

*Full Length Research Paper*

# On the Nutrient distribution and phytoplankton biomass in the Gulf of Guinea equatorial band as inferred from *In-situ* measurements

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Oceanographic *in situ* data collected in the Gulf of Guinea during six cruises carried out between 2005 and 2007 were analysed to study the influence of equatorial upwelling on the productivity of the region. At 10°W, observations during boreal summer and autumn cruises captured seasonal upwelling influences. In response to the shoaling pycnocline in June 2005, higher concentrations of nitrate and chlorophyll fluorescence were recorded at the ocean surface in June than in September. Our findings challenge the paradigm that westward advection from the nutrient-rich African coast is responsible for equatorial enrichment in the Gulf of Guinea. Vertical sections of the parameters under study in the summer of 2005 showed no westward advection from 3°E to 10°W within the equatorial band. This emphasizes the important role of vertical processes in equatorial enrichment at 10°W. An additional aspect of our study provides evidence of the impact on nutrient and chlorophyll distribution of off-equatorial westward recirculation of equatorial undercurrent waters (observed between 2° and 3°S).

**Key words:** Advection, equatorial undercurrent, equatorial upwelling, Gulf of Guinea, nutrients, phytoplankton biomass.

## INTRODUCTION

The equatorial Atlantic Ocean is a region of high productivity, which is a result of seasonal upwelling that uplifts nutrients into the euphotic zone (Voituriez and Herbland, 1977; Christian and Murtugudde, 2003). Upwelling in this region has significant impact on the climate and fisheries of the area (Hardman-Mountford et al., 2000). In the boreal summer, equatorial upwelling is

associated with the Atlantic cold tongue that appears near 10°W owing to the convergence of strong Ekman pumping that is, in turn, associated with the early onset of intensified trade winds near this location (Caniaux et al., 2011). Strong easterly winds that generate upwelling Kelvin waves have been identified during spring in the western tropical Atlantic, and the presence of these

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waves along the Equator is associated with a strong and shallow thermocline in the eastern equatorial Atlantic during the succeeding summer (Hormann and Brandt, 2009; Marin et al., 2009).

The core depth of the subsurface eastward-flowing Equatorial Undercurrent (EUC), with velocity reaching  $90 \text{ cm s}^{-1}$ , has been shown to coincide with the depth of the thermocline in the tropical Atlantic (Schott et al., 1998; Bourlès et al., 2002). In the eastern equatorial Atlantic, the shoaling and nutrient enrichment of the EUC has been linked to the shoaling of the thermocline during summer (Oudot and Morin, 1987; Bourlès et al., 2002). The summer reinforcement of the strong vertical velocity shear between the EUC and the surface westward South Equatorial Current (SEC) has been shown to contribute to the surface layer enrichment through enhanced vertical mixing (Jouanno et al., 2011). According to Jouanno et al. (2011), cooling is not driven directly by the strength of the EUC but by the strength and the direction of the surface current.

Chlorophyll-*a* concentrations have been used to describe biological productivity in the tropical Atlantic (Signorini et al., 1999; Grodsky et al., 2008). Although the seasonal cycle of chlorophyll-*a* in the equatorial belt of the tropical Atlantic has been shown to reflect seasonal variations of equatorial zonal winds and upwelling that follow the seasonal movement of the Intertropical Convergence Zone (Grodsky et al., 2008), there is still a paucity of information with respect to the linkage between physical and biogeochemical processes in this undersampled and poorly understood region. Observing the conditions between  $35^\circ\text{W}$  (that is, to the west of the Gulf of Guinea basin) and  $4^\circ\text{W}$  (within the Gulf), Oudot and Morin (1987) showed that zonal advection from the African coastal upwelling zone, often advanced as an explanation of equatorial enrichment (Kawase and Sarmiento, 1986), does not concur completely with the observed surface distributions of nitrate in the Gulf of Guinea between  $5^\circ\text{N}$  and  $5^\circ\text{S}$ . Oudot and Morin (1987) concluded that zonal advection from the African coast is not sufficient to account for surface nutrient distribution along the Equator, and that other local vertical processes are involved. However, there has been no detailed investigation—using spatial differences within the Gulf of Guinea basin— that explores the hypothesis of zonal advection within the equatorial band (particularly within the EUC latitudinal band) with respect to equatorial enrichment and its associated productivity. Although the presence of off-equatorial westward recirculation of EUC waters has been suggested in the eastern equatorial Atlantic (Mercier et al., 2003), there is a dearth of information on the impact of this process on nutrient distribution and biological productivity in this region.

Our study explores the influence of the seasonal equatorial upwelling on nutrient distribution and phytoplankton biomass in the Gulf of Guinea, reconsiders the paradigm of westward zonal advection within the Gulf

of Guinea basin, and also investigates the impact of off-equatorial westward recirculation of the EUC waters on productivity potential. In order to achieve these objectives, we revisited the seasonality and spatial differences in the physical conditions (specifically upwelling within the EUC latitudinal bands) in the Gulf of Guinea using *in situ* measurements contained in datasets consisting of several physical, biogeochemical and current-related parameters collected during six cruises.

## MATERIALS AND METHODS

### Source of the datasets

The data used in this study were obtained from the EGEE (Etude de la Circulation Océanique et des Échanges Océan-atmosphère dans le Golfe de Guinée) experiment (Bourlès et al., 2007), which was the French oceanographic component of the AMMA (African Monsoon Multidisciplinary Analyses) international program (Redelsperger et al., 2006). It was conducted during the AMMA Enhanced Observing Period (2005–2007) to assess interannual and seasonal variability in the Gulf of Guinea (Bourlès et al., 2007).

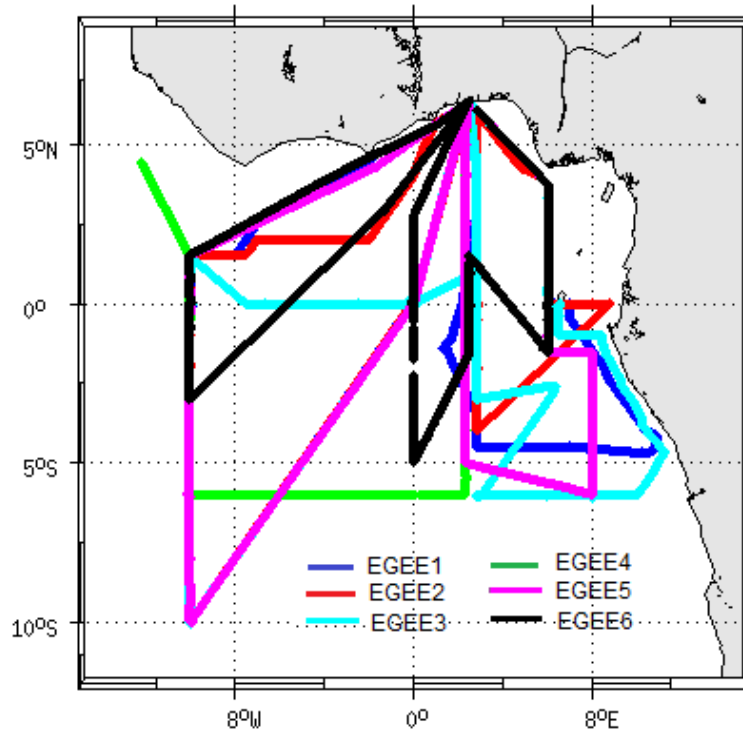
### Sampling and quality control

The variability was measured along several meridional sections, with primary focus given to that of  $10^\circ\text{W}$ , which was sampled several times prior to the EGEE by the PIRATA (Prediction and Research moored Array in the Tropical Atlantic) program (Bourlès et al., 2008) and EQUALANT (Cooperative Survey of the Atlantic Equatorial Zone) cruises (Bourlès et al., 2002). The general track of the six EGEE cruises conducted between 2005 and 2007 is presented in Figure 1 (Kolodziejczyk et al., 2009, 2014; Nubi et al., 2014 for additional details). Seawater samples were collected in 11 or 22 (depending on the cruise/research vessel used) hydrological bottles attached to a rosette, together with a CTD- $\text{O}_2$  (bathysonde) and ship-mounted acoustic Doppler current profiler (SADCP). Conductivity-temperature-depth (CTD) and dissolved oxygen ( $\text{O}_2$ ) measurements were taken using SeaBird probes, and chlorophyll-*a* fluorescence, which is an indicator of active phytoplankton biomass and chlorophyll concentrations in the water column, was measured with a Wetlab ECO FL sensor. The CTD sensors, which were calibrated before and after the cruises, were accurate within  $0.003^\circ\text{C}$  (temperature) and 0.003 (salinity). The horizontal resolution of the CTD profiles along  $10^\circ\text{W}$  was generally of  $\frac{1}{2}^\circ$  of latitude, but  $\frac{1}{3}^\circ$  between  $1^\circ\text{S}$  and  $1^\circ\text{N}$  (Kolodziejczyk et al., 2009). Nitrate analysis (accurate to  $0.1 \mu\text{mol.kg}^{-1}$ ) was conducted according to Benschneider and Robinson (1952), and phosphate analysis (accurate to  $\sim 0.2 \mu\text{mol.kg}^{-1}$ ) according to Murphy and Riley (1962); also, Baurand (2008) provides further detail about nutrient analysis. Duplicate analyses of individual samples were performed regularly to estimate analytical error.

### Rationale for methodology

Zonal currents, temperature, salinity, nitrate, phosphate, and chlorophyll fluorescence were used to describe variability in biological productivity, in relation to hydrology and dynamics of the region. Values for apparent oxygen utilization (AOU) were obtained by subtracting the observed oxygen value from the saturated oxygen value (Weiss 1970):

$$\text{AOU} = \text{O}_{2(\text{saturated})} - \text{O}_{2(\text{observed})}$$



**Figure 1.** Overall track line of EGEE cruises in the Gulf of Guinea. Upper-layer horizontal currents were measured continuously. Stations for hydrological measurements and seawater sampling were located primarily along 10°W and 3°E.

where  $\ln(O_{2(\text{saturated})}[\text{ml}^{-1}]) = -173.4292 + 249.6339(100/\text{TK}) + 143.3483 \ln(\text{TK}/100) - 21.8492(\text{TK}/100) + \text{Salinity} [-0.033096 + 0.014259(\text{TK}/100) - 0.001700(\text{TK}/100)^2]$

where TK is the temperature in Kelvin.

Here, AOU was used to illustrate how much oxygen was taken up during respiration. Following Oudot and Morin (1987), the nitrate-temperature relationship (N-T plot) was used to study the balance between physical and biochemical processes, and also to describe spatial differences in nutrient distribution along the 10°W and 3°E transects. Although data availability varied along the meridians of 10°W and 3°E, our analyses were focused mainly within the equatorial band (1°N–1°S), and in the 0–100 m depth stratum where biological activity is most prevalent. This band encompasses the EUC, and hence some stations were profiled to describe the role of the EUC in the equatorial enrichment processes. While the EUC was characterized primarily by temperature and salinity profiles, it was also expressed through AOU and chlorophyll fluorescence profiles, with maximum chlorophyll fluorescence occurring within the equatorial band.

## RESULTS

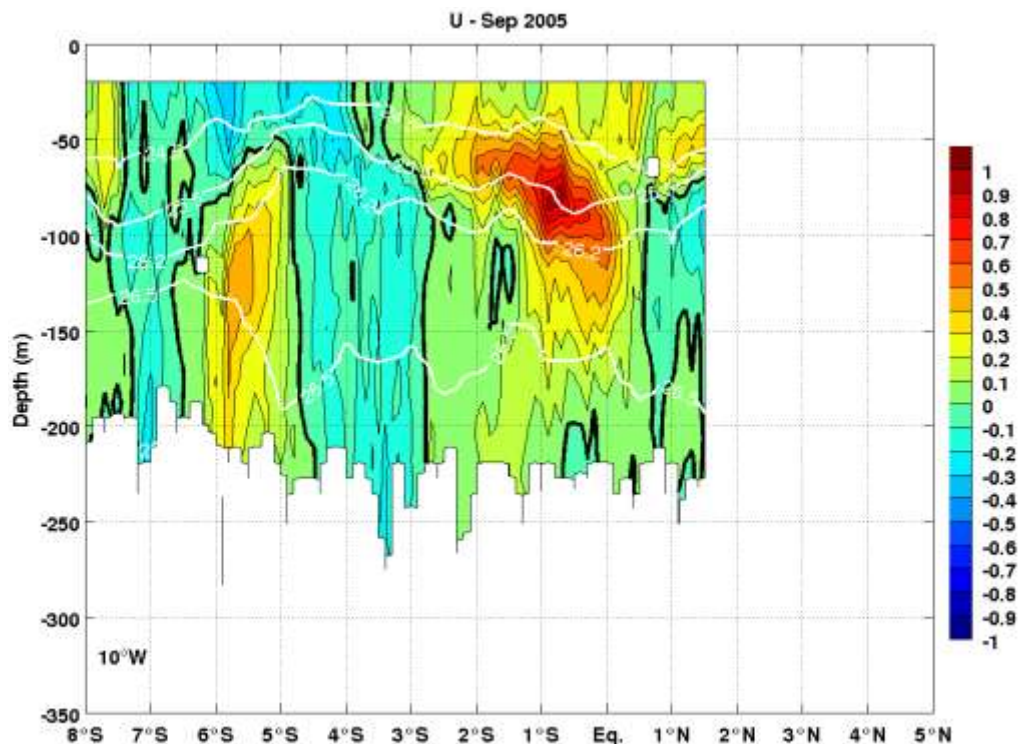
### Seasonal upwelling influence

In order to study the influence of the seasonal upwelling on nutrients and phytoplankton biomass, hydrological structures for the studied parameters within the equatorial

band were analyzed along 10°W during the onset (June - EGEE 1) and final phase (September - EGEE 2) of equatorial upwelling in 2005 (Caniaux et al., 2011). This year was chosen because it exhibited the greatest seasonal variability in the parameters under study.

### Zonal currents

As previously shown by Nubi et al. (2014), the EUC had an eastward velocity core of  $>0.9 \text{ ms}^{-1}$  at depths of  $\sim 50 \text{ m}$  in June 2005. Figure 2 presents the vertical section for the zonal currents in September 2005 with same EUC eastward velocity core value ( $>0.9 \text{ ms}^{-1}$ ) as in June 2005, but with a deeper core in September ( $\sim 70 \text{ m}$ ) than in June 2005 (Table 1). Whereas the EUC extended to  $\sim 250 \text{ m}$  in June (Nubi et al., 2014), the extension was shallower (150 m) in September (Figure 2). The velocity core was more southward in September than in June, and was bordered by the central and northern branches of the westward-flowing SEC in June (Nubi et al., 2014). There was deepening of the pycnocline (represented by the  $25.5 \text{ kg}^{-3} \text{ m}^{-3}$  isopycnal) in September, associated with the deepening of the EUC core (Figure 2). While the  $24.5 \text{ kg}^{-3} \text{ m}^{-3}$  isopycnal was present within the equatorial band in September (Figure 2), it was completely absent north of 3°S in June 2005 (Nubi et al., 2014).



**Figure 2.** Vertical section of the zonal current velocity ( $\text{ms}^{-1}$ ) along  $10^{\circ}\text{W}$  in September 2005. The 24.5, 25.5, 26.2 and 26.5 isopycnals ( $\text{kg}\cdot\text{m}^{-3}$ ) are shown in white lines.

**Table 1.** Positions and values for EUC and chlorophyll fluorescence (CF) maxima within  $1^{\circ}\text{N} - 1^{\circ}\text{S}$ .

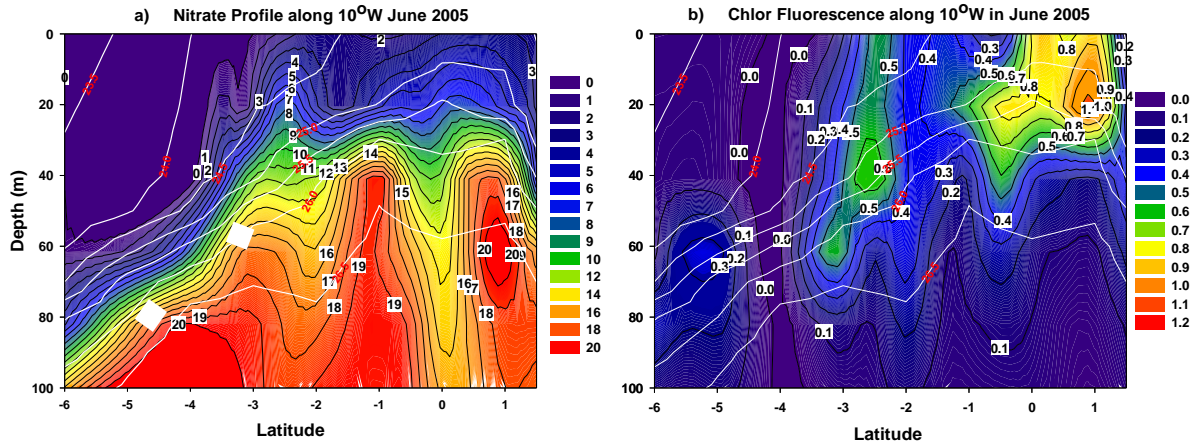
Cruise	Long	EUC core (CF max) lat	EUC core (CF max) depth (m)	EUC (CF) max.
June 2005	$10^{\circ}\text{W}$	$0.5^{\circ}\text{S}$ ( $1^{\circ}\text{N}$ )	50(20)	$>0.9 \text{ ms}^{-1}$ ( $>1.2 \text{ mg}\cdot\text{m}^{-3}$ )
June 2005	$3^{\circ}\text{E}$	$0.5^{\circ}\text{S}$ ( $1^{\circ}\text{N}$ )	50(40)	$0.4 \text{ ms}^{-1}$ ( $<0.5 \text{ mg}\cdot\text{m}^{-3}$ )
Sept 2005	$10^{\circ}\text{W}$	$0.5^{\circ}\text{S}$ ( $0.5^{\circ}\text{S}$ )	70 (40)	$>0.9 \text{ ms}^{-1}$ ( $0.5 \text{ mg}\cdot\text{m}^{-3}$ )

### Nitrate and chlorophyll fluorescence

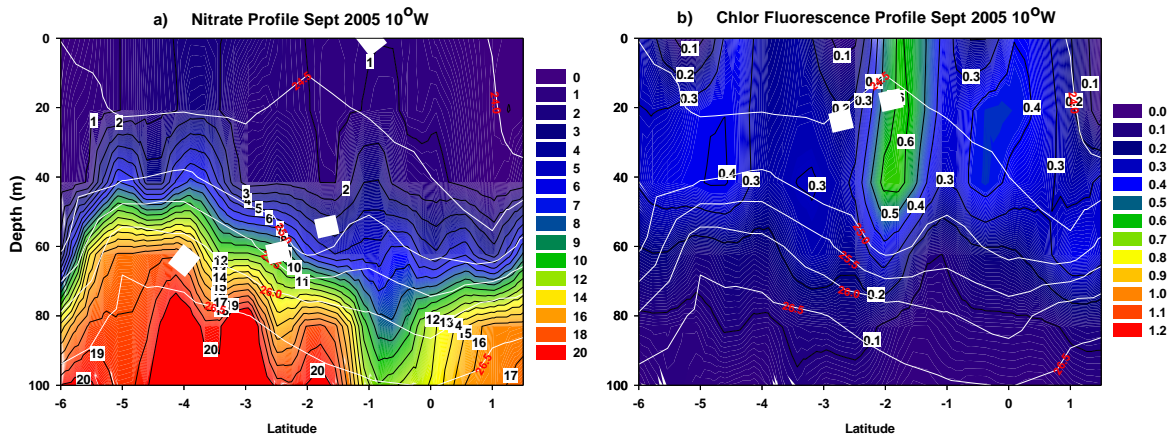
Figures 3 and 4 present nitrate and chlorophyll fluorescence vertical sections along  $10^{\circ}\text{W}$  ( $1.5^{\circ}\text{N}$ – $6^{\circ}\text{S}$ ) in the upper 100 m during June and September 2005, respectively. Nitrate concentration of  $\sim 4 \mu\text{mol}\cdot\text{kg}^{-1}$  was observed within the equatorial band ( $1^{\circ}\text{N}$ – $1^{\circ}\text{S}$ ) at depths  $<20$  m in June (Figure 3a) and  $>50$  m in September (Figure 4a). The presence of off-equatorial surface enrichment of nitrate was noted in June between  $2^{\circ}\text{S}$  and  $3^{\circ}\text{S}$  (Figure 3a), with nitrate concentrations of  $\sim 4 \mu\text{mol}\cdot\text{kg}^{-1}$  at depths  $<20$  m. Along  $10^{\circ}\text{W}$ , the highest values near the surface for chlorophyll fluorescence within the equatorial band in June (Figure 3b) and September (Figure 4b) were  $0.8$  and  $0.4 \text{ mg}\cdot\text{m}^{-3}$ , respectively. Off-equatorial chlorophyll fluorescence maxima ( $0.6 \text{ mg}\cdot\text{m}^{-3}$ ) occurred in June between  $2$  and  $3^{\circ}\text{S}$  at  $40$  m (Figure 3b) and in September at  $2^{\circ}\text{S}$  within the upper  $50$  m (Figure 4b).

### Influence of the EUC

Seasonal variation of the EUC along  $10^{\circ}\text{W}$  in terms of temperature (Figure 5a) and salinity (Figure 5b) was profiled at the location and depth of the EUC velocity core (Table 1). Apparent oxygen utilization (Figure 5c) and chlorophyll fluorescence (Figure 5d) were also profiled at the latitude of maximum chlorophyll fluorescence (Table 1) within the EUC band. The thermocline was shallower in June with an outcropping of colder water ( $<23^{\circ}\text{C}$ ) to the surface, and the halocline was also shallower in June (Figure 5a and b). Relatively high oxygen-saturated water ( $-0.06 \text{ ml}\cdot\text{l}^{-1}$ ) occupied the surface in September, but AOU values were near constant from the surface to  $\sim 50$  m depth, after which they increased with depth to  $\sim 1.75 \text{ ml}\cdot\text{l}^{-1}$  at  $100$  m. Conversely, in June, AOU increased with depth from near the surface to  $\sim 60$  m, remained constant at  $3.5 \text{ ml}\cdot\text{l}^{-1}$  between  $60$  and  $80$  m, and then decreased to  $\sim 2.75 \text{ ml}\cdot\text{l}^{-1}$  at  $100$  m (Figure 5c). The chlorophyll



**Figure 3.** Vertical section of (a) nitrate ( $\mu\text{mol.kg}^{-1}$ ) and (b) chlorophyll fluorescence ( $\text{mg.m}^{-3}$ ) along  $10^{\circ}\text{W}$  ( $1.5^{\circ}\text{N}$ – $6^{\circ}\text{S}$ ) in June 2005. Isopycnals ranging from  $23.5$  to  $26.5 \text{ kg.m}^{-3}$  are shown in white lines (redrawn from Nubi et al., 2014).



**Figure 4.** Vertical section of (a) nitrate ( $\mu\text{mol.kg}^{-1}$ ) and (b) chlorophyll fluorescence ( $\text{mg.m}^{-3}$ ) along  $10^{\circ}\text{W}$  ( $1.5^{\circ}\text{N}$ – $6^{\circ}\text{S}$ ) in September 2005. Isopycnals ranging from  $23.5$  to  $26.5 \text{ kg.m}^{-3}$  are shown in white lines.

fluorescence maximum (Figure 5d) was greater and shallower in June (reaching  $>1.2 \text{ mg.m}^{-3}$  at 20 m) than in September.

**Spatial differences along  $10^{\circ}\text{W}$  and  $3^{\circ}\text{E}$**

In order to confirm if westward zonal advection from the nutrient-rich African coast is responsible for equatorial enrichment in the Gulf of Guinea, we analyzed hydrological structures of some oceanic parameters which reveal upwelling and productivity along  $10^{\circ}\text{W}$  and  $3^{\circ}\text{E}$  during the onset of equatorial upwelling in June 2005.

**Zonal currents**

At  $3^{\circ}\text{E}$ , the EUC had a velocity core of  $0.4 \text{ m.s}^{-1}$  at  $\sim 40 \text{ m}$  depth and extended to  $\sim 200 \text{ m}$  between  $0.5^{\circ}\text{N}$  and  $1^{\circ}\text{S}$

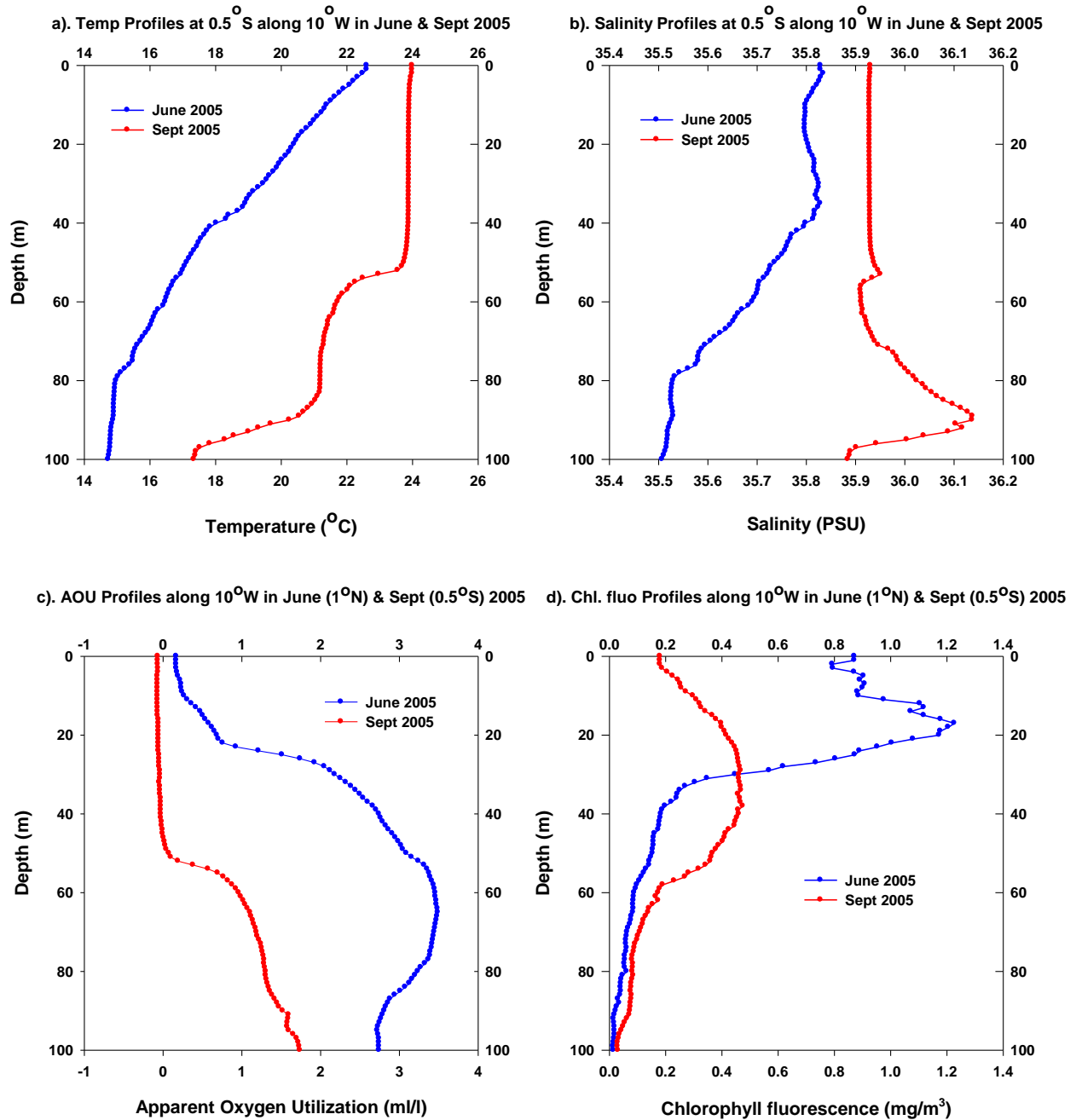
(Figure 6). When compared with the condition along  $10^{\circ}\text{W}$  (Nubi et al., 2014; their Figure 3), there was a significant eastward weakening of the EUC from  $10^{\circ}\text{W}$  to  $3^{\circ}\text{E}$  (Figure 6).

**Nitrate and chlorophyll fluorescence**

Whereas there was equatorial nitrate enrichment near the surface along  $10^{\circ}\text{W}$  (Figure 3a), concentrations of nitrate were very low at the surface within the equatorial band at  $3^{\circ}\text{E}$  (Figure 7a). There were moderate concentrations of chlorophyll fluorescence of  $\sim 0.4 \text{ mg.m}^{-3}$  at  $\sim 40 \text{ m}$  in the equatorial region at  $3^{\circ}\text{E}$  (Figure 7b).

**Influence of the EUC**

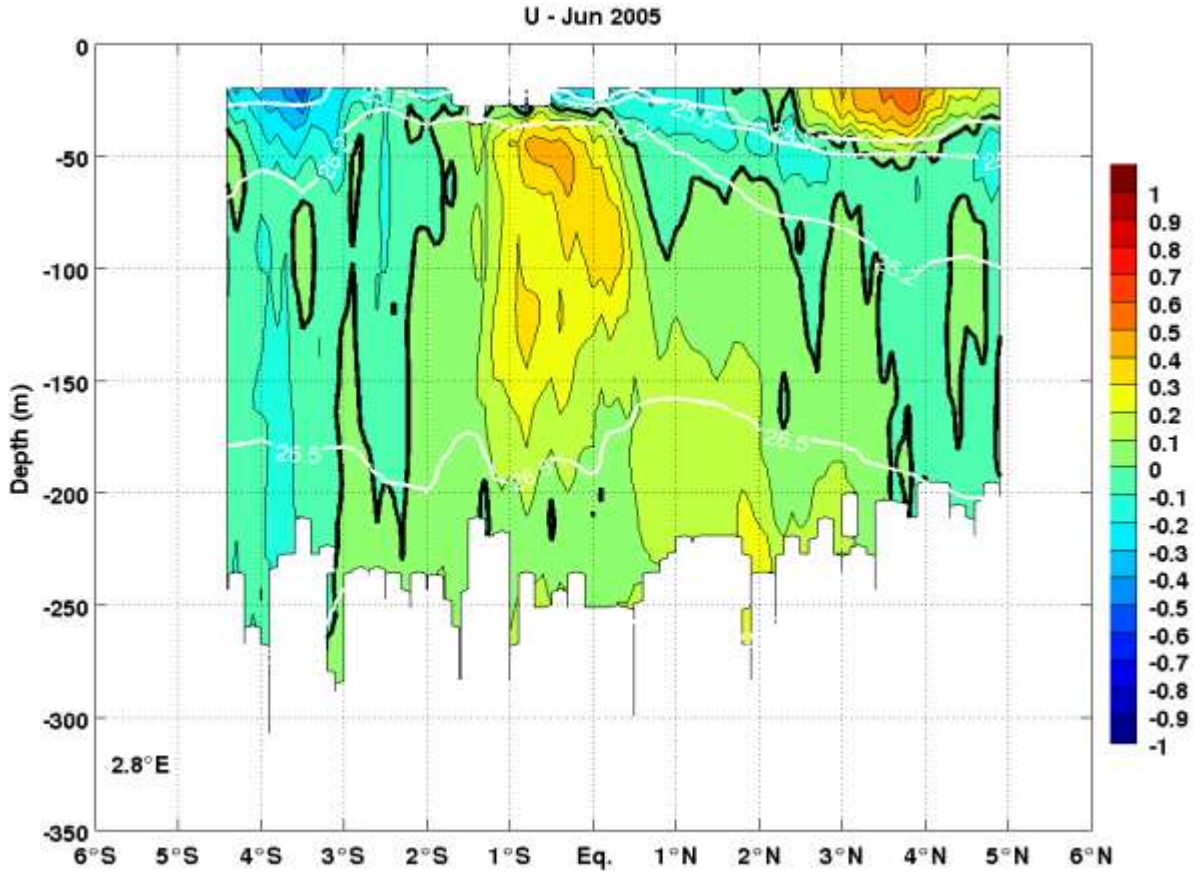
The thermocline was shallow at  $10^{\circ}\text{W}$  (Figure 8a),



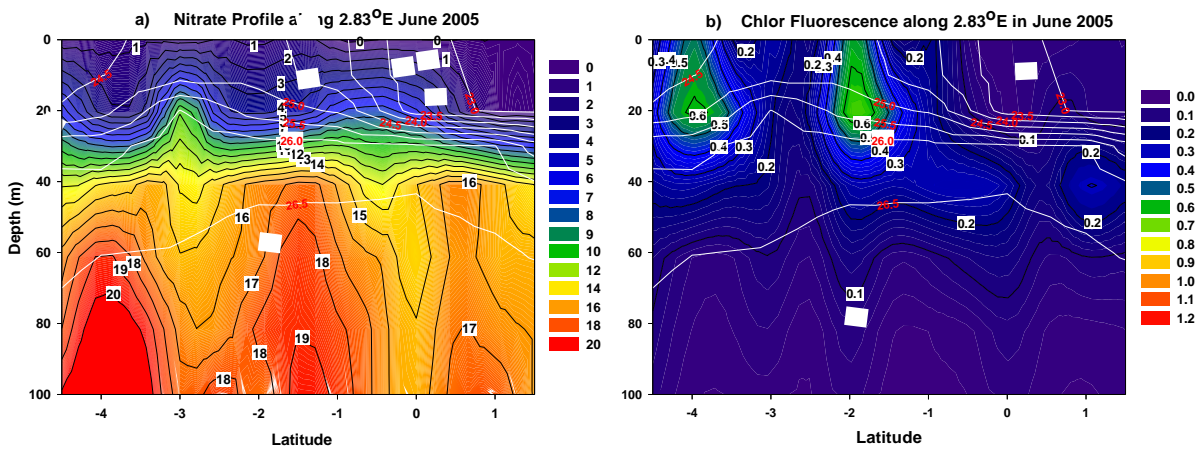
**Figure 5.** Vertical profiles along 10°W at 0.5°S in June and September 2005 of (a) temperature (°C) and (b) salinity (PSU), and at 1°N in June and 0.5°S in September 2005 of (c) apparent oxygen utilization (ml.l<sup>-1</sup>) and (d) chlorophyll fluorescence (mg.m<sup>-3</sup>).

uplifting cold water to the surface. At the mean depth of the EUC velocity core, there was erosion of the EUC salinity maximum along both lines of longitude in June 2005 (Figure 8b), but the net increase in salinity at the surface was mostly expressed at 10°W. Values of AOU were lower at the surface at 3°E, and were constant from the surface to ~20 m (Figure 8c). At both longitudes, there was a strong link between the vertical distribution of

AOU (Figure 8c) and that of chlorophyll fluorescence (Figure 8d). The maximum increase in AOU with depth corresponded to regions of maximum chlorophyll fluorescence (Figure 8c, d). The chlorophyll fluorescence maximum along 10°W (>1.2 mg.m<sup>-3</sup>) and 3°E (<0.5 mg.m<sup>-3</sup>) occurred at 20 and 40 m, respectively (Figure 8d). The slope of the regression line of the relationship between nitrate and temperature (shown in N-T plots



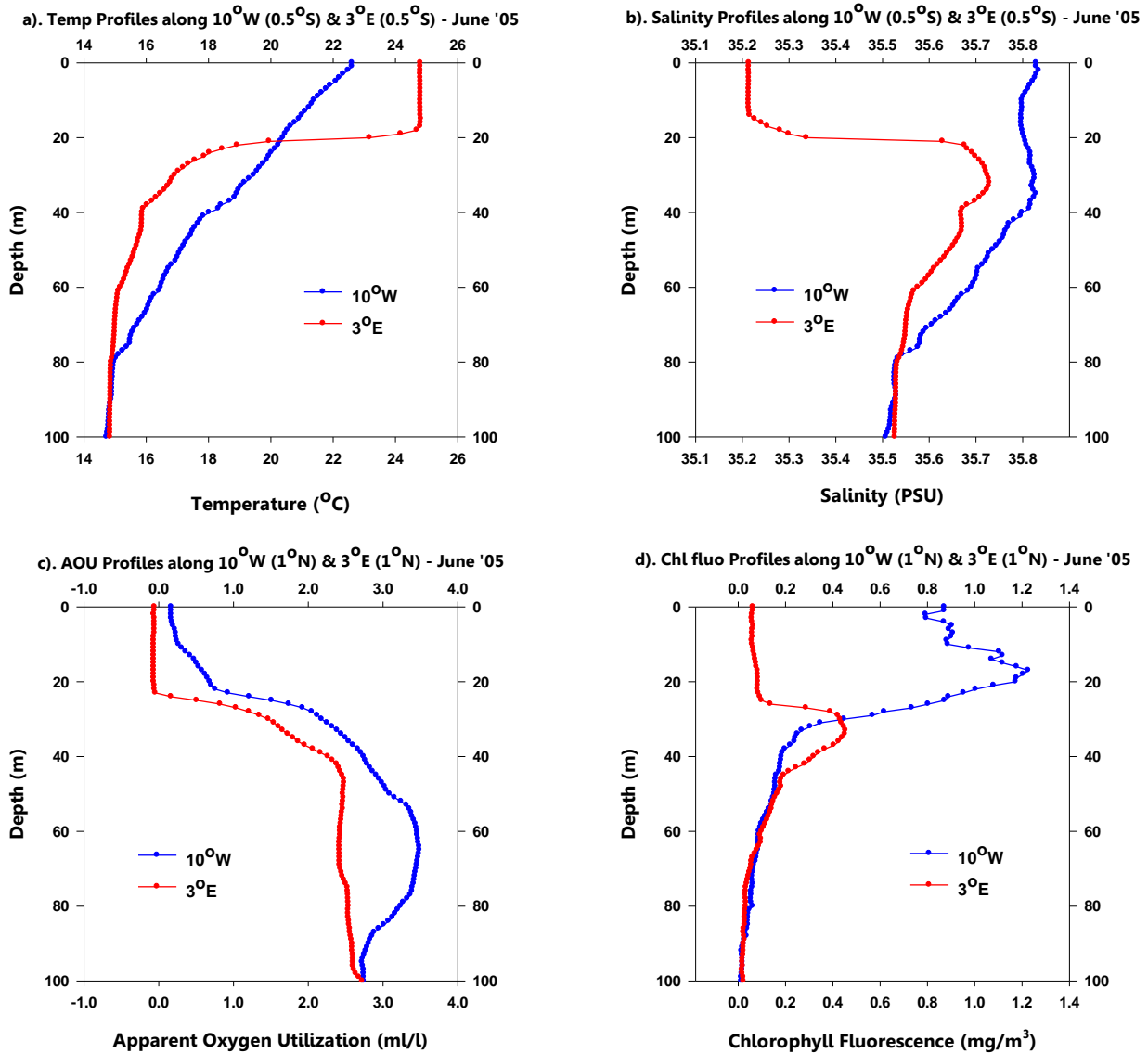
**Figure 6.** Vertical section of the zonal current velocity ( $\text{ms}^{-1}$ ) along  $3^\circ\text{E}$  ( $4.5^\circ\text{S}$ – $5^\circ\text{N}$ ) in June 2005. The 24.5, 25.5, 26.2, and 26.5 isopycnals ( $\text{kg.m}^{-3}$ ) are shown in white lines.



**Figure 7.** Vertical section of (a) nitrate ( $\mu\text{mol.kg}^{-1}$ ) and (b) chlorophyll fluorescence ( $\text{mg.m}^{-3}$ ) along  $3^\circ\text{E}$  ( $1.5^\circ\text{N}$ – $4.5^\circ\text{S}$ ) in June 2005. Isopycnals ranging from 23 to  $26.5 \text{ kg.m}^{-3}$  are shown in white lines.

in Figure 9) was greater (in absolute value) at  $10^\circ\text{W}$  than at  $3^\circ\text{E}$  ( $F_{27, 21} = 2.4698$ ,  $p < 0.05$ ). The coefficient of determination ( $r^2$ ) for the N-T plots along both longitudes

were high. Whereas concentrations of nitrate were lower along  $10^\circ\text{W}$  in the upper nitracline ( $0$ – $10 \mu\text{mol.kg}^{-1}$ ), higher nitrate concentrations were evident in the lower



**Figure 8.** Vertical profiles in June 2005 along 10°W and 3°E and at 0.5°S of (a) temperature (°C) and (b) salinity (PSU), and at 1°N of (c) apparent oxygen utilization (ml.l<sup>-1</sup>) and (d) chlorophyll fluorescence (mg.m<sup>-3</sup>).

nitracline (>10  $\mu\text{mol.kg}^{-1}$ ) (Figure 9).

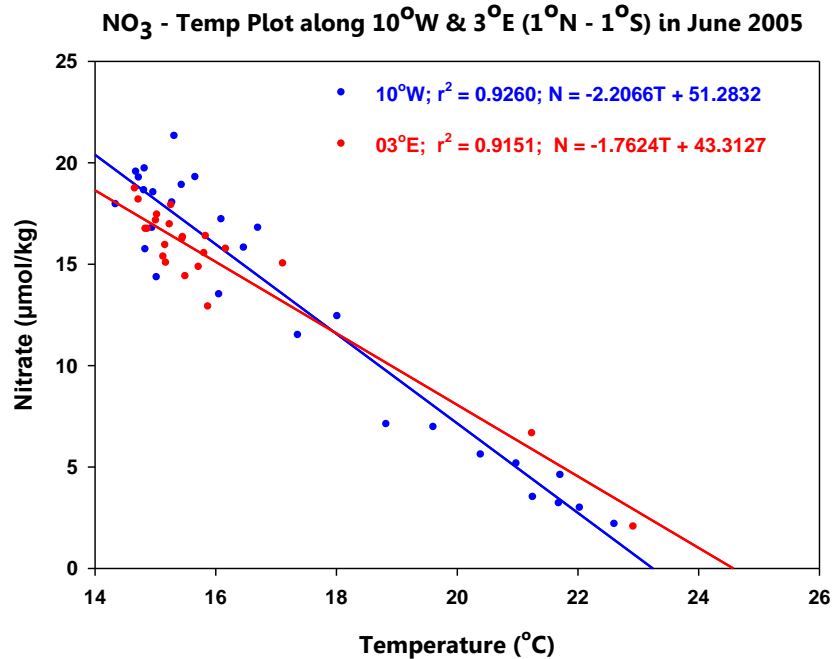
## DISCUSSION

### Seasonal upwelling influence

The vertical profiles of zonal currents depicted in our study show that the EUC in association with the pycnocline is shallower in June 2005. Consistent with the findings of Oudot and Morin (1987), uplift of the pycnocline, which supplies the EUC with nutrients, plays an important role in the enrichment process within the equatorial band. The seasonal differences in various parameters revealed in our study are in agreement with

previous findings regarding seasonal variability in the Gulf of Guinea, where the seasonal equatorial upwelling and thermocline lifting are more enhanced in June than in September (Voituriez and Herbland, 1979; Oudot and Morin, 1987; Kolodziejczyk et al., 2009). Also, in agreement with Jouanno et al. (2011), it is shown here that the intensification of the northern branch of the SEC around 1°N in June 2005 enhanced the vertical shear just above the core of the EUC, causing vertical mixing and equatorial cooling to be stronger in June than in September. According to Jouanno et al. (2011), the cooling in June 2005 was not driven directly by the strength of the EUC, but rather by the strength and direction of the surface current that was westward and more intensified. This explains our finding that the EUC





**Figure 9.** Nitrate-temperature relationship (0–100 m) along 10°W and 3°E for all values of nitrate  $>1 \mu\text{mol.kg}^{-1}$  between 1°N and 1°S in June 2005.

velocity cores in June and September 2005 were equal ( $>0.9 \text{ m.s}^{-1}$ ) (although deeper in September), but net cooling and associated surface enrichment were higher in June 2005. The structures of the thermocline and halocline in June and September were in association with the EUC shoaling in June and deepening in September. The imprint of the EUC salinity maximum was absent at the mean depths of the EUC core in June 2005, which is an indication of an intense mixing of the EUC water with the surface waters in June, as reported by Voituriez and Herbland (1979) and Kolodziejczyk et al. (2014). Higher AOU values at the surface in June are indicative of lower oxygen saturation, whereas the constant AOU value from the surface to about 50 m in September indicates little or no oxygen-consuming processes within this depth range. An increase in AOU with depth, ascribable to oxidation of particulate organic matter, was more pronounced in June. The high concentration for chlorophyll fluorescence ( $>1.2 \text{ mg.m}^{-3}$ ) recorded at about 20 m depth within the EUC latitude band in June was a biological response of phytoplankton to enhanced surface enrichment witnessed in this month.

### Spatial differences along 10°W and 3°E

Within the equatorial band (1°N–1°S), the structure of the pycnocline, which shows complete disappearance of the  $24.5 \text{ kg.m}^{-3}$  isopycnal along 10°W but its presence along 3°E, and the higher concentrations of nitrate ( $\sim 4 \mu\text{mol.kg}^{-1}$

<sup>1)</sup> near the surface at 10°W, did not indicate a westward zonal advection from 3°E to 10°W in June 2005. This was also clear from the currents measurements along 10°W, as there was an eastward-flowing nutrient-rich EUC (weaker along 3°E), which made westward zonal advection within the equatorial band impossible at the EUC depth. Our findings also show a clear indication of stronger equatorial upwelling at 10°W in June 2005. Similar to the finding of Jouanno et al. (2011), the presence of warmer and less saline waters at the upper layer along 3°E establishes a stratification that limits vertical mixing to the upper 20 m depth, and disconnects the surface from subsurface dynamics. Although waters with slightly higher oxygen saturation occurred at the surface at 3°E in June 2005, dissolved oxygen consumption for organic material degradation was higher at 10°W throughout the depths surveyed. Higher values at shallower depths in the vertical distribution of phytoplankton biomass at 10°W is a direct indication that nutrient influx to the upper layer occurred more strongly at that longitude. The N-T plot further supports a higher equatorial nutrient enrichment along 10°W and increased consumption of nutrients by phytoplankton. Significance of the difference between two slopes was performed using the slope, standard error, and sample size for each regression line. A probability value of less than 0.05 indicates that the two slopes are significantly different from each other. An F test statistic ( $F[\alpha(2) = 0.05, 27, 21]$ ) gave a value of 2.4698. Thus, there is significant difference in variability about the regression lines relating

nitrate values to seawater temperature along 10°W and 3°E. As pointed out by Oudot and Morin (1987), the strong correlation between nitrate and temperature at both longitudes in June 2005 shows a balance between physical and biological processes. The lower concentrations of nitrate along 10°W in June 2005 in the upper nitracline are indicative of higher consumption. Conversely, along 3°E consumption and regeneration were lower in the upper and lower nitraclines, respectively.

Further from the equatorial region, the secondary blooms that appeared between 2° and 3°S along 10°W (at depths >50 m) in June of 2005 are biological responses to off-equatorial westward recirculation of the EUC waters, shown by Kolodziejczyk et al. (2014). Also the secondary outcropping between 2° and 3°S of nitrate-rich water to depths <20 m along 10°W and 3°E in June 2005 was not locally induced, but was due to westward recirculation of nutrient-rich EUC waters (Kolodziejczyk et al., 2014).

## Summary

Our study supports the growing body of evidence that not only challenges the paradigm that equatorial surface enrichment in the Gulf of Guinea is supplied from the African coastal upwelling zone, but also improves our understanding of the impact of equatorial upwelling on the nutrient distribution and phytoplankton biomass of this region. The hydrological features of the parameters investigated in our study revealed the seasonal influence of equatorial upwelling on biological productivity in the Gulf of Guinea. Evidence is provided to show that biological response to surface enrichment is stronger within the equatorial band during the onset of upwelling (June) than during its final phase (September). Equatorial upwelling associated with shoaling of the pycnocline was stronger along 10°W than 3°E in the Gulf of Guinea, which suggests the important role of vertical processes in the equatorial enrichment along 10°W. Also, along both longitudes in June 2005, there was an eastward equatorial flow due to the presence of the EUC, the transport and velocity core depth of which decreases eastwards (Hormann and Brandt, 2007; Kolodziejczyk et al., 2009). Westward zonal advection of nutrients from the far eastern part of the Gulf of Guinea to the region along 10°W is therefore not possible within the equatorial band. Off-equatorial maxima for nitrate and chlorophyll fluorescence near 3°S at both longitudes were not locally induced, but rather were a consequence of the westward recirculation of the EUC waters, as suggested by Kolodziejczyk et al. (2014). The off-equatorial distribution of these parameters in the upper pycnocline along 10°W and 3°E around 3°S strongly suggests the continuity of the westward recirculation of saline and nutrient-rich water masses originating from the EUC (Kolodziejczyk et

al., 2014).

## Conflict of Interests

The authors have not declared any conflict of interests.

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## REFERENCES

- Baurand F (2008). Analyses report for nutrient EGEE 1, 2, 3, 4, 5, and 6. US-191 *IMAGO* – Composante océanographique de Brest. Brest: IRD.
- Benschneider K, Robinson RJ (1952). A new spectrometric method for determination of nitrite in sea water. *J. Marine Res.* 11:87-96.
- Bourlès B, D'Orgeville M, Eldin G, Gouriou Y, Chuchla R, DuPenhoat Y, Arnault S (2002). On the evolution of the thermocline and sub-thermocline eastward currents in the Equatorial Atlantic. *Geophys. Res. Lett.* 29:1785.
- Bourlès B, Marin F, Gouriou Y, Grelet J, Chuchla R, Roubaud F, DuPenhoat Y (2007). African Monsoon Multidisciplinary Analysis (AMMA): special measurements in the Tropical Atlantic. *CLIVAR Newsletter Exchanges* 41:7-9.
- Bourlès B, Lumpkin R, McPhaden MJ, Hernandez F, Nobre P, Campos E, Yu L, Planton S, Busalacchi A, Moura AD, Servain J, Trotte J (2008). The PIRATA Program: history, accomplishments, and future directions. *Bull. Am. Meteorol. Soc.* 9:1111-1125.
- Caniaux G, Giordani H, Redelsperger JL, Guichard F, Key E, Wade M (2011). Coupling between the Atlantic cold tongue and the West African monsoon in boreal spring and summer. *J. Geophys. Res.* 116:C04003.
- Christian JR, Murtugudde R (2003). Tropical Atlantic variability in a coupled physical-biogeochemical ocean model. *Deep-Sea Res.* 50:2947-2969.
- Grodsky SA, Carton JA, McClain CR (2008). Variability of upwelling and chlorophyll in the equatorial Atlantic. *Geophys. Res. Lett.* 35:L03610.
- Hardman-Mountford NJ, Koranteng KA, Price ARG (2000). The Gulf of Guinea Large Marine Ecosystem. In *Seas at the Millennium: an Environmental Evaluation* edited by C. Sheppard (Amsterdam: Elsevier), 1:773-796.
- Hormann V, Brandt P (2007). Atlantic equatorial undercurrent and

- associated cold tongue variability. *J. Geophys. Res.* 112:C06017.
- Hormann V, Brandt P (2009). Upper equatorial Atlantic variability during 2002 and 2005 associated with equatorial Kelvin waves. *J. Geophys. Res.* 114:C03007.
- Jouanno J, Marin F, Du Penhoat Y, Molines JM, Sheinbaum J (2011). Seasonal modes of surface cooling in the Gulf of Guinea. *J. Phys. Oceanogr.* 41:1408-1416.
- Kawase M, Sarmiento JL (1986). Circulation and nutrients in mid-depth Atlantic waters. *J. Geophys. Res.* 91:9749-9770.
- Kolodziejczyk N, Boulès B, Marin F, Grelet J, Chuchla R (2009). Seasonal variability of the Equatorial Undercurrent at 10°W as inferred from recent *in situ* observations. *J. Geophys. Res.* 114:C06014.
- Kolodziejczyk N, Marin F, Boulès B, Gouriou Y, Berger H (2014). Seasonal variability of the equatorial undercurrent termination and associated salinity maximum in the Gulf of Guinea. *Clim. Dyn.* 43:3025-3046.
- Marin F, Caniaux G, Boulès B, Giordani H, Gouriou Y, Key E (2009). Why were sea surface temperatures so different in the eastern equatorial Atlantic in June 2005 and 2006? *J. Phys. Oceanogr.* 39:1416-1431.
- Mercier H, Arhan M, Lutjeharms JRE (2003). Upper-layer circulation in the eastern Equatorial and South Atlantic Ocean in January-March 1995. *Deep-Sea Res.* 150:863-887.
- Murphy J, Riley JP (1962). A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 27:31-36.
- Nubi OA, Boulès B, Edokpayi CA, Hounkonnou NM (2014). Inter-annual variability on the influence of equatorial upwelling on biological productivity along 10°W in the Eastern Equatorial Atlantic. *J. Biodivers. Environ. Sci.* 4 (1):72 -80.
- Oudot C, Morin P (1987). The distribution of nutrients in the equatorial Atlantic: relation to physical processes and phytoplankton biomass. Proceedings of an International Symposium on Equatorial Vertical Motion, Paris, 6-10 May 1985. *Oceanologica Acta* pp. 121-130.
- Redelsperger JL, Thorncroft C, Diedhiou A, Lebel T, Parker DJ, Polcher J (2006). African monsoon multidisciplinary analysis (AMMA): an international research project and field campaign. *Bull. Am. Meteorol. Soc.* 87:1739-1746.
- Signorini SR, Murtugudde RG, McClain CR, Christian JR, Picaut J, Busalacchi AJ (1999). Biological and physical signatures in the tropical and subtropical Atlantic. *J. Geophys. Res.* 104(C8):18367-18382.
- Schott FA, Fischer J, Stramma L (1998). Transports and pathways of the upper-layer circulation in the western tropical Atlantic. *J. Phys. Oceanogr.* 28:1904-1928.
- Voituriez B, Herbland A (1977). Production primaire, nitrate et nitrite dans l'Atlantique tropicale. II: Distribution du nitrate et production de nitrite, *Cahiers ORSTOM. Série Océanographie* 15:57-65.
- Voituriez B, Herbland A (1979). The use of the salinity maximum of the equatorial undercurrent for estimating nutrient enrichment and primary production in the Gulf of Guinea. *Deep-Sea Res.* 24:25-33.
- Weiss R (1970). The solubility of nitrogen, oxygen, and argon in water and seawater. *Deep-Sea Res.* 17:721-35.