



## Zooplankton variability on the equator at 140°W during the JGOFS EqPac study

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**Abstract**—The vertical distributions of zooplankton biomass and community composition were measured on the equator at 140°W during March/April (19 days) and October 1992 (21 days). El Niño conditions prevailed during the March/April time series. The average integrated (200 m) zooplankton ( $>64 \mu\text{m}$ ) biomass was  $32 \text{ mM C m}^{-2}$  in March/April and  $41 \text{ mM C m}^{-2}$  in October. The overall cruise means were not significantly different; however during October zooplankton were more aggregated in the upper euphotic zone, there were more copepods  $>200 \mu\text{m}$ , and there were more day/night differences in the vertical distribution of zooplankton biomass as a result of vertical migration behavior. Cyclopoid copepods were more abundant during the El Niño conditions of March compared to October. There were no apparent trends in integrated zooplankton biomass during the March/April time series. However, the species composition of the zooplankton community changed towards the end of the time series when meridional currents flowed to the south. Zooplankton biomass during the October cruise increased nearly five-fold with the passage of a tropical instability wave. A lag in the increase of zooplankton compared to nitrate and chlorophyll as well as changes in the zooplankton community composition over the time series reflect the response times of zooplankton to upwelling events.

### INTRODUCTION

It has been estimated that upwelling in the central equatorial Pacific may support up to 2 gigatons of new production per year (Chavez and Barber, 1987) or approximately half of the estimated annual global new production (Eppley and Peterson, 1979). As such, the central equatorial Pacific was a logical study area for the Joint Global Ocean Flux Study (JGOFS) whose goal is to understand global biogeochemical fluxes.

In the equatorial Pacific as well as in other ocean areas, the composition of the planktonic food-web determines the amount of carbon recycled within the mixed layer and that which sinks below the pycnocline (Frost, 1984; Michaels and Silver, 1988; Longhurst and Harrison, 1989; Peinart *et al.*, 1989). Zooplankton ( $>200 \mu\text{m}$ ), through their processes of ingestion, metabolism and egestion, are important in determining the size and composition of sinking particulate matter. Zooplankton produce rapidly sinking ( $p > 200 \text{ m day}^{-1}$ ) fecal pellets which can dominate the gravitational flux of biogenic material

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(Fowler and Knauer, 1986; Small *et al.*, 1989; Altabet and Small, 1990). In addition, zooplankton can contribute to the flux of biogenic material through their daily vertical excursions in the water column. Recent calculations (Longhurst *et al.*, 1989; Longhurst *et al.*, 1990; Dam and Roman, submitted) suggest that respiratory carbon and excreted dissolved nitrogen from zooplankton that migrate below the euphotic zone during the day can represent significant downward fluxes of carbon and nitrogen relative to measured gravitational fluxes.

The equatorial Pacific study (EqPac) included a combination of survey and time series cruises (Leinen and Murray, 1990; Murray *et al.*, 1992). A major goal of the study was to determine how efficiently the carbon pump (*sensu* Volk and Hoffert, 1985) operates in the equatorial Pacific. Our research included measurements of the biomass, grazing and fecal pellet production of zooplankton. In this paper we present data on the vertical distribution of zooplankton biomass and abundance on the equator at 140°W during March/April (19 days) and October, 1992 (21 days). We focus on the different scales of variability in zooplankton biomass: diel, within cruise, and between cruise. During the October cruise a tropical instability wave passed through the study area changing the hydrography, chemistry and biology of the water column. El Niño conditions (warmer water temperatures, lower nutrients) prevailed during the March/April cruise. On the October cruise, hydrographic conditions were similar to the climatological mean. Thus we will contrast zooplankton during El Niño and "normal" conditions.

## METHODS

Zooplankton ( $>64 \mu\text{m}$ ) were collected from day/night pairs of tows with a 0.25 m<sup>2</sup>-mouth area MOCNESS equipped with nine nets with a 7:1, mouth:length ratio (Wiebe *et al.*, 1985). Transmission by underwater sensors on the MOCNESS through conducting cable to the deck yielded output of fluorescence, temperature, conductivity, depth, frame angle, volume filtered and net closing response at 1-s intervals. Oblique tows were taken from 1000 m and 200 m to the surface. Eight depth strata were sampled on both shallow and deep tows. Descent rates of the MOCNESS were generally between 40 and 50 m min<sup>-1</sup>, and ascent speeds between 10 and 20 m min<sup>-1</sup>. The MOCNESS was towed at a ship speed of 2 kt, which resulted in a net angle of near 45°.

Onboard ship, the contents of each net were split in half with a Folsom Plankton Splitter. One half of the sample was preserved in 4% buffered (Sodium Borate) Formalin. The remaining half of the sample was gently wet-sieved through a 2.0 mm mesh to remove gelatinous zooplankton and micronekton (not caught quantitatively by 0.25 m<sup>2</sup> MOCNESS). The portion passing through this mesh was wet-sieved further through 1000  $\mu\text{m}$ , 500  $\mu\text{m}$ , 200  $\mu\text{m}$  and 64  $\mu\text{m}$  meshes. This procedure yielded four different size classes: 2000–1000  $\mu\text{m}$ : 1000–500  $\mu\text{m}$ : 500–200  $\mu\text{m}$  and 200–64  $\mu\text{m}$ . The samples caught on these size fractions were diluted and thoroughly mixed in a known volume of filtered seawater and duplicate aliquots, drawn with a Henson–Stempel pipette, filtered onto precombusted GF/D filters and rinsed with a small amount of distilled water to eliminate salt. Filters were dried at 60°C. Organic carbon and nitrogen for each filter were measured with a Model 440 Control Equipment CHN analyzer at the Horn Point Laboratory of the University of Maryland. The average error associated with subsampling the zooplankton catch for carbon analysis was 16% (standard deviation/mean). Zooplankton biomass of the different size fractions as well as the amount of total ( $>64 \mu\text{m}$ ) zooplankton is expressed as mM

$\text{C m}^{-3}$  or  $\text{mM C m}^{-2}$  (integrated). The complementary physical measurements described here are discussed in Foley *et al.* (submitted).

## RESULTS

### *Hydrographic changes*

*March/April.* El Niño conditions prevailed at the equator, 140°W station during the March/April, 1992 study. Surface water temperatures averaged 28.7°C (range: 28.2 to 29.3°C); mixed layer depth (surface  $\sigma_t + 0.125$ ) averaged 25.0 m (range: 10.0 to 52.2 m); the depth of the 20°C isotherm averaged 122 m (range: 100 to 146 m); surface nitrate averaged 3.4  $\mu\text{M}$  (range: 2.9 to 3.9  $\mu\text{M}$ ); and the average shipboard measured wind speed was 4.5  $\text{m s}^{-1}$  (range: 1.0 to 11.2  $\text{m s}^{-1}$ ). The greatest variation in temperature occurred in the steepest portion of the thermocline (Fig. 1). *In vivo* chlorophyll fluorescence exhibited a subsurface maximum centered around 58 m.

Surface water temperatures decreased and surface chlorophyll-*a* values increased between Day 95 and 100 (Fig. 2). During this same period, the mixed layer deepened, surface nitrate decreased and the depth of the 0.1% light level shoaled. Current measurements from the TOGO/TAU NOAA/USC mooring located at 0°, 140°W (McPhaden, 1993) show (Fig. 3) meridional currents to the north at the beginning of the March/April time series, switching to the south from Day 95 to 100. This change in meridional current, along with the deepening mixed layer and decreased surface temperatures, suggests the passage of a weak tropical instability wave.

Diel changes in both surface water temperature and the surface mixed layer were apparent over the time series study. On average, surface water temperatures were 0.32°C cooler at 05:00 h (local time) as compared to temperatures measured at 17:00 h. The depth of the mixed layer averaged 8.2 m deeper after the night period (see Gardner *et al.*, 1995; for an alternative analysis of mixed layer dynamics). Chlorophyll-*a* in the mixed layer was usually lower after the night period. Integrated chlorophyll-*a* (to 150 m) measured at the 05:00 cast was lower than integrated chlorophyll-*a* measured at 16:00 h in 5 of 7 day/night pairs.

*October.* Surface water temperatures were cooler during our October 1992 study (average = 25.1°C; range: 24.5 to 25.9°C); the average depth of the mixed layer was 42.1 m, although highly variable (range: 9.3 to 87.2); the depth of the 20°C isotherm averaged 113 m (range: 89 to 139 m); surface nitrate averaged 5.9  $\mu\text{M}$  (range: 6.2 to 9.2  $\mu\text{M}$ ); and shipboard measured wind speeds averaged 8.0  $\text{m s}^{-1}$  (range: 4.1 to 10.7  $\text{m s}^{-1}$ ). The average depth of the chlorophyll fluorescence maximum (50 m) was shallower than March/April (Fig. 1).

The major event that occurred during the October time series was the passage of a tropical instability wave. Colder water with higher nutrients and chlorophyll was advected through the study area, with maximum surface chlorophyll-*a* and minimum temperatures occurring between Days 284 and 286 (Fig. 2). Zonal currents to the west relaxed and there were maximum meridional currents to the north (Fig. 3). The mixed layer depth increased from 26 to 34 m on Day 283 to 78 to 87 m on Day 286 with the passage of the tropical instability wave. The effect of different water masses being advected through the study area is shown by the variability in the temperature/salinity plots from the two cruises (Fig.

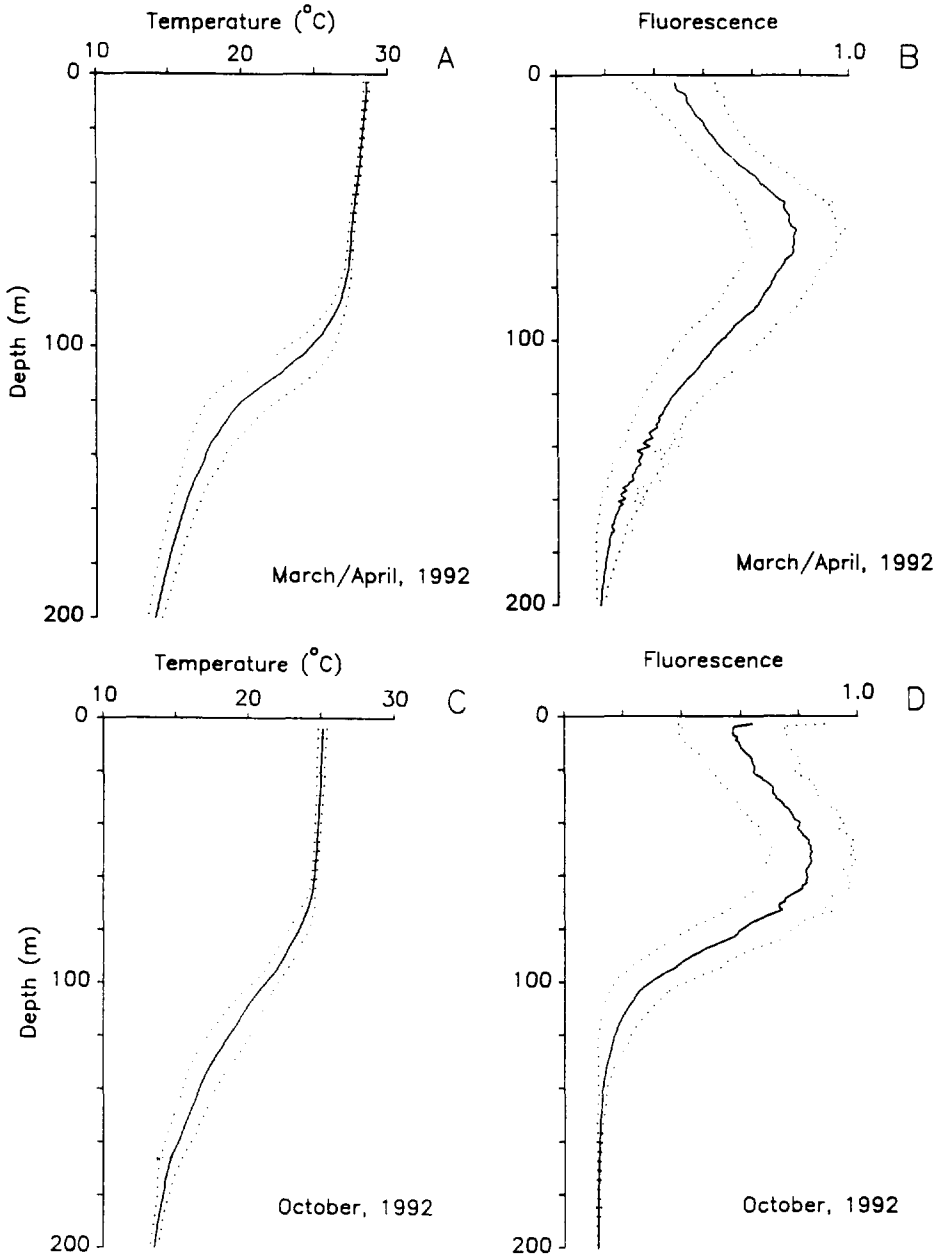


Fig. 1. Mean ( $\pm$  SD) vertical profiles of temperature and *in situ* fluorescence from  $0^{\circ}$ ,  $140^{\circ}\text{W}$  during March/April (A), (B) and October 1992 (C), (D).

4). The higher salinity waters were associated with the tropical instability wave in the October cruise.

Superimposed on the effects of the instability wave were diel changes in the mixed layer. On average, surface water temperatures were  $0.17^{\circ}\text{C}$  cooler at 05:00 h (local time) as

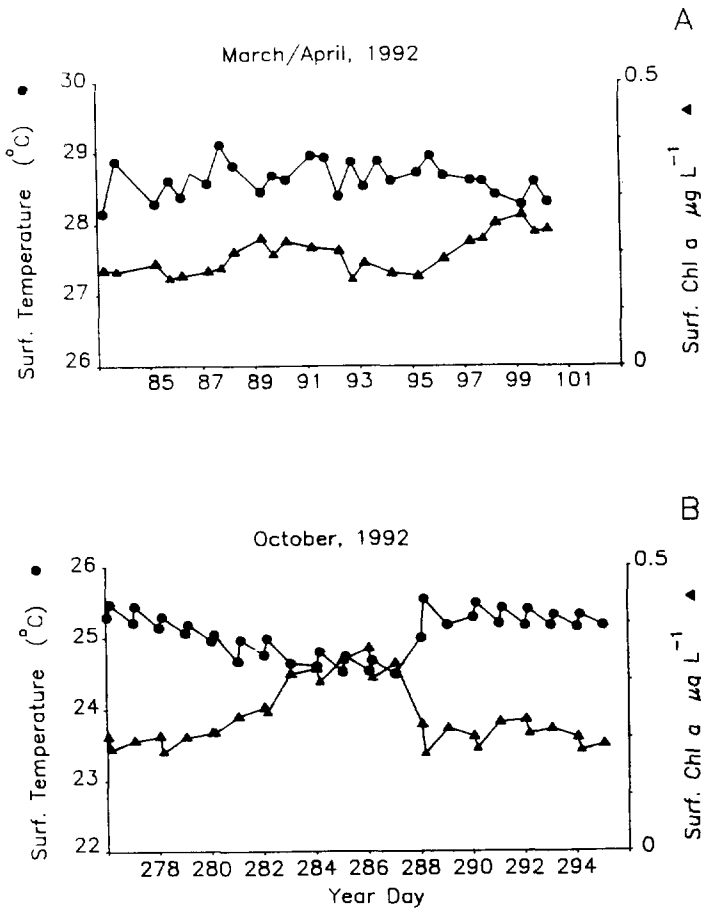


Fig. 2. Surface temperature and chlorophyll-*a* from 0°, 140°W measured at 05:00 and 17:00 h during March/April (A) and October, 1992 (B).

compared to temperatures measured at 17:00 h. The depth of the mixed layer averaged 8.9 m deeper after the night period. Integrated chlorophyll-*a* in the surface waters was lower at the end of the night (05:00 h) as compared to end of the day (17:00 h), the majority of the October time series. More information concerning the physical and optical conditions is given in Foley *et al.* (submitted).

### Zooplankton

The average, integrated (200 m) zooplankton (>64µm) biomass was 32 mM C m<sup>-2</sup> in March/April (range: 17 to 59, SD = 11, SD/mean = 35%, *n* = 21) and 41 mM C m<sup>-2</sup> (range: 13 to 76, SD/mean = 46%, *n* = 24) in October. Thus, the overall cruise means did not indicate significantly reduced zooplankton biomass at the equator, 140°W station during March/April (El Niño) compared to October.

There were no apparent temporal trends in integrated (200 m) zooplankton biomass during the March/April time series (Fig. 5). In contrast, during October integrated

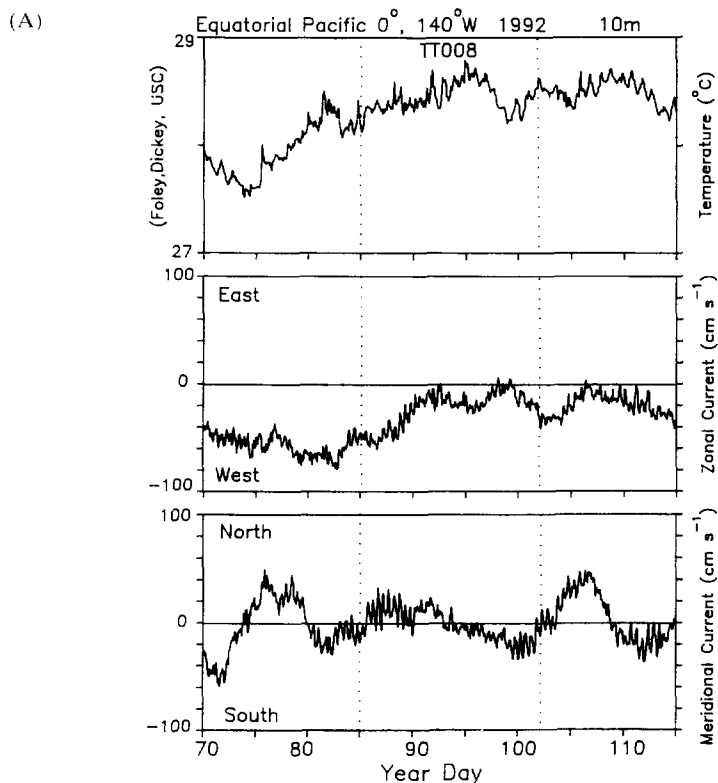


Fig. 3. Temperature, zonal currents and meridional currents from 10 m at 0°, 140°W during March/April (A) and October, 1992 (B).

zooplankton biomass peaked with passage of the tropical instability wave (Fig. 5). Zooplankton biomass was highest on Day 284 when we found low surface temperatures, high surface chlorophyll-*a* and increased depths of the mixed layer. Integrated zooplankton biomass increased two-fold from Days 282 to 286 when the tropical instability wave passed through the area.

Most of the zooplankton in the surface 1000 m were concentrated in the upper 200 m (Fig. 6). A greater percentage and absolute amount of zooplankton were concentrated in surface waters in October as compared to March/April (Figs 6 and 7; Table 1). For example, an average of 40% (day) and 46% (night) of integrated (to 200 m) zooplankton (>64  $\mu\text{m}$ ) biomass was concentrated in the surface 40 m in March/April as compared to October when 48% (day) and 55% (night) of integrated zooplankton were present in the upper 40 m. Thus, although zooplankton biomass integrated to 200 m was not significantly different between the two cruises, there was a greater concentration of zooplankton in the upper euphotic zone during October.

We usually found greater concentrations of zooplankton in surface waters at night both within the surface 200 m and in the euphotic zone (Figs 6 and 7; Table 1). The larger zooplankton size fractions generally exhibited the greatest day/night change. For example, we caught on average  $1.4 \times$  more >1000  $\mu\text{m}$  zooplankton in the euphotic zone at night in

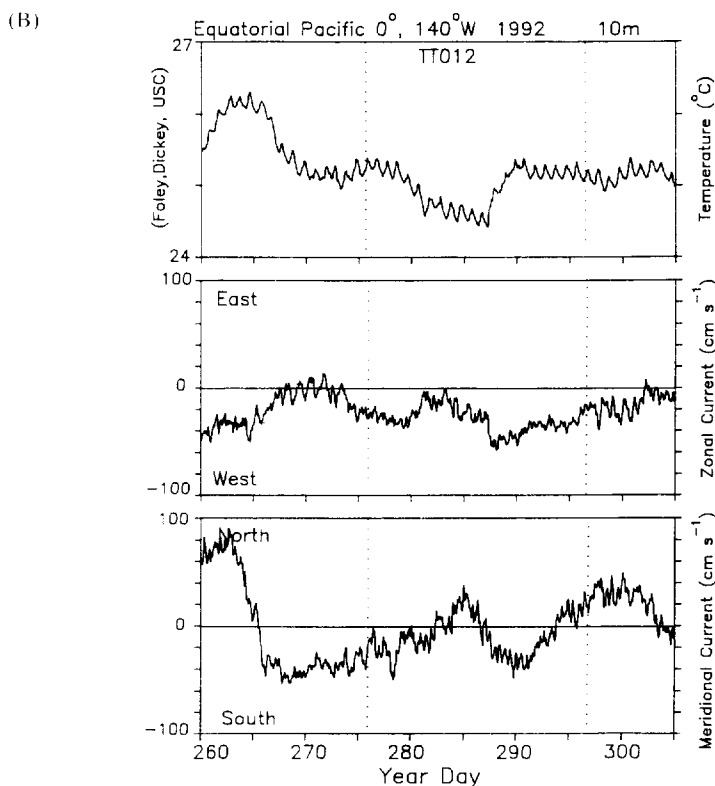


Fig. 3. (Continued)

March/April and  $2.1 \times$  more  $>1000 \mu\text{m}$  at night in October as compared to day samples (Table 1). Overall, there were greater night/day differences as compared to March/April because more copepods  $>200 \mu\text{m}$  migrated into the euphotic zone at night.

The largest category of zooplankton that we enumerated were copepod nauplii (Fig. 8; Table 2). The average number of nauplii in the surface 200 m was  $929 \text{ m}^{-3}$  (range: 193 to 1324) in March/April and  $770 \text{ m}^{-3}$  (range: 661 to 992) in October. The largest difference in the community composition of zooplankton between the two cruises was the greater abundance of cyclopoid copepods during March/April. Although the integrated biomass of total zooplankton was similar for both cruises, we found approximately twice as many cyclopoid copepods on the March/April cruise when water temperatures were warmer, primary production was lower (Barber *et al.*, 1995) and there were less phytoplankton  $>2 \mu\text{m}$  (Bidigare and Ondrusek, submitted). In contrast, we found more calanoid copepods during the October cruise (Table 2). These larger copepods had a greater contribution to total zooplankton biomass and, because of their migratory behavior, the night/day differences in the vertical distribution of zooplankton. Harpacticoid copepods were also more abundant during the October cruise. Poor swimmers, these copepods generally are found associated with the colonial cyanobacteria, *Trichodesmium*, or organic aggregates (O'Neil and Roman, 1992).

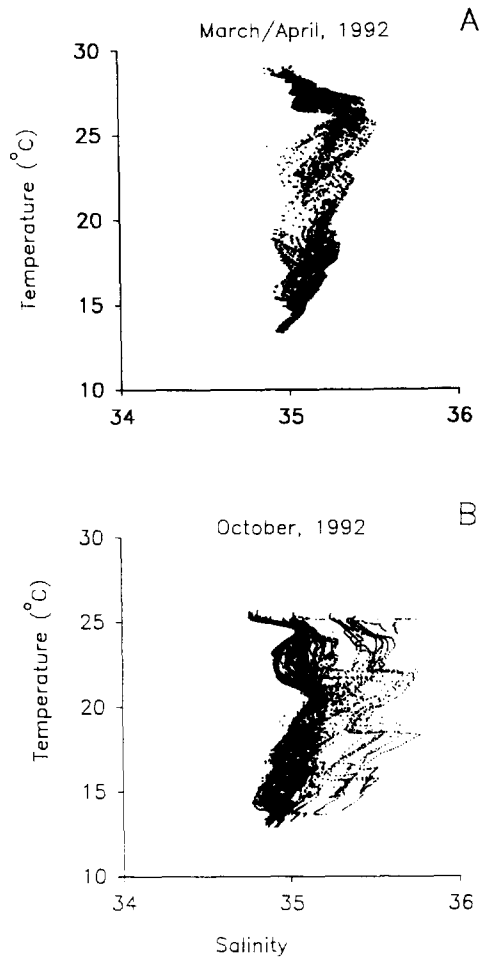


Fig. 4. Temperature-salinity plots for vertical profiles in the surface 200 m at 0°, 140°W in March/April (A) and October 1992 (B).

## DISCUSSION

Time series measurements of physical variables in the open ocean exhibit continuous spectra (Wunsch, 1981). Thus a variety of phenomena ranging from diel heating/cooling, internal waves, storms, mesoscale eddies, equatorial waves, seasonal changes in insolation, inter-annual changes in meteorology and episodic events such as hurricanes have the potential to affect physical, chemical and biological processes. Because biological and chemical sampling programs usually lack *in situ* continuous measurements, studies have been based on discrete (point) measurements that usually can not distinguish the linkages between physical events and subsequent biological responses. Our repeated zooplankton and hydrographic measurements along with continuous measurements of currents and temperature during the equatorial time series (Foley *et al.*, submitted) reveal a number of different scales of variability that influence plankton populations and biogeochemical fluxes.



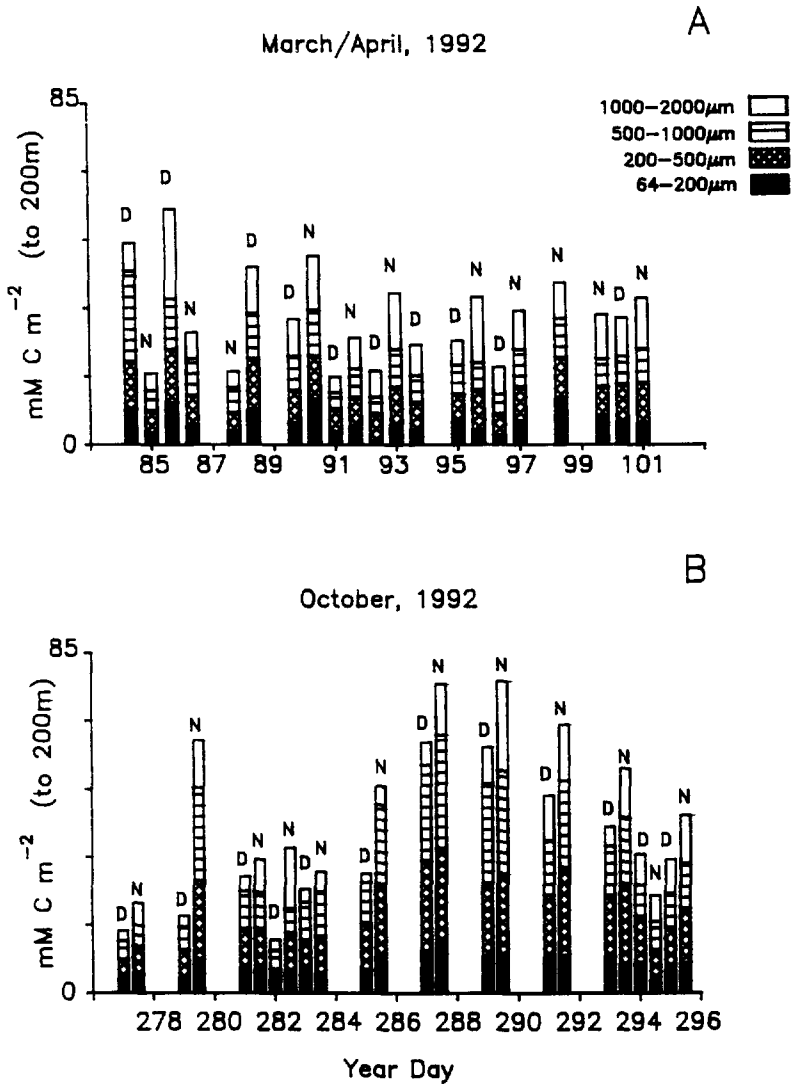


Fig. 5. Integrated zooplankton biomass to 200 m at  $0^{\circ}$ ,  $140^{\circ}$ W in March/April (A) and October 1992 (B). D = day tow; N = night tow.

Diel heating/cooling changed the sea surface temperature and the depth of the mixed layer (Fig. 2). Increased turbulence because of diel heating/cooling (Carr *et al.*, 1992) might increase the contact rate between phytoplankton and zooplankton (Rothschild and Osborn, 1988), thus increasing grazing rates and particle flux.

The day/night difference in integrated zooplankton carbon in the surface 200 m (Fig. 5) and in the euphotic zone (Table 1) was greatest for the largest zooplankton size fraction (1000–2000  $\mu\text{m}$ ). In general, the faster swimming, larger zooplankton size classes exhibit greater vertical migration than do smaller size classes (Longhurst, 1976). Smaller copepods, especially cyclopoids, were more numerous in March/April compared to October

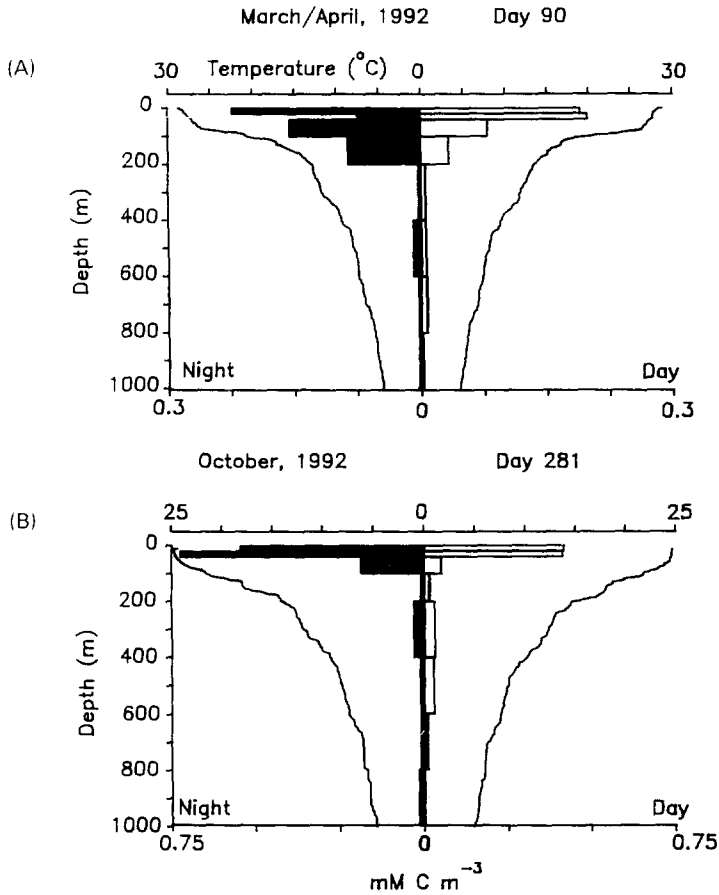


Fig. 6. Vertical profiles of temperature and zooplankton biomass from day (open) and night (shaded) tows to 1000 m at 0°, 140°W in March/April (A) and October 1992 (B).

(Table 2, Fig. 8). This may be one reason why there appeared to be less zooplankton vertical migration in March/April as compared to October.

Increases in the integrated (200 m) night time zooplankton biomass imply that zooplankton were migrating up from below 200 m (Fig. 5). Zooplankton profiles to 1000 m (Fig. 6) indicate that there were day/night changes in the vertical distribution of zooplankton biomass between 200 m and 1000 m. Zooplankton movement in/out of the euphotic zone and in/out of epipelagic waters both would serve to enhance the vertical flux of carbon. Consumption of organic material by zooplankton in surface waters and the production of fecal pellets at depth (Small *et al.*, 1987) as well as respiration at depth (Longhurst *et al.*, 1990; Dam and Roman, submitted) can make significant contributions to the vertical flux of carbon. In October, we found that, on average, 11 mM C m<sup>-2</sup> of zooplankton (>200  $\mu$ m) fed in the euphotic zone at night and resided at depth during the day (Table 1). Assuming a weight-specific production rate of fecal pellets of 50% zooplankton biomass per day (Urban-Rich *et al.*, 1994), this means that 9 mM C m<sup>-2</sup> of fecal pellets would be produced at night, 4 mM C of which were produced by zooplankton

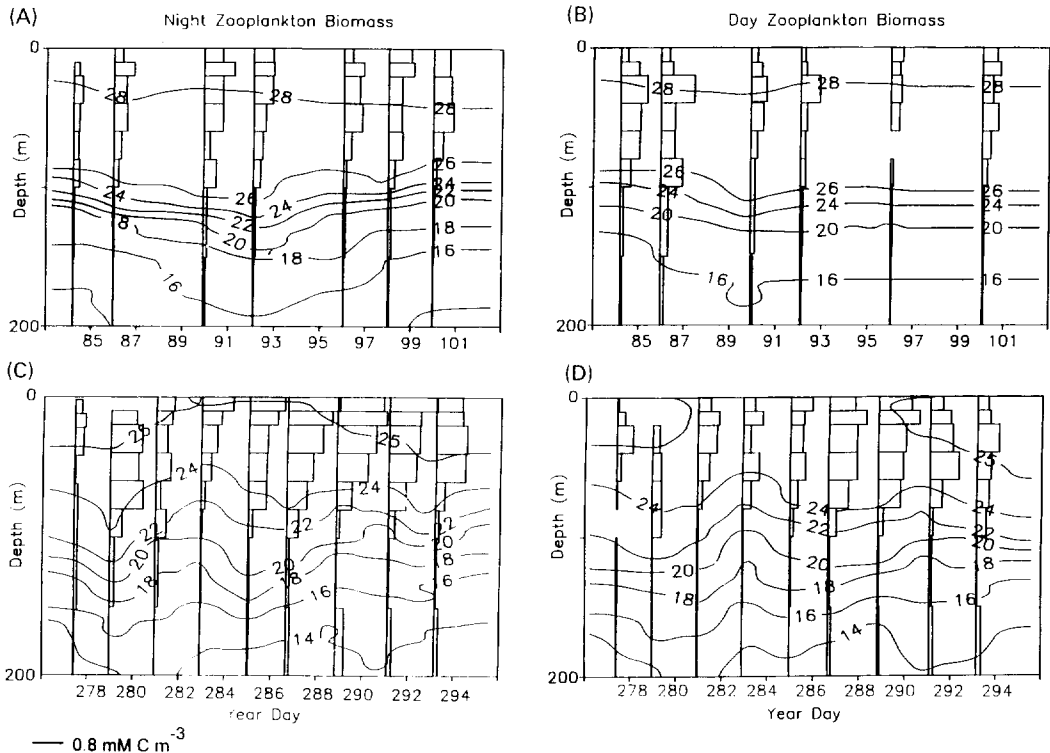


Fig. 7. Vertical profiles of night and day zooplankton biomass and contours of temperature in the surface 200 m at 0°, 140°W during March/April (A), (B) and October 1992 (C), (D).

that resided in the surface waters at night and below the euphotic zone during the day. When the copepods migrate out of the euphotic zone to their daytime depth, some additional number of fecal pellets also would be produced, which contained organic material consumed in the euphotic zone. In addition, daytime respiration would contribute additional carbon flux below the euphotic zone (Dam and Roman, submitted).

In the coastal zone a dominant source of temporal variation is the "event scale" (Walsh *et al.*, 1987) due to the passage of atmospheric fronts (7 to 10 days). Dominant scales of spatial variation at high latitudes are eddies (Robinson, 1983). Neither of these sources of variation are prevalent at our study site. Instead, variability was influenced by remotely forced processes such as Kelvin waves and tropical instability waves which cycle on intermediate (20–60 days) time scales as well as El Niños which dominate the interannual variability.

Westward propagating equatorial waves (tropical instability waves), which have periods of approximately 20 days (Legeckis, 1977; Halpern *et al.*, 1988), are prevalent along the equator during May to December when the trade winds are maximum. A weak tropical instability wave passed through 0°, 140°W during March/April, and a stronger tropical instability wave passed our station during the October time series. Towards the end of the March/April time series (Days 95 to 99) when the meridional currents were to the south (Fig. 3), there was a deepening of the mixed layer and increases in integrated chlorophyll-*a*

Table 1. Integrated zooplankton biomass ( $\text{mM C m}^{-2}$ ) for the euphotic zone for the March/April and October 1992 stations on the equator at  $140^\circ\text{W}$ . Averages (Avg), standard deviations (SD), coefficient of variation ( $Cv = SD/Avg$ ), minimum value (Min), maximum (Max), % of Total  $>64 \mu\text{m}$  biomass (% Total) and Night/Day ratio of euphotic zone integrated biomass (N/D Ratio)

	$>1000 \mu\text{m}$	$1000\text{--}500 \mu\text{m}$	$500\text{--}200 \mu\text{m}$	$200\text{--}64 \mu\text{m}$	Total
MARCH/APRIL DAY					
Avg, $N = 11$	6.9	7.4	7.3	4.5	26.1
SD	4.1	4.9	2.8	2.6	14.4
Cv	59%	67%	38%	58%	47%
Min	2.1	3.5	3.8	0.6	10.0
Max	17.4	21.4	11.6	9.0	59.4
% Total	27%	28%	28%	17%	
MARCH/APRIL NIGHT					
Avg, $N = 10$	9.7	7.3	7.7	5.4	30.1
SD	3.5	1.8	1.8	2.6	9.7
Cv	36%	23%	23%	48%	25%
Min	4.0	4.4	4.6	2.5	15.5
Max	16.0	9.4	9.8	10.3	45.5
% Total	32%	25%	25%	18%	
MARCH/APRIL TOTAL					
Avg, $N = 21$	8.3	7.4	7.4	5.0	28.1
SD	4.1	3.8	2.3	2.7	12.9
Cv	49%	51%	31%	53%	37%
Min	2.1	3.5	3.8	0.6	10.0
Max	17.4	21.4	11.6	10.3	60.7
% Total	29%	26%	27%	18%	
N/D Ratio	1.4	1.0	1.0	1.2	1.2
OCTOBER DAY					
Avg, $N = 12$	4.6	10.3	10.5	5.3	30.7
SD	2.4	6.1	4.8	1.9	15.2
Cv	53%	59%	46%	36%	46%
Min	2.2	4.0	2.3	2.5	11.0
Max	17.7	23.5	20.9	8.7	70.8
% Total	15%	33%	34%	17%	
OCTOBER NIGHT					
Avg, $N = 12$	9.6	13.5	13.3	6.1	42.5
SD	4.9	6.8	5.1	2.1	18.9
Cv	51%	50%	38%	35%	39%
Min	3.7	4.2	5.8	2.5	16.2
Max	20.6	25.4	21.3	10.7	78.0
% Total	23%	32%	31%	14%	
OCTOBER TOTAL					
Avg, $N = 24$	7.1	11.9	11.9	5.8	36.7
SD	4.6	6.6	5.2	2.0	18.4
Cv	65%	56%	43%	36%	44%
Min	2.2	4.0	2.3	2.5	11.0
Max	20.6	25.4	21.3	10.7	78.0
% Total	19%	32%	32%	16%	
N/D Ratio	2.1	1.3	1.3	1.1	1.4

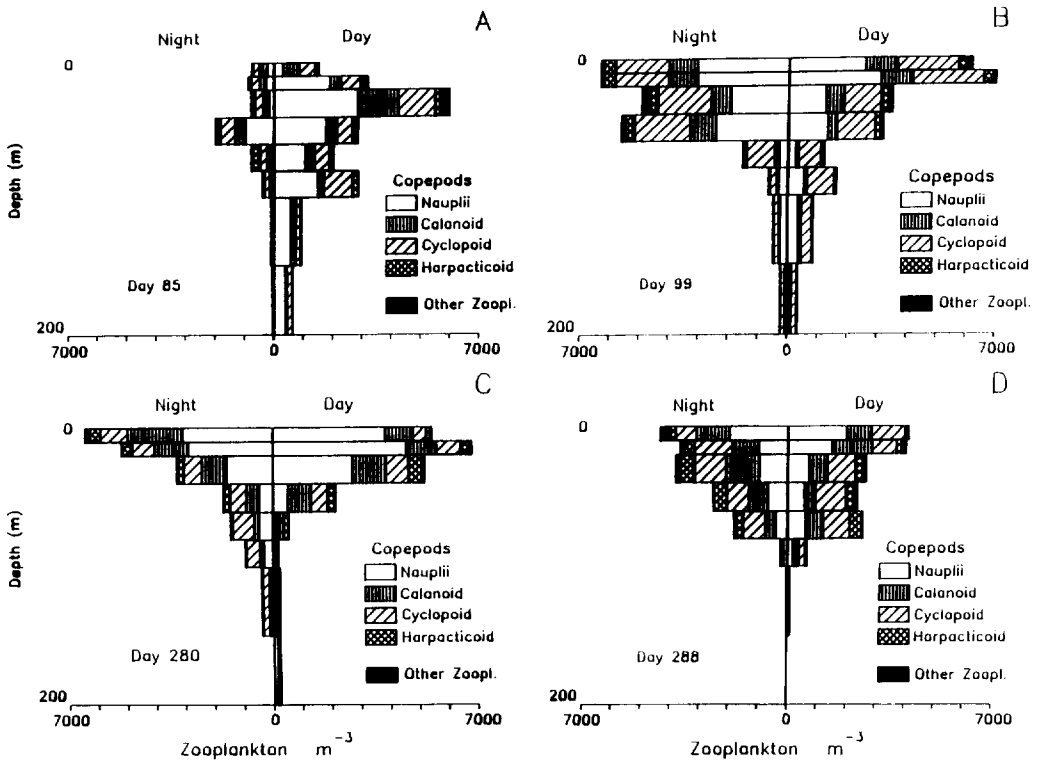


Fig. 8. Night (left) and day (right) vertical profiles of zooplankton taxonomic groups at  $0^{\circ}$ ,  $140^{\circ}$ W during March/April (A), (B) and October 1992 (C), (D).

and primary productivity (Barber *et al.*, 1995). Iriarte and Fryxell (1995) found that the species assemblage of the phytoplankton community changed dramatically over the March/April time series. At the beginning of the time series (Days 85, 89) dinoflagellates and diatoms were similar in abundance in the euphotic zone (roughly  $500$  cells  $liter^{-1}$ ). With southward meridional currents (Days 95, 79; Fig. 3) dinoflagellates decreased and diatoms increased to a maximum of over  $2500$  cells  $liter^{-1}$  at 30 m. These rapid changes, along with changes in both temperature and salinity, suggest that we were seeing more "mature" water from north of the equator. We did not detect any significant trends in zooplankton biomass over the March/April time series. However, we did find that the species assemblage changed towards the end of the cruise (Fig. 8). For example, three- to five-fold increases in the number of copepod nauplii (Fig. 8) and copepods from the families Oncaeidae and Eucheatidae (data not shown) occurred on Day 99 when meridional currents were southward (Fig. 3(A)).

During the October time series, passage of a tropical instability wave was marked by minimum temperatures and maximum concentrations of nitrate, chlorophyll-*a* and zooplankton on Days 284–286 when there was highest meridional flow to the north. Zooplankton biomass increased nearly five-fold from Day 277 with peak concentrations in the euphotic zone of  $68$   $mM$   $C$   $m^{-2}$ . Estimates of fecal pellet flux (Urban-Rich *et al.*, 1994) and phytoplankton ingestion (Dam *et al.*, 1995) were also highest during passage of the tropical instability wave.

Table 2. Zooplankton taxonomic groups (genus, class) collected in integrated tows from 200 m to the surface in March/April and October, 1992. Mean number of animals per m<sup>2</sup> collected in 8 tows (4 day, 4 night)

March/April	No. m <sup>-2</sup>	% of Total	October	No. m <sup>-2</sup>	% of Total
<b>NAUPLII</b>	127752			96438	
<b>CALANOID</b>					
Small calanoids	12797	33.21	Small calanoids	16643	31.64
Clausocalanus	6117	15.87	Calocalanus	10667	20.28
Mecynocera	4025	10.44	Clausocalanus	9256	17.60
Paracalanus	3933	10.21	Mecynocera	3355	6.38
Eucheta	1873	4.86	Unknown calanoids	3341	6.35
Eucalanus	1812	4.70	Eucalanus	2279	4.33
Calocalanus	1645	4.27	Paracalanus	1765	3.36
Undinula	1518	3.94	Eucheata	1304	2.48
Calanus	1273	3.30	Lucicutia	1230	2.34
Lucicutia	688	1.19	Scolecithrix	659	2.25
Pleuromamma	577	1.50	Acartia	583	1.11
Unknown calanoids	478	1.24	Candacia	470	0.89
Scolecithrix	435	1.13	Pleuromamma	381	0.72
Candacia	370	0.96	Undinula	186	0.35
Acartia	198	0.51	Calanus	170	0.32
Centropages	185	0.48	Heterorhabdus	106	0.20
Isocalanus	175	0.45	Euaetideus	53	0.10
Heterorhabdus	155	0.40	Rhincalanus	34	0.06
Rhincalanus	78	0.20	Ctenocalanus	33	0.06
Haloptilus	45	0.12	Gaetanus	30	0.06
Gadius	37	0.10	Haloptilus	26	0.05
Euchirella	33	0.09	Gadius	14	0.03
Euaetidus	25	0.06	Scaphocalanus	8	0.01
Pontellina	18	0.05	Euchirella	5	0.01
Pontella	12	0.03	Centropages	4	0.01
Ctenocalanus	10	0.03	Isocalanus	3	0.01
Aetidus	8	0.02			
Gaetanus	8	0.02			
Scaphocalanus	7	0.02			
TOTAL	38537			52602	
<b>HARPACTICOID</b>					
Microsetella	14280	99.07	Microsetella	28385	90.10
Miracia	105	0.73	Aegisthus	2924	9.28
Macrosetella	22	0.15	Clytemnestra	174	0.55
Aegisthus	7	0.05	Miracia	23	0.07
TOTAL	14413			31505	
<b>CYCLOPOID</b>					
Oncaea	59913	60.68	Oncaea	42819	76.62
Oithona	33548	33.98	Oithona	10364	18.54
Corycaeus	4610	4.67	Sapphirina	1778	3.18
Mormonilla	425	0.43	Corycaeus	914	1.63
Sapphirina	145	0.15	Mormonilla	10	0.02
Copelia	80	0.08	Pachysoma	4	0.01
Pachysoma	18	0.02			
TOTAL	98740			55888	

*Continued*

Table 2. (Continued)

March/April	No. m <sup>-2</sup>	% of Total	October	No. m <sup>-2</sup>	% of Total
<b>OTHER</b>					
Larvaceans	4427	51.65	Larvaceans	5438	55.79
Chaetognaths	1187	13.85	Polycheates	1886	19.35
Decapods	862	10.05	Decapods	988	10.13
Ostracods	523	6.11	Ostracods	864	8.86
Echinoderms	453	5.29	Chaetognaths	284	2.91
Polycheates	425	4.96	Siphonophores	226	2.32
Siphonophores	307	3.58	Cladocerans	29	0.29
Cladocerans	158	1.85	Amphipods	18	0.18
Amphipods	132	1.54	Echinoderms	15	0.15
Fish	52	0.60			
Salps	45	0.53			
TOTAL	8570			9746	
Grand Total	288012		Grand Total	246178	
Nauplii %	44.36		Nauplii %	39.17	
Calanoid %	13.38		Calanoid %	21.37	
Cyclopoid %	34.28		Cyclopoid %	22.70	
Harpacticoid %	5.00		Harpacticoid %	12.80	
Others %	2.98		Others %	3.96	

Studies of zooplankton along the equatorial Pacific upwelling zone have demonstrated that zooplankton biomass is maximum north and south of the equator, or “downstream” of the equatorial upwelling (Vinogradov and Voronina, 1963; White *et al.*, 1995). This spatial separation between the site of upwelling and zooplankton biomass occurs because of the slower growth rates of zooplankton as compared to phytoplankton. Downstream along the meridional flow, there are both increases in zooplankton biomass as well as increases in the adult stages of copepods and increases in predatory copepods as the water matures (Vinogradov and Voronina, 1963). It is interesting to note that during the passage of the tropical instability wave during the October time series, we observed in a temporal sequence, the same features that occur spatially as a result of meridional flows. When zonal currents to the west relaxed and meridional flow began to the north, surface water temperatures decreased (Fig. 3). These lower temperature waters were associated with increased nitrate, chlorophyll-*a* and primary production (Murray *et al.*, 1994; Fig. 2). Examining the variations from the time series means during the October time series ( $[\text{value} - \text{mean}] / \text{standard deviation}$ ) we see that lower than average values of sea surface temperature (Days 281 to 286) coincide with higher than average surface chlorophyll-*a* values (Fig. 9). However, increases in zooplankton biomass relative to the cruise-mean lag the decrease in sea surface temperature and increase in surface chlorophyll-*a* by several days. The absolute (Fig. 5) and relative (Fig. 9) zooplankton biomass remained higher than the time series mean several days after sea surface temperature had increased and chlorophyll-*a* had decreased (Figs 2 and 9). It is likely that the colder, higher nitrate water that initially passed through the study area was followed by “older” upwelled water in which the zooplankton community had a chance to develop. This speculation is confirmed by zooplankton species counts. More “herbivorous” calanoid copepods from the families Calanidae and Paracalanidae occurred with passage of the tropical instability wave (Fig.

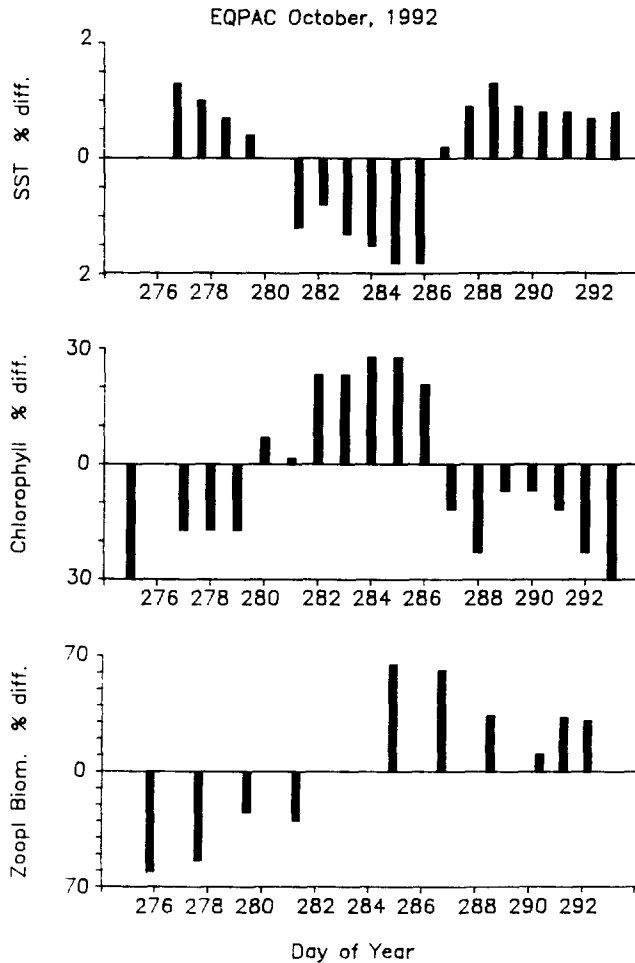


Fig. 9. Difference from the mean ( $[\text{value} - \text{mean}] / \text{standard deviation}$ ) for sea surface temperature, surface chlorophyll-*a* and zooplankton biomass (mean of day and night tow) integrated to 200 m at  $0^\circ$ ,  $140^\circ\text{W}$  during October, 1992.

10). In contrast, the highest abundances of predatory copepods from the family Euchaetidae and cyclopoid copepods from the family Corycaeidae occurred before and after passage of the tropical instability wave (Fig. 10). The rapid changes in zooplankton biomass and species with temperature and salinity confirm that a different water mass passed through our study area as a result of the instability wave. The likely origin of this water was from south of the equator where zooplankton biomass was generally higher than the newly upwelled water of the equator (White *et al.*, 1995). The "older" upwelled water prior to and after the tropical stability wave had a greater number of adult stages and predatory copepods, similar to the pattern observed as one moves downstream meridionally in the upwelled water (Vinogradov and Voronina, 1963).

During the March/April cruise El Niño conditions prevailed at our study site: the average sea surface temperature ( $28.7^\circ\text{C}$ ) was  $2.7^\circ\text{C}$  above the climatological mean



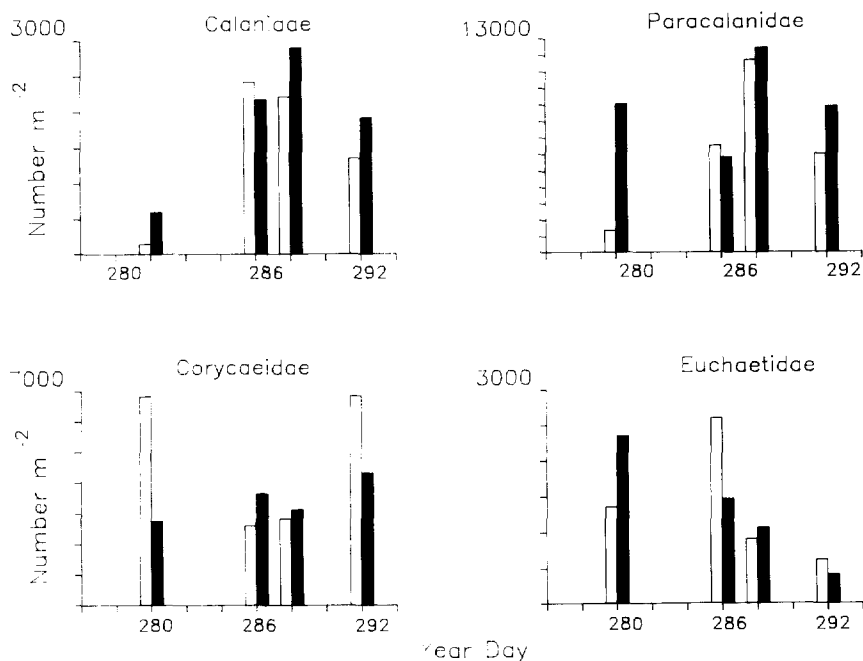


Fig. 10. Integrated (200 m) abundances of copepods from the families Calanidae, Paracalanidae, Corycaeidae and Euchaetidae at 0°, 140°W during October, 1992. Open bars are day samples, shaded bars are night samples.

(McPhaden and McCarty, 1992) and the thermocline was depressed 20–40 m (McPhaden, 1993). During the October time series the average sea surface temperature (25.1°C) equalled the climatological mean and the thermocline had shoaled. Thus we had the unique opportunity to compare plankton biomass, species composition and rate process during time series at 0°, 140°W during El Niño and “normal” conditions. The average integrated (200 m) zooplankton (>64  $\mu\text{m}$ ) biomass was not significantly different during the two cruises. However, there appeared to be more and larger (>200  $\mu\text{m}$ ) zooplankton during the October cruise (Fig. 5, Table 1). Zooplankton biomass was more concentrated in the upper mixed layer during the October cruise (Figs 5 and 6) as compared to March/April. Differences in the species composition and/or avoidance in the warmer surface temperatures during the El Niño condition could have contributed to this different vertical distribution pattern.

Cyclopoid copepods were more abundant during the El Niño conditions (Table 2, Fig. 8). There are several possible causes for this selection. Cyclopoid copepods often dominate in tropical waters (e.g. Newbury and Bartholomew, 1976; Sazhina, 1982; Böttger-Schnack, 1990). With surface water temperatures greater than 28°C during the March/April cruise, it would be advantageous to reduce swimming activity and respiratory demand. Most cyclopoid copepod species do not exhibit continuous swimming; instead they remain relatively motionless and ambush their prey (Paffenhöfer, 1993). This conservation of energy is supported by lower respiration measurements on the cyclopoid copepod *Oithona* (Lampitt and Gamble, 1982). Food resources also might select for more cyclopoid copepods during March/April and more calanoid copepods during October.

During October there was a greater abundance of phytoplankton  $>2 \mu\text{m}$ , primarily diatoms (Bidigare and Ondrusek, submitted). Whereas diatoms are not generally consumed by cyclopoid copepods (Paffenhöfer, 1993), diatoms are the preferred food source of most calanoid copepods (e.g. Frost 1972; Checkley, 1980). Thus there were likely more food resources for calanoid copepods during the more "typical" upwelling conditions in the October time-series. Cyclopoid copepods consume motile prey, mostly protozoa (Paffenhöfer, 1993).

Upwelling of warmer waters with less nutrients at the equator during the El Niño apparently favored the shift to a microbial loop (*sensu* Pomeroy, 1974) based food-web over the diatom-zooplankton pathway. As such, more of the autotrophic carbon should have been recycled in the upper water column and less transported to depth via copepod fecal pellets in March/April as compared to the October time series as a result of less upwelled nitrate and new production as well as a shift in the zooplankton community composition. Export flux of carbon estimated from  $^{234}\text{Th}$  measurements confirmed this hypothesis. Bacon *et al.* (submitted) estimated export flux at the base of the euphotic zone (120 m) as  $1.9 \text{ mM C m}^{-2} \text{ day}^{-1}$  in March/April and  $2.4 \text{ mM C m}^{-2} \text{ day}^{-1}$  during October. These greater export fluxes, as well as higher estimated sinking velocities of particles (Bacon *et al.*, submitted), are consistent with our observations of more zooplankton in the euphotic zone and a shift in the composition of the zooplankton community toward larger, calanoid copepods in October, when hydrographic conditions were similar to the climatological mean.

The amount of zooplankton ( $>200 \mu\text{m}$ ) at  $0^\circ, 140^\circ\text{W}$  is low relative to primary production. For example, we (Roman *et al.*, 1993) found approximately the same amount of zooplankton at the JGOFS station off Bermuda ( $32^\circ\text{N}, 64^\circ\text{W}$ ) as  $0^\circ, 140^\circ\text{W}$ , even though primary production was 3–10 times lower in the Sargasso Sea. As part of the JGOFS North Atlantic Bloom study, Lenz *et al.* (1993) found greater amounts of zooplankton ( $>200 \mu\text{m}$ ) in the euphotic zone of higher latitudes (24, 69, 130, 161  $\text{mM C m}^{-2}$  at  $18^\circ\text{N}, 33^\circ\text{N}, 46^\circ\text{N}, 58^\circ\text{N}$ , respectively) with the ratio of  $>200 \mu\text{m}$  zooplankton biomass/primary production over 10 times greater than we found in the equatorial Pacific. Why do these other oceanic areas have a greater biomass of zooplankton relative to the production of autotrophic carbon that we found at  $0^\circ, 140^\circ\text{W}$ ; or, stated from a different perspective, why aren't there more zooplankton in the equatorial Pacific? Possible causes include both the nature of the pelagic foods webs as well as the physical dynamics of the system. With warmer temperatures at lower latitudes, micro-heterotrophs predominate because of the dominance of small phytoplankton and high bacterial growth rates. In colder waters mesozooplankton ( $>200 \mu\text{m}$ ) may be more abundant relative to primary production because the phytoplankton are larger and thus more available as food. In addition, the lower temperatures depress the growth rate and respiration (C loss) of bacteria and protozoa, potentially allowing more autotrophic carbon utilization by copepods. Thus in the equatorial Pacific, especially during El Niño conditions, small phytoplankton and small heterotrophs (protozoa) dominate the biomass and the cycling of biogenic material.

Our station at  $0^\circ, 140^\circ\text{W}$  was near the center of the equatorial divergence. Thus the newly upwelled source water, initially high in nitrate, low in phytoplankton and low in zooplankton goes through a succession of chemical transformations and species changes as it flows north and south. As shown by previous investigators (Vinogradov and Voronina, 1963) and during EqPac (White *et al.*, 1995), zooplankton biomass is maximum off the equator, or "downstream" from maxima in primary production. This separation is the

result of slower growth rates of the zooplankton compared to the phytoplankton. The plankton food-web is not in equilibrium due to the advective regime of the upwelling system. Both the plankton food web composition and the advective physical regime result in low levels of zooplankton biomass relative to primary production at the equator. As a consequence, the  $>200\ \mu\text{m}$  zooplankton graze  $<10\%$  of daily primary production (Dam *et al.*, 1995). The amount of phytoplankton consumed by zooplankton in the equatorial Pacific increases  $3^{\circ}$ – $5^{\circ}$ N and S of the equator (Zhang *et al.*, 1995) as a result of increases in zooplankton biomass.

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