Primary productivity in the equatorial Pacific during the 1997-1998 El Niño

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Abstract. Shipboard biological and physical measurements made during 1996, 1997, and 1998 in the equatorial Pacific are used to quantify the effect of the 1997-1998 El Niño on the phytoplankton community. This El Niño was by some measures the strongest ever observed and resulted in extremely low phytoplankton biomass and productivity throughout this normally moderately productive region. At the height of the event in late 1997 to early 1998, in the central Pacific, nitrate was absent throughout the entire euphotic zone (~100 m), resulting in chlorophyll concentrations ($0.05\ \mu g\ L^{-1}$) that were among the lowest ever observed in the region and rates of primary production (~$0.41\ g\ C\ m^{-2}\ d^{-1}$) that were approximately half the climatological mean. These conditions persisted until May 1998 when the trade winds resumed and upwelling, with its associated supply of nutrients, was restored along the equatorial Pacific. The phytoplankton community quickly recovered, and by June 1998, nitrate, chlorophyll, and primary productivity levels were comparable to, or in excess of, their respective climatological means.

1. Introduction

The physical oceanography of the equatorial Pacific is dominated by the cool tongue of upwelled water which extends from the coast of south America to at least 180° [*Wyrtki*, 1981]. This upwelling is driven by the coriolis-induced divergence at the equator as a result of the trade winds, which blow from east to west at speeds of the order of 5 m s^{-1} under normal conditions. The trade wind system generates net surface mass transport from east to west and, in conjunction with the upwelling in the central and eastern Pacific, gives rise to slightly higher sea levels and a significantly deeper thermocline in the western region of the basin [*Wyrtki and Wenzel*, 1984]. The upwelled water is high in macronutrients such as nitrate, phosphate, silicate, and carbon dioxide, as well as micronutrients such as iron [*Chavez and Barber*, 1987; *Coale et al.*, 1996a; *Feely et al.*, 1987; *Toggweiler and Carson*, 1995]. The upwelling of CO_2 has global significance as it represents the largest natural source of CO_2 to the atmosphere, at the rate of ~0.5-1.1 × 10^{15} g C y^{-1} [*Tans et al.*, 1990], equivalent to ~10% of the current anthropogenic flux of 6.5 × 10^{15} g C y^{-1} [*Marland et al.*, 1999]. The upwelling of NO_3 accounts for 20% of the global flux to the surface ocean, and ~18% of global new production [*Chavez and Toggweiler*, 1995], yet rates of primary productivity [*Chavez and Barber*, 1987] and new production [*Dugdale et al.*, 1992] remain relatively low given the NO_3 levels observed. This low productivity is primarily responsible for the excess CO_2 in the surface waters, and the flux of CO_2 from the ocean to the atmosphere is almost permanently maintained as long as upwelling continues.

Iron is now widely accepted as the limiting nutrient for the equatorial Pacific ecosystem under normal circumstances [*Coale et al.*, 1996a], although there is some recent evidence for silicate regulation of new production during periods where diatoms dominate the phytoplankton community [*Dugdale and Wilkerson*, 1998]. Upwelling rates and the chemical composition of the equatorial undercurrent (EUC) govern the flux of nutrients to the surface waters. The eastward flowing EUC maintains the mass balance associated with the westward advection of water masses at the sea surface, driven by the trade winds. Under normal conditions, the core of the EUC is located at ~200 m depth in the western Pacific, rising to ~50 m in the east, with a velocity of up to 1.5 m s^{-1} and transport rates of between 13 and 31 Sverdrups [*Tomczak and Godfrey*, 1994]. The high micronutrient concentrations in the EUC are derived from the continental masses in the western Pacific [*Butt and Lindstrom*, 1994; *Tsuchiya et al.*, 1989; *Wells et al.*, 1999], while the observed macronutrient concentrations originate mainly from regeneration of export production from the euphotic zone.

The physical and biogeochemical dynamics of the equatorial Pacific are perturbed on average every 3-4 years by El Niño [*Quinn et al.*, 1987]. During El Niño the trade winds weaken and may reverse, thus removing the driving force for upwelling. This weakening of the trades is usually first observed as westerly wind bursts in the western equatorial Pacific, giving rise to equatorially trapped, downwelling Kelvin waves which propagate from west to east at speeds in excess of 200 km d^{-1}. These Kelvin waves initiate the relaxation of the zonal sea level and thermocline gradients, followed by advection of the western equatorial warm pool into the central Pacific. The warmer waters, usually defined as greater than 28°C [*Picaut et al.*, 1996] are very low in nutrients [*Mackey et al.*, 1995], especially NO_3. Their advection over the central region of the Pacific, combined with the cessation of upwelling leads to dramatically reduced phytoplankton productivity in the equatorial Pacific.

El Niño events may or may not alternate with La Niña conditions, which are characterized by a strengthening of the trade winds and expansion of the equatorial upwelling plume to beyond 180°. Primary productivity in surface waters is enhanced due to increased upwelling rates, and the area characterized by enhanced productivity expands zonally due to the westward contraction of the warm pool. The thermocline and sea level gradients become enhanced, and the EUC is at its strongest and perhaps most nutrient rich.

The onset of the 1997-1998 El Niño was first indicated by two westerly wind bursts centered near 150°E in December 1996 to January 1997 and March-April 1997. These wind events were associated with the 30-60 Madden-Julian Oscillation (MJO) [Madden and Julian, 1971], and each gave rise to a downwelling Kelvin wave which propagated from west to east at a velocity of approximately 200 km d^{-1} [Chavez et al., 1998; McPhaden, 1999]. Because of their direction of propagation, these waves were trapped along the equator by the action of the coriolis force, and as they propagated, resulted in thermocline depressions in excess of 20 m and elevations in sea level. Following the propagation of the second Kelvin wave, which reached the coast of south America in early May 1997, the thermocline shoaled and deepened in the western and eastern equatorial Pacific respectively, a pattern that persisted until May 1998. The propagation of the second Kelvin wave immediately preceded the easterly advection of the western equatorial warm pool, and the 28°C sea surface temperature (SST) isotherm passed 155°W in early May 1997 [Chavez et al., 1998]. Westerly wind bursts associated with the MJO continued into late 1997, and their eastwards extent increased concomitant with the advection of the warm pool [Kessler et al., 1995]. These wind bursts continued to give rise to downwelling Kelvin waves, and in the eastern Pacific by December 1997, the thermocline was depressed by almost 100 m compared to the climatology.

In late 1997, the EUC was nonexistent due to the disappearance of westward advection at the surface and the subsequent lack of a mass balance requirement; a similar phenomenon was observed for the 1982-1983 El Niño [Firing et al., 1983]. SSTs were in excess of 28°C over the entire equatorial Pacific, but SST in the west was in fact cooler than average due to greater evaporative heat loss and deeper mixing associated with the MJO-induced westerly winds [Meyers et al., 1986], which reached velocities of 4-6 m s^{-1}. By late April 1998, thermocline depth anomalies became negative (shallower than normal) as far east as 125°W, thus cool nutrient-rich waters were close to the surface but were not upwelled owing to the absence of trade wind forcing. In May 1998 the trade winds returned, and SSTs rapidly dropped because of the shallow thermocline. During the second half of 1998, upwelling was maintained, and the extent of the cool tongue increased as a strong La Niña developed. In summary, the physical onset and retreat of the 1997-1998 El Niño were extremely rapid, and the event itself was arguably the strongest on record.

Our understanding of the physical processes associated with the El Niño-La Niña cycle has been greatly advanced since the establishment of the Tropical Atmosphere Ocean (TAO) Array, which consists of ~70 moorings across the equatorial Pacific; ~8°N to 8°S, 156°E to 95°W. These moorings record surface wind velocity, air temperature, relative humidity, and ocean temperature from the surface to 500 m. Data are transmitted daily via the Advanced Research and Global Observations Satellite (ARGOS) service, enabling near real-time monitoring and initialization data for modeling studies. In December 1996, the Monterey Bay Aquarium Research Institute (MBARI) installed bio-optical and

chemical sensors on two moorings in the central equatorial Pacific, at 0°, 155°W and 2°S, 170°W, and these data were used by Chavez et al. [1998] to describe the biological-physical coupling observed during the onset of the 1997-1998 El Niño. During 1998 the array of bio-optical instruments was expanded to include smaller, self-contained packages at four additional sites in the TAO Array (2°N, 110°W; 2°N, 140°W; 2°S, 140°W; and 2°N, 180°). The maintenance of the TAO array is performed by the National Oceanic and Atmospheric Administration (NOAA) Ship Ka'imimoana, which visits each mooring site from 95°W to 165°E approximately twice annually. Since October 1997, MBARI has maintained a continuous program of biological measurements on board the Ka'imimoana, including, but not limited to, chlorophyll and nutrient (NO_3, PO_4, and SiO_4) measurements from the surface to 200 m at ~250 stations per year.

In this contribution we focus on in situ ship-based measurements to describe the changes in nutrient concentration, phytoplankton abundance, and primary productivity associated with the 1997-1998 El Niño in the equatorial Pacific. Our specific objectives are to (1) quantify the decrease in phytoplankton biomass and productivity associated with the peak of the El Niño event and the recovery during the onset of La Niña conditions in 1998, (2) identify the physical and chemical mechanisms responsible for the observed biological perturbations, (3) quantify the effect of the productivity perturbations on the carbon uptake of the equatorial Pacific, and (4) disseminate a data set which could serve as validation data for ecosystem models of the region.

2. Materials and Methods

2.1. Location of Data Collection

Data were collected during twelve cruises in the equatorial Pacific aboard the NOAA ships Ka'imimoana and Ronald H. Brown. Figure 1 shows the trackline of the cruises, while Table 1 describes the time periods and locations.

2.2. CTD Sampling Regime

Water samples were drawn from CTD rosette bottles fired at nominal depths of 0 (100%), 10 (50%), 25 (30%), 40 (15%), 60 (5%), 100 (1%), 150 (0.1%), and 200 m. This sampling regime was designed to approximate the percentage light levels in parentheses [Morel, 1988], based on a mean photosynthetically available radiation attenuation coefficient (k_{PAR}) of 0.05 m^{-1} calculated from bio-optical profiles taken during November 1996 along 155°W and 170°W. The validity of this approximation and the potential effects on the resulting data are discussed in section 2.4.

2.3. Chlorophyll profiles

Water samples of 500 ml were taken from eight depths between 0 and 200 m and filtered at a vacuum pressure of < 20 kPa onto Whatman 25 mm diameter GFF filters. Two additional 250 ml samples from the surface were filtered onto 1 and 5 μm polycarbonate membrane filters, respectively. Samples were then extracted in 90% Acetone at −10°C for 24-48 hours, before determination of chlorophyll a and phaeopigments was performed in a Turner Designs model 10-005R benchtop fluorometer [Holm-
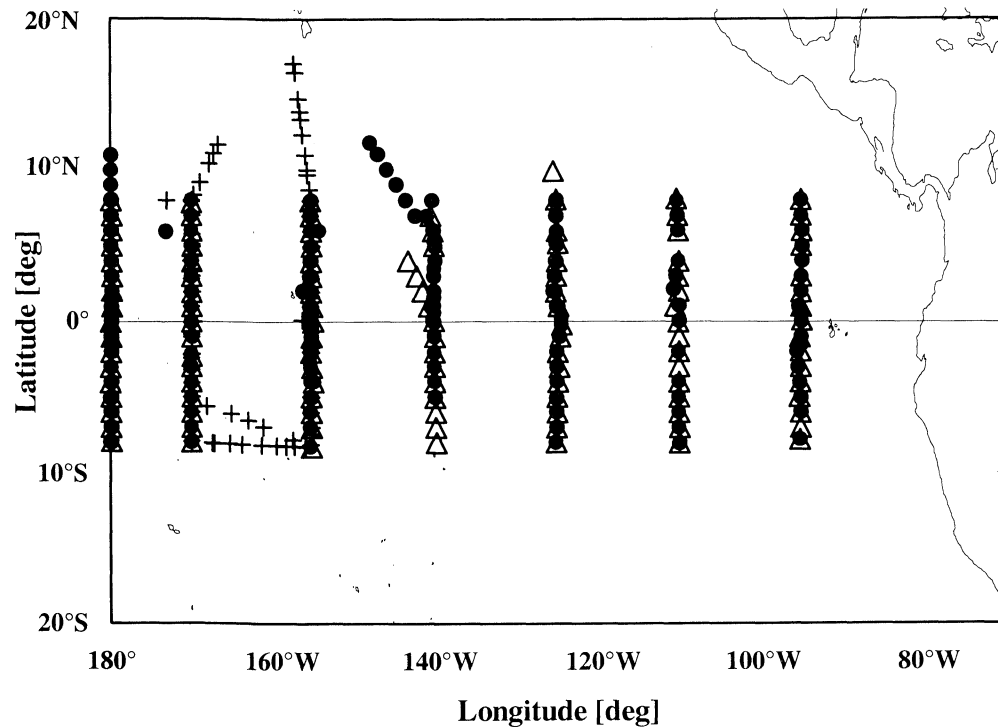
Figure 1. Map showing the location of stations occupied during 1996, 1997, and 1998. CTD locations are shown for GP7-96-KA, GP3-97-KA (pre-El Niño, crosses); GP6-97-KA, GP7-97-KA, GP1-98-KA (El Niño, triangles); GP2-98-KA, GP3-98-KA, GP4-98-KA, GP5-98-KA GP6-97-RB, GP7-98-KA and GP8-98-KA (La Niña, filled circles).

Hansen et al., 1965; *Lorenzen*, 1966]. The fluorometer had been calibrated using known concentrations of chlorophyll *a* (Sigma chemicals), and this method is identical to that used by *Chavez et al.* [1996].

2.4. Primary productivity

Primary productivity measurements were performed at most CTD stations on cruises GP6-97-KA, GP7-97-KA, GP3-98-KA, and GP7-98-KA. In order to minimize the effects of metal contamination or chemical toxicity, the metallic springs and neoprene

o rings in the CTD rosette bottles were replaced with silicone rubber components for the duration of these cruises. In addition, a bottle-washing protocol based on that of *Fitzwater et al.* [1982] was employed at the beginning of each cruise and between longitudinal transects.

For each primary productivity profile, 280 mL water samples were taken from the 100 to 0.1% light depths described above, in polycarbonate bottles that had been washed using a similar procedure as for the CTD rosette bottles. One additional 280 mL sample each was drawn from the 100 and 0.1% depths for determination of the initial isotope uptake, subsequently referred to as the T_0 samples. To determine size-fractionated primary productivity at

Table 1. Description of the Time Periods and Meridional Transects Covered by Cruises Aboard the NOAA Ship *R/V Ka'imimoana*

Cruise Name	Dates	Meridional Transects
GP7-96-KA	Nov. 22, 1996 to Dec. 18, 1996	155°W and 170°W
GP3-97-KA	May 6, 1997 to June 3, 1997	155°W and 170°W
GP6-97-KA	Sep. 27, 1997 to Oct. 30, 1997	125°W and 140°W
GP7-97-KA	Nov. 6, 1997 to Dec. 17, 1997	155°W, 170°W and 180°
GP1-98-KA	Feb. 5, 1998 to March 13, 1998	95°W and 110°W
GP2-98-KA	April 18, 1998 to May 20, 1998	125°W and 140°W
GP3-98-KA	June 2, 1998 to July 3, 1998	155°W and 170°W
GP4-98-KA	July 7, 1998 to Aug. 3, 1998	165°E and 180°
GP5-98-KA	Sep. 5, 1998 to Oct. 9, 1998	125°W and 140°W
GP6-98-RB	Oct. 13, 1998 to Nov. 15, 1998	110°W and 95°W
GP7-98-KA	Oct. 19, 1998 to Nov. 13, 1998	155°W and 170°W
GP8-98-KA	Nov. 18, 1998 to Dec. 12, 1998	170°W and 180°

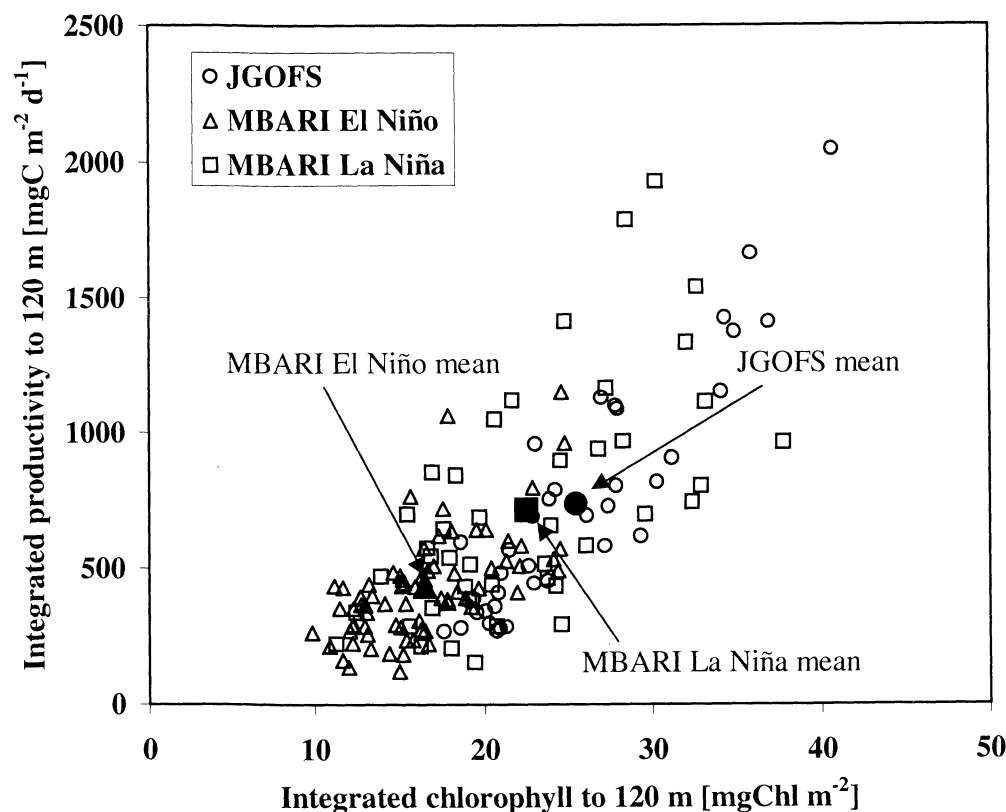GP6-98-RB was conducted aboard the NOAA Ship *Ronald H. Brown*.

Figure 2. Plot of integrated primary productivity versus integrated chlorophyll concentration for the JGOFS Survey cruises (February-March and October 1992, open circles), MBARI 1997-1998 El Niño cruises (October-December 1997, open triangles) and MBARI 1998 La Niña cruises (1998, open squares). Means for the three sets of data are represented in the corresponding solid symbols. The trapezoidal integrations for the JGOFS data were preformed to 120 m using the actual depths at which the bottles were incubated. For the MBARI data, the trapezoidal integrations for productivity were performed to 120 m using the light depths calculated as described in the methods, while the chlorophyll integrations were performed using the actual sample depth.

the surface, an additional 280 mL sample was taken from the 100% light level, subsequently referred to as the SF sample. To each of the 10 280 mL samples, 0.1 mL of $NaH^{14}CO_3$ (activity 0.1 mCi mL^{-1}) was added. The two T_0 samples were filtered immediately onto Whatman 25 mm diameter GFF filters at a vacuum pressure of < 20 kPa. The filters were then placed in 20 mL scintillation vials (Fisher Scientific) with 1 mL of ~0.5N HCl (Fisher Scientific, reagent grade) and left to fume for a minimum of 24 hours. The remaining samples were incubated on deck with running sea surface water in tubes fitted (or not in the case of the 100% samples) with screens designed to reduce the incident light to the levels at which the samples originated.

After 24 hours, samples were removed, filtered and fumed as for the T_0 samples. Prior to filtering, 1 mL was extracted from the 100 and 0.1% samples and combined with 20 mL of Cytoscint ES (ICN Biomedicals) in a scintillation vial which was immediately capped; this was done in order to determine the total activity of the isotope initially added. From the SF sample, 100 mL each was filtered onto a 1 μm Costar and 5 μm Millipore membrane filter, which were then acidified and fumed as above. After a minimum 24 hours fuming, to drive off any abiotic $H^{14}CO_3$, 10 mL of Cytoscint ES liquid scintillation cocktail was added to each scintillation vial. Vials were shaken vigorously and, after a period of 24 hours or more, were analyzed in a Beckman liquid scintillation counter to determine ^{14}C activity, from which primary productivity at each depth was calculated as

$$\text{Carbon uptake (mgC m}^{-3}\text{ d}^{-1}) = \frac{(DPM_t - DPM_0)TIC}{DPM_{total}vt},$$

where DPM_t and DPM_0 are the activities of the samples at 24 and 0 hours, respectively, TIC is the concentration of total inorganic carbon (24,000 mg C m^{-3} ± 1%), DPM_{total} is the activity of the "total activity" samples, v is the volume filtered (280 mL or 100 mL for the SF samples), and t is the incubation time, in days. Using the pigment profile (chlorophyll + phaeopigments) and an algorithm based on *Morel* [1988], the simulated in situ depths of the 100, 50, 30, 15, 5, 1, and 0.1% light levels were calculated for each cast at which productivity measurements were performed. These depths were used to calculate integrated production (mg C or g C m^{-2} d^{-1}) to the same 0.1% light level (120 m) used by *Barber et al.* [1996].

To determine the quality of our deck incubation productivity data, we have compared our integrated productivity and chlorophyll values to the U.S. Joint Global Ocean Flux Study (JGOFS) equatorial Pacific Survey cruises [*Barber et al.*, 1996]. The Survey I and II cruises took place in February-March and October 1992, during El Niño and La Niña conditions, respectively. All incubations were performed in situ, that is with bottles incubated at depth in the water column, attached to a moored line. For our integrated values to be comparable with the JGOFS data, we have performed the trapezoidal integration for productivity using the adjusted "Morel" depths described above, to a maximum depth of
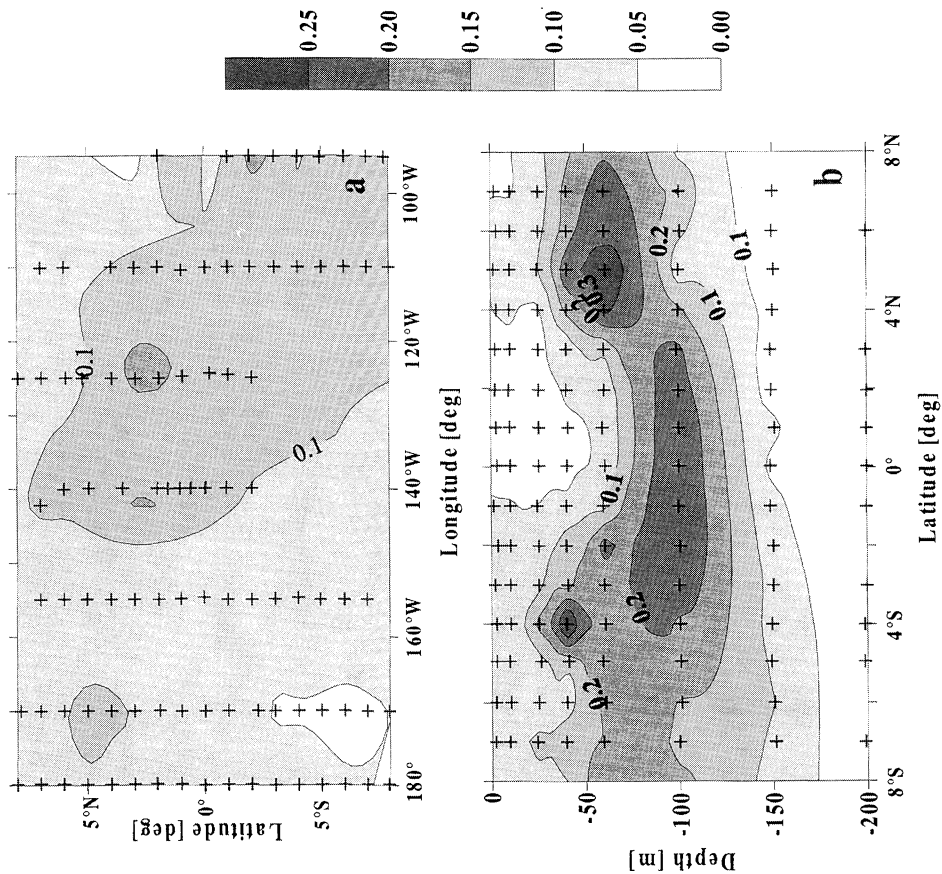
Figure 4. (a) Latitude-longitude map of surface chlorophyll concentrations from 8°N to 8°S, 95°W to 180° for the time period spanning the peak of the 1997-1998 El Niño event, October 1997 to April 1998. Surface chlorophyll concentrations were generally 0.1 μg L^{-1} or lower over the entire region. (b) A latitude-depth section (8°N to 8°S, 0-200 m) along 155°W for the period November 10-17, 1997. Along the equator at this time winds were downwelling favorable (westerly), nitrate was absent in the upper 100 m of the water column, and the vertical profile of chlorophyll at the equator resembled that of the oligotrophic central gyres, with a subsurface maximum at ~100 m, corresponding to the depth of the nitricline.
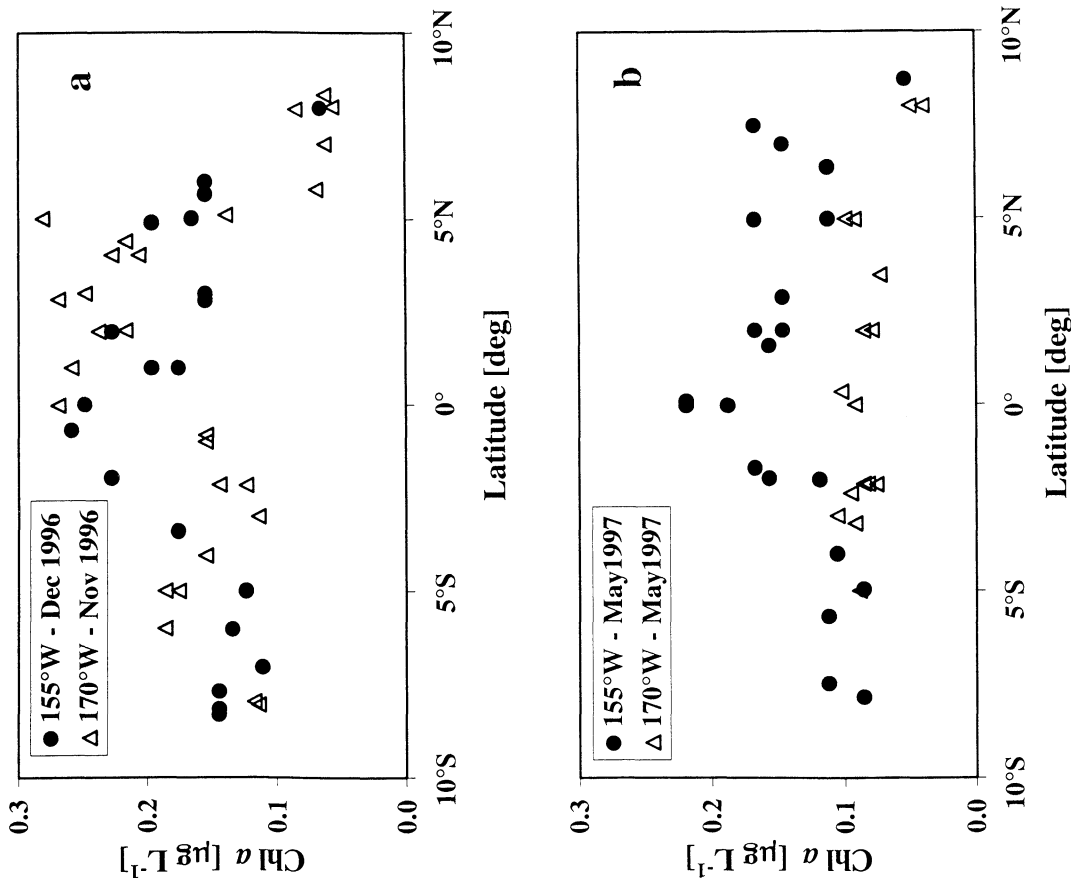
Figure 3. Meridional chlorophyll transects along 155°W and 170°W from (a) November-December 1996 and (b) May 1997.
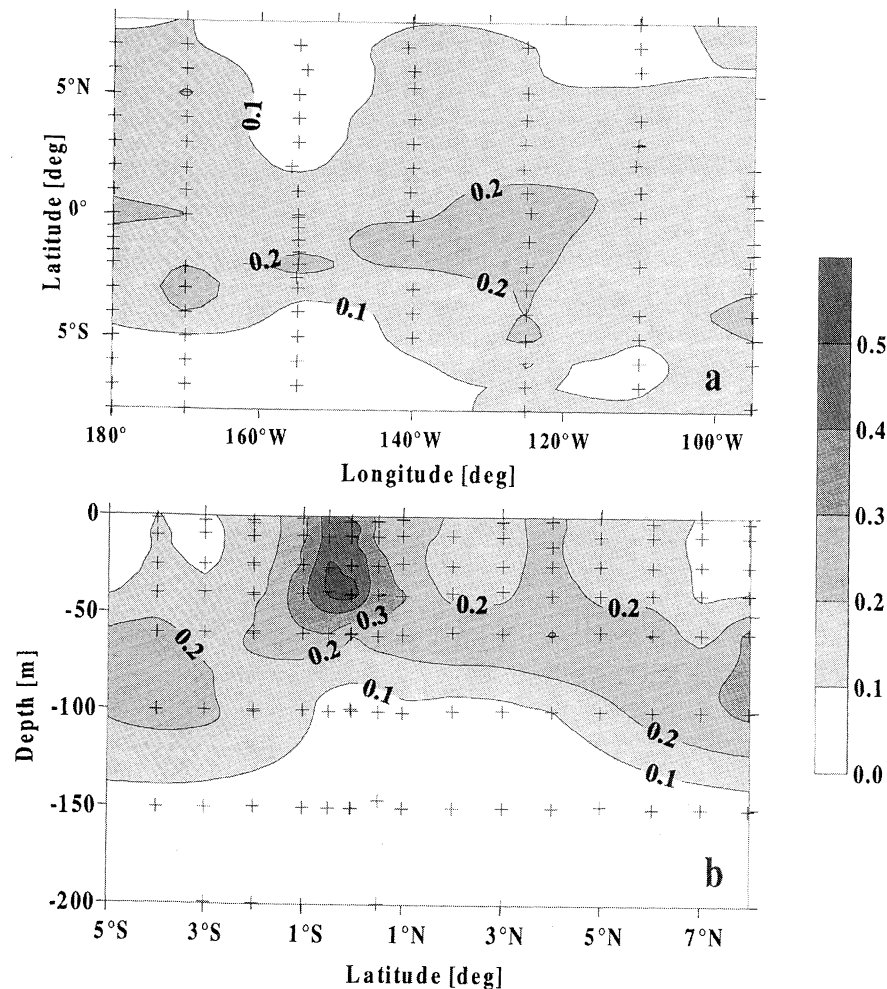
Figure 5. (a) Latitude-longitude map of surface chlorophyll concentration from 8°N to 8°S, 95°W to 180° for the time period spanning the return to cool conditions, September - December 1998. Surface chlorophyll concentrations were ~ 0.1 μg L^{-1} or greater over the entire region. (b) A latitude-depth section (8°N to 5°S, 0-200 m) of chlorophyll concentration along 155°W for the period June 6-16, 1998. Along the equator at this time winds were upwelling favorable (easterly), nitrate was enriched in the euphotic zone, and the subsurface maximum in chlorophyll occurred at ~30 - 50 m.

120 m. The integration for chlorophyll was also performed to 120 m but using the actual sample depths. Figure 2 compares the pooled JGOFS data with our El Niño (October-December 1997) and La Niña (June and October 1998) data. In general, we believe the comparison is favorable, thus confirming the validity of our experimental approach and integration procedure. The MBARI El Niño data cluster at low productivity-chlorophyll values, which is not surprising given the magnitude of the 1997-1998 event and the dramatic effect it had on primary productivity, to be described below. In contrast, the MBARI La Niña data span a wide range of generally higher productivity and chlorophyll values, and the mean for the La Niña period is close to the mean JGOFS Survey data. The MBARI La Niña productivity mean is slightly lower than the JGOFS Survey mean, and this is likely due to the east-west decreasing gradient in productivity associated with the equatorial upwelling tongue; the JGOFS data are from 140°W, whereas the MBARI data are from 155°W and 170°W, closer to the oligotrophic western equatorial warm pool. The similarity of the productivity-chlorophyll relationship between the JGOFS in situ data and the MBARI deck incubation data suggests that the

deck incubation protocol did not significantly affect our estimates of integrated primary productivity.

2.5. Nutrient Measurements

During GP6-97-KA, GP7-97-KA, and GP1-98-KA, surface samples were drawn from all CTD profiles, into plastic 20 mL vials, and then frozen for subsequent analysis of NO_3, NO_2, SiO_4, and PO_4 concentration at MBARI using and Alpkem Rapid Flow Analyzer (RFA) [*Sakamoto et al.*, 1990]. For GP2-98-KA onward, this sampling regime was identical to that of the chlorophyll sampling; that is eight depth (0-200 m) nutrient profiles at all CTD stations.

3. Results

3.1. Chlorophyll distributions

In late 1996, before the initiation of the 1997-1998 El Niño event, chlorophyll concentrations (Figure 3a) were close to the
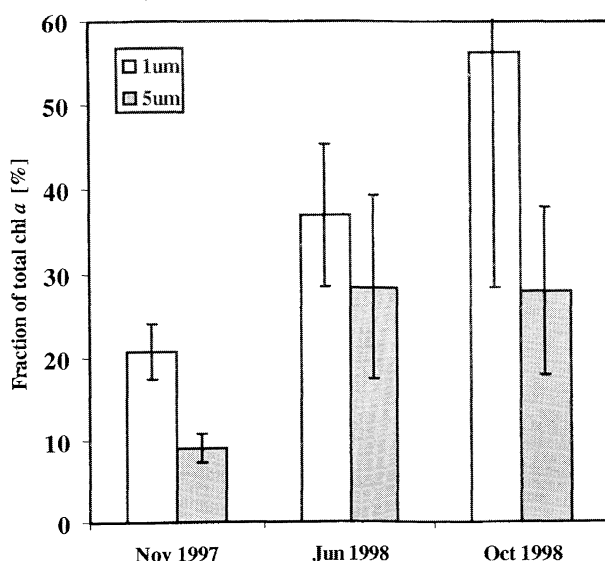
Figure 6. Column chart depicting the increasing importance of larger cells (diatoms) in phytoplankton community composition, concomitant with the return to cool conditions in the equatorial Pacific. During strong El Niño conditions (November 1997), cells > 1 μm in size account for only ~20% of the observed chlorophyll concentration, increasing to ~56% during La Niña conditions in October 1998. Data shown are means ± standard deviation for surface samples collected from CTD casts between 2°N and 2°S and 155°W and 170°W. For November 1997 and October 1998, $n=9$; for June 1998, $n=14$.

climatological means (1980-1989) described by *Chavez et al.* [1996]. During the first half of 1997, fluctuations in chlorophyll of between 0.15 and 0.25 μg L^{-1} were observed at 0°, 155°W associated with the passage of the two downwelling Kelvin waves described above, and *Chavez et al.* [1998] argued that this was due to changes in the flux of iron to the euphotic zone arising from oscillations of the thermocline. By early May 1997, the second of the downwelling Kelvin waves had propagated as far as the coast of south America, and the western edge of the warm pool was located at ~155°W. The effects of this warm, nutrient-poor water are clearly evident in the chlorophyll concentrations along 170°W (Figure 3b), which were lower than the 5°N to 5°S means reported for the same meridian by *Chavez et al.* [1996] during the boreal spring of 1992, when nitrate concentrations were essentially zero.

As the El Niño event matured, surface chlorophyll concentrations were of the order of 0.1 μg L^{-1} or less over the entire equatorial Pacific, and Figure 4a shows the chlorophyll distribution from a composite of cruises spanning October 1997 to April 1997; the peak of the event. In October-November 1997, the trade wind reversal and eastern edge of the warm pool reached as far east as 140°W. Figure 4b shows that these downwelling favorable winds led to an absence of elevated chlorophyll concentration at the equator along 155°W; in fact, the surface concentration at 0°, 155°W at this time was 0.05 μg L^{-1} – one of the lowest values ever recorded for the equatorial Pacific [*Chavez et al.*, 1996]. A subsurface maximum of 0.2 to 0.25 μg L^{-1} was observed at ~100 m, which corresponded to the depth of the nitricline; a similar phenomenon was described by *Mackey et al.* [1995] along 155°E in the oligotrophic western equatorial warm pool during October 1990.

Upwelling favorable winds quickly returned in May 1998, and owing to the proximity of the thermocline to the surface over much of the equatorial Pacific, the nutrient supply to the euphotic zone was rapidly restored. This resulted in a swift recovery of the phytoplankton community, and Figure 5a shows the distribution of surface chlorophyll from a composite of cruises spanning September - December 1998. Figure 5b shows the effect of the rejuvenated upwelling system on the chlorophyll profile along 155°W in June 1998, with concentrations as high as 0.5 μg L^{-1} near the surface at the equator, an order of magnitude greater than the levels observed 7 months previous.

In addition to the gross increase in chlorophyll concentration between El Niño and La Niña conditions, the size distribution of the phytoplankton community also underwent changes, as shown by the percentage chlorophyll contained in the 1 and 5μm fractions (Figure 6). Along 155°W and 170°W, between 2°N and 2°S, the fraction of chlorophyll contained in the 1 μm size fraction more than doubled from November 1997 to October 1998, while the 5 μm fraction increased at least threefold during the same time period. If we consider the 5 μm size fraction to be indicative of diatom abundance, the data indicate that diatoms increased from accounting for ~10% to ~30% of the total chlorophyll.

3.2. Primary Productivity

Mean primary productivity in the equatorial Pacific is ~0.9 g C m^{-2} d^{-1} [*Chavez et al.*, 1996]. During the height of the El Niño in November 1997, measured primary productivity along 155°W and 170°W was approximately half of the climatological mean (5°N to 5°S mean = 0.41 ± 0.22 g C m^{-2} d^{-1}, Figure 7a). Subsequent to the resumption of upwelling and the recovery of the phytoplankton community, primary productivity near the equator along 155°W and 170°W in June 1998 reached 1.0 g C m^{-2} d^{-1} or greater (5°N to 5°S mean = 0.70 ± 0.41 g C m^{-2} d^{-1}, Figure 7b), and in October-November 1998, productivity north and south of the equator also showed signs of the general recovery (5°N to 5°S mean=1.03 ± 0.39 g C m^{-2} d^{-1}, Figure 7c), while productivity at the equator was nearly double the climatological mean.

3.3. Nutrient distributions

Nitrate measurements along 155°W and 170°W in November-December 1996 and May 1997 clearly illustrated the reduction in surface nitrate levels associated with the eastward advection of the warm pool. In late 1996, prior to the first westerly wind burst, nitrate along both 155°W and 170°W was for the most part in excess of the climatological means described by *Chavez et al.* [1996] and *Conkright et al.* [1994], indicative of the upwelling conditions that were still occurring at that time (Figure 8a). The asymmetry of the nitrate field about the equator is a feature of the shape of the upwelling tongue at these longitudes, owing to the presence of the north equatorial counter current (NECC). However, by May 1997, the eastern boundary of the nitrate-deficient warm pool had migrated beyond 170°W to ~155°W, in response to the westerly wind bursts [*McPhaden*, 1999] and to a lesser extent, Kelvin wave propagation [*Kessler and McPhaden*, 1995]. Winds were downwelling favorable as far east as the date line at this time, and their easterly extent increased with the expansion of the warm pool, as described above. Nitrate was essentially absent along 170°W and near the equator along 155°W had decreased
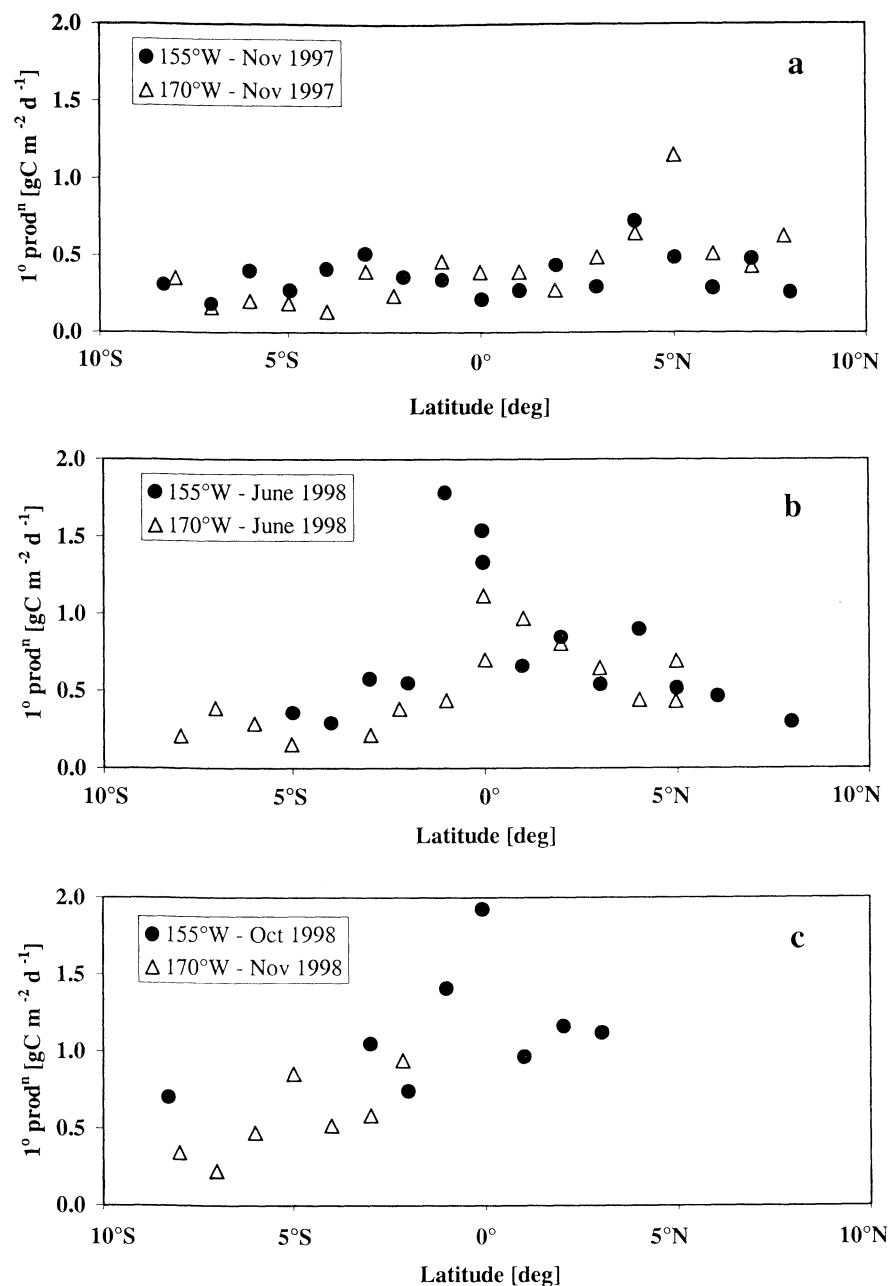
Figure 7. Integrated primary productivity (g C m^{-2} d^{-1}) along 155°W and 170°W, for (a) November 1997, (b) June 1998, and (c) October-November 1998.

40% from 5 μmol L^{-1} in December 1996 to 3 μmol L^{-1} in May 1997 (Figure 8b).

During the mature phase of the event, surface nitrate was depleted to almost zero across the equatorial Pacific (Figure 9a). West of ~140°W (Figure 9b), this nitrate depletion extended over the entire euphotic zone and was presumably correlated with iron depletion. By June 1998 when the transition to La Niña conditions was occurring, the surface nitrate field along 155°W (Figure 10) very closely resembled the climatological field described by *Conkright et al.* [1994]. At this time there was a strong nitricline between 100 and 150 m, poleward of ~4°N and 4°S, respectively, but near the equator, elevated levels reached the surface and presumably coexisted with elevated levels of upwelled iron.

4. Discussion

The fluctuations in chlorophyll concentration and quantum yield of fluorescence [*Chamberlin et al.*, 1990] observed by *Chavez et al.* [1998] during the onset of the 1997-1998 El Niño event were attributed to fluctuations in the iron supply to the euphotic zone. The mechanisms responsible for this reduced flux were twofold. First, while upwelling was still occurring, as it was at 0°, 155°W until May 1997, the depth of the thermocline was perturbed as a result of the passage of two downwelling Kelvin waves. These waves moved the high-nutrient source waters deeper, such that the iron concentration of the upwelled water, whose source depth presumably remained constant, was dimin-
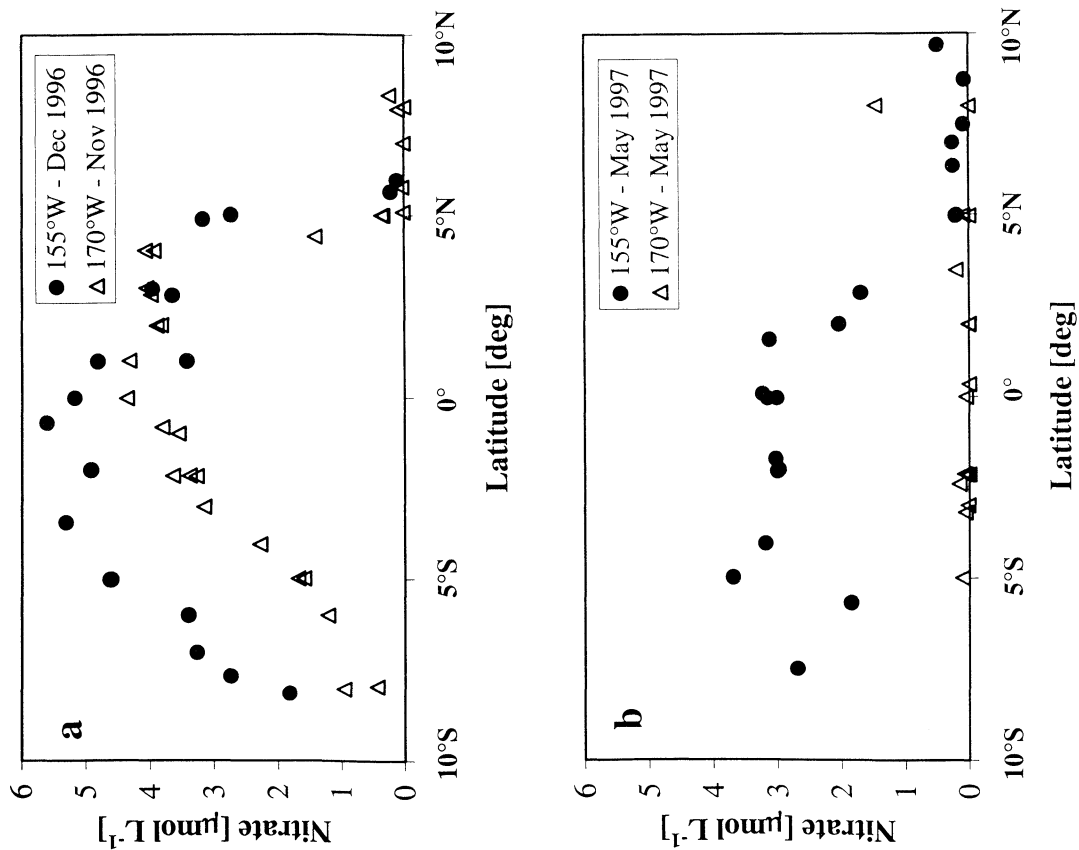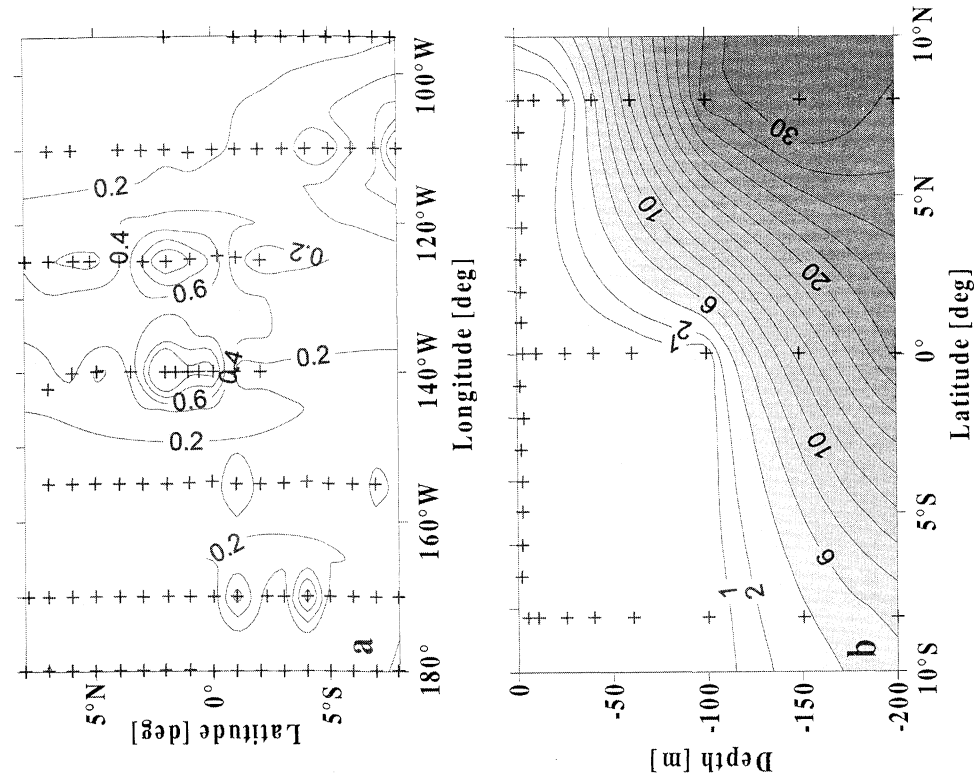
Figure 9. (a) Latitude-longitude map of surface nitrate concentrations from 8°N to 8°S, 95°W to 180° for the time period spanning the peak of the 1997-1998 El Niño event, October 1997 to April 1998. Surface nitrate concentrations were < 2 μmol L^{-1} over the entire region. (b) A latitude-depth section (10°N to 10°S, 0-200 m) along 155°W for the period November 10-17, 1997. Along the equator at this time, winds were downwelling favorable (westerly) and nitrate was absent in the upper 100 m of the water column south of the equator, similar to the oligotrophic open ocean gyres.
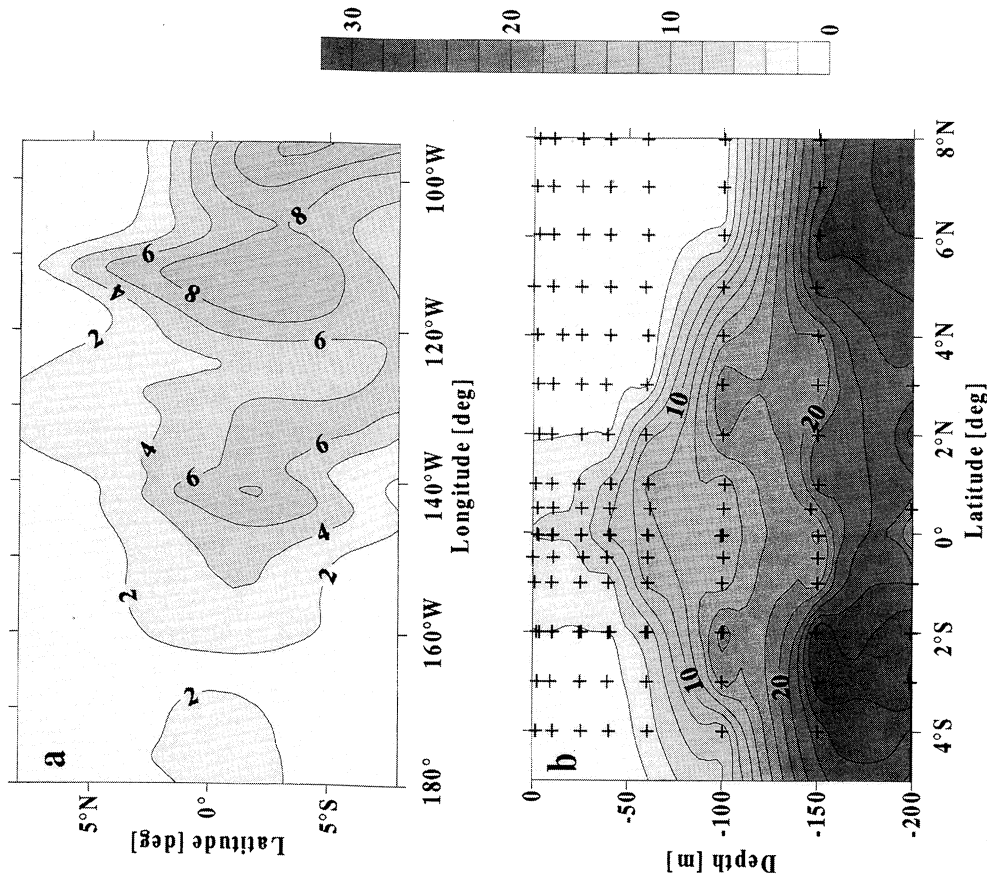

Figure 8. Nitrate concentrations from ~8°N to 8°S along 155°W and 170°W for (a) November-December 1996 and (b) May 1997. The asymmetry of nutrient concentrations about the equator is due to the presence of the north equatorial counter current (NECC) and the resulting greater southward advection of water upwelled at the equator.

Figure 11. Comparison of the climatological and El Niño conditions at 0°, 155°W with a station in the south Pacific gyre (27.5°S, 103°W, March 1994) and the climatology for the Hawaii Ocean Time series (HOT) site. (a) Nitrate profiles. For the south Pacific gyre, the HOT site, and the central equatorial Pacific during El Niño (November 1997), nitrate is essentially absent in the euphotic zone, but for 0°, 155°W under climatological conditions (from *Conkright et al.*, 1994), nitrate is ~ 3 - 4 µmol L⁻¹ at the surface, increasing to > 20 µmol L⁻¹ at depth. (b) Chlorophyll profiles. Under normal conditions in the central equatorial Pacific, the subsurface chlorophyll maximum is located at ~50 - 60 m, but under conditions of depleted nitrate in the euphotic zone, this maximum occurs at ~100 m, corresponding to the depth of the nitricline. This profile is similar to that observed in oligotrophic regions, such as the south Pacific site and the HOT site. The chlorophyll climatology at 0°, 155°W was derived from data collected between 1980 and 1998.

Figure 10. (a) Surface nitrate climatology from 8°N to 8°S, 95°W to 180°. Surface nitrate concentrations are generally greater than 2 µmol L⁻¹ over most of the region. (b) A latitude-depth section (8°N to 5°S, 0 to 200 m) of nitrate along 155°W for the period June 6-16, 1998. Along the equator at this time, winds were upwelling favorable (easterly), resulting in enriched nitrate in the euphotic zone.
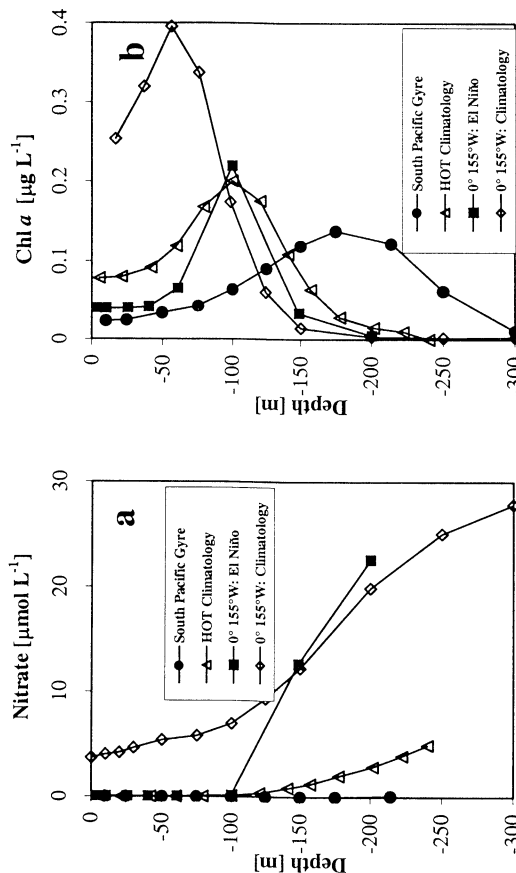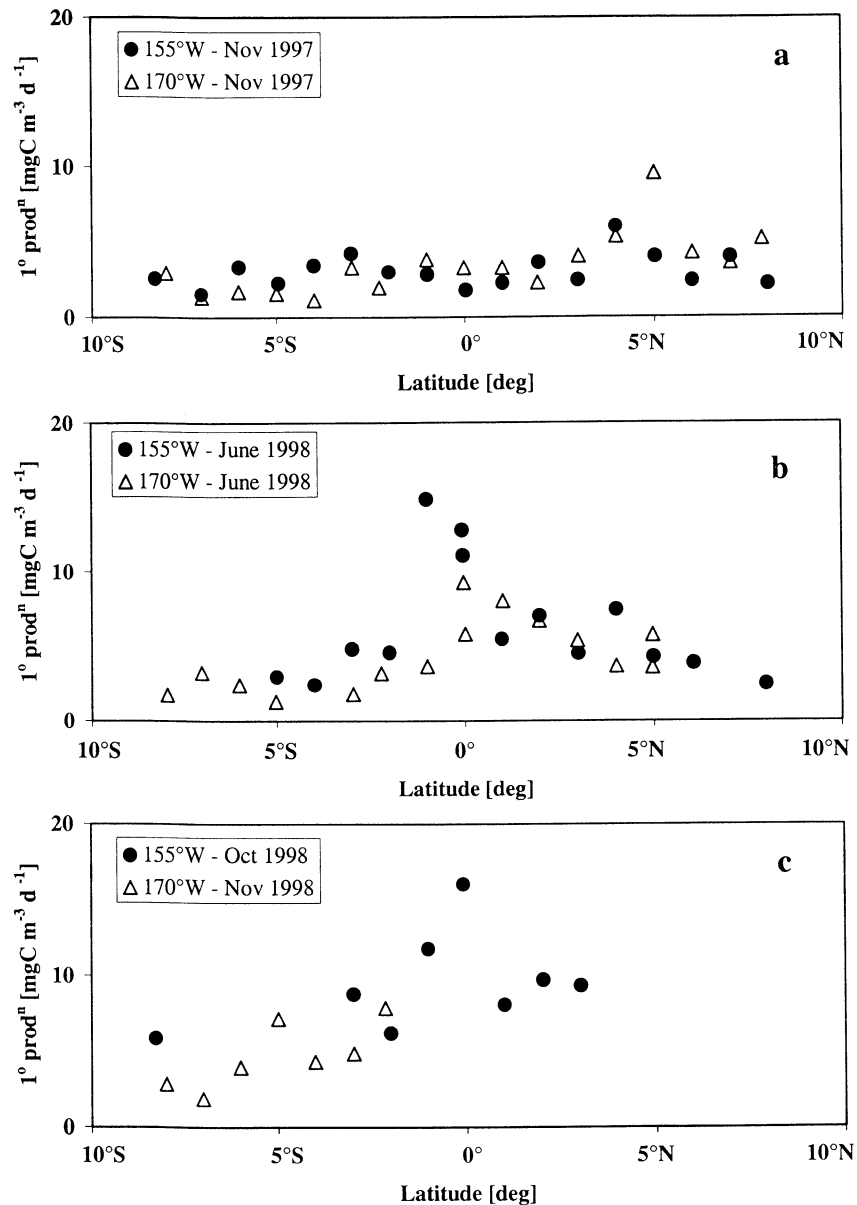
Figure 12. Mean productivity in the euphotic zone along 155°W and 170°W for the same time periods depicted in figure 7 as integrated primary productivity. (a) November 1997, (b) June 1998, and (c) October-November 1998. Data are from deckboard incubations and have been multiplied by 1.39, as described by *Chavez et al.* [1996] to be compared to the in situ incubations of *Barber et al.* [1996].

ished. Second, the EUC progressively deepened during early 1997, and the vertical velocity gradient between its core and the surface decreased owing to the simultaneous weakening of the trade winds and the EUC. This led to a decrease in the shear-induced diffusive flux of iron to the surface from the EUC. It should be noted that the amount of iron introduced to the euphotic zone via this diffusive process is probably very small; *Coale et al.* [1996b] and *Leonard et al.* [1999] calculated that upwelling accounted for 85-95% and 85-99%, respectively, of the vertical iron flux, while *Gordon et al.* [1997] used a value of 0.2 nmol m^{-2} d^{-1} for the vertical Fe diffusion, equivalent to 0.3% of the total flux.

Until May 1997, nitrate concentrations in the central equatorial Pacific were ≥ 3 μmol L^{-1} [*Chavez et al.*, 1998], sufficient for phytoplankton growth [*Barber and Chavez*, 1986]. However, during the latter half of 1997, when the warm pool began to dominate the equatorial Pacific, nitrate concentrations in the

euphotic zone, at least west of 140°W, were ubiquitously less than 1.0 μmol L^{-1}. While the nitrate depletion alone is sufficient to explain the extremely low phytoplankton biomass and productivity described above, iron depletion was also presumably responsible for some of the phytoplankton response. Nitrate levels were indeed at or near conventional detection limits during the height of the event, and in the absence of any direct measurements, all of the physical evidence suggests that iron concentrations were ~0.03 nmol L^{-1} during this period. If iron was present in higher concentrations, its uptake would have been hindered by the lack of nitrate. This macronutrient and/or micronutrient limitation resulted in the extremely low biomass and productivity described above.

At 0°, 140°W during the moderate El Niño conditions of early 1992, both empirical [*Barber et al.*, 1996] and modeled [*Leonard et al.*, 1999] vertical chlorophyll distributions exhibited almost

uniform concentrations of ~0.2 μg L^{-1}, and the absence of a deep chlorophyll maximum, usually observed near 60 m. With the return to cool conditions in late 1992, a general increase in chlorophyll occurred from the surface to ~80 m, and a pronounced subsurface chlorophyll maximum of ~0.4 μg L^{-1} evolved [Barber et al., 1996; Bidigare and Ondrusek, 1996], which is also visible in the model data of Leonard et al. [1999]. In contrast, the chlorophyll data presented here for the mature phase of the 1997-1998 El Niño, from 155°W, did exhibit significant vertical structure, particularly at the equator. This was primarily associated with the shape of the nitrate profile, which resulted from a combination of downwelling and biological depletion in the euphotic zone. While nitrate and chlorophyll concentrations were close to zero from the surface to 100 m during the 1997-1998 El Niño, nitrate remained above 3 μmol L^{-1} at the surface in early 1992. We attribute these differences in the chlorophyll profiles between 1992 and 1997-1998 to the differing strengths of the two El Niño events.

In order to illustrate the extent to which nutrient limitation altered the vertical distribution of chlorophyll, we have compared the nitrate and chlorophyll profiles at 0°, 155°W for El Niño and climatological conditions with an extremely oligotrophic station in the south Pacific, and the climatological data for the Hawaii Ocean Time series (HOT) site (Figure 11). Climatological nitrate concentrations for the euphotic zone in the central equatorial Pacific are between 4 and 7 μmol L^{-1}, increasing to ~20 μmol L^{-1} at 200 m. However, during the intense El Niño of 1997-1998, the nitrate concentration of the upper 100 m was essentially 0 μmol L^{-1}, similar to the profile observed at 27.5°S, 103°W in March 1994, and the HOT climatology, both of which represent nitrate limited systems. Below 100 m at 0°, 155°W in November 1997, nitrate was close to climatological values, which is perhaps surprising given that the EUC, a major source of nutrients to the euphotic zone at the equator, was essentially nonexistent at that time. From the meridional section in Figure 9b and from previous work [Tsuchiya and Talley, 1996], there is evidence for a potential source to the north and perhaps south. In the oligotrophic environments of the north and south Pacific gyres, subsurface chlorophyll maxima of 0.15 - 0.20 μg L^{-1} are observed at ~100 - 200 m, while in the central equatorial Pacific, concentrations of up to 0.4 μg L^{-1} are observed between 50 and 60 m. The nitrate depletion at 0°, 155°W during late 1997 altered the chlorophyll profile such that it closely resembled that of the HOT climatology, with a subsurface maximum of 0.22 μg L^{-1} at 100 m, corresponding to the depth of the nitricline.

The phytoplankton assemblage of the equatorial Pacific is dominated by the smaller size class organisms such as prochlorophytes and Synechococcus, but Chavez et al. [1996] encountered several sites dominated by larger diatoms. These sites generally corresponded to regions of higher productivity due to physical phenomena such as upwelling or the equatorial front. The model of Leonard et al. [1999], centered at 0°, 140°W, produced a 40% increase in total chlorophyll from El Niño conditions in 1991-1992 to the cooler conditions of 1994. This increase was largely due to increases in the netphytoplankton, whose contribution to total chlorophyll ranged from 0.1 to 30% throughout the duration of the simulation. Similarly, Bidigare and Ondrusek [1996] measured chlorophyll concentrations in the < 2 μm fraction that were virtually unchanged between February-March 1992 (El Niño) and August-September 1992 (upwelling). In the same time period, the eukaryotic biomass (including diatoms) underwent significant increases, most notably at several sites near the equator. During El Niño conditions, the < 2 and > 14 μm size fractions accounted for 92 and 3% of the total chlorophyll, respectively, while during

cooler conditions these percentages were 81 and 12%, indicative of the increased importance of larger cell classes. The size fractionated chlorophyll data from 155°W and 170°W spanning the peak of the 1997-1998 El Niño through until late 1998 (Figure 6) suggest a change in species composition from dominance of the smaller size classes to an assemblage where diatoms contributed ~30% of the total chlorophyll. This change in species composition undoubtedly has consequences for nutrient consumption and export, specifically relative rates of silicate uptake.

Fluctuations in integrated productivity during the 1997-1998 El Niño-La Niña transition were ecologically significant, but the magnitude of the observed perturbations is more dramatic if the mean productivity in the euphotic zone is considered. During El Niño, the euphotic depth is greater because of reduced attenuation of light by chlorophyll and other particles. Hence, the greater depth over which integration is occurring will inflate productivity integrated over the euphotic zone. During La Niña, the opposite is true, and so comparison of integrated productivity between El Niño and La Niña may not reflect the true effect of the productivity perturbations on the ecosystem. Figure 12 shows the mean productivity of the euphotic zone for the same time periods and stations that were depicted as integrated values in Figure 7. During the height of the El Niño event, in November 1997, mean productivity in the euphotic zone, 5°N to 5°S, along 155°W and 170°W was 3.4 ± 1.8 mg C m^{-3} d^{-1} (where 1.8 is the standard deviation of the mean). By June 1998 this figure had increased to 5.8 ± 3.4 mg C m^{-3} d^{-1} owing mainly to the enhanced productivity close to the equator, and as productivity at the poleward stations increased, the 5°N to 5°S mean reached 8.5 ± 3.3 mg C m^{-3} d^{-1}. Between 1°N and 1°S productivity increased from 2.9 ± 0.7 to 11.9 ± 4.0 mg C m^{-3} d^{-1}. Higher trophic levels, zooplankton and their predators, likely respond to this mean productivity, as it corresponds to lower density of prey items during El Niño. Thus fluctuations in higher trophic level organisms are perhaps greater than would be inferred from the integrated productivity data [Lehodey et al., 1998]. This phenomenon also has consequences for particle export in the form of zooplankton fecal matter and perhaps also particulate aggregation, as these processes depend on the mean density of particles, rather than integrated particle abundance in the euphotic zone.

The above-stated mean primary productivity along 155°W and 170°W between 5°N and 5°S in November 1997 was 0.41 ± 0.22 g C m^{-2} d^{-1}. Incorporating additional measurements made along 125°W, 140°W (October 1997) and 180° (November 1997), the mean primary productivity for 5°N to 5°S, 125°W to 180° equates to 0.47 ± 0.21 g C m^{-2} d^{-1}. This is probably a slight over estimation of the mean "El Niño primary productivity," as it includes data from 125°W and 140°W at a time when the event was not fully developed in that region. Nonetheless, this is approximately half the climatological mean of 0.9 g C m^{-2} d^{-1} described by Chavez et al. [1996] and, if extended to 90°W, implies an annual primary production in the Wyrtki [1981] box of ~1.90 × 10^{15} g C y^{-1}, compared to 3.65 × 10^{15} g C y^{-1} determined by Chavez et al. [1996]. Given these productivity levels and the very low levels of surface nitrate depicted in Figure 9a, rates of new production must have also declined dramatically during late 1997 to early 1998. During 1998, as upwelling returned, productivity in the central Pacific exceeded the climatological mean. In June and October/November 1998, the 5°N to 5°S mean productivity along 155°W and 170°W was 0.70 ± 0.41 and 1.03 ± 0.39 g C m^{-2} d^{-1}, respectively. These figures extrapolate to 2.84 and 4.15 × 10^{15} g C y^{-1} in the Wyrtki box, respectively. Our observations suggest that primary productivity in the equatorial

Pacific fluctuated at least twofold between the El Niño and the cool conditions that followed in 1998. On longer timescales, after accounting for the dramatic decrease in productivity described above, our 1998 productivity data suggest a continuation of the general increasing trend, observed since 1986 by *Chavez et al.* [1996]. Continued observations in the equatorial Pacific may help to further elucidate this phenomenon.

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