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Particulate organic matter and chlorophyll in the surface layer of the equatorial Pacific Ocean along 135° W

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ABSTRACT: Vertical and horizontal distributions of chlorophyll (chl) *a*, phaeopigment, particulate organic carbon (POC) and nitrogen (PON) in the euphotic zone were studied on a transect across the equatorial Pacific at ca 135° W from 12° S to 15° N. POC, PON, chl, and nutrient concentrations were highest near the equator. Despite a coincidence of maximum POC, and PON levels with the subsurface chl maximum (SCM), photoadaptation appears to play the predominant role in the vertical distribution of chl along this equatorial transect. The size distribution of the above properties was examined within the mixed layer and SCM across the same transect. Small particles (< 10 µm) dominated at both depths. In general, phytoplankton cells constituted only a small proportion of the particulate organic matter, particularly in the < 1 µm fraction which had higher proportions of detritus than the other fractions. The residence time of POC outside the equatorial region was 14 d. In the equatorial upwelling region the residence time was shorter (6 to 7 d), indicating that the suspended particles were turning over more rapidly. Results suggest that particulate loss by grazing is the predominant removal mechanism rather than advection or sedimentation. This suggestion is supported by the distributions of phaeopigment to chl *a* ratios, and the observed particle size distributions.

INTRODUCTION

The equatorial Pacific region has enhanced autotrophic production (Betzer et al. 1984, Chavez & Barber 1987, Peña et al. 1990) due to large-scale divergence in the ocean circulation which increases concentration of plant nutrients in the euphotic zone. It has been estimated that this region could account for 10 to 56 % of global new production (as defined by Dugdale & Goering 1967, Chavez & Barber 1987), and hence for a large part of the global downward flux of organic matter (Eppley & Peterson 1979). A notable feature of this region is that, in spite of the high level of nutrients available, chlorophyll (chl) levels are low (Walsh 1976, Thomas 1979, Peña et al. 1990).

Despite its large area and the potential importance in the removal of atmospheric carbon through biological processes, there are relatively few biological data from the equatorial Pacific, in contrast to the more intensively studied subtropical ocean. In the equatorial Atlantic, the distribution of particulate organic carbon (POC) and its size structure has been well documented (Herbland & Le Bouteiller 1981, 1983). In the equatorial Pacific, it is only along 150° W that the distribution of POC has been reported (Wangersky 1976, Eppley et al. 1991). POC is a heterogeneous mix of living planktonic organisms and organic detritus. Detrital carbon consists mainly of fine particles, although larger particles of fecal material, crustacean molts, and aggregates of mucous-like material from gelatinous organisms are also present (Banse 1977). The living plankton usually account for less than half of the total POC collected by water bottle sampling (Sharp et al. 1980, Eppley et al. 1983). In the surface layer, the POC levels are a function of productivity (Wangersky 1976) and particulate organic matter (POM) composition is usually similar to that of phytoplankton (Copin-Montegut & Copin-Montegut 1983).

Information on the size composition of phytoplankton biomass is important for understanding the utilization of primary production in the surface layer and the flux of organic matter out of the surface layer. In tropical systems, size-fractionation studies (Herbland et al. 1985, Chavez 1989, Peña et al. 1990) have shown that

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chl concentrations are dominated by small organisms passing through a 10 µm mesh screen. Together with the low chl and high production observed, this observation has led to the suggestion that equatorial upwelling systems may be more similar ecologically to subtropical systems, with a close coupling between rates of phytoplankton growth and zooplankton grazing and excretion, than to coastal upwelling zones, where grazing and recycling are relatively less important (Walsh 1976, Minas & Minas 1986, Murray et al. 1989, Peña et al. 1990).

In an attempt to better understand the distribution and dynamics of phytoplankton biomass in equatorial regions, the distribution of POM, chl *a* and phaeopigment and their size-structure in the upper water column were investigated in a transect crossing the equatorial Pacific at 135° W.

METHODS

Twelve stations were occupied by the RV 'Wecoma' in the equatorial Pacific Ocean along a transect crossing the equator within a few degrees of 135° W longitude and between 12° S and 15° N during April of 1988 (see Table 1). At each station, water samples were collected with twelve 5 l Niskin bottles on a rosette sampler to which the CTD was attached.

Duplicate water samples from 5 or 6 depths within the euphotic zone (between the surface and 150 m) were obtained for POM and from 6 to 12 depths (between the surface and 200 m) for total and size-fractionated chl. At 9 of the stations (Stns 20 to 78), duplicate water samples for size-fractionation of particulate matter were collected at two of these depths, one from the mixed layer region and another from the depth where the subsurface chl maximum (SCM) was expected, based on CTD cast.

Samples for total particulate organic carbon (POC) and nitrogen (PON) were obtained by filtering 1 l of seawater through combusted glass fiber filters (Whatman GF/F). For the size fractionation 1 to 2 l samples, depending on the quantity of particulate material, were passed through a 10 µm or 1 µm Nuclepore filter, and each filtrate was immediately filtered on a Whatman GF/F. After the filtration, the filters were stored at −20 °C, then dried at 60 °C and placed in a desiccator with silica gel until analysed with a Perkin Elmer elemental analyser (model 2400) calibrated with a cyclohexanone standard.

For total chl *a* measurements, 100 ml of seawater were filtered through glass fiber filters (Whatman GF/F). Samples of 200 ml were size-fractionated by passing the sample serially through a 10 µm and a 1 µm Nuclepore filter, and finally through a Whatman GF/F filter. The samples were then extracted with 10 ml of 90 % acetone for 24 h and the fluorescence was measured (Turner Design fluorometer) to derive chl *a* and phaeopigments values (Holm Hansen et al. 1965). The fluorometer was previously calibrated against pure chl *a* (Sigma). At 2 stations, comparisons were made of chl *a* concentration values obtained by following the filtration procedure used in the size-fractionation of POM, and by the chl size-fractionation procedure; the values from the 2 procedures agreed to within 5 %.

Nitrate samples were taken from 12 fixed depths at each station (between 0 and 200 m) and determined by the method described by Strickland & Parsons (1972) with an autoanalyser.

Chl *a*, POC and PON data were subjected to linear regression analysis (Model II; as recommended by Laws & Archie 1981) after pooling the data by: (1)

Table 1. Latitudinal distribution of average concentrations of chlorophyll (chl) *a*, particulate organic carbon (POC) and nitrogen (PON) at each station sampled

Stn	Location		POC (µM)		PON (µM)		Chl *a* (µg l^{-1})	
	Latitude	Long. (W)	Avg.	SD	Avg.	SD	Avg.	SD
11	12°09.4'S	134°19.5'	7.9	3.7	1.01	0.6	0.22	0.06
20	5°58.0'S	134°59.4'	4.1	1.3	0.62	0.3	0.23	0.08
34	1°59.9'S	133°00.2'	5.1	1.7	0.66	0.2	0.26	0.16
39	0°59.9'S	133°35.5'	5.8	2.1	0.77	0.3	0.35	0.13
50	0°30.8'N	133°18.8'	6.1	1.9	0.96	0.5	0.40	0.12
55	2°03.0'N	133°37.9'	6.4	2.3	0.85	0.3	0.36	0.11
60	4°17.2'N	133°30.5'	5.6	1.3	0.62	0.2	0.33	0.07
65	5°45.1'N	135°00.0'	5.5	0.7	0.75	0.4	0.31	0.09
73	7°13.7'N	137°33.3'	5.7	0.7	0.78	0.2	0.30	0.03
78	9°03.4'N	136°47.5'	5.3	1.0	0.46	0.1	0.27	0.08
88	11°05.2'N	136°26.8'	7.1	0.3	0.87	0.3	0.29	0.13
96	15°40.9'N	143°05.7'	6.8	0.3	0.77	0.3	0.11	0.03

regions according to the nitrate available in the water, (2) size of the organisms, or (3) by grouping all data available.

RESULTS

Distribution of chl, POC and PON

The average concentrations of chl *a*, POC and PON in the euphotic zone along the transect are summarized in Table 1. The geographic variation of POC and PON concentrations was similar. For both, the variation was about 2-fold (range 4.1 to 7.9 μM of POC and 0.46 to 1.01 μM of PON) between 12° S and 15° N, and both showed highest values near the equator and at the most poleward stations. In contrast, chl *a* concentration showed an increase coincident with POM concentration only near the equator. Details of the chlorophyll distribution along this transect were given by Peña et al. (1990).

The vertical profiles of suspended particulate matter (POC and PON) and chl *a* (Fig. 1) at each station share several features. Subsurface maxima were observed in some of the stations along the transect, although they were less prominent for POC and PON than for chl. The concentration of chl *a* at the maximum ranged from 0.26 to 0.59 μg l^{-1} and was, on average, about twice (range = 1.2 to 4.0) that in the overlying waters. POC concentrations ranged from 5.05 to 13.09 μM and were, on average, only about 1.3 (range = 1 to 2.2) times the values of the upper layer. Near the equator (Stns 34 to 55), the subsurface POM maxima were more pronounced and located around 30 to 60 m in the vicinity of the SCM. Out of the equatorial zone, no coincidence between POC and chl maxima was observed.

Considering the entire transect, linear regression analysis (Table 2) gave C/N molar ratios of 5.7 in the particulate matter (slightly lower than the Redfield ratio of 6.6). When the data were grouped by regions according to nutrient status – equatorial region (Stns 20 to 55, with elevated nutrient concentration at the surface (>4 μM)) and outside the equatorial region (Stns 11 and 60 to 96, where nutrient was depleted) – similar ratios (5.8 and 5.4 respectively) were estimated. The correlation coefficients were high (r = 0.82 to 0.86) for both regression lines. In contrast, a significant linear regression model of POC or PON on chl *a* ($p < 0.01$ and < 0.5 respectively) was obtained only for the equatorial region. The slope of POC on chl *a* regression (Table 2) was 178 (w/w) and that of PON on chl *a* was 36 (w/w). The differences in absolute magnitude of correlation coefficients between POC vs PON and POC or PON vs chl found between the regions indicate that compositional variability in the POM is occurring over the latitudinal range studied.

Size distribution of POM in the mixed layer and SCM

The latitudinal variation in the size distribution of POC and PON at 2 depths in the euphotic zone between 6° S and 9° N is shown in Fig. 2. In general, the biomass within all size-fractions increased in the region of the equator. The only exception occurred at 1° S (Stn 39) at the SCM depth, which was in fact a POC and PON minimum (Fig. 1). An unusual feature of the data was that the greatest POC concentrations occurred at the SCM depth whereas the greatest concentrations of PON were found within the mixed layer. Most of the latitudinal variation in POC and PON appeared to be associated with variations in the < 10 μm size-fraction.

The relative contributions of each size-fraction to total biomass at each depth horizon is shown in Fig. 3. At all the stations sampled, most of the POM (> 70 % of POC and > 50 % of PON) passed through a 10 μm pore

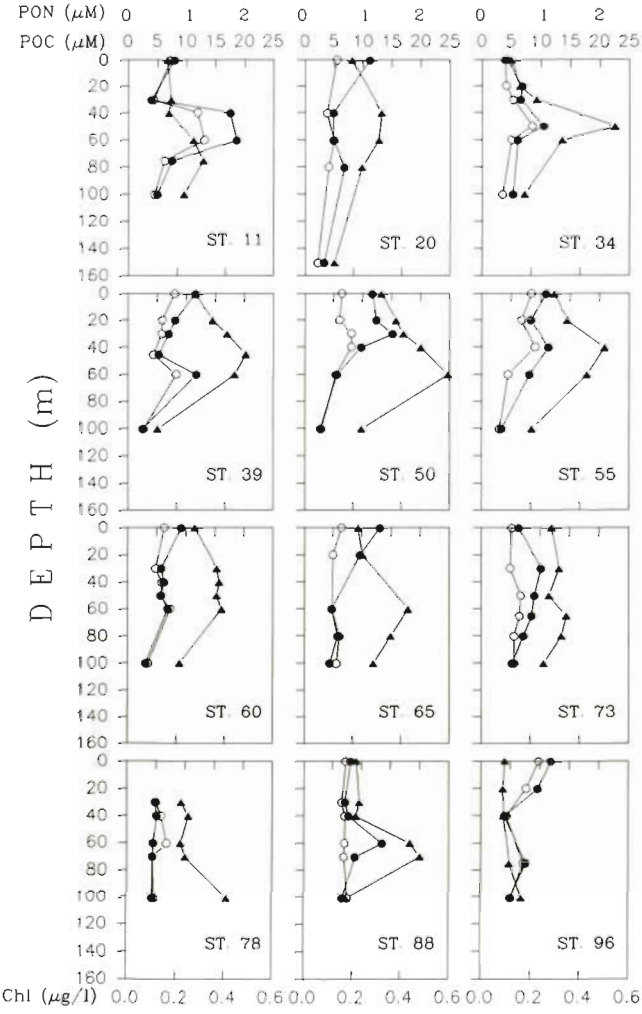

Fig. 1. Vertical profiles of chlorophyll (▲), particulate organic carbon (POC; ●) and nitrogen (PON; ○) at each station

Table 2. Linear regression between POC, PON and chl *a* computed for each region

Regression lines	Correlation coefficient	No. of samples
All stations		
POC ($\mu g\ l^{-1}$) = 203.1 chl *a* ($\mu g\ l^{-1}$) + 12.9	0.16	67
PON ($\mu g\ l^{-1}$) = 41.5 chl *a* ($\mu g\ l^{-1}$) – 1.4	0.19	67
POC (μM) = 5.7 PON (μM) + 1.6	0.82••	67
Equatorial		
POC ($\mu g\ l^{-1}$) = 177.9 chl *a* ($\mu g\ l^{-1}$) + 9.3	0.64••	28
PON ($\mu g\ l^{-1}$) = 35.5 chl *a* ($\mu g\ l^{-1}$) + 0.56	0.46•	28
POC (μM) = 5.8 PON (μM) + 1.05	0.86••	28
Out of equatorial region		
POC ($\mu g\ l^{-1}$) = –231.1 chl *a* ($\mu g\ l^{-1}$) + 135.9	0.19	39
PON ($\mu g\ l^{-1}$) = –47.7 chl *a* ($\mu g\ l^{-1}$) + 23.0	0.05	39
POC (μM) = 5.4 PON (μM) + 2.2	0.83••	39

•• Highly significant ($p \ll 0.01$)
• Significant ($p < 0.05$)

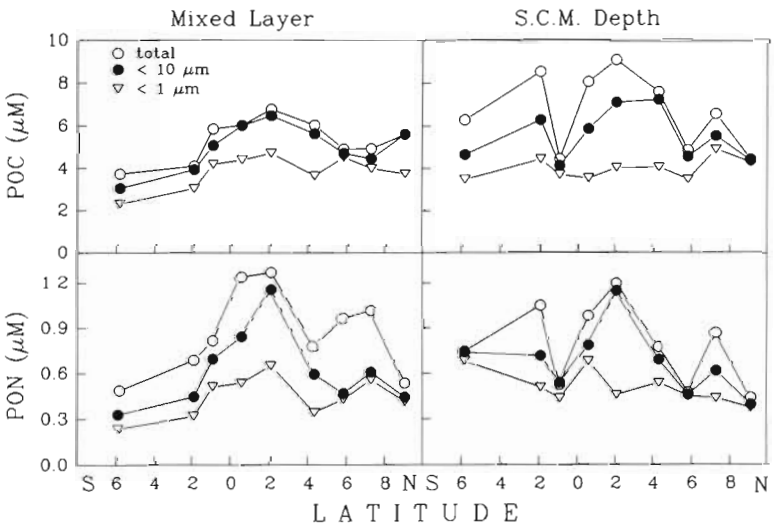

Fig. 2. Size distribution of POC and PON concentration at the depth of the SCM and mixed layer between 6° S and 9° N along the transect

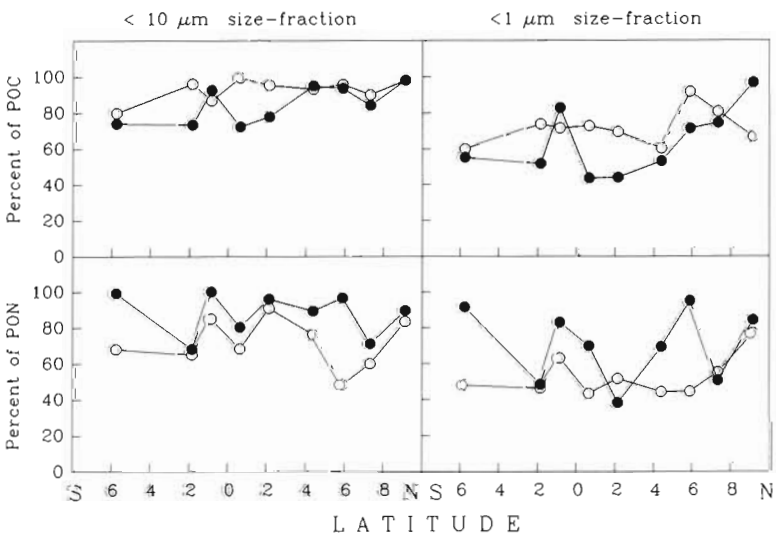

Fig. 3. Relative concentration of POC and PON in the < 10 and < 1 μm size-fraction at the depth of the SCM (●) and mixed layer (○) along the transect

Table 3. Linear regression between POC, PON and chl *a* for each size-fraction, all data combined (n = 18)

Regression lines	Correlation coefficient
Total	
POC (μg l^{-1}) = 188.5 chl *a* (μg l^{-1}) + 5.1	0.61••
PON (μg l^{-1}) = 38.6 chl *a* (μg l^{-1}) – 2.1	0.35
POC (μM) = 5.8 PON (μM) + 1.2	0.65••
< 10 μm	
POC (μg l^{-1}) = 165.0 chl *a* (μg l^{-1}) + 17.4	0.44•
PON (μg l^{-1}) = 39.8 chl *a* (μg l^{-1}) – 1.8	0.51•
POC (μM) = 4.9 PON (μM) + 2.0	0.75••
< 1 μm	
POC (μg l^{-1}) = 150.0 chl *a* (μg l^{-1}) + 22.7	0.04
PON (μg l^{-1}) = 37.7 chl *a* (μg l^{-1}) + 0.94	0.23
POC (μM) = 5.1 PON (μM) + 1.5	0.41

•• Highly significant ($p << 0.01$)
• Significant ($p < 0.05$)

filter. In both small size-fractions (<10 and <1 μm), greater proportions of POC were found within the mixed layer than at the SCM, except at Stns 39 and 78. In contrast, the contribution of PON showed the opposite tendency, with higher contributions of both size-fractions at the depth of the SCM and with higher variability along the transect than that of POC.

The POC on PON linear regression analysis (Table 3) yielded a slope of 5.8 for unfractionated samples and a lower value (4.9) for the <10 μm size-fraction. Both regressions showed a positive intercept. The slope of the POC on chl *a* regression was 188 (w/w) for unfractionated samples. No significant correlations were associated with the POC on chl *a* regression for the <10 μm size-fraction or with any regression for the <1 μm size-fraction.

Relationship between POM and nutrient concentration

In Fig. 4 the ratios of POC/PON, POC/chl *a* and PON/chl *a* have been averaged in 4 groups according to the amount of nitrate present: (1) the upper euphotic zone out of the equatorial region, (2) the upper euphotic zone at the equatorial upwelling region, (3) the lower nutrient containing part of the euphotic zone out of the equatorial region, and (4) this level within the equatorial region. Similar trends were observed in variation in the POC/chl and PON/chl with changing nitrate concentration. Both ratios tended to decrease with an increase of nitrate in the environment. The POC/PON ratio, in contrast, showed a slight increase at higher nitrate concentrations. Higher variability in the ratios was found outside the equatorial region compared with ratios in the equatorial region.

Distribution of chl *a* to phaeopigment ratio

Chl *a* was the most abundant pigment along the transect with the exception of deep in the water column, where phaeopigment dominated. This is evident in the vertical section (Fig. 5) of the ratio of the 2 pigments, chl *a*/phaeo, which ranged in value from 0.8 to 4 with values higher than 1.4 above the 60 m depth horizon. In the upper layer, lowest values were found south of 4° S with highest north of 10° N; intermediate, more vertically variable values were observed at latitudes between those.

The vertical distribution of the ratio chl *a*/phaeo (Fig. 6) showed a similar trend in both regions, reaching highest values in the top 30 m and then decreasing with depth. However, lower average ratios (1 to 2.8) were found in the upper 100 m in the equatorial region than away from the equator (2.1 to 3.7). Below that depth no difference between regions was observed.

The mean vertical profiles of chl *a*/phaeo ratio for the 3 size-fractions are shown in Fig 7. Ratios ranged from 0.4 to 1.5 for the >10 μm and from 1 to 1.9 for the 10 to 1

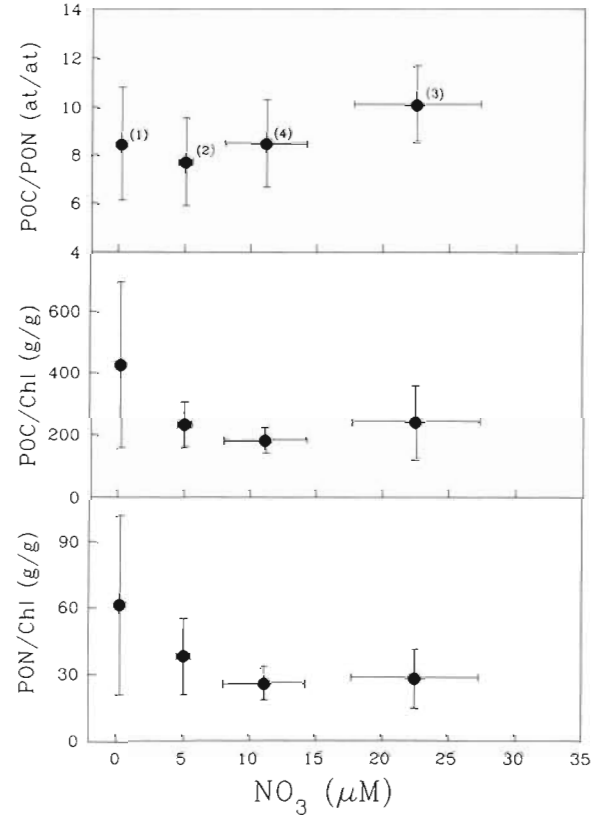

Fig. 4. Relationship between nitrate concentration and ratios of POC/PON, POC/chl and PON/chl. Values represent the mean ratio and the standard error of: (1) the upper euphotic zone outside the equatorial region, (2) this level within the equatorial region, (3) the lower euphotic zone outside the equatorial region, and (4) this level within the equatorial region

μm size-fraction, while the < 1 μm fraction ranged from 0.4 to 3.8. In the latter fraction higher ratios were observed at the surface layer, decreasing with depth, until values similar to those of the > 10 μm size fraction were observed (below 80 m). This pattern indicates that for particles > 1 μm in size, the vertical distribution of phaeopigment was similar to the vertical distribution of chl *a*, whereas for the < 1 μm size a different vertical distribution existed. Thus, the vertical variation in chl *a*/phaeo ratios between regions was due predominantly to variations within the < 1 μm size-fraction.

DISCUSSION

The concentrations of POC and PON observed in this study were within the range of values found in earlier studies of the equatorial Pacific (Wangersky 1976, Eppley et al. 1991), and around twice the values typically observed in the North Pacific gyre (Gordon 1971, Sharp et al. 1980, Eppley et al. 1988). The observed increase in POC and PON concentration at the equator, where nutrients were high, was similar to the pattern previously shown for chl *a* concentration and primary productivity (Peña et al. 1990). Although POC and PON concentrations were higher at the equator, the differ-

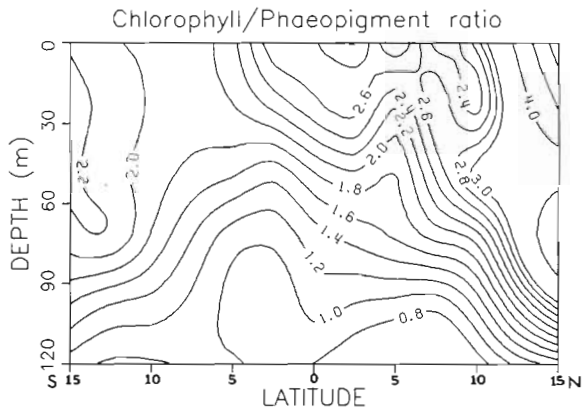

Fig. 5. Vertical section of chl *a*/phaeopigment ratio along the cruise track. Longitudinal variations between stations were ignored

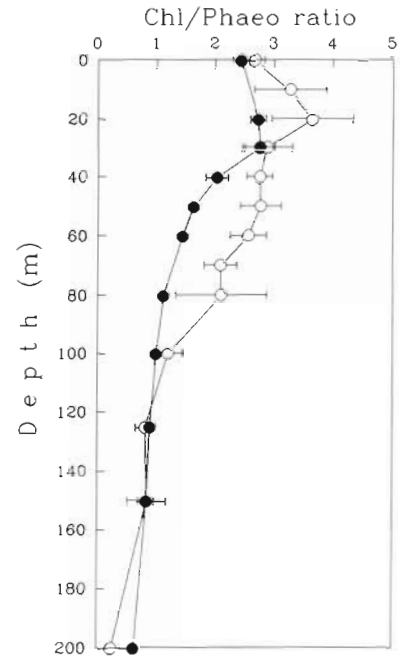

Fig. 6. Vertical distribution of the mean chl *a*/phaeopigment ratio at the equatorial region (•) and outside the equatorial region (○) and its standard error

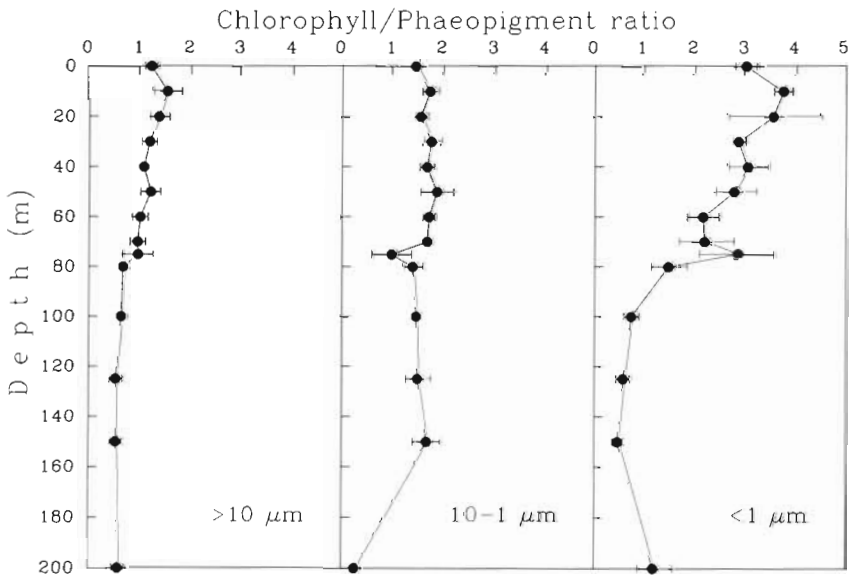

Fig. 7. Vertical distribution of the mean chl *a*/phaeopigment ratio in the different size fractions and its standard error (n = 120) at all stations along the transect

ences were less than 2-fold. Given the potential importance of the equatorial Pacific upwelling region to global new production (Chavez & Barber 1987), biological properties varied much less than might be expected across this region.

Within the resolution of the bottle casts, maxima in suspended particulate matter in the euphotic zone were observed near the SCM layer in the equatorial region, but this increase was less than that of chl *a*. Therefore, although part of the increase in chl *a* at this depth may have been due to an increase in phytoplankton standing stock (particularly at the equatorial region), most of it was probably due to a higher content of chl in the cells at the SCM than at the upper layer. Similarly, in a transect across the equatorial Pacific at 150° W, Pak et al. (1988) concluded that the vertical distribution of chl was predominantly caused by photoadaptation of cells, although a particle maximum was observed near the depth of the SCM within the latitude of equatorial upwelling. Moreover, Bienfang et al. (1983) based on experimental and modelling results also concluded that shade adaptation alone could account for the SCM in subtropical waters. In contrast, Eppley et al. (1991) found a uniform vertical distribution of both POC and PON over the euphotic zone in the same region. In the equatorial Atlantic region, a subsurface particulate maximum has also been observed (Herbland & Le Bouteiller 1983).

In the equatorial region, the SCM was located at around 40 to 60 m above the Equatorial Undercurrent in the 'high shear' zone (Carr et al. 1991). In this region diffusion can disperse cells faster avoiding the development of non-uniformities in biomass. Phytoplankton cells in this layer would have to be growing at a considerably higher rate than in the upper layer if the SCM were the result of a local increase in phytoplankton standing stock. Hence, as previously suggested, the observed vertical distribution of chl is most likely to be the result of photoadaptation which can increase the cellular chl content on shorter time scales (e.g. Cullen & Lewis 1988).

Away from the equator, the average POC/chl *a* ratio was greatest (Fig. 4) in the mixed layer and lowest at the bottom of the euphotic zone. Although this pattern is consistent with expected changes due to physiological adaptation, the values obtained were considerably greater than most C/chl ratios for the living phytoplankton. This suggests a large component of heterotrophs and detritus within the suspended matter. Although high light levels in surface waters may cause low chl *a*/cell, a lack of trace metals such as Fe also might limit the chl synthesis of phytoplankton, resulting in variable POC/chl ratios (Rueter & Ades 1987). In this study, the presence of a high and variable content of POC not covarying with chl was reflected in the lack of or low correlation coefficient found for POC or PON on chl *a* and in particular for the <1 µm size fraction. The low phytoplankton content in the POM found in this region is consistent with previous observations across 150° W (Eppley et al. 1991), where *Synechococcus* was found to be the most numerous component of phytoplankton, although it contributed no more than 6 % of POC and less than 7 % of PON.

Within the regions, a significant POC on chl regression was obtained only at the equatorial region. The slope found (178) was considerably higher than those reported previously for this region. Zeitzschel (1971), using phytoplankton carbon derived from microscopical measurements, found a phytoplankton C/chl ratio of 67 ± 43 in the EASTROPAC area of the eastern tropical Pacific at 120° W. Using the same method as the present study, but a different regression model (Model I instead of II), Eppley et al. (1991) found the slope of the POC/chl regression to be 58 (w/w) in the equatorial Pacific at 150° W, and Herbland & Le Bouteiller (1983) found a slope of 54 to 57 in the equatorial Atlantic. A detailed discussion of the limitations of the regression approach was given by Banse (1977).

C/N ratios for the suspended matter (5.7) in the euphotic zone were intermediate between the values obtained in the equatorial Pacific at 150° W (C/N 5.0; Eppley et al. 1991), and those from the equatorial Atlantic (C/N 6 and 6.1; Herbland & Le Bouteiller 1983), and within the values observed in several oceanic regions (Copin-Montegut & Copin-Montegut 1983). All these values are significantly lower than the ratio of 8.9 found in the Panama Basin region (Murray et al. 1989). The increase in the C/N ratio for particulate material below the upper euphotic zone (Fig. 4) suggests some preferential removal of N relative to C by recycling process within the lower layer or, alternatively, the vertical introduction of small-sized, detritus-rich water from below.

The quotient POC/total ^{14}C production can be used to estimate POC residence time (Eppley et al. 1983). Using the productivity values previously reported for this transect (Peña et al. 1990), we obtained an average residence time of 6 to 7 d in the equatorial region and nearly 14 d away from the equator. Values similar to these have been obtained in the equatorial Pacific across 150° W (Eppley et al. 1991). The shorter residence time at the equatorial upwelling region indicates a faster removal of suspended particles in this region. Phytoplankton cells can be directly removed from the euphotic zone by lateral advection and sinking, and indirectly by zooplankton grazing.

In the equatorial Pacific region, particle losses due to advection and sinking do not seem to be the main mechanisms of removal. Equatorial divergence can

replace surface waters only on longer time scales (Lewis et al. unpubl.). Moreover, in this region, as well as in the equatorial Atlantic, size-fractionation of chl has shown the dominance of small phytoplankton cells (Herbland et al. 1985, Chavez 1989, Peña et al. 1990) with negligible settling velocities (Bienfang & Harrison 1984). Results from this study confirmed the dominance of small particles in this region, since most of the POC and PON concentrations in the mixed layer and SCM depth consisted of particles smaller than 10 µm. Therefore, zooplankton grazing seems to be the most reasonable explanation for phytoplankton biomass losses here. The lack of seasonality in the equatorial waters would imply a similar lack of seasonality in microheterotrophs, and should allow a closer coupling between phytoplankton and zooplankton than in more temperate populations. This should increase the effective control of phytoplankton populations by grazing.

It has been suggested that chl degradation products, phaeopigments, sampled in the water column can be used as a measure of grazing pressure (Lorenzen 1965, 1967). Considering that probably the major source of phaeopigments is grazing by zooplankton (Lorenzen 1967, SooHoo & Kiefer 1982), increased amounts of phaeopigments relative to chl *a* indicate a higher herbivorous grazing pressure, although some production within senescent cells also occurs. We found lower chl *a*/phaeo ratios in the upper layer of the equatorial region (Fig. 5) suggesting higher grazing rates than away from the equator. Phaeopigments measured in routine pigment samples represent a net result of grazing and photooxidation on short time scales (Yentsch 1965, Lorenzen 1976, SooHoo & Kiefer 1982, Welschmeyer & Lorenzen 1985). According to SooHoo & Kiefer's model (1982) of grazing and photooxidation in the upper layer, we have estimated that more than 86 % of primary production is grazed by zooplankton, using average light conditions observed in the first 40 m (4.2 mE cm^{-2} d^{-1}) and a growth rate of 0.7 d^{-1} (Cullen et al. 1991).

Several authors (Yentsch 1965, Lorenzen 1967, Gibbs 1979, Vernet & Lorenzen 1987) have recognized that the presence of chl *b* may cause overestimates of phaeopigments and underestimates of chl *a* determined by the fluorometric technique and, therefore, would cause an overestimation of zooplankton grazing as estimated previously. In tropical waters chl *b* has been found to be considerable at depth, whereas near the surface only traces have been observed (Gieskes & Kraay 1986). Since, in this study, the average chl *a*/phaeo ratio found in the first 40 m was used in the estimation of zooplankton grazing, the effect due to the presence of chl *b* is expected to be small. Furthermore, we have found that the vertical distribution of the ratio chl *a*/phaeo varies among the different size-fractions; only in the <1 µm fraction did the chl/phaeo ratios decrease with depth. This could be due to the presence of green algae and prochlorophytes, which contain chl *b* (Chisholm et al. 1988), in the SCM depth as observed in the Pacific Ocean and in the western equatorial Pacific (Takahashi & Hori 1984, Everitt et al. 1990). In the upper layer, considerably higher ratios were found in the <1 µm fraction than in the other size fractions. This could be the result of a lower grazing pressure over this size fraction or that the fecal pellets of microzooplankton are bigger than this size.

Because feces of macrozooplankton are not effectively or quantitatively sampled by water bottles, the vertical distribution of phaeopigment corresponds more to features associated with smaller particles processed by micro- and nanozooplankton. Larger fecal material can be retained in the upper layer only if the fecal pellets are fragile and fragmented easily. However, due to its small size and low or negligible sinking rate, the pigmented fecal debris of microzooplankton herbivores would be expected to contribute to the pool of suspended phaeopigments and consequently would not be sampled by sediment traps (SooHoo & Kiefer 1982, Welschmeyer & Lorenzen 1985). As a consequence of the close coupling between producers and microzooplankton grazers we hypothesize to hold in the equatorial Pacific region, this suspended fraction may be very important to carbon flux out of the euphotic zone and should be considered in future models of the region.

The estimation of primary production from satellite chl data requires appropriate light-production models in conjunction with information about the total pigment content in the water column and its vertical distribution. Morel & Berthon (1989) have distinguished several trophic situations according to the surface chl concentration, representing waters from very oligotrophic to very eutrophic. For each trophic category they obtain a mean vertical profile and an average value of the ratio chl *a* to (chl *a* + phaeo). In their analysis, the ratio decreases from eutrophic systems to oligotrophic waters and it also seems to be constant with depth. In contrast, in this study, the ratio increased from the more eutrophic equatorial region to outside this region (Fig. 6) and the value varied with depth. Moreover, although a similar vertical profile of chl has been observed, the SCM seems to be a poor indicator of phytoplankton biomass at the equatorial. Therefore, the equatorial Pacific region seems to be different from other regions and these differences should be considered when remote estimations of production are attempted. Particularly important is the ratio chl *a* to (chl *a* + phaeo) which responds almost linearly to the production estimates in Morel & Berthon's model (1989).

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