Zonal variability of plankton and particle export flux in the equatorial Pacific upwelling between 165° E and 150° W

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Abstract – Observations made during a "La Niña" situation (April–May 1996) in the equatorial Pacific upwelling, between 165° E and 150° W, show the classic deepening of hydrological isolines from east to west, resulting in zonal gradients for surface temperature and macronutrients. However, contrasting with such a gradient, no clear zonal variation could be seen for integrated planktonic biomasses and carbon fluxes, namely: chlorophyll *a*, bacterial abundances, particulate organic phosphorus, mesozooplankton ash-free dry weight, primary production, and the sinking flux of particulate organic carbon (POC). Moreover, mean values of these parameters along the zonal equatorial transect, are not significantly different from those of a 7-day-long time series station made at 0°, 150° W in October 1994 during an El Niño period. Such a steady zonal distribution of planktonic parameters seems to be characteristic of equatorial Pacific upwelling west of the Galapagos Islands so that the spatial distributions of nutrient concentrations and planktonic biomass appear to be uncoupled. This is consistent with the High Nutrient-Low Chlorophyll (HNLC) concept, in which primary production is not controlled directly by macronutrient concentrations. The lack of zonal gradient also suggests that carbon budget of the equatorial Pacific is primarily controlled by oscillations in the zonal and meridian extension of the HNLC area, rather than by values of planktonic biomasses and carbon fluxes within the upwelled water, which are quite constant. © Elsevier, Paris / Ifremer / Cnrs / Ird

Equatorial Pacific / zonal variations / plankton / carbon sinking flux / primary production

Résumé – Variabilité zonale des paramètres planctoniques et du flux de particules exportées dans l'*upwelling* équatorial du Pacifique entre 165° E et 150° W. Des observations réalisées en situation de la Niña (avril–mai 1996) dans l'*upwelling* équatorial du Pacifique, considéré entre les longitudes 165° E et 150° W, font apparaître l'approfondissement bien connu des isothermes et isolignes de nitrate d'est en ouest. La conséquence en est la présence d'un gradient zonal de température et de concentrations de sels nutritifs de surface. On n'observe cependant pas de gradient analogue dans les valeurs intégrées des biomasses planctoniques et des flux de carbone, les paramètres suivants étant considérés : chlorophylle *a*, nombre de bactéries, phosphore organique particulaire, poids sec sans cendre de mésozooplancton, production primaire et sédimentation de carbone organique particulaire. De plus, les valeurs moyennes de ces paramètres mesurés le long de la radiale équatoriale, ne sont pas significativement différentes de celles calculées sur les données d'un point fixe équatorial de 7 j à 150° W, réalisé en octobre 1994 pendant un épisode El Niño. Ce caractère monotone de la distribution zonale des paramètres planctoniques semble être typique de l'*upwelling* équatorial du Pacifique, tout au moins dans sa partie située à l'ouest des îles Galapagos. Il apparait ainsi qu'il y a découplage entre les distributions spatiales des sels nutritifs et des biomasses planctoniques, ce qui est en accord avec le concept de situation HNLC (High Nutrient - Low Chlorophyll) pour lequel la production primaire n'est pas sous le contrôle direct des concentrations de sels nutritifs majeurs. Cette absence de gradient zonal des paramètres planctoniques nous amène également à conclure que tout bilan de carbone établi pour le Pacifique équatorial doit avant tout prendre en compte les variations temporelles de superficie de la zone HNLC et non celles des valeurs de biomasse et de flux qui sont relativement constantes au sein de l'*upwelling* équatorial. © Elsevier, Paris / Ifremer / Cnrs / Ird

Pacifique équatorial / variabilité zonale / plancton / sédimentation de carbone / production primaire

1. INTRODUCTION

The equatorial Pacific ocean is considered as the main ocean export source of carbon dioxide to the atmosphere [15, 40]. At the same time it is an important sink of particulate carbon [30]. The absolute magnitudes of these two processes are directly related to the zonal extension of the equatorial upwelling, which appears to oscillate in step with ENSO, El Niño Southern Oscillation [31, 34]. During El Niño events, which are characterized by a negative Southern Oscillation Index (SOI), the western limit of the nutrient-rich upwelling moves to the east, whereas it is west of the dateline during the opposite situation, La Niña, when the SOI is positive. Recently, Inoue et al. [18] presented a correlation between SOI and the longitude of the western border of the upwelling position (as defined by high values of pCO_2), which ranged from 160° W to 150° E during the 1987–1994 period, corresponding to a zonal excursion of 5500 km. Thus, survey of zonal displacement of the cold-tongue upwelling boundary is an important goal of international programmes dealing with the global carbon budget, such as JGOFS (Joint Global Ocean Flux Study).

The cold-tongue upwelling itself is characterized by clear east–west positive temperature and negative nutrient gradients. The zonal variations have been presented in climatological studies [3, 8, 10, 24] and in data of equatorial transect cruises including Alizé 1 in 1964–1965 between 95° W and 162° E [17, 25], Alizé 2 in 1991 between 95° W and 165° E [23, 37], Japanese equatorial transects between 1987 and 1994 [18], US-JGOFS/NOAA meridian transects in 1992 between 90° W and 170° W [11], Flupac equatorial transect in 1994, between 165° E and 150° W [19] and Russian cruises between 90 and 150° W [42]. It was originally hypothesized that planktonic parameters should exhibit a similar zonal gradient, with a "well-known decrease from east to west" [17]. This hypothesis has been difficult to test, owing to both the limited number of observations in this vast area and data heterogeneity, particularly as far as the fluxes are concerned. More recently, however, the increasing data base and knowledge of the functioning of the equatorial upwelling (i.e. a region of "High Nutrient-Low Chlorophyll", HNLC, [29]) led several authors to contest the E–W gradient for phytoplankton [9, 11, 21] and zooplankton biomass and size structure [20].

In the present report, we want to bring additional support of the lack of zonal variability of biological properties on the equator, which seems to be characteristic of this area. Thus, more structural (e.g. biomasses) and functional (e.g. carbon fluxes) parameters of the equatorial upwelling ecosystem will be considered, using data from two cruises which had comparable sampling and analytical methodologies. On purpose, however, no detailed account of any one parameter will be given, since this will be made in other papers. Zonal variations of planktonic biomasses and carbon fluxes were measured during the Zonal Flux cruise (*figure 1*), which was conducted on the R.V. *Thompson* in April–May 1996, during La Niña conditions when the cold tongue extended west of the dateline. Such spatial variations will be compared with short-term ones, obtained during a 7-day time series station made at 150° W in the equatorial upwelling during the Flupac cruise on board R.V. *l'Atalante* in October 1994 [19]. El Niño conditions prevailed at that time and the time series station was representative of the HNLC area encountered east of 172° W.

2. CRUISES

2.1. Zonal Flux equatorial transect

The Zonal Flux cruise (April 15–May 14, 1996) was a joint operation of US JGOFS and ORSTOM/Flupac programme of Noumea. Its equatorial transect included ten stations between 165° E and 150° W (*figure 1*). Six lasted for 24 hours and were sampled several times at night and day for hydrographic, nutrient and plankton parameters. Four short stations were only sampled once for CTD-rosette and plankton, whatever time of day they occurred. Primary productivity and vertical flux measurements were only performed at the 24-hour stations.

2.2. Flupac time series station

A 7-day station was occupied at 0°, 150° W during the R.V. *L'Atalante* Flupac cruise (23 September–30 October 1994) and consisted of hydrographic/nutrient casts every four hours, plankton hauls during the day and night, in situ primary production measurements every day and the deployment of sediment traps for 48 hours. Details are given in Le Borgne et al. [19] and Rodier and Le Borgne [38].

3. MATERIAL AND METHODS

Hydrographic data were obtained with a SeaBird® SBE9 + CTD attached to a 24 Niskin bottle General Oceanics® rosette. Seawater samples for biological observa-

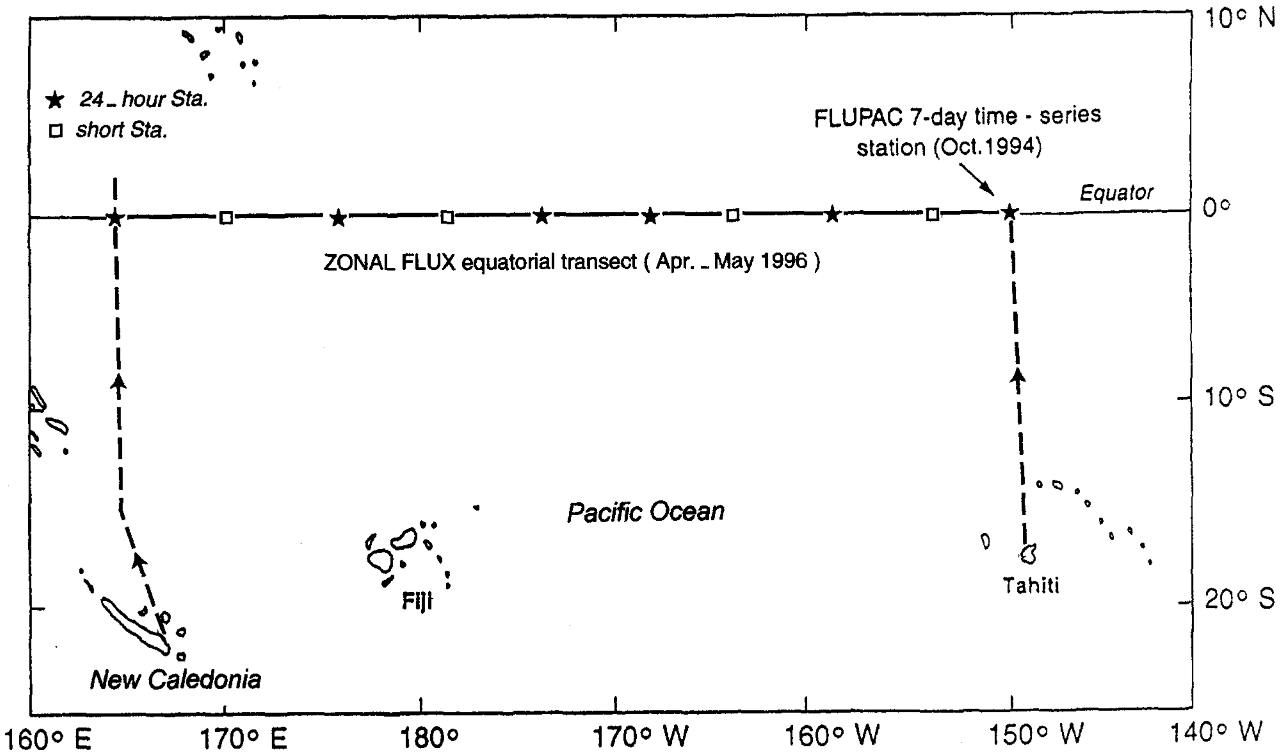

Figure 1. Equatorial stations of "Zonal Flux" cruise on board R.V. *Thompson* and location of Flupac time series station at 150° W on board R.V. *l'Atalante*.

tions were collected from the surface to 400 m. Data on light absorption with depth originated from a QSP-200L Biospherical Instruments® sensor for Flupac and a Satlantic® OCP200 spectroradiometer coupled to a surface reference cell, mounted on a floating frame during Zonal Flux (courtesy of S. Pegau, Oregon State University).

Nutrient analyses were performed immediately on board with a Technicon® Auto-analyser, using the colorimetric methods described in Bonnet [6].

Chlorophyll *a* concentrations were analysed with a Turner® fluorometer. Water samples (0.125 L) were filtered through Whatman® GF/F filters (diameter: 25 mm) and pigments were extracted in 95 % methanol, according to the method described in Le Bouteiller et al. [22]. Because chlorophyll *a* data present diel variations, the average integrated values have been calculated on night and morning casts. For the short stations of Zonal Flux, however, a correction factor for afternoon or morning casts has been applied, using a mean afternoon/morning ratio of 1.23, calculated from the cruise data.

Seawater samples (2.3 to ~ 4 L) were filtered on precombusted GF/F filters (diameter 25 mm) for determination of particulate organic phosphorus (POP) and analyses were performed with the wet oxidation method, following the procedures of Pujo-Pay and Raimbault [35]. POP is quite representative of the detritus-free biomass [33].

Bacteria were collected by filtration of 10–20 mL of seawater on black 0.2 µm Nuclepore® filters (diameter: 25 mm), stained with DAPI and counted using epifluorescence microscopy, following the methodology of Torreton and Dufour [41]. Six depths were sampled from the surface to 300 m on afternoon casts of the 24-hour long stations of Zonal Flux.

Mesozooplankton (200–2000 µm size-fraction) was sampled in vertical hauls by a Hydrobios® "multiple plankton sampler" (MPS II). Five different layers were successively sampled between 400 m and the suface. Living plankton were sieved on 2 mm metal grids, rinsed with freshwater and dried at 60 °C on board. Ash-free dry weight (AFDW) was measured in the shore laboratory after combustion at 550 °C for 1.5 h. Biomass data refer to filtered volume measured with Hydrobios® flowmeters. For details, see Le Borgne and Rodier [20].

AFDW data are the means of day and night hauls made at the 24-hour long stations. For the short stations during

Zonal Flux, a correction factor for day or night hauls has been applied, using mean night/day ratios observed during the cruise, i.e. 1.06, 1.14, and 1.14, respectively for 0–400, 0–200 and 0–125 m biomasses.

Primary production was measured by the ^{14}C method at twelve depths between 0 and 150 m. The method was similar to that described by Barber et al. [5], except water was gently dispensed with silicone tubes from Niskin bottles into 250 mL sterile tissue-culture flasks. In situ incubations were performed from dawn to dusk (about 12 h) using a drifting array, and followed by deck incubations for the night to complete the 24 h.

The flux of sinking particles was measured using drifting sediment traps. During Flupac, these traps were deployed for 48 h at four depths from 100 m to 300 m while during Zonal Flux they were deployed for 24 h at three depths from 100 to 250 m. The traps consisted of 3–4 frames, each equipped with 6–8 cylindrical (pit style) collectors (diameter: 0.0053 m², aspect ratio = 6.5). Traps contained non-poisoned brine solution in their lower part and were closed prior to retrieval to prevent wash out. The flux samples were analysed for a variety of parameters, including particulate organic carbon (POC), after swimmers had been removed. For details, see Rodier and Le Borgne [38].

Data processing. In this paper, chlorophyll *a*, POP, bacteria abundances, and primary production have been integrated from 0 to 120 m, a layer which is close to the photic zone as defined by the depth of the 0.1 % light level. The sinking fluxes, Fz, have been standardized to 120 m. Fz was estimated from measured trap fluxes using a log-transformed normalized power function of the form $Fz = Fo\ (z/zo)^b$, where Fo is the flux at the reference depth, zo, and b = 0.80, the log-log slope derived from trap data of the Zonal Flux equatorial transect.

Comparisons between two data sets have been made using the Wilcoxon non-parametric test. Trends are evaluated using the significance of the Spearman rank correlation coefficient between each parameter and the longitude.

4. RESULTS

4.1. Temperature, nitrate and light absorption with depth

During the Zonal Flux equatorial transect in April–May 1996, the isotherms and isolines of nitrate (*figure* 2) and other macronutrients (not represented) shoaled from west to east. As a result, zonal gradients were observed for surface temperature and nitrate concentration. Temperature decreased from 28.4 °C at 165° E to 26.4 °C at 150° W, and nitrate concentration increased from 2.7 to 5.2 µM. Such characteristics are representative of the cold-tongue equatorial upwelling, which covered most of the Pacific during the cruise. The position of the western boundary was located west of 165° E, probably around 158° E considering Inoue et al. [18] correlation between SOI (0.6 in April 1996) and the western boundary of the cold water upwelling. This corresponds to an usual extension of the equatorial upwelling during La Niña situations [36].

For comparison, Flupac time series station at 150° W also took place in the equatorial HNLC structure, but during the onset of an El Niño. In October 1994, the western boundary of the upwelling was located at 172° W, surface temperature was 27.7 °C at 150° W while nitrate concentration was 3.14 µM [14].

Light absorption with depth is a function of the particulate biomass in the open ocean, but it is measured independently from chlorophyll *a* and particulate organic phosphorus concentrations. It was extremely constant from east to west during Zonal Flux. The 1 % light level ranged from 70 to 80 m and the 0.1 %, from 110 to 140 m (*figure 2*). During the Flupac time series station, the average depth of the 1 % light level was 73 m, close to that of Zonal Flux, thus indicating similar particle loads in both cases.

4.2. Plankton biomass and particulate organic phosphorus (POP) (*figure 3, table I*)

During Zonal Flux, integrated values of particulate organic phosphorus, chlorophyll *a*, bacteria and zooplankton displayed a slight, although significant, increase (Spearman rank correlation, 5 % significance level) from east to west which may be ascribed to extreme values at both ends of the transect (*figure 3*). This feature contrasts with the clear zonal gradient in hydrographic properties. The mean values of the Zonal Flux transect were quite similar to that observed during the Flupac time series study, but their standard deviations (*table I*) and range (*figure 3*), were somewhat higher for the equatorial transect. POP, chlorophyll *a*, and zooplankton AFDW data of the two cruises were not significantly different at the 1 % level.

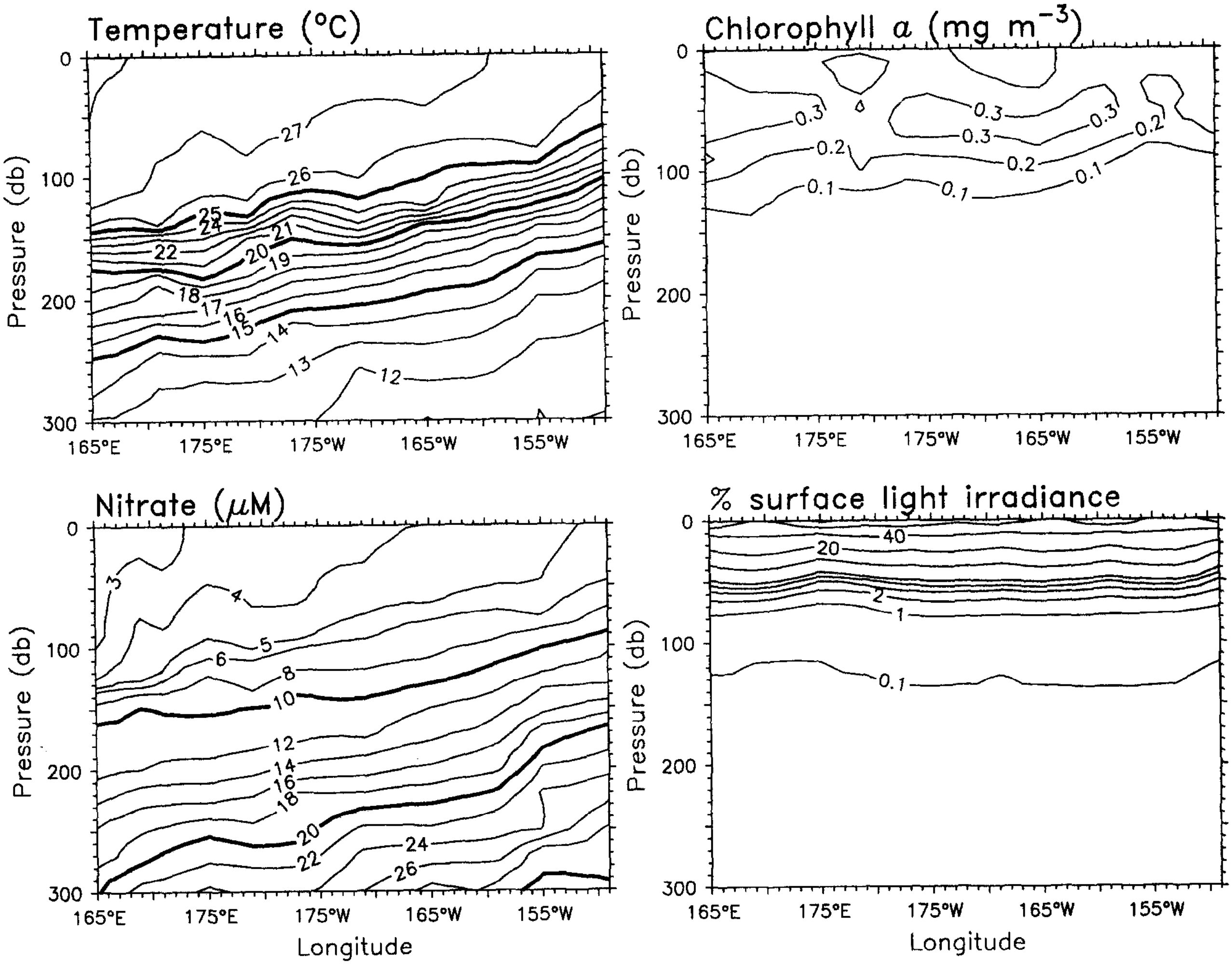

Figure 2. Potential temperature, nitrate concentration, chlorophyll *a*, and percentage of surface light irradiance at the equator between 165° E and 150° W during Zonal Flux cruise (April 15–May 14 1996).

4.3. Primary production and POC export flux

Primary production values did not show any zonal gradient during Zonal Flux and were comparable to the Flupac observations (*figure 4*). The difference between the two data sets (88 mmol C m^{-2} d^{-1} during Zonal Flux vs. 92 mmol C m^{-2} d^{-1} during Flupac, *table I*) was not significant at the 1 % level.

POC export flux out of the photic layer (0.1 % depth) did not show a significant (5 % level) zonal gradient during Zonal Flux and was less than that measured during Flupac for four of six stations (*figure 4*): 13.0 vs. 17.0 mmol C m^{-2} d^{-1} (*table I*). During Zonal Flux, the average POC sinking flux was equal to 15 % of the 0–120 m ^{14}C uptake.

5. DISCUSSION

Data from the 5000-km-long Zonal Flux equatorial transect (i.e. 45 degrees of longitude) during HNLC conditions show a very clear zonal gradient for hydrological parameters (temperature and nutrients). However, planktonic parameters did not present a similar gradient and their average values were very similar to those observed at the Flupac time-series station, in HNLC conditions, also.

The slightly increasing trend from east to west, observed for planktonic biomass, is ambiguous because it relies on a small number of stations and is influenced by the end-member values. It could be due, either to a zonal evolution of the equatorial ecosystem towards more heterotro-

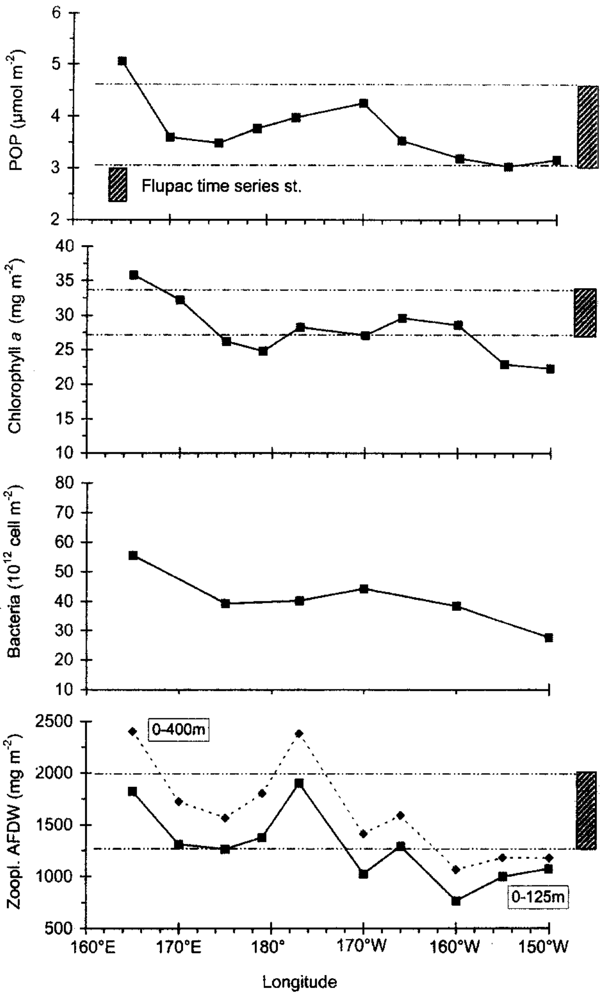

Figure 3. 0–120 m integrated particulate organic phosphorus (POP), chlorophyll *a*, bacterial abundances (Bacteria), and mesozooplankton (200–2000 µm) ash free dry weight (Zoopl. AFDW) during Zonal Flux equatorial transect and comparison with the range observed during Flupac 7-day time series station at 150° W (October 1994). Note that the range of Flupac Zoopl. AFDW refers to the 0–400 m water column. Zoopl. AFDW peak at 177°W is due to high values for both night and day hauls in the 0–65 m layer.

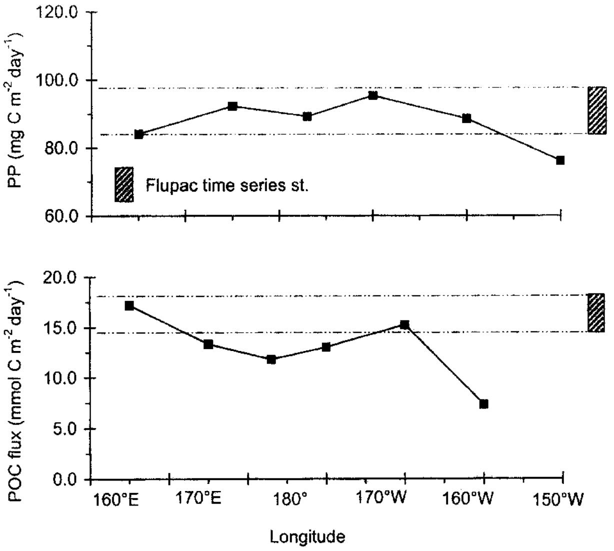

Figure 4. 0–120 m integrated primary production (^{14}C uptake, PP) and particulate organic carbon sinking flux (POC flux) at 120 m during Zonal Flux equatorial transect (April–May 1996) and comparison with the range observed during Flupac 7-day long time series station at 150° W (October 1994).

phy when moving to the west, or to the influence of the zonal distribution of a factor limiting primary production. The first hypothesis is dubious since both autotrophic (i.e. chlorophyll *a*) and heterotrophic (bacteria and zooplankton) parameters display parallel evolutions and do not show a variable heterotroph/autotroph ratio. The second explanation, dealing with a possible E–W positive gradient of a limiting factor does not stand since such a gradient has not yet been documented. More likely, the observed increasing trend could simply be due to mesoscale variability, an explanation which is suggested by results of previous long equatorial transects, such as Alizé 1 [17] and Alizé 2 [21]. In that case, an extension of Zonal Flux equatorial leg would have shown biomass values oscillating around an average value along the HNLC area, as shown on *figure* 5 for Alizé 2. We conclude, therefore, that there are no significant E–W variations in biological properties, in contrast to the hydrological features.

This feature of equatorial upwelling is evident in previous studies dealing with phytoplankton biomass and production, although it was not always mentioned. Thus, the lack of an obvious zonal gradient for integrated chlorophyll *a* was reported by Le Bouteiller and Blanchot [21], Chavez and Brusca [9] and Barber and Chavez [4] for the region extending westward from the Galapagos Islands to the dateline. But it appeared also in results presented by Guérédrat [17] and Chavez et al. [11]. Similar results were presented for small phytoplankton cells (counted by epifluorescence microscopy), and the size-structure of phytoplankton, by Le Bouteiller and Blanchot [21] for the Alizé 2 cruise of 1991, for which surface nitrate decreased from 11 µM at 95° W to 0 µM at 168° E.

Less data are available for primary production along the equatorial Pacific. In their synthesis work, Barber and Chavez [4] wrote: "in contrast with the Chl result, plots of the Chl-specific P^B for the euphotic zone show a con-

Table I. Mean values of components of the "biological pump", integrated from 0 to 120 m (unless otherwise stated). Measurements were made during the zonal Flux (*ZF*) equatorial transect (165° E–150° W) and the Flupac (*Fl*) equatorial time series (7 days) station at 150° W (AFDW= ash free dry weight; s = standard deviation, n= number of stations).

Parameter	Zonal Flux (April–May 96)	Flupac (Oct. 94)
Particulate organic phosphorus (µmol m^{-2})	3.70 (s = 0.60; n = 10)	3.81 (s = 0.48; n = 7)
Chlorophyll *a* (mg m^{-2})	27.8 (s = 4.1; n = 10)	30.5 (s = 2.65; n = 7)
Mesozooplankton AFDW (*ZF*:0–125m; *Fl*: 0–100m) (mg m^{-2})	1283 (s = 303; n = 10)	1331* (s = 213; n = 13)
Mesozooplankton AFDW (0–400m) (mg m^{-2})	1630 (s = 549; n = 10)	1718* (s = 284; n = 13)
^{14}C uptake (mmol m^{-2} d^{-1})	87.6 (s = 6.8; n = 6)	91.7** (s = 3.3; n = 7)
Vertical flux of particulate organic carbon (mmol m^{-2} d^{-1})	13.0 (s = 3.4; n = 6)	17.0** (s = 2.5; n = 3)

* in: Le Borgne and Rodier [20].
** in: Rodier and Le Borgne [38].

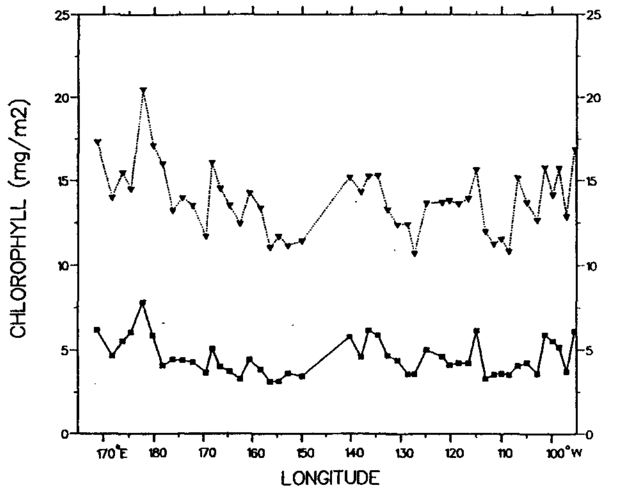

Figure 5. Depth integrated values of chlorophyll *a* along the equator during Alizé 2 cruise. Squares: 0–20 m. Triangles: euphotic layer [21].

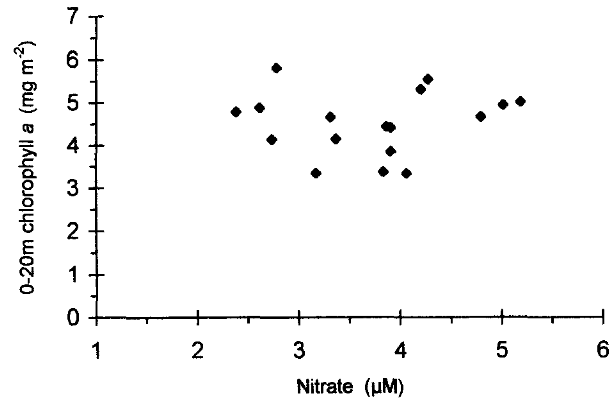

Figure 6. Plots of 0–20 m chlorophyll *a* vs. surface nitrate concentration during Zonal Flux equatorial transect.

sistent gradient from the warm pool eastward to the eastern boundary". However, it appeared on their data, particularly those presented in their table II, that neither chlorophyll, primary production, nor productivity (P^B) presented any significant zonal gradient between 93° W and 160° W. We conclude from their table II that primary production and chlorophyll display an invariant distribution across a 70° of longitude equatorial belt. Chavez et al. [11] reached the same conclusion, using 1992 EqPac data from five equatorial longitudes (between 90 and 170° W).

Data on zonal variations of other planktonic parameters are very scarce and deal only with zooplankton. Guérédrat [17] reported that the total number of copepods decreased from east to west during the Alizé 1 cruise. In fact, this was primarily due to higher values in the easternmost part of the transect (east of 120° W). Zooplankton numbers were actually quite stable between 120° W and 169° E. Vinogradov's [43] data on zooplankton wet weight show no zonal variations between 122° W and 155° W. The same is true for the HNLC part of the Flupac transect between 150° W and 172° W [20].

Therefore, the results from the Zonal Flux cruise provide additional support of the invariant phytoplanktonic and zooplanktonic biomass zonal distribution in the equatorial upwelling, and extend this conclusion to all observed parameters acting in the "biological pump". Such an observation means that planktonic biomasses and fluxes are independent of the zonal distribution of macronutrients as shown in *figure 6* and this is in agreement with what we know of HNLC situations, in which primary production is not limited by nitrate or phosphate, but by other limiting factors, such as iron [26, 28] or silicate [12]. Present results suggest that the equatorial ecosystem functioning would be more or less the same for all longitudes west of the Galapagos Islands and in quasi steady-state, taking the comparison of the Zonal Flux and Flupac results, into account. Steady-state implies an equilibrium balance between predators and prey and control of phytoplankton biomass by grazing, following Walsh [44], Banse [2], Frost and Franzen [16], Loukos et al. [26], and others who have advocated "grazing" controls in the equatorial HNLC.

Provided the zonal variability of plankton parameters is small and of the same magnitude as the short-term variability, average values of *table I* may be used in carbon budgets of the equatorial Pacific HNLC area. The following discussion shows values of *table I* are often close to other recent data from the literature dealing with the same region. Thus, integrated chlorophyll *a* values of Chavez et al. [11] are similar to ours: an average 29 mg m^{-2} may be calculated from their *table II* and compared with 28 and 30.5 in *table I*. Their average value of primary production for the area spanning 90 to 180° W and 5° N–5° S (75 mmol C m^{-2} d^{-1}) is somewhat lower than our value of 88 mmol C m^{-2} day^{-1} for Zonal Flux cruise. Average chlorophyll *a* (30 mg Chl *a* m^{-2}) and primary productivity (95 mmol C m^{-2} d^{-1}) values of Barber et al. [5] for the photic zone (ca. 120 m) at 140° W (1° N–1° S) are very close to those of the present paper (*table I*). There seems to be no zooplankton AFDW data for the equatorial Pacific in the literature. Most recent results are those of Roman et al. [39] at 0°, 140° W during EqPac, obtained with the same net mesh size (200 μm) and sampling depths as ours but with a different design plankton net (Mocness). Their carbon biomass values for the 200–>1000 μm size-class (21.6 and 30.9 mmol C m^{-2}, for the two studied periods, respectively) may be converted into AFDW, assuming carbon makes up half of the organic matter. The converted values (518 and 742 mg AFDW) are lower than those in *table I*. Finally, POC sinking fluxes of the present paper are higher than those obtained by Buesseler et al. [7], Luo et al. [27], Murray et al. [32] and Bacon et al. [1], but are in agreement with those of Dunne et al. [13]. Based on this brief comparison, using the most recent literature values for the equatorial Pacific, and knowing variability of plankton parameters is small, it appears values of *table I* may be tentatively used to assess the carbon budget and its time variations. The main question, in fact, deals with zonal and meridional extensions of the upwelling and therefore, its overall area, rather than with temporal and spatial variations of biological parameters within the upwelling, which are of small amplitude.

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