysis of spatial distances. Non-metric MDS (KRUSKAL, 1964) is less subject to distortion of true distances (GAUCH,

WHITTAKER and SINGER, 1981). In non-metric MDS a geometric configuration of distances between sample points is derived from a matrix of similarities between points by minimizing a 'badness of fit' function termed stress (KRUSKAL and WISH, 1978). Non-metric MDS was performed with the program MINISSA (ROSKAM and LINGOES, 1977) on a Euclidean distance similarity matrix. Factor analysis was done with an SPSS program (NIE *et al.*, 1975).

In univariate comparisons, to match station pairs where two stations were sampled in summer and only one in winter (see Fig. 1), a value interpolated between the two adjacent stations was compared with the corresponding value from the single winter station. Non-parametric tests can be found in HOLLANDER and WOLFE (1973) and ZAR (1974). The correction for multiple-testing is based on the Bonferroni inequality (MILLER, 1977).

#### HYDROGRAPHY OF THE REGION

The study area is dominated by the northern equatorial current system, but there are numerous features that do not correspond to the mean flow. Meridional gradients typify the wind and current systems; a thermal ridge separates the westward-flowing North Equatorial Current (NEC) and the eastward-flowing North Equatorial Counter-Current (NECC, Fig. 2). The NEC and the NECC typically intensify in August and September as the Intertropical Convergence Zone (ITCZ) migrates northward ( $11^{\circ}\text{N}$  at  $119^{\circ}\text{W}$ , TSUCHIYA, 1974) and the northeast trades weaken (WYRTKI, 1974). In February to April when the ITCZ is near its southernmost position ( $4$  to  $5^{\circ}\text{N}$ ) and the northeast trades are strongest, both the NEC and the NECC are weaker (WYRTKI, 1974) and the NECC tends to be discontinuous in the eastern Pacific (TSUCHIYA, 1974).

Upper ocean currents are variable, although the east-west component reveals less temporal variability than the north-south component (HALPERN, 1979). The east-west component  $u$ , measured at 20-m depth, averaged  $-17 \pm 15 \text{ cm s}^{-1}$  at Sta. C in September and October 1975,  $4 \pm 11 \text{ cm s}^{-1}$  at Sta. B in March and April 1976, and  $20 \pm 20 \text{ cm s}^{-1}$  at Sta. A in August to October 1976 (HALPERN, 1979). SECKEL (1975) reported the occurrence of mesoscale eddies in the NEC. Long-period fluctuations ( $>20$  days) are also apparent in the region (WYRTKI, 1978; HALPERN, 1979).

A surface mixed layer typically overlies a pycnocline of high hydrostatic stability. The depth of the surface mixed layer ranges from 15 m in the divergence zone along the thermal ridge to 135 m in the convergence region at the southernmost stations along transect A (Fig. 2). A salinity minimum of high latitude origin (REID, 1973) is usually found in the pycnocline. At Sta. A in August 1976, short-term vertical displacement of isotherms, as detected by thermistor arrays, averaged  $\pm 5.2$  m (standard deviation of hourly-averaged values) in the thermocline and  $\pm 13.5$  m below the thermocline. HALPERN (1979) ascribed the fluctuation predominantly to internal gravity waves.

Surface concentrations of nitrate range from undetectable to  $5.20 \mu\text{M}$ , depending on proximity to the divergence zone (Fig. 3). A primary nitrite maximum typically occurs near the top of the nitracline (50 to 100 m); a secondary nitrite maximum is most evident near Sta. C ( $15^{\circ}\text{N}$ ,  $126^{\circ}\text{W}$ ), at 175 to 200 m (ANDERSON and RICHARDS, 1977). The oxygen minimum zone that develops in the eastern tropical Pacific extends westward into the DOMES area as a tongue along approximately  $15^{\circ}\text{N}$  (REID, 1965; ANDERSON, 1979).

Small phytoplankton cells predominate across the region: an average of 84% of the chlorophyll *a* and 77% of the primary production is in the nanoplankton size fraction ( $<20 \mu\text{m}$ , EL-SAYED and TAGUCHI, 1979). A subsurface chlorophyll maximum (ANDERSON, 1969; VERNICK,

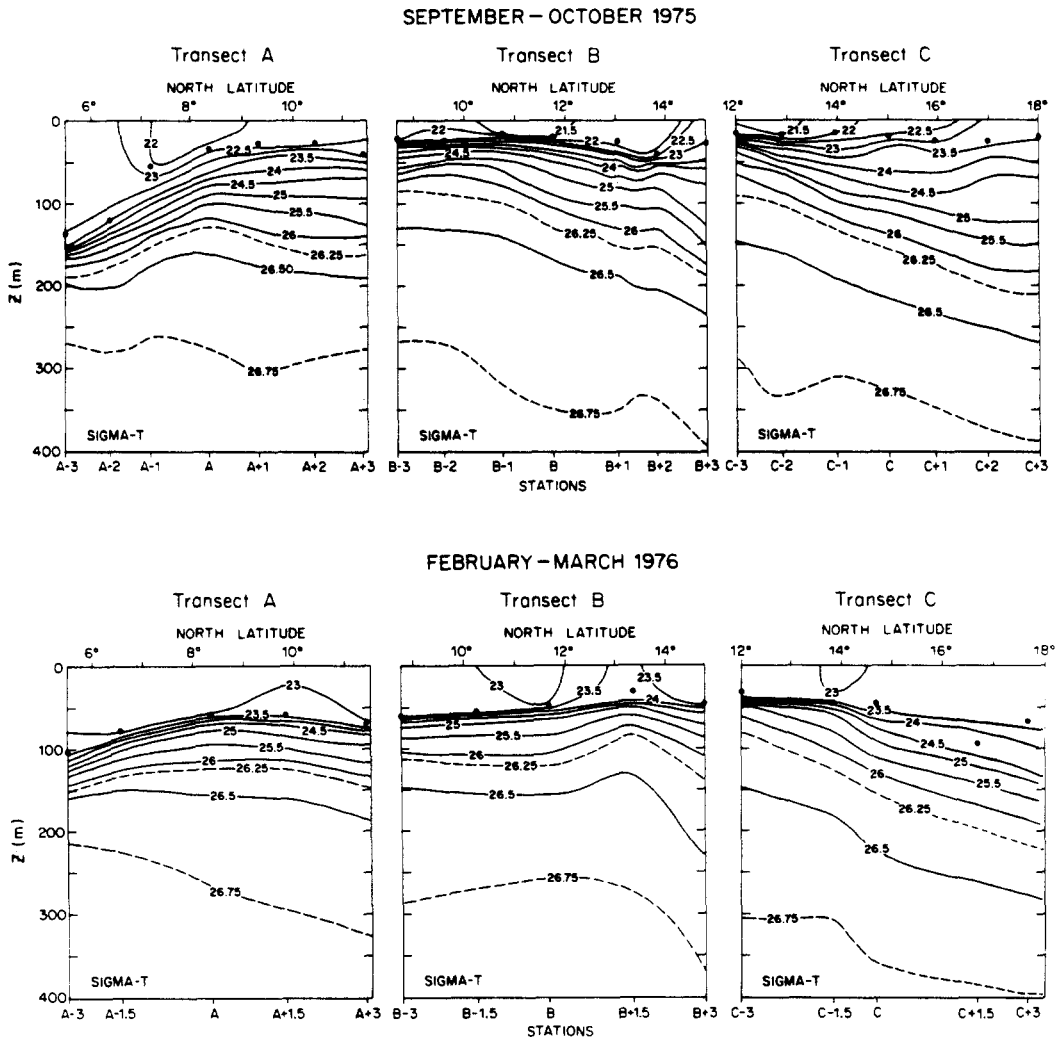


Fig. 2. Sigma- $t$  sections along A, B, and C in 1975 and in 1976. Dots indicate surface mixed-layer depths determined from vertical profiles of the Brunt–Väisälä frequency.

MCGOWAN and MANTYLA, 1973) is a persistent feature of the area, occurring at an average depth of 62 m ( $\pm 28$  m); this corresponds to the 14% ( $\pm 21\%$ ) light level (EL-SAYED and TAGUCHI, 1979). Coccolithophorids (especially *Gephyrocapsa huxleyi*) are the most abundant cells in the chlorophyll maximum layer (FRYXELL *et al.*, 1979).

The zooplankton is dominated by a diverse assemblage of small copepods (*ca.* 1 mm long; HIROTA, 1977b). Zooplankton standing stock decreases monotonically with depth, both day and night. The fraction of zooplankton in the upper 200 m exhibiting a diel vertical migration is relatively small as indicated by a median night : day catch ratio of 1.28. Areal changes in standing stock are small but appear to exhibit a gradient of decreasing concentration from east to west in the EASTROPAC region (BLACKBURN *et al.*, 1970) and possibly southeast to northwest in the DOMES region (HIROTA, 1977b).

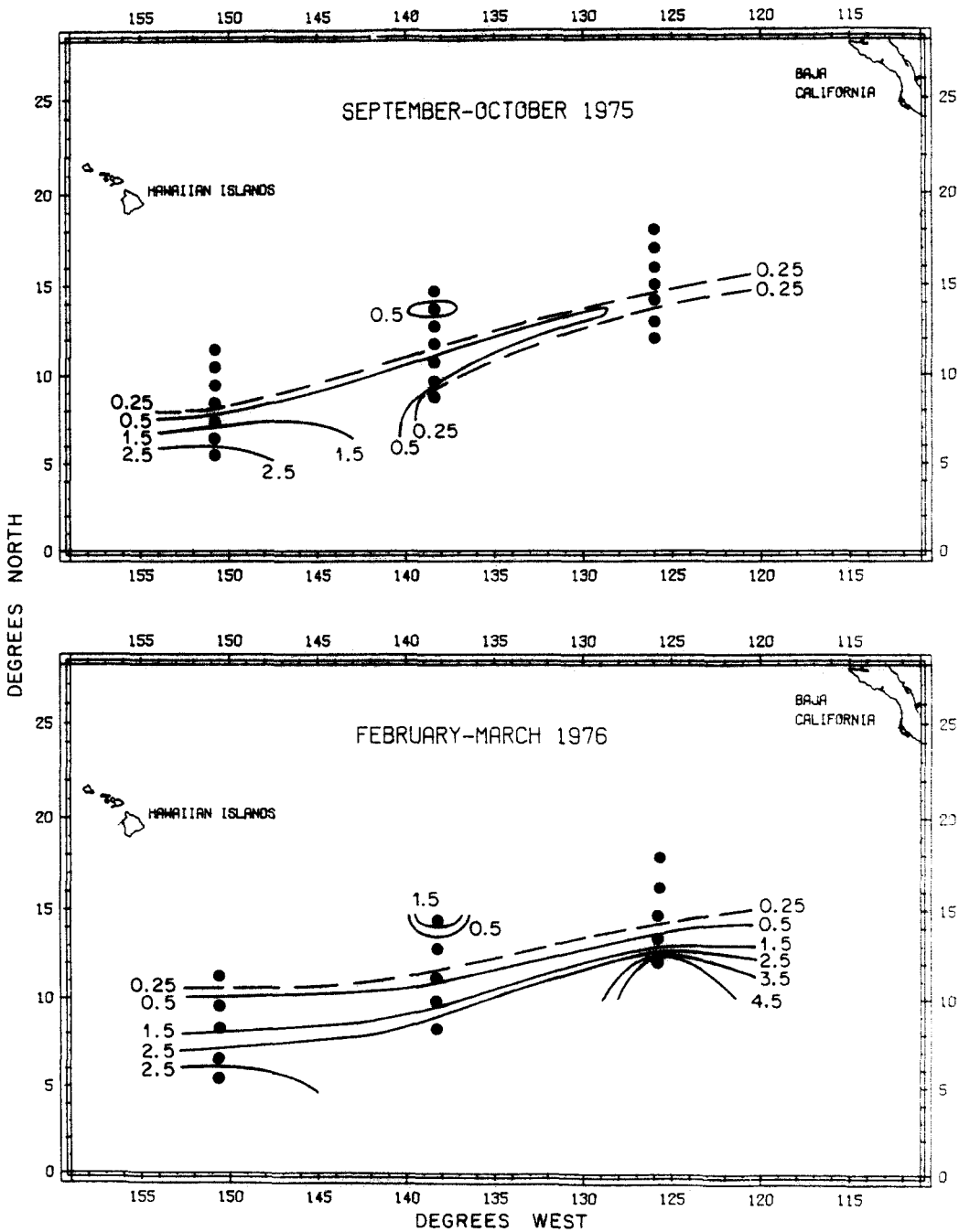


Fig. 3. Contours of average  $\text{NO}_3^-$  concentration ( $\mu\text{M}$ ) in the surface mixed layer. High  $\text{NO}_3^-$  values in the northern region of transect B are interpreted as mesoscale features.

## RESULTS

*Multivariate analysis*

The factor matrix resulting from factor analysis of 606 depths sampled in the upper 400 m of the water column in 1975 and 1976 is shown in Table 1. The first two factors recover 78.5% of the variance in the original data set. Factors 3 and 4 have eigenvalues smaller than unity and are not considered further here (HARMAN, 1976). A plot of the points sampled, in the reduced dimensions of the first two factors, reveals three primary data clusters (Fig. 4). Surface mixed-layer points have low scores on factor 1 (corresponding to low nutrients, high temperature, and high dissolved oxygen) and a broad range of factor 2 scores (phytoplankton properties). Pycnocline depths show increasing scores on factor 2 and on factor 1. Depths below the pycnocline tend toward a narrow range of factor 1 scores and low factor 2 scores.

When winter scores on factor 2 were compared with summer scores, winter scores appeared higher within the surface mixed layer. To examine this pattern further, independently of the variance contributed by deeper samples, the mixed-layer data were analyzed separately by two techniques, another FA and non-metric MDS. In the mixed-layer FA, the first three factors account for 70.7% of the common variance in the original 12 variables (Table 2). Factor 4 (dominated by salinity) and subsequent factors contribute substantially less to explaining the common variance in the data set. Mixed-layer factor scores for each station are plotted in Fig. 5 excepting Sta. B-3 in winter, for which most data were missing. Comparison of the relative positions of stations between cruises reveals that winter stations differ significantly from summer stations along factor 1, a phytoplankton pigment-productivity factor ( $P < 0.001$ ), and along factor 3, a temperature-density factor ( $P < 0.001$ ), but not along factor 2, a nutrient-oxygen factor ( $P = 0.205$ ; all Mann-Whitney U test, two-tailed).

Results of analysis of the mixed-layer data by non-metric MDS are presented for the two-dimensional solution. The dimensionality of the data set was determined from Fig. 6 and from M-SPACE analysis (SPENCE and GRAEF, 1974; KRUSKAL and WISH, 1978), which indicated

Table 1. Factor matrix: 0 to 400 m. Varimax-rotated factor solution. Factor loadings larger than 0.4 are italicized. [Bartlett's test is rejected ( $P < 0.0001$ ), off-diagonal elements  $> 0$  total 6 (4.55%), and the Kaiser-Meyer-Olkin measure = 0.84 (see Methods)]

	Factor 1	Factor 2	Factor 3	
Eigenvalue:	5.780	1.913	0.968	
% Variance:	59.0	19.5	9.9	Communality
NO <sub>3</sub> <sup>-</sup>	<i>0.9166</i>	-0.2166	-0.1737	0.9645
PO <sub>4</sub> <sup>-3</sup>	<i>0.9070</i>	-0.2247	-0.1611	0.9304
Si(OH) <sub>4</sub>	<i>0.9011</i>	-0.2766	-0.1610	0.9362
Temperature	-0.8977	0.2741	0.2376	0.9817
Sigma-t	<i>0.8898</i>	-0.1871	-0.2106	0.9846
O <sub>2</sub>	-0.8446	0.3214	0.2430	0.9281
Primary production	-0.6243	<i>0.4392</i>	0.1755	0.6585
Chlorophyll <i>a</i>	-0.5357	<i>0.8396</i>	0.0640	1.0024
Phaeopigments	-0.1558	<i>0.7709</i>	0.1089	0.6310
ATP	-0.1282	0.0645	<i>0.6422</i>	0.4356
ETS	-0.4648	0.1652	<i>0.5113</i>	0.5716
Salinity	0.2466	-0.0493	-0.0718	0.7699



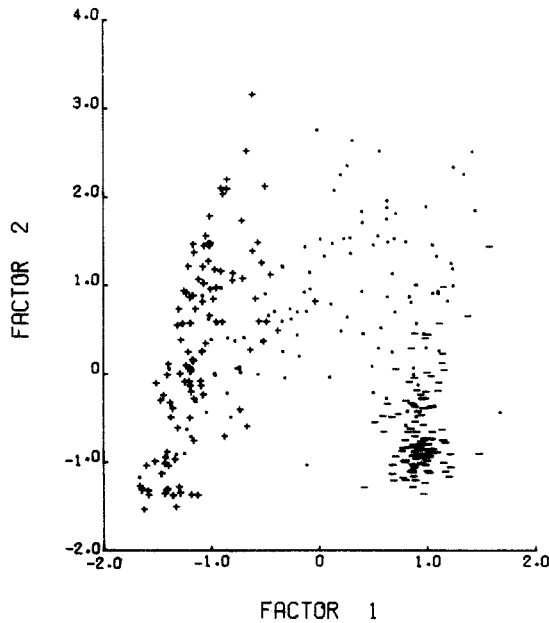


Fig. 4. Scatter plot of factor scores in the upper 400 m of the water column (+, mixed-layer depths; ■, pycnocline depths; -, depths below the pycnocline).

that the appropriate dimensionality is 2 (with an error level of 23%). The two-dimensional MDS solution (Fig. 7) shows a clear summer–winter distinction along axis 1 ( $P < 0.001$ ) but not along axis 2 ( $P = 0.424$ ).

In the MDS solution, spatial heterogeneity is apparent in both summer and winter (Fig. 7). Stations in the NEC and the NECC appear as nearly separate clusters. The divergence zone stations appear distinct from the NEC and NECC clusters on transects B and C, but on

Table 2. Factor matrix: surface mixed layer. Varimax-rotated factor solution, as in Table 1. [Bartlett's test is rejected ( $P < 0.0001$ ), off-diagonal elements  $> 0$  total 20 (15.15%), and the Kaiser–Meyer–Olkin measure = 0.54]

	Factor 1	Factor 2	Factor 3	Factor 4	
Eigenvalue:	2.350	2.037	1.773	1.225	
% Variance:	27.0	23.4	20.3	14.1	Communality
Chlorophyll <i>a</i>	0.9433	0.0179	-0.1639	0.0695	0.9397
Phaeopigments	0.9177	0.1875	-0.0618	0.1872	0.9122
Primary production	0.4522	0.0633	-0.0137	-0.0718	0.3401
ATP	-0.4277	0.0075	0.2524	0.0643	0.4668
PO <sub>4</sub> <sup>3-</sup>	0.2110	0.8480	-0.1768	0.1341	0.8324
NO <sub>3</sub> <sup>-</sup>	0.3405	0.7924	0.0241	0.2890	0.8811
O <sub>2</sub>	0.1378	-0.6573	-0.920	-0.0727	0.5057
Temperature	-0.1209	0.0628	0.9255	0.2113	0.9996
Sigma- <i>t</i>	0.1860	0.1732	-0.8824	0.3955	1.0020
Salinity	0.1154	0.3653	-0.0066	0.9176	1.0020
Si(OH) <sub>4</sub>	-0.0583	0.1999	0.1544	-0.0112	0.3852
ETS	-0.0183	0.1060	0.2848	-0.1606	0.4490

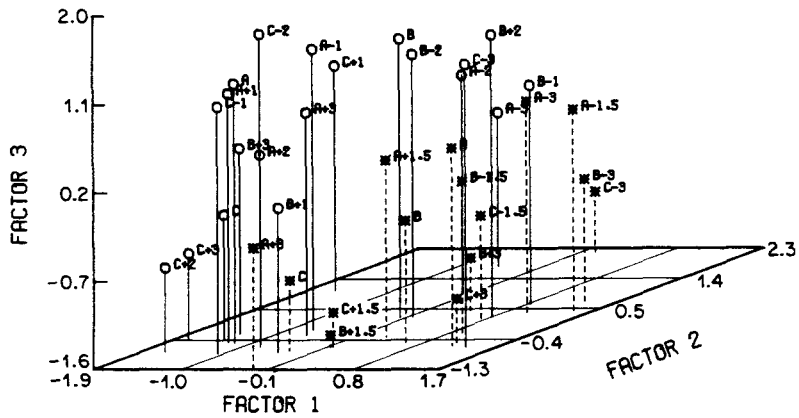


Fig. 5. Plot of mixed-layer factor scores for summer 1975 (O, solid line) and winter 1976 (\*, dashed line).

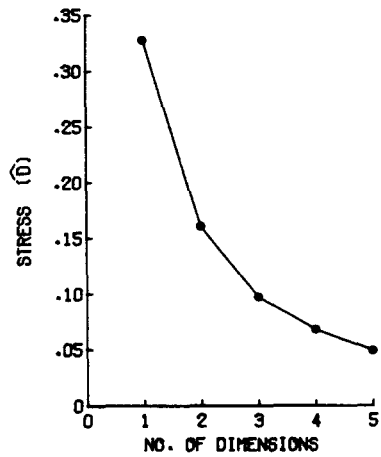


Fig. 6. Stress vs number of dimensions for the multidimensional scaling analysis.

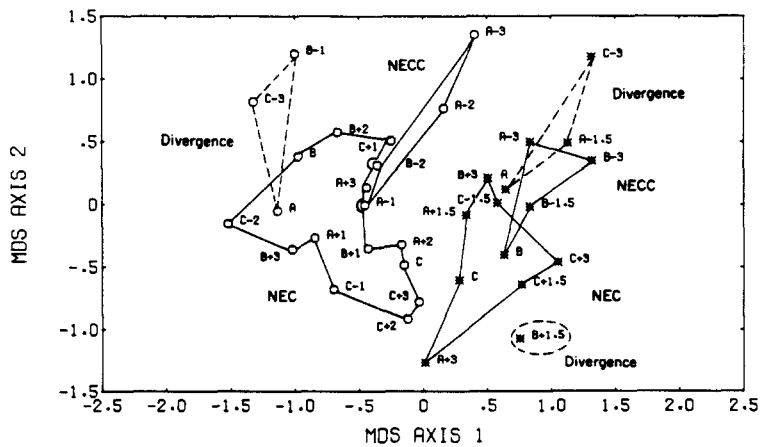


Fig. 7. Scatter plot of mixed-layer scores for the multidimensional scaling solution in summer (O) and winter (\*). Clusters drawn on the figure are derived from examination of Fig. 2 and meridional sections of nitrate, phosphate, silicate, dissolved oxygen, and submarine light transmittance.

transect A, farther to the west, the divergence zone stations are imbedded within other station clusters.

### *Spatial associations*

Correlations between variables were examined for summer 1975 and winter 1976 (Table 3). Note that in summer no significant correlations are found. In winter, however, vertically integrated primary production is positively correlated with both mixed-layer  $\text{NO}_3^-$  concentrations and with incident PAR. Further analysis showed that mixed-layer primary production is highly correlated with mixed-layer  $\text{NO}_3^-$  but is uncorrelated with incident PAR, while photosynthesis at the 1% light level shows a weak relationship with PAR. This suggests that increments of either nutrients near the surface or light at depth enhanced primary production in the appropriate depth region of the water column, in winter 1976 (cf. DUGDALE, 1967).

Also in winter, a significant inverse correlation was detected between primary production and the nitracline depth, and integrated chlorophyll *a* showed a weak association with primary production rate but not with mixed-layer nitrate. Zooplankton standing stock covaried significantly with mixed-layer nitrate in 1976. Winter associations between zooplankton standing stock and both integrated primary production rate ( $r_s = 0.660$ ) and the nitracline depth ( $r_s = -0.700$ ) were also observed, though neither correlation was significant, due to small sample sizes. However, zooplankton standing stock was more strongly associated with primary production rate than with chlorophyll *a*.

Results from summer 1975 differed from those in winter 1976, not only in a lack of strong correlations but also in the magnitude of short-term variability observed near a single station. Time series of repeated pump casts over a 30 to 60-h period at the central station on each of

Table 3. Spearman's rank correlations between properties, for summer 1975 and for winter 1976

	Summer 1975			Winter 1976		
	<i>N</i>	$r_s$	<i>P</i> -value	<i>N</i>	$r_s$	<i>P</i> -value
PProd vs Nitrate <sub>ML</sub>	19	0.034	>0.10	13	0.736	0.002 < <i>P</i> < 0.005*
PProd <sub>ML</sub> vs Nitrate <sub>ML</sub>	19	0.123	>0.10	14	0.821	<0.001†
PProd vs Z <sub>nitracline</sub>	19	-0.008	>0.10	12	-0.802	0.001 < <i>P</i> < 0.002†
PProd vs PAR	17	-0.136	>0.10	13	0.727	0.002 < <i>P</i> < 0.005*
PProd <sub>ML</sub> vs PAR	17	-0.436	0.05 < <i>P</i> < 0.10	14	0.426	>0.10
PProd <sub>1% light</sub> vs PAR	16	0.075	>0.10	13	0.562	0.02 < <i>P</i> < 0.05*
Chl <i>a</i> vs Nitrate <sub>ML</sub>	21	0.247	>0.10	15	0.411	>0.10
Chl <i>a</i> vs PProd	19	-0.300	>0.10	13	0.551	<i>P</i> = 0.05*
Chl <i>a</i> vs Z <sub>nitracline</sub>	21	-0.292	>0.10	14	-0.424	>0.10
Zoop vs Nitrate <sub>ML</sub>	8	-0.048	>0.10	9	0.750	0.01 < <i>P</i> < 0.02*
Zoop vs PProd	7	0.455	>0.10	7	0.660	0.05 < <i>P</i> < 0.10
Zoop vs Chl <i>a</i>	8	0.071	>0.10	9	-0.179	>0.10
Zoop vs Z <sub>nitracline</sub>	8	-0.101	>0.10	8	-0.700	0.05 < <i>P</i> < 0.10

\* Significant at  $\alpha = 0.05$ .

† Significant at  $\alpha = 0.002$ , the  $\alpha$ -level corrected for 26 tests of the null hypothesis.

PProd, integrated primary production rate; PProd<sub>ML</sub>, Nitrate<sub>ML</sub>, average value in the mixed layer; PProd<sub>1% light</sub>, primary production rate at 1% light level; PAR, incident photosynthetically active radiation; Chl *a*, integrated chlorophyll *a*; and Zoop, day-night average of zooplankton (>183  $\mu\text{m}$ ) dry weight in upper 200 m.

Table 4. Coefficient of variation (s.d./ $\bar{x} \times 100\%$ ) of surface chemical properties (modified from ANDERSON, 1979) and of integrated chlorophyll *a* (0 to 160 m, modified from EL-SAYED et al., 1977) at Stas A, B, and C in 1975 and 1976. Pump casts for nutrients and dissolved oxygen were made 4 to 10 times over a 30 to 60-h period, and 7 to 10 chlorophyll casts were made over a 20 to 29-h period at each station

Variable	Station	Coefficient of variation	
		1975	1976
A. Surface chemical properties			
O <sub>2</sub>	A	10.9%	4.8%
	B	25.8	8.7
	C	—	3.0
NO <sub>3</sub> <sup>-</sup>	A	0.0	20.0
	B	71.4	16.7
	C	100.0	100.0
PO <sub>4</sub> <sup>-3</sup>	A	54.5	23.1
	B	47.0	14.3
	C	33.3	50.0
Si(OH) <sub>4</sub>	A	142.8	35.5
	B	29.2	15.0
	C	85.7	11.5
B. Integrated chlorophyll <i>a</i>			
Chl <i>a</i>	A	20.0	12.6
	B	15.1	6.6
	C	51.5	17.8

the three transects (A, B, C) illustrate that in 1975 the variability in surface chemical properties was greater than in 1976 (Table 4A; paired differences significant at  $P = 0.024$ , Wilcoxon signed-rank test). The coefficient of variation of surface dissolved chemical constituents [O<sub>2</sub>, NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>-3</sup>, Si(OH)<sub>4</sub>] averaged 47.1% in 1975 but only 15.8% in 1976. Short-term variations in integrated chlorophyll *a* over a 24-h period also exhibited a higher coefficient of variation in 1975 than in 1976 (Table 4B).

#### Between-cruise comparisons

Some of the statistical comparisons summarized here, particularly in Table 5, have been reported differently (e.g., EL-SAYED and TAGUCHI, 1979; FRANCESCHINI, 1979). We justify further analysis of some of the same data as follows: (1) we used non-parametric statistical tests exclusively, because inspection of the data set showed frequent violations of the assumptions of parametric tests. (2) Our design for comparisons attempted to be consistent for all components of the data set, facilitating intercomparison of results. (3) Our analysis detected patterns not yet reported.

The hypothesis that there were significant differences between the 1975 and 1976 cruises was tested explicitly by examining individual variables using the Wilcoxon matched-pairs signed rank test. One-tailed tests were made only where the expected direction of a difference was predicted *a priori*. Only chlorophyll *a* exhibits a significant between-cruise difference, when a correction for multiple-testing is applied ( $\alpha = 0.0030$ , for 17 related comparisons in Table 5). However, as only a small number of samples are available for most comparisons, this conservative correction increases the danger of accepting a false null hypothesis (Type II error). Relaxing the rejection level to  $\alpha = 0.05$ , additional between-cruise differences are detected. A significant increase in PAR was evident in winter 1976, because of a decrease in

Table 5. Comparison between summer 1975 and winter 1976 using the Wilcoxon matched-pairs signed rank test (parts A, B, C) or the Wilcoxon rank sum test (part D)

Variable	N	P-value	Average % change summer to winter	Comments
<b>A. Water column properties</b>				
Mixed-layer depth	15	0.004*	+135.7%	Winter deepening north of 7°N
Nitracline depth	14	0.152	(+ 11.8%)	
Euphotic zone depth	13	0.146	(- 9.2%)	
Cloudiness	15	0.010*	- 30.6%	
Incident PAR‡	14	0.004*	+ 20.4%	
<b>B. Vertically integrated values</b>				
Chlorophyll <i>a</i>	15	0.001†	+133.8%	Greatest increases south of 11°30'N
Phytoplankton abundance	6	0.078	(+ 62.0%)	Transects B and C only
Particulate organic carbon	9	0.150	(+ 46.8%)	Transects A and C only; winter increases south of 11°30'N
Primary productivity	11	0.232	(+ 29.7%)	Winter increases south of 11°30'N
Microzooplankton abundance (day)	5	0.031*	+ 72.3%	
Macrozooplankton dry wt. (day)	8	0.020*	+104.6%	
Macrozooplankton dry wt. (night)	8	0.156	(+ 88.2%)	
<b>C. Individual light depths</b>				
Productivity/chlorophyll <i>a</i>	61	0.008*	- 36.1%	
<b>D. Mixed-layer averages</b>				
Suspended particulate matter	12	0.017*	+ 45.0%	
NO <sub>3</sub> <sup>-</sup>	15	0.042*	+ 87.5%	
PO <sub>4</sub> <sup>-3</sup>	15	0.281	(+ 3.7%)	
Si(OH) <sub>4</sub>	15	0.402	(+ 13.0%)	

\* Significant at  $\alpha = 0.05$ .

† Significant at  $\alpha = 0.003$ , the  $\alpha$ -level corrected for 17 tests of the null hypothesis.

‡ Photosynthetically active radiation.

cloudiness rather than a greater clear-sky irradiance (see FRANCESCHINI, 1979). Mixed-layer depth, microzooplankton abundance, and daytime macrozooplankton standing stock were greater in winter 1976. The average mixed-layer concentration of suspended particles and of nitrate were also greater in winter. Productivity:chlorophyll *a* ratios showed a significant decrease on the winter cruise.

Between-cruise changes were not uniform across the entire region. Winter increases of chlorophyll *a* were greater south of 11°30'N ( $P = 0.05$ , Runs test). Particulate organic

Table 6. Correlations between summer to winter differences ( $\Delta$ ) in primary production rates and other properties, from Kendall's coefficient of concordance ( $W$ ) or Spearman's rank correlation coefficient ( $r_s$ )

	N	Correlation	P-value
$\Delta$ PProd† vs $\Delta$ PAR† vs $-\Delta$ cloudiness‡	10	$W = 0.865$	$0.005 < P < 0.05^*$
$\Delta$ PProd vs $\Delta$ mixed-layer nitrate	11	$r_s = 0.697$	$0.01 < P < 0.02^*$
$\Delta$ PProd vs $\Delta$ mixed-layer depth	11	$r_s = -0.380$	$P > 0.10$

\* Significant at  $\alpha = 0.05$ .

† Integrated primary production rate.

‡ Incident photosynthetically active radiation.

§ Inverse change in cloudiness.

|| Average nitrate concentration in the mixed layer.

carbon (POC) showed a winter increase south of 11°30'N and a winter decrease in three out of four paired comparisons north of 11°30'N. Primary production rates were greater in winter south of 11°30'N. In only one comparison north of 11°30'N was there a winter increase in integrated production rates, i.e., at Sta. C-3, which appears to exhibit strong winter upwelling. If this station is deleted from the analysis, there is a significant ( $P = 0.05$ , Runs test) trend toward a February–March increase in primary production rates south of 11°30'N and decrease north of 11°30'N.

The greatest winter increases in primary production rates tend to occur at those stations where the greatest decrease in cloudiness and largest increase in incident light were found (Kendall's coefficient of concordance,  $W = 0.865$ ; Table 6). Between-cruise differences in integrated primary production rates are also correlated with differences in mixed-layer nitrate concentration, but not with differences in mixed-layer depth (Table 5).

## DISCUSSION

### *Spatial structure*

The predominant spatial pattern observed from the initial FA is the vertical structure of biological, physical, and chemical properties of the water column (factor 1, Fig. 4). Depth-related variations do not fully account for the variance of phytoplankton properties (see Table 1), suggesting that phytoplankton growth rates and standing stocks are not completely controlled by vertical gradients of nitrate or other nutrients. Other controlling factors are discussed below.

From the MDS analysis, horizontal structure is also apparent. Within the surface mixed layer, clusters corresponding to the NEC, the NECC, and the divergence zones were detected in both 1975 and 1976 (Fig. 7). As the source waters for the two major currents differ (TSUCHIYA, 1968), planktonic populations entrained in the NEC and NECC will have come from distinct source populations and will have experienced different temperature, nutrient, and mixing histories, which may contribute to differences in growth rates and in standing stocks.

### *Spatial associations*

Unanticipated in this analysis was the qualitatively different pattern of correlations observed during the two cruise periods. In 1975, the lack of statistically significant correlations between primary production rates and mixed-layer nitrate concentration, or between zooplankton standing stocks and chlorophyll *a* or primary production rates, suggests nutrient supply, phytoplankton growth, and zooplankton grazing were less predictably related in summer 1975 than in winter 1976. The difference provides evidence that *qualitative* changes may occur in the interrelationships between producers and consumers in the tropical Pacific, even if the quantitative changes in abundance of phytoplankton and zooplankton are few at all times of the year (BLACKBURN *et al.*, 1970; OWEN and ZEITZSCHEL, 1970).

The pattern of weaker correlations in 1975 than in 1976 may be affected by the greater short-term variability in 1975. In a highly variable environment, nutrient patches, primary producers, and suspension-feeding zooplankton may co-occur only transiently, making their interrelationships difficult to detect. WALSH (1978), for example, argued that variability in the physical environment can lead to "more frequent mismatches of energy transfer up the food chain" in the tropical Pacific.

One source of physical variability in the region is mesoscale eddy fields (SECKEL, 1975). Eddies have been suggested to influence variations in phytoplankton activity off Hawaii (BIENFANG and SZYPER, 1981). Mesoscale eddies also introduce waters of different origin and promote major changes in planktonic communities in the Sargasso Sea (e.g., WIEBE *et al.*, 1976; ORTNER, WIEBE, HAURY and BOYD, 1978). SECKEL (1975) suggested that in the Pacific, eddy-induced spatial variability increases with higher current speeds. As current speeds are typically greater in September and October than in February and March (WYRTKI, 1974), eddy-related variability would be more significant in September and October, coincident with the time when weaker biological correlations were observed.

Vertical mixing may also influence short-term variability and the strengths of correlations among biological properties. Correlations may be more readily detected in a more homogeneous system. Enhanced vertical mixing could reduce small-scale gradients in physical microstructure and in patches of phytoplankton and small grazers. If these gradients were reduced, less variability would also be expected in concentrations of nutrients and dissolved oxygen, as observed in winter 1976. Greater vertical mixing would be expected in February and March in this region of the tropical Pacific (WYRTKI and MEYERS, 1975). Additionally, inspection of continuous vertical profiles of nitrate, phosphate, and dissolved oxygen (ANDERSON and RICHARDS, 1977) shows that fewer inversions and less microstructure were evident within the surface mixed layer in February and March 1976 than in September and October 1975, consistent with the suggestion of greater vertical mixing in winter.

Finally, an explanation for the difference in correlation patterns between 1975 and 1976 that cannot be ruled out is that some trace constituents of waters in the euphotic zone were different in the two years. Phytoplankton growth may be limited by an imbalance of Mn:Cu in newly upwelled water (SUNDA, BARBER and HUNTSMAN, 1981) or possibly by a deficiency of organic chelators (BARBER and RYTHER, 1969; BARBER, DUGDALE, MACISSAC and SMITH, 1971). If the composition of waters transported to the surface by upwelling and vertical mixing were different in 1975 and 1976, then the ability of the waters to support phytoplankton growth may differ. For example, the absence of an association in 1975 between mixed-layer nitrate and either primary production rates or zooplankton standing stock was particularly apparent at the southernmost stations along transect A. Such nitrate-rich water—presumably recently upwelled or mixed into the surface layer—does not support high phytoplankton growth, perhaps due to trace nutrient effects. Alternatively, major nutrients may be upwelled faster than they can be assimilated, or grazing activity (by grazers included in the  $^{14}\text{C}$  incubation bottles) may be unusually high (cf. THOMAS, 1979). Further observations in tropical divergence regions will be necessary to distinguish these hypotheses.

In the western EASTROPAC region, significant correlations were observed between day zooplankton standing stock and primary production rates during some cruise periods but not others (BLACKBURN, 1973). However, other regression relationships between lower trophic levels did not appear to vary seasonally.

In the eastern tropical Atlantic, HERBLAND and VOITURIEZ (1979) and LEBORGNE (1981) proposed that vertically integrated primary production rates, chlorophyll, zooplankton standing stock, and other quantities can be predicted from correlations with relatively easily measured quantities such as the nitracline depth. They suggested that the correlations they observed are applicable to a 'typical tropical structure', defined as the absence of nitrate in the mixed layer (LEBORGNE, 1981). While the present study area is clearly influenced by near-surface nutrients, we consider this structure to represent much of the tropical Pacific Ocean (cf. REID, 1962; LOVE, 1970 to 1978). As significant correlations between the nitracline depth

and other properties were not detected during one of the two cruise periods, we conclude that no single correlation is sufficient to predict biological interrelationships in a 'typical' tropical Pacific environment. Also, in a subtropical environment off Hawaii where the surface nitrate concentration was nearly always near zero, BIENFANG and SZYPER (1981) observed no correlation between the depth of the nitracline and variations in primary productivity.

#### *Between-cruise differences*

The significant differences between cruises detected by FA and MDS were confirmed by analysis of individual measurement variables. Chlorophyll *a* shows the greatest between-cruise difference, although the 2.3-fold winter increase appears not to be due entirely to an increase in phytoplankton standing stock. In contrast to the chlorophyll *a* pattern, phytoplankton abundance (excluding flagellates) did not exhibit a winter increase (although the great variability in cellular volumes makes cell number an inadequate estimate of standing stock). Particulate organic carbon did not increase in winter across the entire region. Suspended particulate matter in the mixed layer was greater on the winter cruise, although the increase was less (1.4 ×) than in chlorophyll *a*. Therefore, although part of the winter 1976 increase in chlorophyll *a* may have been due to an increase in phytoplankton standing stock (particularly south of 11°30'N), part was probably due to higher cellular chlorophyll content in February and March than in September and October. Thus in the central North Pacific gyre the phytoplankton carbon:chlorophyll *a* ratio and the ratio of ATP:chlorophyll *a* were higher in mid-summer (June and July) than in winter (December to March; EPPLEY *et al.*, 1977).

Similarly, the significant winter decline in productivity:chlorophyll *a* observed across the region might also be due to elevated levels of chlorophyll *a* per unit cell biomass. Temperature decreases do not appear to be sufficient (average 2.6°C in the mixed layer) to account for the observed change in productivity:chlorophyll *a* ratio (EPPLEY, 1972). There is no evidence for decreased availability of nutrients (either inorganic or organic), so greater nutrient limitation (CURL and SMALL, 1965; THOMAS, 1970) does not appear to be decreasing productivity:chlorophyll *a*. Hence, the winter depression of productivity:chlorophyll *a* is probably due to increased cellular chlorophyll *a* content, resulting from either altered cell physiology or from shifts in phytoplankton size composition (FALKOWSKI, 1980).

EL-SAYED and TAGUCHI (1979) reported that the light utilization efficiency per unit chlorophyll *a* (mg C E<sup>-1</sup> mg Chl *a*<sup>-1</sup> m<sup>-2</sup>) was higher in summer than in winter. This suggests greater shade adaptation of cells in winter than in summer, a surprising result in this tropical region where a 20 to 30% average increase in incident solar radiation was observed in winter. The probable mechanism promoting greater shade adaptation is enhanced vertical mixing in winter. Vertical mixing would lower the daily average light intensity for much of the phytoplankton community within the surface mixed layer. Calculations from data presented in FRANCESCHINI (1979) show that the average mixed-layer irradiance (PAR) in summer 1975 was 288 μE m<sup>-2</sup> s<sup>-1</sup>, but 104 μE m<sup>-2</sup> s<sup>-1</sup> in winter 1976. In further support of the mixing hypothesis is the winter decrease in productivity:chlorophyll *a* at light depths with the mixed layer (12% of surface irradiance and shallower), in contrast to the similarity between winter and summer assimilation numbers at light depths below the mixed layer (Table 7).

The P vs I experiments of CHAN, OZTURGUT, JACOBSEN and ANDERSON (1980) are also consistent with the suggestion of increased cellular chlorophyll *a* in late winter. Near-surface phytoplankton populations from waters near Sta. C exhibited greater shade adaptation in March 1979 than in early November 1978, despite higher incident solar radiation in March.



Table 7. *Phytoplankton productivity:chlorophyll a as a function of light level (modified from EL-SAYED and TAGUCHI, 1979). Each value is the median for that depth and season*

Light level (%)	P:Chl <i>a</i> [mg C m <sup>-3</sup> day <sup>-1</sup> (mg Chl <i>a</i> ) <sup>-1</sup> ]	
	1975	1976
100	20.58	13.32
50	25.10	16.80
25	11.26	8.80
12	9.61	5.36
6	5.86	6.76
1	2.24	2.13

Again, the deeper mixed layer in March 1979 (85 m) than in November 1978 (45 m) may have reduced the average light field for near-surface phytoplankton cells.

The greatest between-cruise differences in primary production rates, chlorophyll *a*, and POC tend to occur at the southernmost stations. Either *in situ* growth processes or advection of different populations in the NECC could lead to the apparent changes between 1975 and 1976 in both chlorophyll *a* and POC.

As anticipated from the apparent increase in some measures of phytoplankton standing stock, zooplankton standing stock was greater in February and March 1976 than in September and October 1975. The winter increase in daytime, but not night-time, zooplankton standing stock parallels that observed in the EASTROPAC investigation (BLACKBURN *et al.*, 1970). The magnitude of the difference observed between the two cruises of the DOMES study (approximately 2-fold) is similar to the maximum difference observed over an annual cycle in the western area of the EASTROPAC region (approximately 1.6-fold, BLACKBURN *et al.*, 1970).

As only two seasons were sampled in the present study, we cannot establish that the differences observed between September and October 1975 and February and March 1976 represent 'seasonal' changes. Conceivably, interannual variations, advection of waters of different origins, or stochastic changes could lead to the observed patterns. BIENFANG and SZYPER (1981), for example, detected no seasonal periodicity in variations in phytoplankton pigments, ATP, and primary production rates in waters off Hawaii over a 14-month period. However, because many of the changes that were observed between 1975 and 1976 in the DOMES region recurred in approximately the same two seasons in 1978 and 1979 (CHAN *et al.*, 1980; OZRETICH, 1979), and the changes were largely in phase with the seasonal patterns observed earlier in the EASTROPAC region (BLACKBURN *et al.*, 1970; OWEN and ZEITZSCHEL, 1970), the most likely basis for the differences appears to be underlying seasonal cycles in the tropical Pacific.

#### CONCLUSIONS

Statistical analysis of biological and supporting hydrographic data from two cruise sequences to the eastern tropical North Pacific show that the concentrations of some biological properties, the magnitude of short-term (30 to 60 h) variations in properties, and the patterns of correlation between properties differ significantly at two different times of year. The intensity of correlations between biological variables may be influenced by

mesoscale eddy-induced variability and by vertical mixing. The absence of statistically significant correlations in summer 1975, in contrast to those observed in winter 1976, suggests that processes of vertical transport of nutrients, phytoplankton growth, and grazing and excretion by zooplankton may be more closely coupled at some times of year than at other times.

Tropical ocean regions are classically characterized as experiencing only low-amplitude seasonal variations. However, temporal changes in physical forcing functions should be considered in future investigations concerning the dependence of phytoplankton growth rates on vertical nitrogen fluxes, trace-metal and chelator effects on phytoplankton growth, vertical mixing and phytoplankton shade adaptation, and the interactions between phytoplankton growth and zooplankton grazing in the tropical ocean.

*Acknowledgements*—We express particular thanks to the investigators who designed and carried out the research discussed in this paper. Critical comments on the manuscript by K. BANSE, B. W. FROST, B. A. TAFT, D. WARTENBURG, and the anonymous referees are gratefully acknowledged. We benefited from early discussions with P. A. JUMARS concerning statistical design and from discussions with R. W. EPPLEY and B. A. TAFT on specific topics. To B. E. TAYLOR go thanks for the three-dimensional plotting program. Supported by NOAA Contract No. 03-6-022-35101 to G.C.A.

#### REFERENCES

- ANDERSON G. C. (1969) Subsurface chlorophyll maximum in the northeast Pacific Ocean. *Limnology and Oceanography*, **14**, 386–391.
- ANDERSON J. J. (1979) Nutrient chemistry in the tropical north Pacific: DOMES Sites A, B, and C. In: *Marine geology and oceanography of the Pacific Manganese Nodule Province*, J. L. BISCHOFF and D. Z. PIPER, editors. Plenum Press, New York, pp. 113–161.
- ANDERSON J. J. and F. A. RICHARDS (1977) Continuous profiles of chemical properties in the euphotic zone of the DOMES study area in the Equatorial North Pacific. University of Washington, Department of Oceanography Special Report No. 78, 97 pp.
- BAARS M. A., J. J. ZIJLSTRA and S. B. TUISSEN (1979) Investigations in the euphotic zone of the tropical North Atlantic: Programme and hydrography during the NECTAR cruises. *Netherlands Journal of Sea Research*, **13**, 40–57.
- BARBER R. T., R. C. DUGDALE, J. J. MAC ISSAC and R. L. SMITH (1971) Variations in phytoplankton growth associated with the source and conditioning of upwelling water. *Investigacion Pesquera*, **35**, 171–193.
- BARBER R. T. and J. H. RYTHER (1969) Organic chelators: Factors affecting primary production in the Cromwell Current upwelling. *Journal of Experimental Marine Biology and Ecology*, **3**, 191–199.
- BIENFANG P. K. and J. P. SZYPER (1981) Phytoplankton dynamics in the subtropical Pacific ocean off Hawaii. *Deep-Sea Research*, **28**, 981–1000.
- BISCHOFF J. L. and D. Z. PIPER, editors (1979) *Marine geology and oceanography of the Pacific Manganese Nodule Province*. Plenum Press, New York, 842 pp.
- BLACKBURN M. (1973) Regressions between biological oceanographic measurements in the eastern tropical Pacific and their significance to ecological efficiency. *Limnology and Oceanography*, **18**, 552–563.
- BLACKBURN M., R. M. LAURS, R. W. OWEN and B. ZEITZSCHEL (1970) Seasonal and areal changes in standing stocks of phytoplankton, zooplankton, and micronekton in the eastern tropical Pacific. *Marine Biology*, **7**, 14–31.
- CHAN A. T., E. OZTURGUT, R. JACOBSEN and G. C. ANDERSON (1980) Environmental investigation of the effects of deep-sea mining on the phytoplankton in the tropical eastern Pacific Ocean, with special attention on primary productivity. University of Washington, Department of Oceanography Special Report No. 92, 48 pp.
- CURL H. and L. F. SMALL (1965) Variations in photosynthetic assimilation ratios in natural marine phytoplankton communities. *Limnology and Oceanography* (Supplement), **10**, R67–R68.
- DUGDALE R. C. (1967) Nutrient limitation in the sea; dynamics, identification and significance. *Limnology and Oceanography*, **12**, 685–695.
- DZIUBAN C. D. and E. C. SHIRKEY (1974) When is a correlation matrix appropriate for factor analysis? Some decision rules. *Psychological Bulletin*, **81**, 358–361.
- EL-SAYED S. Z. and S. TAGUCHI (1979) Phytoplankton standing crop and primary productivity in the tropical Pacific. In: *Marine geology and oceanography of the Pacific Manganese Nodule Province*, J. L. BISCHOFF and D. Z. PIPER, editors. Plenum Press, New York, pp. 241–286.

- EL-SAYED S. Z., S. TAGUCHI, G. A. FRANCESCHINI, G. A. FRYXELL and C. E. GATES (1977) Phytoplankton and primary productivity studies. (In connection with the Deep Ocean Mining Environmental Study (DOMES.) Department of Oceanography, Texas A & M University Report, 197 pp.
- EPPLEY R. W. (1972) Temperature and phytoplankton growth in the sea. *Fishery Bulletin*, **70**, 1063–1085.
- EPPLEY R. W., E. H. RENGER, E. L. VENRICK and M. M. MULLIN (1973) A study of plankton dynamics and nutrient cycling in the central gyre of the north Pacific Ocean. *Limnology and Oceanography*, **18**, 534–551.
- EPPLEY R. W., J. H. SHARP, E. H. RENGER, J. J. PERRY and W. G. HARRISON (1977) Nitrogen assimilation by phytoplankton and other microorganisms in the surface waters of the central North Pacific Ocean. *Marine Biology*, **39**, 111–120.
- FALKOWSKI P. G. (1980) Light-shade adaptation in marine phytoplankton. In: *Primary productivity in the sea*. P. G. FALKOWSKI, editor, Plenum Press, New York, pp. 99–119.
- FASHAM M. J. R. (1977) A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines, and coenoplanes. *Ecology*, **58**, 551–561.
- FRANCESCHINI G. A. (1979) The solar radiation environment in the eastern tropical north Pacific Ocean. In: *Marine geology and oceanography of the Pacific Manganese Nodule Province*, J. L. BISCHOFF and D. Z. PIPER, editors, Plenum Press, New York, pp. 1–41.
- FRYXELL G. A., S. TAGUCHI and S. Z. EL-SAYED (1979) Vertical distribution of diverse phytoplankton communities in the central Pacific. In: *Marine geology and oceanography of the Pacific Manganese Nodule Province*, J. L. BISCHOFF and D. Z. PIPER, editors, Plenum Press, New York, pp. 203–239.
- GAUCH H. G., JR., R. H. WHITTAKER and S. B. SINGER (1981) A comparative study of nonmetric ordinations. *Journal of Ecology*, **69**, 135–152.
- GAUCH H. G., JR., R. H. WHITTAKER and T. R. WENTWORTH (1977) A comparative study of reciprocal averaging and other ordination techniques. *Journal of Ecology*, **65**, 157–174.
- HALPERN D. (1979) Observations of the upper ocean currents at DOMES sites A, B, and C in the tropical central North Pacific Ocean during 1975 and 1976. In: *Marine geology and oceanography of the Pacific Manganese Nodule Province*, J. L. BISCHOFF and D. Z. PIPER, editors, Plenum Press, New York, pp. 43–82.
- HARMAN H. H. (1976) *Modern factor analysis*, 3rd edition, revised, University of Chicago Press, 487 pp.
- HERBLAND A. and B. VOITURIEZ (1979) Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean. *Journal of Marine Research*, **37**, 87–101.
- HIROTA J. (1977a) DOMES zooplankton (data report). Hawaii Institute of Marine Biology and Department of Oceanography, University of Hawaii, 710 pp.
- HIROTA J. (1977b) DOMES zooplankton. Hawaii Institute of Marine Biology and Department of Oceanography, University of Hawaii, 247 pp.
- HOLLANDER M. and D. A. WOLFE (1973) *Nonparametric statistical methods*. John Wiley, New York, 503 pp.
- JACKSON G. A. (1980) Phytoplankton growth and zooplankton grazing in oligotrophic oceans. *Nature, London*, **284**, 439–440.
- KRUSKAL J. B. (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, **29**, 1–27.
- KRUSKAL J. B. and M. WISH (1978) Multidimensional scaling, Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-011, Sage Publications, 93 pp.
- LEBORGNE R. L. (1981) Relationships between the hydrological structure, chlorophyll and zooplankton biomasses in the Gulf of Guinea. *Journal of Plankton Research*, **3**, 577–592.
- LONGHURST A. R. (1976) Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. *Deep-Sea Research*, **23**, 729–754.
- LOVE C. M. (1970 to 1978) EASTROPAC Atlas. United States Fish and Wildlife Circular 330. Vol. 2, 4, 6, 8, 10, 11.
- MCCARTHY J. J. and J. C. GOLDMAN (1979) Nitrogenous nutrition of marine phytoplankton in nutrient-depleted waters. *Science, New York*, **203**, 670–672.
- MILLER R. G., JR. (1977) Developments in Multiple Comparisons 1966–1976. *Journal of the American Statistical Association*, **72**, 779–788.
- NIE N. H., C. H. HALL, J. G. JENKINS, K. STEINBRENNER and D. H. BENT (1975) *Statistical package for the social sciences*, 2nd edition, McGraw-Hill, New York, 675 pp.
- ORTNER P. B., P. H. WIEBE, L. HAURY and S. BOYD (1978) Variability in zooplankton biomass distribution in the northern Sargasso Sea: the contribution of Gulf Stream cold core rings. *Fishery Bulletin*, **76**, 323–334.
- OWEN R. W. and B. ZEITZSCHEL (1970) Phytoplankton production: seasonal change in the oceanic eastern tropical Pacific. *Marine Biology*, **7**, 32–36.
- OZRETICH R. J. (1979) Final Report on the experiments and field measurements to assess the stimulation of bacterial growth as an impact of prototype deep ocean mining. University of Washington, Department of Oceanography Special Report No. 90, 61 pp.
- OZTURGUT E., G. C. ANDERSON, R. D. BURNS, J. M. LAVELLE and S. A. SWIFT (1978) Deep ocean mining of manganese nodules in the North Pacific. Premining environmental conditions and anticipated mining effects. National Oceanic and Atmospheric Administration Technical Memorandum ERL MESA-33. 133 pp.

- REID J. L., JR. (1962) On circulation, phosphate phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. *Limnology and Oceanography*, **7**, 287–306.
- REID J. L., JR. (1965) *Intermediate waters of the Pacific Ocean*. Johns Hopkins Press, Baltimore, MD, 85 pp.
- REID J. L., JR. (1973) The shallow salinity minima of the Pacific Ocean. *Deep-Sea Research*, **20**, 51–68.
- ROSKAM E. E. and J. C. LINGOES (1977) MDS (X) programs, Program Library Unit, University of Edinburgh. Edinburgh EH8 9LN, Scotland.
- SECKEL G. R. (1975) Seasonal variability and parameterization of the Pacific north equatorial current. *Deep-Sea Research*, **22**, 379–401.
- SHARP J. H., M. J. PERRY, E. H. RENGER and R. W. EPPLEY (1980) Phytoplankton rate processes in the oligotrophic waters of the central North Pacific Ocean. *Journal of Plankton Research*, **2**, 335–353.
- SPENCE I. and J. GRAEF (1974) The determination of the underlying dimensionality of an empirically obtained matrix of proximities. *Multivariate Behavioral Research*, **9**, 331–342.
- SUNDA W. G., R. T. BARBER and S. A. HUNTSMAN (1981) Phytoplankton growth in nutrient rich seawater: importance of copper–manganese cellular interactions. *Journal of Marine Research*, **39**, 567–586.
- THOMAS W. H. (1970) On nitrogen deficiency in tropical ocean phytoplankton: photosynthesis parameters in poor and rich water. *Limnology and Oceanography*, **15**, 380–385.
- THOMAS W. H. (1979) Anomalous nutrient–chlorophyll interrelationships in the offshore eastern tropical Pacific Ocean. *Journal of Marine Research*, **37**, 327–335.
- TRANter D. J. (1973) Seasonal studies of a pelagic ecosystem (Meridian 110°E). In: *The biology of the Indian Ocean*, B. ZEITZSCHEL, editor. Springer-Verlag, New York, pp. 487–520.
- TSUCHIYA M. (1968) *Upper waters of the intertropical Pacific Ocean*. Johns Hopkins Oceanographic Studies No. 4, 50 pp.
- TSUCHIYA M. (1974) Variation of the surface geostrophic flow in the eastern intertropical Pacific Ocean. *Fishery Bulletin*, **72**, 1075–1086.
- VENRICK E. L., J. A. MCGOWAN and A. W. MANTYLA (1973) Deep maxima of photosynthetic chlorophyll in the Pacific Ocean. *Fishery Bulletin*, **71**, 41–52.
- VINOGRADOV M. E. (1977) Pelagic ecosystems studies on the upwellings of the eastern Pacific Ocean: Cruise 17 of the R/V "Akademik Kurchatov." *Polskie Archiwum Hydrobiologii* (Supplement) **24**, 7–19.
- VINOGRADOV M. E., I. I. GITELZON and YU. I. SOROKIN (1970) The vertical structure of a pelagic community in the tropical ocean. *Marine Biology*, **6**, 187–194.
- WALSH J. J. (1978) The biological consequences of interaction of the climatic, El Niño, and event scales of variability in the eastern tropical Pacific. *Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, **173**, 182–192.
- WESTMAN W. E. (1975) Edaphic climax pattern of the pygmy forest region of California. *Ecological Monographs*, **45**, 109–135.
- WIEBE P. H., E. M. HULBERT, E. J. CARPENTER, A. E. JAHN, G. P. KNAPP, III, S. H. BOYD, P. B. ORTNER and J. L. COX (1976) Gulf Stream cold core rings: large-scale interaction sites for open ocean plankton communities. *Deep-Sea Research*, **23**, 695–710.
- WYRTKI K. (1974) Equatorial currents in the Pacific 1950 to 1970 and their relations to the Trade Winds. *Journal of Physical Oceanography*, **4**, 372–380.
- WYRTKI K. (1978) Lateral oscillations of the Pacific Equatorial Countercurrent. *Journal of Physical Oceanography*, **8**, 530–532.
- WYRTKI K. and G. MEYERS (1975) The trade wind field over the Pacific Ocean. Part I. The mean field and the mean annual variation. University of Hawaii Institute of Geophysics, HIG-75-1, 64 pp.
- ZAR J. H. (1974) *Biostatistical analysis*. Prentice-Hall, New York, 620 pp.