The Western Boundary of the Equatorial Pacific Upwelling: Some Consequences of Climatic Variability on Hydrological and Planktonic Properties

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The longitude of the western limit of the equatorial Pacific upwelling is a key parameter for studies of carbon budget and pelagic fisheries variability. Although it is well defined at the surface on the equator by a salinity front and a sharp variation of the partial pressure of CO2, data from two equatorial cruises make it clear that this hydrological limit does not necessarily coincide with the boundary of the nitrate and chlorophyll enriched area. In January–February 1991 during a non-El Niño period, when trade winds and the South Equatorial current (SEC) were favorable to upwelling, the two limits were at the same longitude. Conversely, in September–October 1994 during El Niño conditions, when the equatorial upwelling had stopped, the nitrate and chlorophyll enriched zone was found a few degrees of longitude east of the hydrological boundary (5.5° at the surface and 2.5° for the 50 m upper layer), whereas no such offset was observed for zooplankton biomass. A simple model, based on the HNLC (High Nutrient - Low Chlorophyll) ecosystem functioning, was initialized with nitrate uptake measurements and estimates of upwelling break duration. The model results support the hypothesis that zonal separation of the limits arises from biological processes (i.e. nitrate uptake and phytoplankton grazing) achieved during that upwelling break.

1. Introduction

The equatorial Pacific is the domain of an upwelling which makes it both a source of CO2 to the atmosphere, and a carbon sink due to its increased primary production (Murray et al., 1994). Since the equatorial Pacific upwelling usually covers more than 100° of longitude (ca. 11,000 km), it is recognized as being the major source of CO2 to the atmosphere on Earth (Tans et al., 1990) which also contributes to more than 18% of global “new biological production” (Chavez and Toggweiler, 1995). Most of all, the surface area of the upwelling undergoes significant temporal changes, resulting in a close control of the equatorial Pacific carbon budget. The key factor underlying such control is probably the zonal displacement of the upwelling which makes its surface change by a factor of up to two, depending on the climatic situation (Boutin et al., 1999). It turns out that monitoring the upwelling western boundary is crucial in temporal variability studies of equatorial carbon fluxes. Beyond its role on the carbon budget, the zonal displacement of the upwelling western boundary also has significant impacts on the location of tuna catches, as Lehodey et al. (1997) have shown.

Although it is not well defined in sea surface temperature (Picaut et al., 1996; Ando and McPhaden, 1997), the western edge of the equatorial upwelling is clearly marked by a surface salinity front (Kuroda and McPhaden, 1993; Picaut et al., 1996; Vialard and Delecluse, 1998; Delcroix and Picaut, 1998) which separates the “warm, fresh pool” to the west, from the colder and saltier upwelled waters to the east. At interannual time scales, zonal displacements of the front are closely correlated with the Southern Oscillation Index (SOI), which has been shown by Delcroix and Picaut (1998). This salinity front is also manifested by a sharp change in the surface seawater pCO2 (CO2 partial pressure), with higher values in the upwelling area (Inoue et al., 1996). According to these authors, and similar to the sea surface salinity, the pCO2 front is also zonally displaced in relation to the
SOI. Recently, Boutin et al. (1999) found that the pCO₂ variability in the western part of the equatorial Pacific was primarily governed by the displacement of the boundary between the warm pool and the upwelling. They also considered that this process exerted a strong control on CO₂ exchanges with the atmosphere over the entire equatorial Pacific region.

In the equatorial Pacific, the upwelling zone is known as an HNLC area (High Nutrient - Low Chlorophyll, Minas et al., 1986), which means that surface chlorophyll is low compared to the concentrations of nutrients present. The HNLC situation indicates lack of macronutrient (e.g. NO₃) control over primary production and a steady-state of the epipelagic ecosystem. The consequence of such a feature is that the zonal displacement of the upwelling western boundary may also be monitored by surface nutrient concentration measurements (Inoue et al., 1996) or chlorophyll biomass estimates from satellite imagery (Dupouy et al., 1993). To our knowledge, however, fine resolution observations of nutrient or plankton concentrations at the western edge of the upwelling are very scarce, and no detailed descriptions of their temporal variability in relation to the hydrological front are yet available.

Here we use data from two French (ORSTOM/CNRS) equatorial cruises (ALIZÉ 2 in January–February 1991 and FLUPAC in October 1994) in order to describe features of the upwelling western boundary during two contrasting climatic conditions: non-El Niño conditions in 1991, during ALIZÉ 2 and El Niño conditions in 1994, during FLUPAC. Physical, chemical and biological data were also obtained simultaneously during these multidisciplinary cruises and thus allowed a rather accurate description of the boundary in terms of both the physical and biological aspects. This paper introduces some evidence on the impact of upwelling variability on the connection between the salinity/pCO₂ front and the HNLC area western limit. It proposes an explanation for some specific features observed in the chemical and plankton “frontal” signatures in relation to the physical structures.

2. Sampling and Analytical Methods

2.1 Sampling

The primary datasets used for this study were collected during the ALIZÉ 2 cruise (3 Jan.–5 Mar. 1991) on board R/V Le Noroît (Reverdin et al., 1991) and the FLUPAC cruise (23 Sept.–29 Oct. 1994) on board R/V L’Atalante (Le Borgne et al., 1995). Equatorial stations were set up every two degrees of longitude from 95.39°W to 165°E during ALIZÉ 2, and from 150°W to 165°E during FLUPAC (Fig. 1). In this paper, we use only ALIZÉ 2 data obtained west of 150°W, in the same area as FLUPAC.

Conductivity-temperature-depth (CTD) casts with water sampling, and underway measurements were performed along each equatorial transect. During the FLUPAC cruise, zooplankton hauls were carried out at hydrographic stations.

Additional observations from TAO moorings (data distributed by TAO Project Office, NOAA, Seattle, WA, USA) were used to replace each cruise in a large-scale climatic context.

2.2 Material and analytical procedures

Temperature and salinity data were acquired with a Neil-Brown Mark III CTD probe during ALIZÉ 2 and two sets of Sea-Bird SBE-911+ probes during FLUPAC. Additionally, continuous measurements of sea surface salinity (SSS) and temperature (SST) were gathered with a Sea Bird thermosalinograph during both cruises. Note, however, that during ALIZÉ 2, underway measurement of SSS and SST along the equator stopped at 167.75°E, so no continuous data are available west of this longitude.

Currents were continuously measured with two VM-ADCPs from RDI (300 kHz and 75 kHz). More details on data processing are given by Eldin et al. (1997).

Nutrient, chlorophyll and particulate matter were measured on samples collected with a Rosette sampler mounted on the CTD, in the upper 1000 m and 200 m during ALIZÉ 2 and FLUPAC, respectively. Nitrate (NO₃) and phosphate (PO₄) analyses were performed immediately on board with a Technicon Autoanalyzer using colorimetric methods, as described by Radenac and Rodier (1996). Chlorophyll a (Chl a) was determined on methanol (95%) extracts by the fluorometric technique using a Turner fluorometer (Le Bouteiller et al., 1992). Chl a analyses were performed on frozen samples. Particulate phosphorus (POP) analyses were carried out only during FLUPAC, by the wet oxidation and colorimetric method.
on filtered samples (1000 ml), according to the method of Pujo-Pay and Raimbault (1994).

Mesozooplankton biomass was measured on samples collected with 0–500 m vertical hauls, made with a WP-2 net (mesh size = 200 µm; UNESCO, 1968). Biomasses refer to mg of ash-free-dry weight (AFDW) in the 0–100 m layer, calculated from the 0–500 m biomass and the (0–100)/(0–500) m biomass ratios for the “warm pool” (0.61) and the HNLC area (0.69). More details are given by Le Borgne and Rodier (1997).

Underway sea surface pCO2 measurements were made during FLUPAC, following the method described in Le Borgne et al. (1995). Data on ALIZÉ 2 pCO2 used in this paper have already been presented by Lefèvre et al. (1994).

3. Results

3.1 Large-scale climatic conditions and upper layer structures during ALIZÉ 2 (non-El Niño)

ALIZÉ 2 took place during a non-El Niño period (SOI~0, Fig. 2). During the cruise, the eastward trade winds were slightly stronger than climatological monthly winds. However, from 180° to 165°E, average winds were weak and highly variable (Lefèvre et al., 1994). Furthermore, a westerly wind burst (WWB) of 11 days appeared from February 25 to March 7 in the western Pacific "warm pool" at the time the ship had reached 165°E (Delcroix et al., 1993). Sustained trade winds during the cruise caused a strong westward flowing South Equatorial Current (SEC) and active equatorial upwelling which extended to the western Pacific. In these conditions, the upwelled waters reached ~167°E and consequently, the warm, fresh, nutrient-depleted “pool”, appeared only in the westernmost part of the transect (Fig. 3).

The zonal distribution of salinity, both at depth and in surface, reveals a well-defined salinity limit between the “warm/fresh pool” (SSS < 35.0) to the west and the colder/saltier upwelling (SSS around 35.2) to the east (Fig. 3). This salinity boundary of the upwelling was crossed between stations set up at 167.75°E and 169.75°E. Thanks to continuous SSS measurements (not shown), the position of the salinity front can be determined more accurately at 167.83°E, with a 0.1 surface salinity change in less than 0.08 degree (SSS gradient = 1.25 degree–1).

According to Lefèvre et al. (1994), the hydrological front, well evidenced in salinity but not in temperature, also coincides with a sharp east-west discontinuity of pCO2.

As is apparent from Fig. 3, the HNLC waters of the upwelling are also clearly isolated from the nitrate/chlorophyll-poor (oligotrophic) waters of the “warm pool”, with a marked boundary. This feature is also evident for PO4, as already noted by Lefèvre et al. (1994). As for salinity, the western edge of the HNLC area is located between hydrological casts at 167.75°E and 169.75°E (Fig. 3). The lack of continuous nutrient and chlorophyll
data makes it impossible to be more precise about its exact longitude. However, due to almost nil surface concentrations (0.2 μM) at 167.75°E and moderately high NO₃ values (1.8 μM) at 169.75°E, the western boundary of the HNLC zone is probably very close to 167.75°E. Since this longitude is near the salinity and pCO₂ front (167.83°E), it turns out that the nutrient/chlorophyll and salinity/pCO₂ western boundary of the upwelling are closely associated in these conditions of active upwelling.

Within the sampled HNLC area, nitrate increases steadily to the east, whereas chlorophyll exhibits no clear zonal trend and fluctuates around a mean value (mean 0–50 m Chl a ± SD = 0.282 ± 0.065 mg m⁻³). The monotonous distribution of both Chl a and phytoplankton size distribution, have already been reported by Le Bouteiller and Blanchot (1991). Consequently, the 0–50 m NO₃ concentration at the salinity front (167.83°E) can be inferred from the nitrate-to-longitude related gradient within the HNLC area: calculation gives a value of 0.96 μM. On the other hand, chlorophyll at the salinity front is assumed to be close to the mean HNLC value given above.

3.2 Large-scale climatic conditions and upper layer structures during FLUPAC (El Niño)

In contrast to ALIZÉ 2, the FLUPAC cruise took place during a moderate El Niño event that was developing in the Pacific at the time of the cruise (negative SOI, Fig. 2). During the cruise the trade winds weakened and there was a westerly wind burst at the end of September 1994, which triggered a downwelling Kelvin wave; these conditions induced: (i) a reversal of the surface current (from westward initially to eastward); (ii) a convergence at the equator; and (iii) a cessation of the upwelling (Eldin et al., 1997). The fresh/warm “pool” progressed eastward and the equatorial salier/colder tongue retreated: the limit between the two systems was at that time displaced to the central Pacific (Fig. 4). The salinity front, which delimited the cold tongue at 172°W, was abrupt with a 0.7 salinity change in two degrees (SSS gradient = 0.35 degree⁻¹). However, a finer resolution given by underway SSS measurements (Fig. 5) reveals that the front is particularly abrupt in the first 40 km going out of the saltier tongue: SSS decreases by 0.4 over 0.4 degree of longitude (gradient = 1 degree⁻¹), which is comparable in magnitude to the gradient observed during ALIZÉ 2. The transition between the “warm pool” and the upwelling is much less pronounced in temperature than in salinity, as shown by Fig. 5, which confirms that SST alone is not sufficient to detect the western boundary of the upwelled waters. As was also found during ALIZÉ 2, the salinity front coincides with a well-marked change in pCO₂.

Although active upwelling had ceased, the nitrate and Chl a enriched area was still present east of the salinity/pCO₂ limit, which may be considered as the signature of previously upwelled waters (Fig. 4). This enriched area is found a few degrees east of the salinity front, however, which contrasts with the ALIZÉ 2 observations where the two fronts coincided. The longitudinal offset between the salinity/pCO₂ and nitrate/Chl a limit is 5.5 degrees for surface data (Fig. 4) and about 2.5 degrees for the 0–50 m upper layer average concentrations (Fig. 5). It is important to bear in mind that sampling was done every two degrees, which does not permit an accurate definition of the offset. As observed for NO₃, the increase in PO₄ also occurred east of the salinity front. The distribution of particulate phosphorus (POP), which is an indicator of living plankton (mainly phytoplankton and micro-heterotrophs, owing to the small filtered volume) confirms that the HNLC boundary shifted east of the salinity front during the FLUPAC cruise. In contrast, greater zooplankton biomasses are associated with higher salinity indicating there was no gap between the increase of zooplankton and the salinity front at the time of observa-
tion (Fig. 5). The zooplankton biomasses east and west of this limit are quite constant through the cruise period, with values 2.8 times higher in the enriched area than in the oligotrophic zone.

In the HNLC area, the NO$_3$ concentrations increased regularly to the east (slope of the linear regression $\frac{\partial \text{NO}_3}{\partial x} = 0.210 \text{ mmol NO}_3 \text{ m}^{-3} \text{ deg.long}^{-1}$), despite local variations due to Tropical Instability Wave (TIW) activity observed between 162°W and 156°W (Eldin et al., 1997). Such NO$_3$ concentrations are below both the values observed at the same longitudes during ALIZÉ 2 and the NOAA Atlas climatology (Eldin et al., 1997). This decrease of nitrate stocks in the “cold tongue” is not followed by a decline in the phytoplankton biomass, at least through the time of the cruise. Note, indeed, that the mean HNLC 0–50 m Chla (0.301 ± 0.056 mg m$^{-3}$) measured during FLUPAC was nearly the same as that observed during ALIZÉ 2 in the HNLC zone west of 150°E (0.282 ± 0.065 mg m$^{-3}$), although climatic and nutrient conditions were different. Such results are consistent with the general idea that NO$_3$ is not limiting in the HNLC regions and that the ecosystem is in a steady-state until NO$_3$ becomes depleted.

Finally, in the NO$_3$-depleted warm pool (0–50 m mean NO$_3$ close to the detection limit), the mean 0–50 m Chla concentration is equal to 0.093 ± 0.029 mg m$^{-3}$, which is 3.2 times less than in the HNLC area.

4. Discussion

In active upwelling conditions (ALIZÉ 2 cruise), nitrate, phosphate and chlorophyll limits between the oligotrophic “warm pool” and the HNLC upwelling region, coincide quite well with the hydrological limit defined by a salinity front and a sharp transition in pCO$_2$. Conversely, no such coincidence is observed during the FLUPAC cruise, when the equatorial upwelling had been inhibited by weakening of the trade winds and propagation of equatorial downwelling Kelvin waves: in such a case, the nutrient and chlorophyll enriched zone was found further east of the SSS, and pCO$_2$ limit.

We hypothesize that the specific structure observed during FLUPAC at the western boundary of the upwelling (i.e., offset between the SSS/pCO$_2$ and NO$_3$(PO$_4$)/Chla limits) is most likely related to the large-scale climatic forcing variability, and particularly to the recent cessation of the upwelling. From TAO array data obtained during the July to December 1994 period, it may be inferred that the upwelling had stopped around Sept. 5–10, i.e. 31–36 days before the salinity front was crossed at 172°W. Indeed, time-longitude plots of zonal wind field and depth of the thermocline (figure 8 in Eldin et al., 1997) show: (i) a rapid decrease of easterly winds between 170°W and 160°W after Sept. 5–10, followed by a depression of the thermocline, and (ii) westerly wind bursts in the western Pacific, and propagation of a downwelling Kelvin wave which reaches the central Pacific around Sept. 5–10. TAO array data also indicate that the upwelling did not restart during these 31–36 days. In such conditions of upwelling cessation, where nutrient inputs to the euphotic zone stop, NO$_3$ and Chla stocks are being taken up progressively until NO$_3$, and later Chla, become depleted. The W-E positive NO$_3$ gradient causes the depletion to start at the western boundary of the upwelling and to propagate east-
wards. According to this scenario, the offset of a few degrees observed in October 1994, between the salinity front and the boundary of the HNLC equatorial waters, results from nitrate uptake and phytoplankton grazing, achieved during the upwelling break.

In order to test this scenario, we have developed a simple model and compared modeled outputs with observed data. Our model considers the upper 0–50 m layer only, where most of the NO₃ uptake (70%) occurs (Navarette, 1998; Raimbault et al., 1999). For clarity of the demonstration, the discussion is divided into two parts, dealing with NO₃ and Chla distributions, respectively.

4.1 Zonal offset of the NO₃-enriched water boundary during FLUPAC

Our initial hypothesis is that salinity and nitrate fronts were coincident at longitude xₒ and time tₒ, when the upwelling ceased. This hypothesis is based on ALIZÉ 2 observations made during active upwelling conditions. Let NO₃(x,xₒ) be the mean 0–50 m NO₃ concentration at tₒ and at any longitude x along the equator (x being positive when moving from xₒ to the east). Then,

\[ \text{NO}_3(x,t_o) = 0 \quad \text{if } x < x_o \]  
\[ \frac{\partial \text{NO}_3}{\partial x}(x,x_o) \times (x - x_o) + C_o \quad \text{if } x \geq x_o \]

where xₒ is the front longitude, \( \partial \text{NO}_3 / \partial x \) is the zonal NO₃ gradient in the HNLC region, and Cₒ is the mean NO₃ concentration in the 0–50 m upper layer at the salinity/NO₃ front at tₒ.

If we consider that nitrate uptake during the upwelling break is the only process responsible for the observed offset between nitrate and salinity limits, the NO₃ concentration (mmol m⁻³ or µM) along the equator at time t (t ≥ tₒ) is given by:

\[ \text{NO}_3(x,t) = \text{NO}_3(x,t_o) - \rho_{\text{NO}_3} \times (t - t_o) \]  

where \( \rho_{\text{NO}_3} \) is NO₃ uptake rate (mmol m⁻³day⁻¹).

NO₃ uptake, \( \rho_{\text{NO}_3} \), is taken as a constant value between tₒ and t under HNLC (i.e. NO₃ non-limiting) conditions and is negligible as soon as NO₃ becomes depleted (i.e. <0.1 µM). During FLUPAC, \( \rho_{\text{NO}_3} \) was measured at 150°W by the ¹⁵N method (Navarette, 1998) and its 0–50 m average was 0.044 mmol m⁻³day⁻¹, a value within the range presented by McCarthy et al. (1996) for NO₃ < 4 µM during the EqPac cruises along 140°W. Therefore, such a \( \rho_{\text{NO}_3} \) value may be considered as a good estimate of the NO₃ uptake at the time of FLUPAC and will be used in our model.

The zonal NO₃ gradient (\( \partial \text{NO}_3 / \partial x \)) in the HNLC area is approximated by a constant value with longitude. Such an assumption is not crucial to our demonstration and is simply a convenient approximation for the longitudinal distribution of NO₃ because the shape of the distribution will not change with time in the constant uptake hypothesis. We use here the value of \( \partial \text{NO}_3 / \partial x = 0.210 \text{ mmol NO}_3 \text{ m}^{-3} \text{deg. long}^{-1} \), as measured in the NO₃-enriched area of the FLUPAC transect (see Subsection 3.2).

Finally, the initial nitrate condition at the salinity front before cessation of the upwelling, \( C_o = 0.96 \text{ µM} \) (~1 µM, for convenience), is deduced from observations made during ALIZÉ 2 (see Subsection 3.1). To our knowledge, these observations are the only ones available in that area to estimate \( C_o \).

The results of a run over time of the simple model defined by Eqs. (1)–(3) using the numerical values defined above, are shown in Fig. 6(a). Starting at the cessation of upwelling (tₒ = day 1), NO₃ is progressively taken up until the initial front disappears (day 23). Then, considering the limits of uncertainty in upwelling break duration (i.e. 31–36 days according to TAO data), the western boundary of the HNLC area has moved eastward between 1.7 and 2.8 deg. of longitude from its initial position at the salinity front. With the model, a displacement of 2.5 degrees (such as observed from FLUPAC data) is reached after 34 days, and predicted NO₃ concentrations are fairly close to those measured during FLUPAC. These results suggest that NO₃ uptake can account for a good part of the observed eastward displacement of the NO₃-enriched area during the upwelling break.

However, one must bear in mind that some rather crude assumptions had to be made. For instance, the model outputs depend on the estimate of the frontal initial concentration, \( C_o \), and modifying the 1.0 µM value used in our calculations by ±0.1 µM would imply a different time span (±2 days) to obtain the observed frontal displacement. Besides, the discrepancy between observed and modeled NO₃ concentrations (Fig. 6(a)) derives from the use of an average zonal NO₃ gradient (\( \partial \text{NO}_3 / \partial x \)), although the zonal offset between the hydrological and NO₃ boundary is very well predicted. Other processes than NO₃ uptake can also play a role in NO₃ distribution, including physical processes like mixing or horizontal advection of depleted waters from out of the equator. Although no observation were available to assess such processes at the time of the cruise, the effect of meridional transport is assumed to be minor in the observed shift, otherwise the salinity distribution west of the salinity front would have also been affected. Finally, as shown below, applying a related mechanism to the variability of Chla at the same time also leads to agreement with observations made during FLUPAC, which adds to the coherence of our hypotheses.

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4.2 Zonal offset of the Chla-enriched area during FLUPAC

Following our previous interpretation of the NO₃ offset, we assume again that salinity and nitrate fronts were coincident during the active upwelling phase, and that a Chla “front” was associated with them. We then hypothesize that grazing by micro- and mesozooplankton is the main cause for phytoplankton biomass changes in the upper layer and that grazing remains constant east of the salinity front after cessation of the upwelling. In that area, Chla will only vary in regions where NO₃ becomes a limiting factor following the eastward shift of the HNLC region.

Before the upwelling stops, the HNLC system is in a steady state, implying constant phytoplankton biomass (P) values (Le Borgne et al., 1999). Provided sinking losses are negligible, the grazing rate on phytoplankton (gₑ) will be equal to total primary production (Landry et al., 1995) or to the sum of new (-ρNO₃) and regenerated (-ρNH₄) production rates, so that:

\[ \frac{dP}{dt} = (\rho_{NO₃} + \rho_{NH₄}) - gₑ = 0 \]  

or

\[ (\rho_{NO₃} + \rho_{NH₄}) = gₑ. \]

After upwelling has stopped, NO₃ becomes depleted (< 0.1 µM) east of the salinity front and new production (ρNO₃) becomes negligible. Thus, grazing gₑ exceeds production, which is now nearly equal to regenerated production ρ′₄₅, leading to a decrease of phytoplankton biomass:

\[ \frac{dP}{dt} = ρ₄₅ - gₑ. \]

It turns out that the loss of phytoplankton by grazing after the upwelling break is approximated by nitrate uptake in the HNLC area, ρNO₃. Relation (7) can be expressed in terms of chlorophyll biomass as:

\[ \frac{dChla}{dt} = \frac{12R}{C/Chla} \cdot ρ_{NO₃}, \]

where R is the ratio (atm/atm) used to convert phytoplankton N into C and C/Chla is the ratio used to convert carbon weight into chlorophyll weight. In our calculation, R is taken as equal to the Redfield ratio, R = 6.6. A large range of C/Chla values can be found in the literature for the 0–50/70 m upper layer in the mesotrophic Pacific on the equator: 57–81 (Chavez et al., 1991), 55 (Eppley et al., 1992), 133 (Landry and Brown, 1999) and about 40–120 for surface values (Chavez et al., 1996). C/Chla = 90 will be used to test our hypothesis because it is the mean value estimated at 150°W during the FLUPAC cruise (Navarette, 1998) and because it falls in the range of C/Chla ratios given in the literature mentioned above.
The time variation given by Eq. (8) is shown on Fig. 6(b). The modeled Chla distribution at the time the upwelling stopped \( (t_a = \text{day 1}) \) is deduced from FLUPAC results, with an average of 0.09 mg m\(^{-3}\) in the oligotrophic zone west of the salinity front, and 0.30 mg m\(^{-3}\) in the HNLC area east of the front (see Subsection 3.2). As shown in Fig. 6(a), NO\(_3\) becomes depleted at day 23, and Chla starts to decrease following Eq. (8). At day 34 (time of FLUPAC observations), the predicted Chla transition zone fits reasonably well with the observed Chla. Note that using the extreme C/Chla values found in the literature (55–133) does not significantly alter the agreement (dotted lines on Fig. 6(b)). Conversely, one cannot determine the exact C/Chla ratio that would lead to a best fit of the data points, owing to the low zonal resolution of Chla sampling.

The present results show that, for NO\(_3\), field Chla values at the western boundary of the HNLC area during FLUPAC (“non active” upwelling) are correctly predicted by our model based on grazing and nitrate uptake. Thus, in spite of crude assumptions on the upwelling cessation time from TAO data and on the functioning of the HNLC ecosystem, there is a good agreement between modeled and observed NO\(_3\) and Chla values and their zonal distribution.

It is noteworthy that the scenario and model proposed to explain the offset between hydrological and NO\(_3\)/Chla boundaries are not incompatible with the quite constant pCO\(_2\) and mesozooplankton biomass observed between the two boundaries. In the case of CO\(_2\), it may be shown that biological activity has no significant effect on observed pCO\(_2\) during the upwelling break (31–36 days). Thus, the CO\(_2\) uptake over this period (9.0–10.5 mmol m\(^{-3}\)), as estimated from NO\(_3\) uptake via the C/N Redfield ratio of 6.6, amounts to only 0.5% of the total inorganic carbon (TCO\(_2\)) stocks in the 0–50 upper layer (=1967 mmol m\(^{-3}\), Le Borgne et al., 1995), which is almost undetectable in pCO\(_2\). In the case of mesozooplankton, a longer upwelling break would probably lead to a decrease of its biomass at the salinity/pCO\(_2\) front, in a similar way as for nitrate and chlorophyll, but with a longer time lag.

5. Conclusion

Data collected during two equatorial transects introduced some new information on the structure of the western edge of the Pacific equatorial upwelling. In October 1994, when equatorial upwelling had been temporarily stopped by a weakening of the trade winds and propagation of a downwelling Kelvin wave, a complicated zonal structure was observed: while a strong front in salinity and pCO\(_2\) was still present at 172°W, the western limit of HNLC waters was found several degrees of longitude east of the front. Observations made during an active upwelling period (ALIZÉ 2 cruise) and runs of a simple model based on the HNLC ecosystem functioning, support the hypothesis that the front and the western limit of the enriched area were coincident during active upwelling, and became separated after the upwelling cessation, due to nitrate uptake and grazing. However, available data do not allow resolution of either the fine structure of the upwelling western boundary or the detail of the processes involved. Obviously, further studies will be needed to refine our understanding of this limit and to integrate new observations in coupled biological-physical models.

The consequences of such an offset between the hydrological front and the western boundary of the HNLC enriched waters may have some impacts on higher levels of the trophic chain, including the spatial distribution of tuna forage (Lehodey et al., 1997, 1998). Another consequence may also be envisioned in the use of sea color imagery in carbon budget estimates since the chlorophyll enriched area does not necessarily coincide with the zone of higher pCO\(_2\). Finally, one question arises concerning the time evolution of both areas after a several-month cessation of upwelling instead of only one as in the present case.

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