Biogeochemical Conditions in the Equatorial Pacific in Late 1994

New Production, Oct 15, 1994 (mmol m$^{-2}$ d$^{-1}$)

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Stocks and fluxes of biogenic silica in the western oligotrophic equatorial Pacific

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Abstract. During a cruise along the 165°E meridian (6°N-15°S), distributions of biogenic silica (BSi) and of chlorophyll a were studied. BSi ranged between 10 and 60 nmol L⁻¹ in the nitrate-depleted surface layer. A deep BSi maximum (DBSiM) layer was located at the base of the photic layer. The high mesoscale variability in BSi distribution is explained as resulting from a combination of physical and chemical forcings. For studying the response of the tropical/equatorial ecosystem to physical forcing, BSi is a more sensitive tracer than chlorophyll a. Daily variations of stocks and fluxes of biogenic silica in the 0-340 m layer were measured at a drifting station during a 5-day experiment at 0°S, 167°E. Displacement of the pycnocline occurred at the drifting station, allowing injection of new nutrients in the photic layer to which the ecosystem reacted by an increase of BSi in the DBSiM layer. We hypothesize that this BSi increase is explained by increased diatom growth (at a rate of 0.6 doublings d⁻¹). At this drifting station, sediment traps were deployed below the photic layer (at 125, 175, 240, and 340 m depths) to estimate export fluxes of BSi. They ranged between 60 μmol m⁻² d⁻¹ at 125 m and 180 μmol m⁻² d⁻¹ at 340 m. Compared to a BSi production of 960 μmol m⁻² d⁻¹ measured 1 week later during the same cruise in similar oligotrophic equatorial waters, such low export fluxes suggest that dissolution of BSi might be high in the warm equatorial Pacific waters.

1. Introduction

The strong net flux of CO₂ from the surface ocean to the atmosphere located in the eastern and central equatorial Pacific [Tans et al., 1990] has triggered numerous biogeochemical studies in these regions [Murray, 1995, 1996]. Most studies, including interannual variations due to El Niño-Southern Oscillation (ENSO) events, were focused on the nutrient rich zone located east of the date line. Nevertheless, the western equatorial Pacific, although less studied so far, has been identified as playing a key role in the interaction between the ocean and the atmosphere, driving the ENSO cycles [McPhaden and Picaud, 1990]. The comparison between El Niño and non-El Niño situations demonstrates their impact on the biomass and primary production in the warm pool [Barnett et al., 1988; Blanchot et al., 1992; Le Bouteiller et al., 1992]. From a biogeochemical point of view the western equatorial Pacific exhibits most of the features of oligotrophic areas and has been considered similar to the subtropical gyres [Barber and Chavez, 1991]. The phytoplankton biomass is largely dominated by small-sized cells taking part in an active microbial loop. New production, as well as the export of biogenic matter from the euphotic layer, is low. The water column is characterized by nitrate-depleted surface waters separated from deep water by a sharp nutricline. As pointed out by Mackey et al. [1995], however, the analogy between subtropical gyres and the oligotrophic western tropical Pacific does not extend to oceanic circulation: four regions with different distributions of nitrate and chlorophyll relative to thermohaline structure have been distinguished along 165°E by Radeac and Rodier [1995].

It is generally accepted that in the world ocean, diatoms should account for a significant part of the export production from the euphotic zone [Goldman, 1988]. In the oligotrophic ecosystems the nutrient-depleted warm surface waters are unfavorable to diatoms [Smeltekop, 1985], and they principally grow at low levels of light near the base of the euphotic zone where high nutrient concentrations exist. Blain et al. [1997] estimated that 10% of the carbon production in the oligotrophic water of the equatorial Pacific can be attributed to diatom growth. The magnitude and variability of their contribution to the primary production of these systems are highly dependent on the input of new nutrients in the euphotic zone. These inputs are suspected to be stochastic and difficult to document. Jenkins [1988] gives indirect evidences of such events in the Sargasso Sea, and McGowan and Hayward [1978] suggested physical processes such as shear-induced turbulence and breaking of internal waves acting as a nutrient pump in the oligotrophic central gyre of the North Pacific. Theoretical supports have also been reported to explain episodic mixing events and biological mesoscale variability [Klein and Coste, 1984; Klein and Hua, 1988].

Biogenic silica (BSi) is exported to the deep ocean by different way of transportation including direct sedimentation of diatoms...
or faecal pellets settling down. The prediction of the sinking of diatoms is complex because they have physiological control over buoyancy [Smetacek, 1985; Bienfang et al., 1982]. Thus the sinking rate is highly dependent upon environmental conditions. In addition, sporadic events previously described could be considered hydrodynamic singularities in the bifurcation model of Legendre and Le Fèvre [1989]. These singularities could favor, at different bifurcations, production export over in situ recycling, leading to high variability in the contribution of diatoms to export fluxes. Despite the potential role of diatoms in export production in oligotrophic waters the minor contribution of diatoms to biomass and production had likely precluded the silica cycle from further investigations until very recent times.

The first extensive study of the silica cycle in an oligotrophic area has been reported by Brzezinski and Nelson [1995] for the Sargasso Sea (Joint Global Ocean Flux Study (JGOFS)/Bermuda-Atlantic times series study). A tight coupling between BSi accumulation in the surface waters and export from the euphotic zone has been evidenced. Brzezinski and Nelson estimated that the diatom contribution of new and export N production had to be over 26%. They suggested that this could be a lower limit due to low subsurface [Si(OH)4]:[NO₃⁻].

This paper reports on variations of stocks and fluxes of BSi in the oligotrophic equatorial Pacific in October 1993. Export of biogenic silica was simultaneously measured at a drifting station for 5 days. A rapid response of the diatoms to modification of the environmental conditions has been assumed to explain the observed increasing in BSI production and export following injection of nutrients in the surface layer. The combined role of environmental factors and hydrodynamical structures is also illustrated by the BSI distribution along a 5°N-16°S transect.

2. Methods

Data were collected during the Flux dans l'ouest du Pacific Equatorial (FLUPAC)/JGOFS cruise. The results we report hereafter refer to the first part of the cruise (Figure 1) including a transect along 165°E from 16°S to 5°N (from September 23 to October 1, 1994) and a drifting station around 0°N, 167°E where the ship followed the drift of floating sediment traps (from October 2 to October 7, 1994). Conductivity-temperature-depth (CTD) casts were carried out every 4 hours at each station. Ocean currents were also obtained from onboard acoustic Doppler current profiler (ADCP) instruments. A short-range 300 kHz instrument of 4 m vertical resolution and first bin at 12 m was used in the first 140 m. Deepest measurements (up to 700 m) resulted form a long-range 75 kHz instrument with a vertical resolution of 16 m. Details on validation and data processing are given by Le Borgne et al. [1995] and Eldin et al. [1997]. Samples for nutrient determinations were collected at 12 depths between 0 and 200 m. The samples were analyzed onboard with Technicon II analyzers, according to Strickland and Parsons [1972].

2.1. BSi

One or two liters of seawater were filtered immediately after collection under a gentle vacuum through 0.6 µm nuclepore membranes. The filter was dried for 12 hours at 60°C and stored in plastic petri dishes before analysis. BSi analyses were performed using the NaOH digestion method [Paasche, 1973] modified by Raguenneau and Tréguer [1994]. The blank was 8 nmol L⁻¹ and the limit of detection determined as 3 times the standard deviation of the blank was 5 nmol L⁻¹.

2.2. Trap Deployments

The fluxes of settling material were measured with short-term free-drifting sediment traps. The trap systems were designed by Technicap (France) and consisted of six or eight individual baffled polycarbonate cylinders mounted on a stainless steel circular frame. Each cylinder (collection area = 0.005 m²) was opaque and had a 7:1 aspect ratio (height: diameter). The trap arrays deployed three times for ~43 hours during the first FLUPAC time series station at 167°E. Four depths below the mixed layer and euphotic zone were sampled: 125, 175, 240, and 340 m. Exact deployment depths were continuously recorded by two internal recording pressure-sensor-temperature systems (Micrel) fixed on the first and third trap arrays. Traps were closed prior to retrieval by a programmable release system.

Prior to deployment the collectors (capacity of 2.850 L each) were filled with 0.2 µm of filtered surface seawater for two thirds of the volume. A high-density solution (adding 50 g of NaCl to each liter of filtered water) was added at the bottom up to the last third [U.S. JGOFS, 1989]. No preservatives were added to the brine solution. A portion of this trap was saved for analysis of the blank.

Immediately upon recovery, the entire contents of each trap were water-sieved through a 700 µm mesh, and only the fraction <700 µm was included in the analysis and the determination of the fluxes. BSi was measured with the same analytical method as the water column samples. The brine was analyzed at the end of the trap deployment to get the Si that dissolved from trapped material.

![Figure 1. Location of the transect and the drifting station (square) during the Flux dans l'Ouest du Pacifique Equatorial (FLUPAC) cruise. Hydrocasts were performed each degree of latitude during the meridional transect and every 4 hours at the drifting station. The track of the ship following the drifting sediment traps is also shown. The numbers are related to the stations discussed in the text.](image-url)
3. Results

3.1. BSI Distribution Along 165°E

The distribution of BSI along 165°E varied greatly (Figure 2), ranging from <8 to 338 nmol L⁻¹. The regions with high integrated BSI alternated with regions with lower integrated BSI. The locations of the different areas varied by only 3° latitude. At 15°S the profile showed a slight deep maximum of 54 nmol L⁻¹ at 135 m deep. Moving northward, the deep BSI maximum (DBSiM) reached 60 m, and the maximal concentration reached 108 nmol L⁻¹ at 11°S. Then, from 11° to 6°S the DBSiM stayed roughly the same, and few variations were observed in the BSI content of the water column. In this area the integrated BSI was maximal at 7°S, and high concentrations of BSI were measured up to the surface vicinity at this station. The stations at 5° and 4°S had some of the lowest concentrations encountered along the transect. Other areas with concentrations ~100 nmol L⁻¹ were located from 3° to 1°S. The DBSiM was between 80 and 40 m deep. From the equator to 2°S the concentrations were still very low, and DBSiM sank to between 80 and 100 m deep. Finally, the region from 3° to 5°S showed the highest integrated BSI measured along the transect. As observed at 7°S, a BSI concentration of 80 nmol L⁻¹ was observed in surface waters at 3°N. The last sampled station along the transect, at 6°N, was separated from the previous rich BSI area by a very strong gradient of biogenic silica; that is, the maximum BSI concentration decreased from 233 to 65 nmol L⁻¹.

3.2. Drifting Station

3.2.1. Hydrodynamic context. At a free-drifting station the ship is expected to follow the same water mass. However, wind-current interactions on the floating buoy as well as complex vertical profiles of current-generating shears (Figure 3) could more or less invalidate this assumption. The zonal component of the currents was very stable during the 5 days of the study. In the surface waters (0-100 m) the current (measured by ADCP) flowed westward (velocity maximum at 90 m), whereas the flow was eastward between 140 and 260 m because of the equatorial undercurrent. Below 260 m the current was again flowing westward. Thus the resulting zonal drift of the floating traps was westward (Figure 1). During the first 2 days of the study, meridional currents were in opposite directions above and below 120 m (Figure 3). The resultant drift was slightly southward (Figure 1). After station 37 and by the end of this study the meridional component was northward in the whole water column (Figure 3), leading to the same direction for the meridional component of the drift (Figure 1).

The density profiles are shown in Figure 4a. A strong pycnocline was generally observed at ~100 m. However, evidence of the variability of the depth and the shape of the pycnocline from one station to another was found in the 80-100 m layer, probably associated with vertical displacements by internal waves. The density stratification was estimated from the computation of the Brunt-Väisälä frequency $N^2 = g \, \text{d} \phi / \text{dz}$ and the squared vertical shears from the calculation of $\text{Sh}^2 = (\text{dU}/\text{dz})^2 + (\text{dV}/\text{dz})^2$. The dynamic stability of the water $R_i = N^2/\text{Sh}^2$ column was then deduced from the Richardson number (Figure 4b). In the upper part of the water column, $R_i$ was close to 1, indicating that static stability and vertical shear balanced each other to create moderate mixing conditions. In the core of the pycnocline, $R_i$ reached maximum values (Figure 4b), resulting from the high static stability. This area is closely encompassed between two regions with small $R_i$. In particular, at the top of the pycnocline, $R_i$ was below the critical value $R_i = 0.25$, indicating instability in the shear flow. The nitrate profiles (Figure 4c) are typical of oligotrophic waters. Nutrient-depleted surface waters, with concentration below the limit of detection (3 nM) of the nitrate sensitive colorimetric method [Oudot and Montel 1988], were separated from deep nitrate-enriched waters by a strong gradient region. Silicic acid presented the same sort of profile, but the upper mixed layer was depleted, with concentrations varying from 1 to 2 μM.

3.2.2. BSI distribution. The time course of the vertical distribution of BSI at the drifting station is shown in Figure 5a. The mean vertical profile is reported in Figure 5b. The concentrations in the surface layer (0-60 m) ranged from 10 to 20 nmol L⁻¹, and all the profiles showed a clear maximum of BSI at ~100 m depth. This maximum, located near the nutricline, coincided with that of chlorophyll (Figure 5). During the first 3 days (stations 23, 29 and, 35), BSI showed little variation. The standing stock of BSI in the upper 120 m (Figure 5) slightly decreased from 2.44 to 2.08 mmol m⁻³. At station 41, below 30 m, BSI increased for all depths (Figure 5a). The integrated BSI increased to 3.00 mmol m⁻³ (Figure 6). During the following 2 days, above 70 m the BSI decreased to <15 nmol L⁻¹ (Figure 5a). The values then were very similar to those measured during the first 3 days. However, near the maximum of BSI the concentrations stayed roughly 25% higher than at stations 23, 29, and 35.

3.2.3. BSI fluxes measured from drifting sediment traps. The BSI fluxes measured at the four depths (125, 175, 240, and 340 m) are reported in Figure 7. Numerous studies indicate that particle fluxes deduced from surface-tethered sediment traps may be altered by various biases [Buesseler, 1991], and this issue still generates lively debates [Boyd and Newton, 1997; Rivkin et al., 1997]. Zooplankton entering the trap and the exchange of water contained within the trap with surrounding seawater have been identified as the main causes of biases and called "swimmers" and "hydrodynamic effects," respectively.

Collection efficiency has been estimated [Dunne, 1995] from ²³⁵Th method [Moore et al., 1981; Coale and Bruland, 1987]. The results show a slight overestimation of the fluxes deduced from the trap in relation to the model of Murray et al. [1996]. At 125 and 170 m the ratio between the flux measured in the trap and the flux calculated by the model are 1.7 ± 0.1 and 1.4 ± 0.3, respectively. Little bias was observed at 240 m (1.1 ± 0.4). No estimation existed for 340 m; but there is no reason to believe that the bias was dramatically different from the estimations at upper depths. Thus the high current velocities in the studied area did not seem to alter significantly from the flux measurements [Rodier and Le Borgne, 1997].

For all the deployments, except at 175 m during the third, we observed an increase in the fluxes with depth (Figure 7). This pattern is frequently described for deep or shallow sediment traps [Takahashi, 1986; Brzezinski and Nelson, 1996]. Siegel et al. [1990], performing a Lagrangian analysis of particle sinking through a random mesoscale eddy field, concluded that such a process may explain the observed "inverted" flux profiles. This analysis is rigorously applicable only to fixed sediment traps, but Siegel et al. [1990] suggested that similar features may also be observable with free-drifting sediment traps. In the particular case of the equatorial Pacific another explanation might be
Figure 2. Contour of (a) chlorophyll and (b) biogenic silica (BSi) concentrations along the south-north transect at 165°E. (c) The integrated (0-180 m) BSi concentration.

proposed. Indeed, a qualitative observations, of the material collected within the traps showed an increase in the number of radiolarians with depth (M.J. Chrétiennot-Dinet, personal communication, 1997). Radiolarians are siliceous organisms and no methodological work exists to demonstrate whether or not they dissolve during the alkalin digestion used in the BSi measurement. Nevertheless, it seems reasonable to assume that a part dissolves and, consequently, that radiolarians contribute more or less to BSi. The increase in the BSi flux related to the increase of radiolarians with depth then may be an alternative explanation to the variation of the silica fluxes with depth.

The dissolution of the collected material within the trap was not exactly calculated. We deduced the maximum amount of BSi that may have dissolved assuming no seawater mixed with the
brine solution initially filling the trap and measuring the silicic acid concentration in the supernatant at the end of the deployment. As shown in Figure 7, the contribution of the dissolution was within the standard deviation for a duplicate analysis of material from different traps at the same depth. In the discussion then we used the BSI fluxes estimated from BSI measurements without any correction.

Except for a low value at 175 m the fluxes were very similar for the first and the third deployments (Figure 7). During the first deployment they increased from 60 μmol m^-2 d^-1 at 125 m to 123 μmol m^-2 d^-1 at 340 m. During the second deployment we observed higher fluxes varying from 89 μmol m^-2 d^-1 at 125 m to 159 μmol m^-2 d^-1 at 340 m.

4. Discussion

4.1. Standing Stock and Fluxes of BSI During Steady Oligotrophic Conditions

The standing stock of BSI was 3.0 ± 0.5 mmol m^-2 (mean and standard deviation) in the upper 150 m during the 5 days, very similar to the value of 2.7 ± 0.9 mmol m^-2 reported by Brzezinski and Nelson [1995] for the Sargasso Sea during nonbloom conditions. The BSI fluxes measured during our cruise were also comparable to those reported by Brzezinski and Nelson [1995] for the months following the bloom periods (March-July 1992) and slightly higher than the fluxes for fall and early winter (August-December 1991). Because these fluxes prevailed most of the year, the observed agreement between values measured at different sites would suggest that a range of 50-100 μmol m^-2 d^-1 is a good estimation of the BSI flux through 300 m in oligotrophic waters of the world ocean.

Except for station 41, which will be discussed in the next section, the constancy of the integrated BSI stock from day to day suggests that steady state conditions might prevail for the silica cycle. In other words the net BSI production should be nil, and Si assimilation by phytoplankton should be balanced by losses, dissolution, and export. The silica export at 125 m deep, deduced from the material collected in sediment traps, was 60 μmol m^-2 d^-1. BSI production was not measured at the drifting station; however, during the following week a BSI production of 960 μmol m^-2 d^-1 was measured in the 0-125 m layer at stations located along the equator [Blain et al., 1997]. Because nutrient profiles and light availability were similar at the drifting station and at the stations along the equator, we believe the estimate of BSI production to be realistic for our study period. If this is correct, the export of BSI at 125 m represented only 60/960 = 6.3% of the BSI production. This suggests that the dissolution of BSI might be high in the warm oligotrophic equatorial water. The percentage of Si production that dissolves in the surface waters of the world ocean varies over a wide range [Nelson et al., 1995; Tréguer et al., 1995], from 10% of the production in the coastal upwelling of Peru or southern California [Nelson et al., 1981] to nearly 100% in the Atlantic Ocean west of the Sahara [Nelson and Goering, 1977]. Temperature is recognized as a major factor regulating the silica dissolution [Kamatani et al., 1988]. Sea surface temperatures of the warm equatorial pool were 28-30°C, among the highest in the world ocean. Thus it is so not surprising that the Si dissolution process were so efficient. However, it is likely that dissolution did not operate at the same rate in the warm mixed layer and below the DBSiM because environmental conditions (temperature, nutrient abundance, and stratification) and biological features (species composition and specific surface area of diatom cells) were highly different in both regions. By comparison, in the Sargasso Sea, 80% of the Si produced in the 0-150 m layer dissolves [Nelson and Brzezinski, 1998; Brzezinski and Nelson, 1996]. Although preliminary, our estimate strengthens Nelson and Brzezinski's [1996] hypothesis that the high ratio of Si dissolution to Si production is not necessarily associated with diatom abundance and may be a common pattern of oligotrophic ecosystems.

Dugdale et al. [1995] and Dugdale and Wilkerson [1998] identified the silica pump as a potential cause of limitation of the diatom growth in some ecosystems. In our case, 60 μmol m^-2 d^-1 of "new" silicic acid was required at 100 m to sustain the steady state. Despite the poor resolution of the nutrient profiles in the nutricline (scale 20 m) we estimated d(Si)/dz, in the range 0.16-0.05 mmol m^-4 at 100 m. Using the vertical average diffusivity KE, 10^-5 m^2 s^-1 estimated by Mackey et al. [1995] at 155°E in the equatorial Pacific, we deduce a Si flux ranging from 0.140 to 0.043 mmol m^-2 d^-1, high enough to prevent depletion of the surface water and consistent with the steady state hypothesis.

4.2. Impact of a Mixing Event on the Stocks and Fluxes of BSI

4.2.1. Variability of nitrate availability. As shown in Figure 6, integrated BSI in the 0-120 m layer significantly
Figure 4. Density profiles for 30 stations (23 - 53) with a 4 hour time interval resolution (4 m). (b) Richardson number profiles for the stations 35 and 36 with a 12 m resolution space scale. (c) Nitrate profiles for stations 23-53.

Figure 5. (a) Time course of BSi concentration (nmol L\(^{-1}\)) in the upper 200 m at the equator during the 5 days at the drifting station. (b) Mean BSi profile. The error bars represent 1 standard deviation. The mean chlorophyll profile (dotted line) is also shown.
increased during the fourth day (station 41). The understanding of the origin of such events is of prime importance because they could important contributors to the annual Si production.

The variability of oligotrophic ecosystems has been known for a long time. Menzel and Ryther [1960, 1961] described a seasonal variability associated with a spring bloom in the Sargasso Sea. Recent time series studies in subtropical gyres (Atlantic and Pacific) have definitely confirmed the variability of these ecosystems at different timescales. During the Bermuda Atlantic Time Series Study (BATS), seasonal and interannual variabilities were clearly evidenced [Michaels and Nisbet, 1996; Bates et al., 1996]. Doney et al. [1996], using a one-dimensional biological-physical model, successfully reproduced these long-term seasonal cycles. The biological component of the model was only based on carbon and nitrogen cycles. However, Brzezinski and Nelson [1995] clearly demonstrated the impact of this annual winter-spring bloom on the cycle of another major nutrient such as Si.

In the same manner the now available time series data set [Karl and Michaels, 1996] in the North Pacific gyre (The Hawaiian Ocean Time-series stresses the unexpected and high variability of this open-ocean ecosystem [Bingham and Lukas, 1996; Letellier et al., 1996; Karl et al., 1996]. In particular, the times series studies [Karl and Lukas, 1996] confirm the previously reported discrepancy between the measured rates of primary production and the required nutrient supply [Hayward, 1987]. Several hypothesis have been emitted to reconcile both approaches. The steady state across-isopycnal nitrate diffusion rates for the oligotrophic Pacific has been rejected by Karl et al. [1992]. Nitrogen fixation by diazotrophic organisms, such as Trichodesmium [Karl et al., 1992], the transfer of nutrient from the deep nutrient rich water to the surface layer by Rhizosolenia [Villareal et al., 1993], or mixing events driven by advection [Jenkins, 1987] may also contribute to the nutrient pump. Klein and Coste [1984], using a one-dimensional model, demonstrated that the windstress-current interaction is also a possible mechanism for nutrient injection.

The time course of integrated nitrate (0-100 m; Figure 8), demonstrated the very high variability of this parameter at short time scales. For example, the time course increased from near 0 (station 35) up to 125 μmol m⁻² (station 36) in less than 4 hours. Such events have already been reported for the oligotrophic region. During the 5 years of the HOT study, Karl et al. [1996] reported four episodic events which are believed to be manifestations of mixing/stirring processes. However, a one-dimensional analysis of time series data could lead to erroneous conclusions if horizontal advection caused a number of the observed vertical features. Siegel et al. [1995] and Michaels et al. [1994] highlighted the likely role of mesoscale eddies in the biological variability. In our case, considering a maximum horizontal velocity of 60 cm s⁻¹ in the upper part of the water column, water located 100 km northward of the equator (roughly

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Figure 6. Time courses of integrated BSI (0-120 m). The horizontal rectangles represent the duration of the three deployments of the sediment traps.

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Figure 7. Export flux of Si measured in drifting sediment traps. The error bar represents 1 standard deviation of duplicate analysis. The non-shaded areas represent the contribution to the total flux of the dissolution of the collected material within the traps (see text for details and discussion).
between the equator and 1°N) may have been advected through the studied place during the first 2 days. The north-south transect carried out a few days prior to the study did not reveal any strong horizontal gradient in density or nutrient concentrations on this space scale [Radenac and Rodier, 1996]. This supports our hypothesis that the observed features resulted from local vertical processes.

Among the numerous mechanisms proposed for explaining episodic nutrient injections, a physical model based on the breaking of internal waves has been described by McGowan and Hayward [1978]. Karl et al. [1996] reported measurements consistent with such a mechanism at Airborne Lidar Observations of Hawaiian Aflow (ALOHA) station. In the central equatorial Pacific (140°W), Moun et al. [1992] deduced from microstructure measurements that internal waves are the main source of mixing in the thermocline above the Equatorial Undercurrent. For the same area, McPhaden and Peters [1992] brought evidences of diurnal variations in turbulent dissipation rates which penetrated into the stable thermocline. During our study at site 0°, 167°E, the water column was also characterized by low Richardson number regions (Figure 4b). Microstructure measurements were not performed during the cruise; nevertheless, the time courses of density and nitrate concentrations at 100 and 80 m show (Figure 9) vertical displacements, suggesting internal wave activity at the pycnocline level. It is thus likely that this activity, associated with high shear, produced irreversible mixing.

### 4.2.2. Biological response.

Several hours after the nutrient injection, a peak of integrated BSI was measured in the 0-120 m layer (Figure 6). It reached up to 3.0 nmol m⁻², i.e., 0.7 nmol m⁻² higher than the mean value of 2.3 nmol m⁻². Twenty-four hours later, it had disappeared. We assume the biomass increase is linked to the episodic injection of nitrate. However, this cannot be done without a thorough examination of the situation because the nutrient injection also coincided with the shoaling of the pycnocline. Using a theoretical model, Kamykowski [1974] concluded that internal tides can contribute significantly to the biological variability at a geographic location. Supporting field observations have also been reported [Cullen et al., 1983; Vandevelde et al., 1987]. The vertical motion of water may have concentrated the biomass in a shallower layer, leading to an increase of the BSI concentration. In the upper part of the water column (above 100 m) a vertical motion of water (amplitude of 20 m), rather than production, is thus likely to explain the unusual observed pattern at station 41. In contrast, if one considers a deepest layer (140-100 m) the results are different. At station 35 the (140-100 m) integrated BSI was 0.73 nmol m⁻². The upwelling of this water column (amplitude 20 m) cannot explain by itself the (120-80 m) integrated BSI of 1.41 nmol m⁻² measured at station 41. At the base of the euphotic zone, BSI production rather than vertical motion of water may thus explain the vertical distribution observed at station 41. The upwelling of dense and nitrate rich water at 100 m deep occurred at station 36 (Figure 9). The ecosystem thus seems to respond quickly to the perturbation. Twenty hours later, the biogenic silica concentration was 67% higher at 100 m. This increase corresponds to a net Si production of

\[ [(BSI)_{40}-(BSI)_{35}] \Delta t = 0.8 \text{ nmol L}^{-1} \text{ h}^{-1} \]

or to a net specific growth rate of

\[ [(BSI)_{40}-(BSI)_{35}] / \Delta t = 0.6 \text{ d}^{-1} \]

Actually, this value is in good agreement with the specific growth rate of 0.7 ± 0.3 d⁻¹ measured by the ³²Si method along the equator at stations where similar environmental conditions prevailed (light level of 1% of the surface incident light and nitrate concentration of 3 μM) [Blain et al., 1997]. This estimated growth rate is also in good agreement with the value reported by Goldman [1983], who demonstrated that values of 1.0 ± 0.1 doubling per day may be common for the growth rate of large diatoms under low light level conditions. The injection of nitrate was also effective at 80 m but on a shorter timescale (< 8 hours) (Figure 9). If production was the single cause of the BSI peak, the net production rate would have been of 2 nmol L⁻¹ h⁻¹ or 3.7 doubling per day. Obviously, the latter value is out of the acceptable range as far as rates of biological processes are concerned. Thus physical mechanisms must be the major cause of the anomalously high BSI concentration at 80 m. At stations 47 and 53 the BSI concentrations above 80 m were very similar to those of stations 23, 29 and 35 (Figure 5). Downwelling would explain this pattern in the same way as upwelling caused the increase. At 100 m the decrease was weaker; BSI concentration higher than 30 nmol L⁻¹ persisted for the next 48 hours. However, the similarity between BSI profiles at these two stations suggests that the system was back to a steady state.

### 4.2.3. BSI export.

The biomass excess produced was rapidly exported or regenerated. As shown in Figure 6 the peak of BSI stock was included in the second period of trap deployment. In Figure 7 the expected increase in BSI export is evident. At 125 m depth the increase of BSI export was 30 μmol m⁻² d⁻¹. This feature was similar at all deeps. It is accordingly possible to estimate a total additional export of 48 μmol m⁻² d⁻¹ during the second deployment, which is the difference between the mean of the fluxes at all depths during the second deployment and the mean of the fluxes at all depths during the first and third deployments. Only 7% of the additional BSI production due to the nutrient injection is exported. Consequently, 632 μmol m⁻² of silicic acid should dissolve in the 0-340 m water column. However, this leads to an undetectable variation in silicic acid concentration. On the other hand, assuming that the increase in export flux at 340 m resulted from particles produced, at the most, 24 hours earlier in the surface layer we estimate a sinking rate within the range 100-200 m d⁻¹. This is much higher than sedimentation rates for single cells [Smayda, 1970]. Aggregation

![Figure 8. Time courses of vertically integrated nitrate and silicic acid in the 0-100 m layer at the drifting station.](image)
is now recognized as a major way of controlling the sinking of diatoms [Smetacek, 1985]. Aggregates with chains connected at a central mass composed of faecal material have also been reported by Buck and Chavez [1994] for the equatorial Pacific. The excretion of exopolymer by diatoms and the aggregation as transparent exopolymer particles (TEP) [Alldredge et al., 1995; Passow and Alldredge, 1995] is another well-studied mechanism which explains high sedimentation rates. Examination of the material collected in the water column shows that the first cited mechanism for aggregation may contribute to the sinking of diatoms in the equatorial Pacific. However, the direct aggregation of diatoms themselves is the only mechanism which could support the short time lag observed between production and export during the episodic growth event. Unfortunately, conventional sampling and observation procedures preclude the microscopic confirmation of this assumption. However, the microscopic observations at a very similar location [Blain et al., 1997] indicated that pennate diatoms were dominant in the water column. Large pennate (50-1000 μm size) contributed 40% of the total BSI at 90 m. The occurrence of such species can be considered as favorable to the formation of floculant masses. Sancetta et al., [1991] suggested that massive fluxes of Rhizosolenids may be a common feature because of a rapid loss of buoyancy by a slowly growing population. This hypothesis applied very well to diatom growing at low light levels near the nutricline in the oligotrophic system. In conclusion, the high variability in the environmental conditions, mainly light and nutrient availability at the depth of the deep maximum of chlorophyll in oligotrophic water, at very short timescales can drive a rapid increase in diatom growth when conditions become more favorable and rapid export when they deteriorate.

4.3. BSI Distribution and Mesoscale Hydrodynamic Structure Along 165°E

Radenac and Rodier [1996] reported a further description of the nitrate and chlorophyll distributions associated with the thermohaline and current structures in the western tropical Pacific (165°E, 20°S-10°N). This study was based on 14 transects carried out from 1985 to 1989, and different typical situations resulting from El Niño, La Niña, and reference conditions were described. The situation encountered in October 1994 was very similar to what were called “reference conditions.” The highest concentrations observed in the biogenic silica transect (Figure 2) were all associated with particular thermohaline and current structures. The South Equatorial Current flowed westward from 4°N to 4°S. At these latitudes it was flanked by two eastward flows, the North Equatorial Countercurrent and the South Equatorial Countercurrent. This led to moderate convergence and salinity fronts. The highest subsurface maxima of BSI were associated with these structures and may result from the accumulation of diatoms near the barrier layer.

Another important feature of the distribution of the BSI along 165°E is the occurrence of two regions where relatively high concentrations (> 40 nmol L⁻¹) reached surface waters but no nitrate was detected. Two hypotheses can be suggested to explain this fact.

1. High biomass in nitrate-depleted surface waters have been reported occasionally at 10°S [Le Borgne et al., 1992; Blanchot et al., 1992]. This feature appears to be associated with a doming structure but is highly variable in time and space [Radenac and Rodier, 1996; Dandonneau, 1992]. In 1987, nitrate enrichment, which caused enhanced chlorophyll concentrations in surface water, had disappeared 3 weeks later, whereas anomalous chlorophyll concentrations higher than usual were still measured. In our case the variation of the BSI signal was not associated with the variation of the chlorophyll signal with a similar amplitude. A possible explanation then is that a few days or weeks before a pulse of nitrate had led to diatom production in surface water but that most of the living cells had vanished at the time of observation and the biogenic silica was mainly detritic material.

Figure 9. Time courses of density and nitrate concentrations at (a) and (b) 80 m and (c) and (d) 100 m.
2. The two places were the unique regions of the transect with surface water flowing eastward (North and South Equatorial Countercurrents). The biogenic silica may have been advected from region of highest Si productivity located west of 165°E. This hypothesis would be most plausible at 6°-8°S, where numerous islands are located close enough upstream of the studied site. The hypothesis is more speculative at 2°-4°N, where the nearest coastal waters are 3000 km away and where no data exist to assess the occurrence of an offshore enriched BSi region at this latitude.

This interpretation of the distribution of BSi along 165°E is preliminary because a single transect is an insufficient basis upon which to conclude firmly the origin of most of the observed features and whether they exist permanently. As demonstrated at the equator in the previous section, it is probable that short-term events contribute to the spatial and time variability. However, the most important information resulting from this first report of BSi in the tropical Pacific comes from the comparison between the chlorophyll a and BSi distribution (Figure 2). Except for surface waters where the BSi increase was noted, at some places, without any correspondent variations in chlorophyll concentration, both distributions presented the same features. However, the variations of BSi concentrations had a much higher amplitude than the variations of chlorophyll. For example, between the stations at 1° and 4°N, BSi increased from 46 to 338 nmol L⁻¹ associated with a chlorophyll increase only from 0.27 to 0.36 mg m⁻³. Thus, whereas the silica cycle study has been neglected in this areas, likely because of the low diatom abundance, the BSi distribution may be a very powerful tool for detecting and studying the spatial and temporal biological variability of the tropical ecosystem in relation to the physical forcing (hydrodynamic and current structures).

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