Influence of the Orinoco River Plume on the balance between plankton primary production and respiration in the Caribbean Sea

by

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Abstract

Influence of the Orinoco River Plume (ORP) on plankton metabolic balance in the Eastern Caribbean was estimated along the plume's dispersal axis. Planktonic gross primary production (GPP), net community production (NCP) and community respiration (CR) were determined from changes in dissolved oxygen concentration after 24h light/dark incubations. ORP has marked influence on near surface plankton metabolism; less impact was observed at low irradiance. GPP and CR showed maximum values in the near field. NCP shows this area to be highly autotrophic. Dilution of the ORP with Caribbean waters results in reduction of GPP and CR. Comparing GPP and CR with studies in the Atlantic show the highly productive southern ORP region to fit well into a subsidized region regression. The mid to far field exhibit metabolic ratios closer to those observed in isolated regions. This suggests that riverine DOC in the mid and far fields is refractive to planktonic respiration.

Resumen

La influencia de la descarga del Río Orinoco (ORP) en el balance metabólico en el Mar Caribe se estimó a través de un gradiente de dispersión. La producción primaria bruta (GPP), la producción neta (NCP) y la respiración (CR) de la comunidad planctónica se determinaron analizando cambios en la concentración de oxígeno disuelto después de 24 horas de incubación. Nuestros resultados indican que la ORP influye en el metabolismo planctónico cercano a la superficie y un menor impacto en las profundidades de baja irradianza. GPP y CR muestran valores máximos en áreas cercanas a la desembocadura del río y la NCP calculada indica que esta es una región altamente autotrófica. La dilución de la ORP en las aguas del Caribe resulta en una reducción en la GPP y la CR con un movimiento hacia el norte. Al comparar la relación entre la GPP y la CR con estudios realizados en el Atlántico se observó que la alta productividad de la región sur de la OPR concuerda con la regresión de la región subsidiada con carbono alóctono. Por otro lado las regiones medias y lejanas demostraron tasas metabólicas cercanas a las observadas en regiones aisladas no productivas. La relación GPP:CR sugiere que el carbono orgánico disuelto en la región media y lejana, asociado a la descarga, es refractario y no utilizado en la respiración planctónica.

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I. Introduction

The threat posed to society and ecosystems by climate change has prompted the need for an improved understanding the role of the oceans in the global carbon cycle. Current assessments of the carbon cycle evidence the importance and the urgency to understand the transformation and flux of organic and inorganic carbon (Ducklow et al., 2001). Recent reviews on the role of the ocean in the carbon cycle largely focused on carbon dioxide (CO_2) flux have been published by Raven & Falkowski (1999) and Falkowski (2002).

Exchange between ocean and atmosphere is controlled by physical and biological processes. Two biological processes that play a part in the fate of carbon in the ocean are primary production (PP) and respiration (R). In primary production autotrophs convert inorganic material, CO_2 into new organic compounds through photosynthesis. Through respiration organisms obtain their vital energy needs by oxidizing organic compounds while producing CO_2. Understanding what drives the balance between plankton gross primary production (i.e. GPP, the total amount of inorganic carbon converted to organic compound) and community respiration (i.e. CR, oxygen consumption of organic compounds in plankton communities) is vital for the accurate determination of the ocean's role in the carbon cycle. These two biological processes are responsive to environmental conditions such as temperature, salinity, and irradiance (López et al., 2006). Irradiance effects are seen as photoinhibition and photorespiration. Photoinhibition is a reduction in photosynthetic capacity which occurs when photosynthetic organisms are exposed to strong irradiance. The latter is a biological process associated with the competition between O_2 and CO_2 which reduce

the primary production rates in areas that have high levels of irradiance. If significant photorespiration rates occur it is important to evaluate the definition of gross and net primary production and the relationship to ^{14}C assimilation or light-dark CO_2 exchange (Geider and MacIntyre, 2002).

Oceanic communities act as sources or sinks of CO_2 depending on the metabolic balance discussed above. If we consider the ocean as open system, the balance between primary production and respiration should be sustained by the import or export of organic material. Over the years oceanographers assumed planktonic primary production in oligotrophic waters to be in or near equilibrium with planktonic respiration (del Giorgio and Duarte, 2002). This assumption has been recently questioned by studies in oceanic surface waters evidencing R exceeding PP in large areas of the oceans (del Giorgio et al., 1997, Duarte et al., 2001). Several studies have estimated and extrapolated measurements of PP and R to the open ocean (Hernández and Ikeda, 2005; Barber& Hilting, 2002; Longhurst et al., 1995).

The organic carbon required to support the net heterotrophy (R>PP) in oligotrophic areas must be supplied by allochthonous inputs from productive areas (e.g. coastal areas, freshwater and estuarine ecosystems) (Duarte et al., 2001). The conclusion that allochthonous inputs of organic carbon are necessary for metabolic balance of the oligotrophic ocean has generated several efforts aimed at identifying its source and the transportation mechanism (Duarte and Agustí, 1998; RiOMar, 2001; Hansell et al., 2004).

Even though planktonic communities of tropical and subtropical waters have been reported to exhibit a net heterotrophic metabolism (Duarte et al. 2001; Serret et al.

2002), tropical oceans influenced by major rivers have been identified as areas of high potential for carbon sequestration (Cooley et al., 2006; Cooley et al., 2007; Subramaniam et al., 2008). Studies by Cooley et al. (2007) indicate 15 $\pm$ 6 Tg C yr^{-1} carbon uptake from the Amazon River plume. In 2008, Subramaniam et al. estimated that diazotrophs present in the Amazon plume uptake 1.7 Tmol C yr^{-1}. The Mississippi River plume has been shown to influence primary production of the 71 % of the northeastern of Gulf of Mexico (Wawrik and Paul, 2004). Approximately 900 Tg C is delivered by river plumes to the global ocean (RiOMar, 2001).

The Orinoco River (OR) discharge supplies nutrients as well as dissolved organic matter (DOM) and particulate organic matter (POM) totaling of 6.8 X 10^6 metric tons (t) of organic carbon per year into the Caribbean Sea (Corredor and Morell, 2001; Corredor et al., 2004; Morell and Corredor, 2001). The fate of the DOM, POM and nutrients is influenced by the physical structure and the dynamics of the river plume. The river discharges freshwater into the tropical Atlantic which is advected into the Caribbean Sea and extends northward to the southern coast of Puerto Rico (Muller-Karger et al., 1994; Hu et al., 2004; Odriozola, 2004; Morell and Corredor, 2001; Corredor and Morell, 2001). The highest Orinoco River discharges occur from June to October (Lewis and Saunders, 1989).

The objective of this study was to determine the influence of the Orinoco River Plume (ORP) on the balance between plankton primary production and respiration in a gradient along the plume's dispersal axis. The study addresses the hypothesis that riverine influence supports a net autotrophic balance and therefore, stimulates sequestration of CO_2 in the Eastern Caribbean Sea. In order to test the above

hypothesis, measurements of PP (O_2 evolution and ^{14}C techniques) and R (O_2 evolution and electron transport system (ETS) techniques) were performed along the ORP dispersal axis (10.3°N-17.6°N) during fall 2006. Data from previous cruises throughout the plume (ORI-III, fall 1995; ORI-IV, fall 1996; ORI-VII, fall 2005) is also included for documenting planktonic metabolism in the ORP.

II. Literature Review

Influence of the River Plumes

Global freshwater discharge by major rivers has been estimated at 35 x 10^3 km^3 y^{-1} (Cauwet, 2002). Large river plumes dispersing over the ocean surface have been intensely studied due to their effects on physical and bio-optical properties, high content of nutrients dissolved organic matter and , phytoplankton biomass and high biological productivity (Lewis, 1988; Lohrenz et al., 1997; Del Castillo et al., 1999; RiOMar, 2001; Cauwet, 2002; Wawrik and Paul, 2004; Hu et al., 2004; Cooley and Yager, 2006; Chérubin and Richardson, 2007; Cooley et al., 2007; Subramaniam et al., 2008). Annually, rivers deliver ~900 Tg total carbon, making delta areas the highest in primary production in the ocean (RiOMar, 2001). River plume inputs of dissolved organic matter are ~0.25 Gt C y^{-1} (Cauwet, 2002). Due to the weakened Coriolis Effect at low latitudes, tropical rivers extend particularly far into the surrounding ocean (RiOMar, 2001).

The riverine waters of the Orinoco River Plume (ORP) exert profound influence on the hydrographic and biological conditions of the estuarine system of the Gulf of Paria and adjacent Caribbean Sea (Lewis, 1988; Corredor and Morell, 2001; Hu et al., 2004). Coastal water masses in the Caribbean, while typically oligotrophic, become rich in nitrogen, phosphorus and silicon under the influence of the buoyant ORP (Bonilla et al., 1993). Studies of the ORP influence on primary production show that, during spring, its waters have covered areas ranging from high (31.0 µg Cm^{-3} h^{-1}, Boca de Dragón) to low (1 µg Cm^{-3} h^{-1}, ocean) productivity (Bonilla et al., 1993). In the Orinoco main stem the average biomass carbon production has been found to range from 19 to 43 mg m^{-2} d^{-1} (Lewis et al., 1988).

The ORP covers the eastern and northern Caribbean Basin on a seasonal basis with the highest discharge occurring from June to October (Lewis and Saunders, 1989; Muller-Karger et al., 1989; Del Castillo et al., 1999; Corredor et al., 2004; Chérubin and Richardson, 2007). Remote sensing studies indicate enhanced phytoplankton biomass and, presumably, enhanced primary production. Muller-Karger et al. (1989) attribute high biological productivity of the eastern Caribbean to the high concentration of surface nutrients arising from both river discharge (e.g. ORP) and upwelling.

Relationship between gross primary production and community respiration (GPP:R)

In the past, respiration measurements in the ocean were infrequent due to the generalized assumption that planktonic primary production must be near equilibrium with planktonic respiration (del Giorgio and Duarte, 2002). While primary production (particulate carbon fixation) was routinely measured in marine biogeochemical studies respiration was not (Robinson and Williams, 2005; del Giorgio et al., 1997). This changed when scientific evidence arose for respiration rates (R) in excess of primary production in large areas of the ocean (del Giorgio et al., 1997; Duarte et al., 2001; López et al., 2006). A vigorous debate ensued in part because it was difficult to compare between the existing databases of primary production and respiration. Not only was the respiration database smaller than that of primary production but measurements were performed using different methods and scales (Robinson and Williams, 2005).

Currently, ocean primary production and respiration are estimated respectively at 35 - 65 Gt C yr^{-1} and 143 Gt C yr^{-1} (del Giorgio and Duarte, 2002). The estimate of respiration is three times greater than that of primary production. The observed rate of

GPP at which CR > GPP was found to vary between productive (<0.001 m mol O_2 m^{-3} d^{-1}) and unproductive (~1.5 mmol O_2 m^{-3} d^{-1}) conditions thus, indicating the absence of a universal relationship between net metabolism and the magnitude of photosynthesis in the pelagic ecosystem (Serret et al., 2002).

In unproductive ecosystems community respiration declined at a slower rate than gross primary production (Duarte and Agusti, 1998). In transition from unproductive to productive ecosystems bacterial respiration was almost two orders of magnitude less variable than net primary production among systems (del Giorgio et al., 1997). Serret et al. (2001) found that in the eastern Atlantic Ocean, integrated community respiration was constant over a range of integrated gross primary production of three orders of magnitude. In field observations (in volumetric rates) the frequency distribution of photosynthesis and respiration indicates that respiration rates show a narrower distribution than photosynthetic rates (Robinson and Williams, 2005).

Relationship between oxygen evolution and ^{14}C methods

The rate of photosynthesis can be measured very early in the evolution of oxygen or later in the fixation of carbon (Marra, 2002). In the two cases the measurements involves incubation for a period of time. Methods, such as ^{14}C, O_2 and CO_2 light-dark bottle, ^{18}O and fluorescence properties of photosynthesis, have been used to estimate primary production in the ocean (Bender et al., 1987; Marra, 2002).

The use of the light /dark bottle method with Winkler titration was developed by Garder and Gran in 1927 (Mountford, 1969). The analysis is performed by measuring dissolved oxygen before and after an incubation period. This method uses oxygen

evolution (in the light bottle) and consumption (in the dark bottle) in order to determine gross primary production and community respiration to calculate net community production. For years the main drawback for its use was the poor sensitivity and precision of the Winkler method (Marra, 2002).

The introduction of the ^{14}C method in 1952 presented a more sensitive and efficient technique for estimating primary production in the ocean. Its widespread application resulted in an improvement of the primary production database that allowed obtaining global primary production estimates (Barber and Hilting, 2002). The ^{14}C technique is a method of rate measurements that needs the addition of a tracer (Marra, 2002). However, there is uncertainty about what the ^{14}C technique actually measures. It is still unknown whether it measures gross or net primary production. In 1983, Williams et al. reported the first comparison of planktonic photosynthesis based on ^{14}C and O_2 measurements in oligotrophic waters. They concluded that the ^{14}C technique measures gross rather than net primary production. In theory, biological autotrophic ^{14}C fixation should estimate gross photosynthesis within the first few minutes of incubation since the isotope has not had sufficient time to enter the respiratory pool (Marra, 2002). Table 1 compares ^{14}C and O_2 evolution techniques.

Table 1. Comparison of ^{14}C and O_2 evolution techniques (Marra, 2002).

Technique	Estimates
O_2 light-dark bottle method	Net community production (change in bottle kept in light) Gross primary production (change in light plus change in dark)
^{14}C assimilation	P>>R (very short incubation period): gross photosynthesis P>R: net primary production P=R: net community production (at community isotopic equilibrium) and biomass increase

Some of the organic carbon that is photosynthesized by phytoplankton is released as dissolved organic carbon (DOC). The rate of such release is extremely important for estimating the ocean carbon budget but primary production is mainly derived from ^{14}C incorporation into particulate organic carbon (Sakshaug, et al., 1998). In 2005, Marañón et al. determined the photosynthetic production of dissolved (DOCP) and particulate organic carbon (POCP) to verify the integrated percentage of extracellular release of DOC (mean 22 $\pm$ 2 %) in oligotrophic waters. Other authors reported percentages of extracellular release (PER) ranging from 4 to 42 % (Karl et al., 1998 and Teira et al., 2001). The variability in DOCP could be determined by changes in the POCP rates. Extracellular release is a major process that contributes to the quantity of DOC in marine ecosystems (Marañón et al., 2004).

Relationship between electron transport system (ETS) and respiration (R)

The introduction of the electron transport system method by Packard in 1971 as a respiratory index brought the opportunity to expand the measurements of community respiration (Arístegui and Montero, 1995). This method presents important points of the distribution of respiratory metabolism and estimates the instantaneous rate avoiding problems with *in vitro* effects (Arístegui and Montero, 1995). ETS measurements provide estimates of the potential plankton respiration rates. The ratio of respiration to ETS indicates the fraction of the respiratory capacity that the organism is currently using (Packard, 1985).

In practice, electron transport system activity measurements are converted to *in situ* respiration using an empirical equation derived from oxygen consumption experiments (Packard, 1985). Most studies of the R:ETS relationship were carried out under laboratory conditions in cultured phytoplankton experiments (Packard, 1985). The R:ETS relationship obtained from natural marine ecosystems has been scarce and difficult to compare because each study was done using a different variation of the method.

The regression equation obtained by Arístegui and Montero (1995) in a log transformed R:ETS relationship in the upper ocean microbial community for different ocean regions was log R (mg O_2 $m^{-3}d^{-1}$) = 0.357 $\pm$ 0.750 log ETS . The ratio of the respiration rate to the ETS activities of zooplankton and marine bacteria ranges from 0.54 to 2.16 and 0.66 to 1.87 respectively (King et al., 1975; Packard, 1985). In upwelling areas, assuming that phytoplankton dominate the euphotic zone, the mean phytoplankton R:ETS ratio was 0.15 (Packard ,1985). A significant correlation between

ETS and R indicates that ETS can be used to estimate plankton respiration in marine communities (Arístegui and Harrison, 2002; Arístegui and Montero, 1995).

III. Methodology

Study site: A total of ten stations were sampled during Cruise ORI-VIII in September 2006 in the Eastern Caribbean Sea. This cruise extended from the Caribbean Time Series (CaTS) station off the south coast of Puerto Rico to the Gulf of Paria (Figure 1). Table 2 includes date, location, salinity and classification (N-near field, M-midfield and F-far field) for all stations sampled.

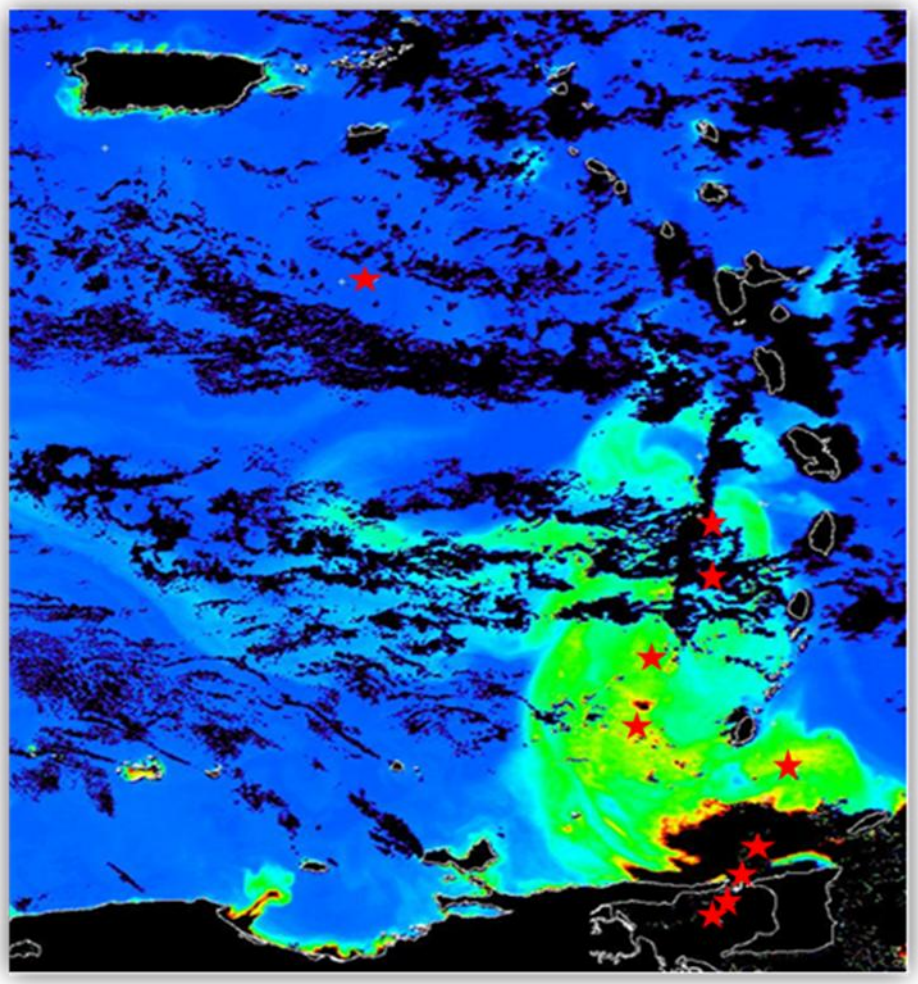

Figure 1. Cruise track. Red stars indicate stations.

Table 2. Date, coordinates, salinity value and respective abbreviation for sampled stations.

Date	Latitude (ºN)	Longitude (ºW)	Salinity	Station
September 19	16.35	-64.70	34.929	2(F)
September 20	14.10	-62.00	33.266	3(F)
September 21	12.83	-62.50	32.188	6(M)
September 22	11.06	-61.63	25.769	10(N)
September 23	10.35	-61.93	19.440	11(N)
September 23	10.51	-61.83	18.641	12(N)
September 26	10.65	-61.78	15.536	1L2(N)
September 27	11.48	-61.52	31.112	2L2(M)
September 28	12.20	-62.57	32.602	4C2(M)
September 30	14.64	-61.98	33.281	6L2(F)

Optical Characterization: Diffuse attenuation of solar irradiance was characterized using a Biospherical Instruments PRR600 instrument. The instrument was lowered from the ship stern while orienting the vessel in such a manner as to avoid shading the instrument. To assure adequate light, instrument casts were performed around 10:00 AM local time. The correct depth was obtained from the derivation of the irradiance equation:

$$I/I_0 = e^{-kz} \qquad (1)$$

where I = irradiance at depth z, I_0 = irradiance at surface water, z = depth and k = the attenuation coefficient. For k values we use the diffuse attenuation coefficient (Kd(PAR)) determined from the profile for each station following the equation:

$$Kd\ (PAR) = 1/(z_2 - z_1) * \ln (Ed_1/Ed_2) \qquad (2)$$

where Ed_1 and Ed_2 represent the measured downwelling irradiance values at depths z_1 (reference surface water) and z_2 (change with depth).

GPP, NCP, CR sampling procedures: Planktonic gross primary production (GPP), net community production (NCP) and community respiration (CR) were determined from changes in dissolved oxygen concentration after 24h light/dark simulated *in situ* incubation. Water samples were collected each day from the CTD rosette in 300mL BOD bottles from depths equivalent to 100, 72, 32, 4 and 1 percent of surface irradiance.

BOD bottles were rinsed twice, then water samples were carefully siphoned (to avoid air bubbles) using silicon tubing. Water at least equal to the volume of the bottle was overflowed twice before taking the sample. Nine replicates for each depth were taken for the analysis. For each depth, three replicate samples were fixed with manganous sulphate and alkaline iodide solutions immediately after collection (zero time, t_0). Three replicate for each depth were incubated in the dark (24h dark) and three were incubated under irradiance conditions (24h light) that simulated the original sampling depth. Dark bottles were covered with black plastic to avoid light contamination before incubation.

Light/dark simulated *in situ* incubation: A wood (covered with fiberglass) and aluminum incubator was built (Figure 2). The incubations were performed in a polycarbonate tube (3"o.d. x 2 ¾" i.d. x 4') with continuous flowing sea water. Six tubes were positioned in the upper part of the incubator for light sample incubation. *In situ* irradiance for each depth was simulated using light attenuation Roscolux filters (Appendix A). Six tubes for dark bottle incubations were covered with black plastic poly film and positioned in the bottom of the incubator.

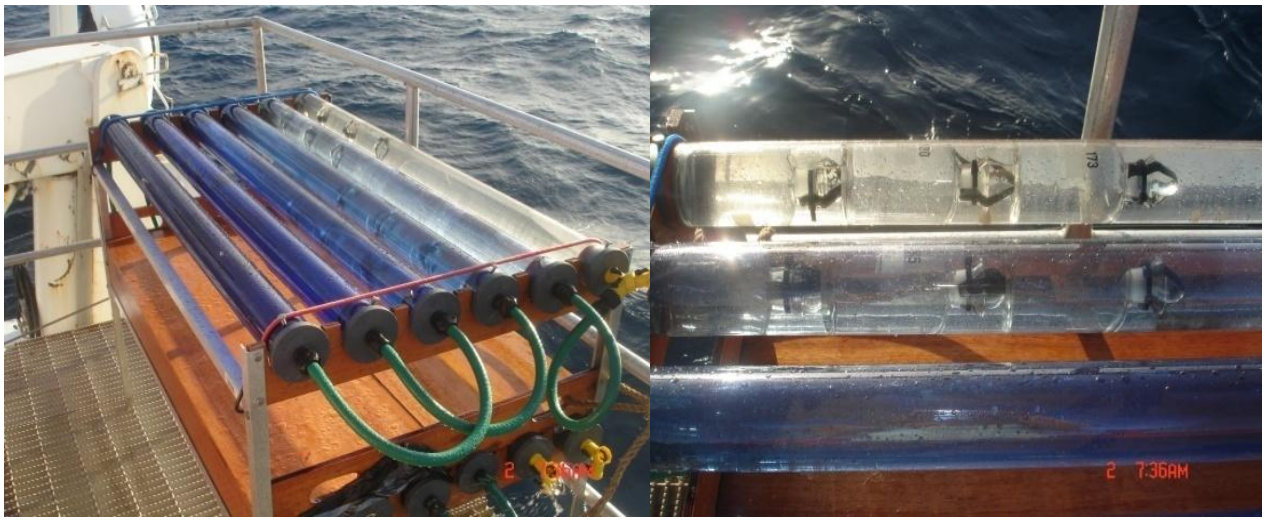

Figure 2. On deck simulated *in situ* incubator.

GPP, NCP, CR sample analysis: After 24h of incubation, dark and light samples were fixed with manganous sulphate and alkaline iodide solutions. A 100mL aliquot of each sample was analyzed for dissolved oxygen by a modified Winkler method (Parkson et al., 1984) in a Mettler Toledo DL50 Graphix Titrator, utilizing a potentiometric end point. Production and respiration were calculated by differences using the means of the three dark, light and zero time samples. NCP was obtained using the following equation:

$$NCP = \text{mean } [O_2] \text{ 24h light} - \text{mean } [O_2]\ t_0 \quad (3)$$

R was calculated as the difference between the means of t_0 and 24hr dark samples:

$$CR = \text{mean } [O_2]\ t_0 - \text{mean } [O_2] \text{ 24h dark} \quad (4)$$

GPP was the sum of measured changes in the light and dark bottles:

$$GPP = NCP + R \quad (5)$$

Electron transport system (ETS) sampling procedure: Samples were collected using 10L Niskin bottles mounted on a rosette sampler. Four liters of sea water were filtered through 47 mm Whatman GF/F to 100, 72, 32, 4 and 1 % of surface irradiance. Filters

were folded in aluminum foil, placed in cryotubes, stored in liquid nitrogen and then transferred to a deep freezer set to -80ºC until time of analysis.

ETS samples analysis: Electron transport system determinations were carried out according to Kenner and Ahmed (1975) modification of the tetrazoliun reduction technique proposed by Packard (1971). The sample absorbance at 490 and 750 nm was read in a Shimadzu UV-Visible Spectrophotometer, UV-1601. ETS activity was calculated by the equation:

$$ETS\ (\mu l\ O_2\ h^{-1}d^{-1}) = 60 \times H \times S \times (corr\ OD) / (1.42 \times V \times f \times t) \qquad (6)$$

where 60 converts minutes to hours, H is the homogenate volume (ml), S is the volume of quenched reaction mixture (ml), corr OD is the absorbance of the sample at 490 nm corrected for blank absorbance, 1.42 converts the INT-formazan formed to oxygen units (µl), V is the volume of the seawater filtered (L), f is the volume of the homogenate used (ml) and t is equal to the incubation time (min).

IV. Results

Orinoco River Plume (ORP) water column

Mean salinity and Chl *a* concentration in the upper 6 meters of the ORP are presented are Figure 3. Surface salinity increased along the plume from 17.9 within the Gulf of Paria (GOP), at 61.78°W, 10.65°N, to 34.9 in the northeastern Caribbean. Surface Chl *a* concentration decreased along the plume's axis from 2.09 in the GOP to 0.15 mg/l at 64.98°W, 16.33°N. Chl *a* concentration in the GOP exhibited high variability (1.37 $\pm$ 1.06 ug/l) and decreased sharply to ca. 0.25 ug/l near latitude 13ºN and remained relatively constant into the northeastern Caribbean. The plume depth observed, identified as the upper halocline, averaged 13.5 m. The diffuse attenuation coefficients [Kd(PAR)] (Figure 4) decreased along the plume from 0.6, within the Gulf of Paria, to 0.08 in the northeastern Caribbean. The above observations of salinity, Chl *a* and Kd (PAR) showed similar N-S gradients as those observed on previous cruises (i.e. ORI-III, ORI-IV and ORI-VII) (Figure 5).

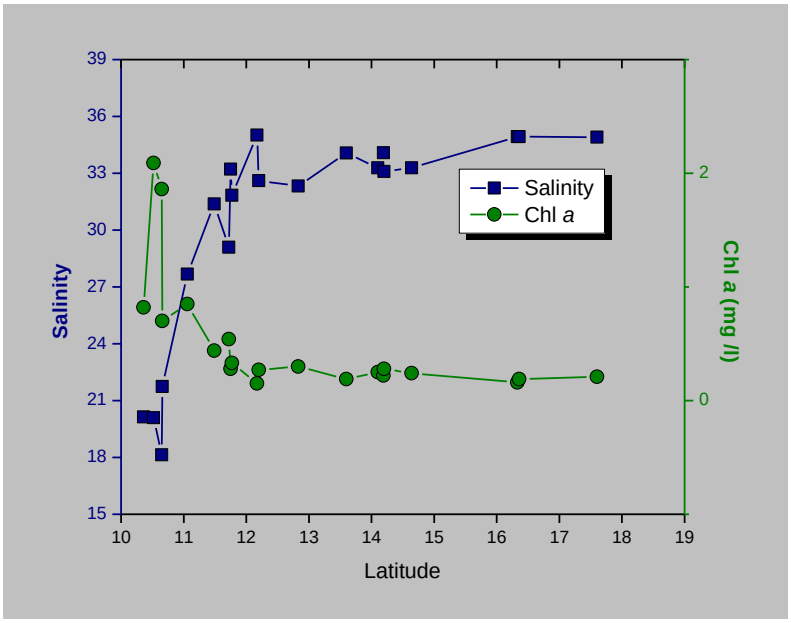

Figure 3. Average salinity and Chl *a* concentration in the upper 6 m along the latitudinal gradient across the eastern Caribbean.

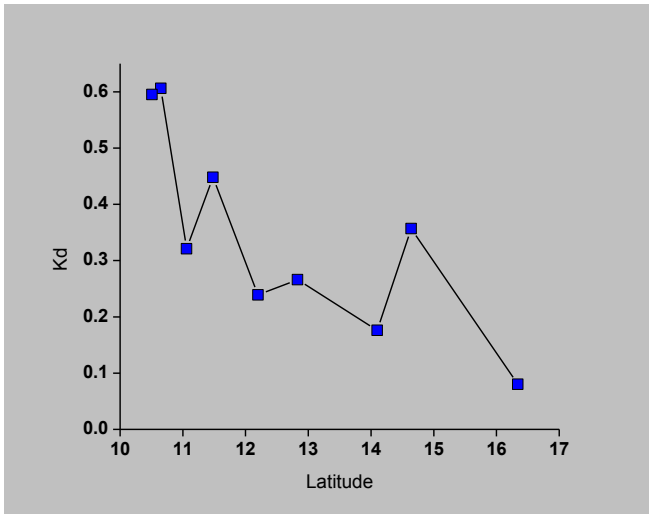

Figure 4. Surface diffuse attenuation coefficient (Kd(PAR)) along the latitudinal gradient across the eastern Caribbean Sea.

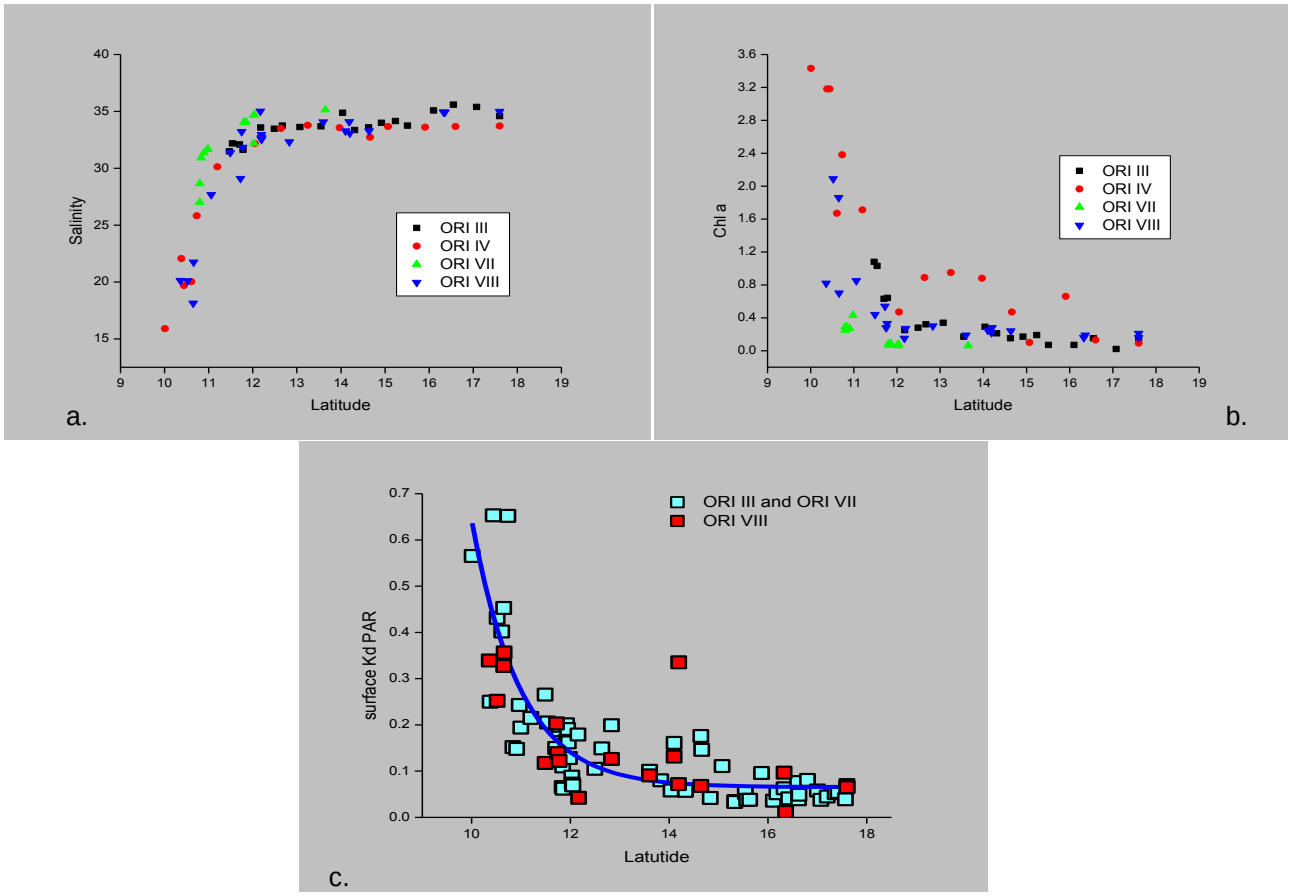

Figure 5. Surface salinity (a), Chl *a* concentration (b) and diffuse attenuation coefficient (Kd(PAR)) (c) along the latitudinal gradient across the eastern Caribbean Sea for cruises ORI-III, ORI-IV, ORI-VII and ORI-VIII.

Gross primary production estimates (GPP) computed from the NCP and CR estimates are presented in Figure 6. GPP at depths corresponding to 72 and 32 percent of the surface irradiance (I/I_0*100) levels show a marked gradient with GPP decreasing along the plume dispersal axis. Contrastingly, GPP at 1 % irradiance remained relatively constant.

Rates of Community Respiration (CR) (Figure 7) showed a behavior analogous to GPP with higher values measured in near surface samples (collected at the 72 % irradiance depth) at stations closer to the river delta and lower quasi constant CR values at depth (1 % irradiance).

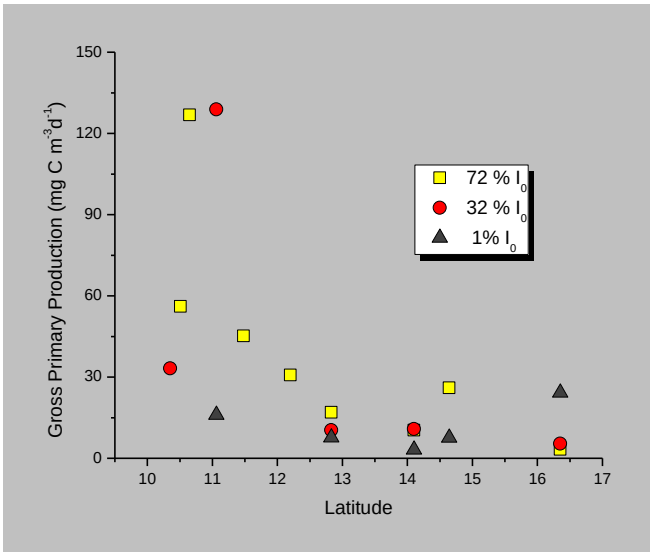

Figure 6. Gross primary production using light/dark bottle oxygen technique for samples incubated at 72, 32 and 1 % irradiance along the latitudinal gradient across the ORP during ORI-VIII, fall 2006.

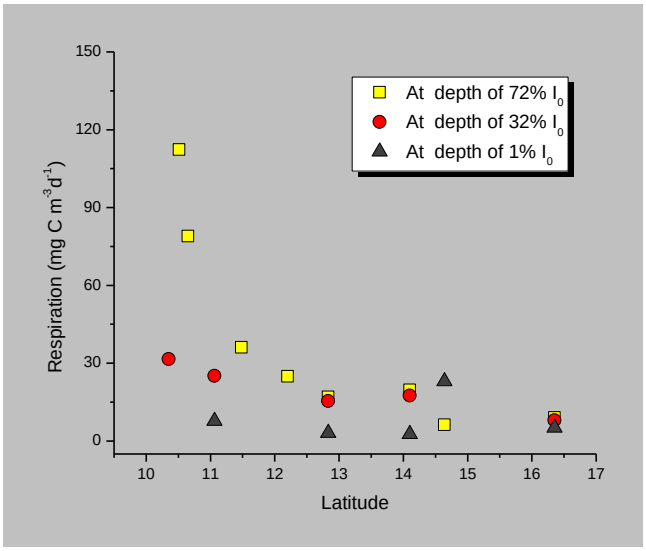

Figure 7. Respiration measurements using light/dark bottle oxygen technique for samples corresponding to depth equivalent to 72, 32 and 1 % irradiance along the latitudinal gradient across the ORP during ORI-VIII, fall 2006.

As with CR and GPP, potential plankton respiration (ETS) rates (Figure 8) at the depth of 72 % of the surface irradiance, exhibited a marked gradient decreasing along the plume. At the depth corresponding to 32 % irradiance, ETS remained approximately constant (13.00 $\pm$ 0.33) between 11.71 and 16.35°N. A much lower value (3.87 mg C m^{-3} d^{-1}) was observed near Boca de Dragón. Results from samples collected at 4 and 1 % irradiance depth show limited respiratory potential (<10 mg.C.m^3.d^{-1}) and remained relatively constant along the river plume.

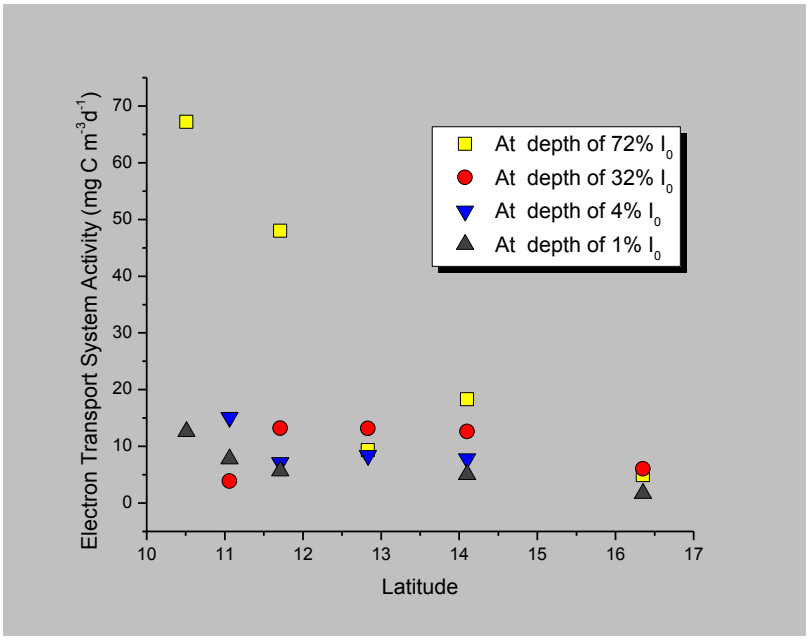

Figure 8. Latitudinal distribution of potential respiratory activity (ETS) for samples corresponding to depths of 72, 32 and 1 % of surface irradiance along the ORP.

A regression analysis comparing CR with ETS yields a significant correlation where CR = 0.41 + 1.28 ETS (r^2=0.78). An outlier value (ETS = 3.87 and R = 25.14) was observed and not considered for the regression analysis (Figure 9).

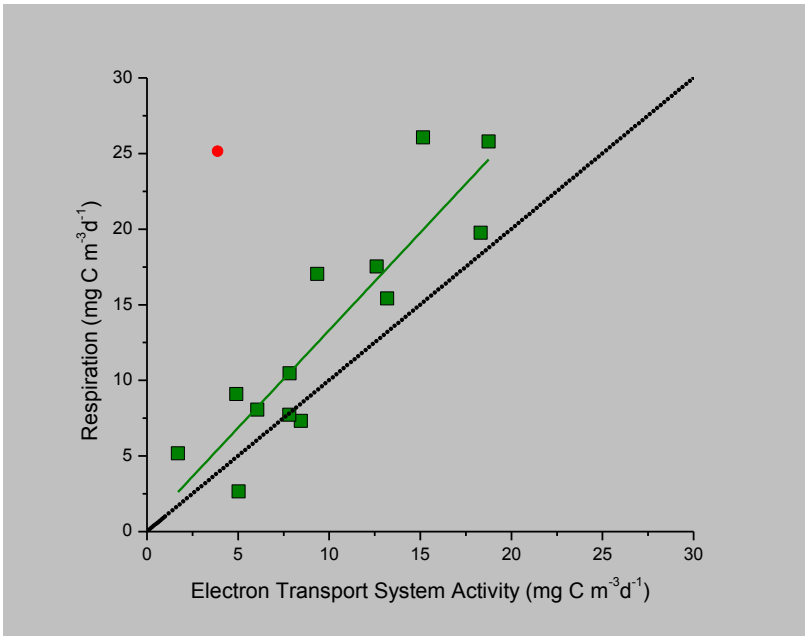

Figure 9 .Relationship between electron transport system activity and community respiration along the ORP during ORI-VIII. Green line represents the fitted regression equation (R = 0.41 + 1.28 ETS, R^2 =0.78) while the dashed one is the 1:1 proportion line.

Net community production (NCP) estimates from simulated *in situ* incubations are shown in Figure 10. NCP for samples collected at depths of 72 and 32 % irradiance show net autotrophy in most of the sampled stations with the exception of samples collected at the very near (Gulf of Paria) and far fields (northeastern Caribbean). Maximum NCP results, 47.7 (72 %) and 103.7 (32 %) mg C m^{-3} d^{-1}, were obtained in samples collected near Boca de Dragón. NCP at depth (one percent irradiance samples) averaged 3.4 mg C m^{-3} d^{-1} and did not show a discernable trend along the plume.

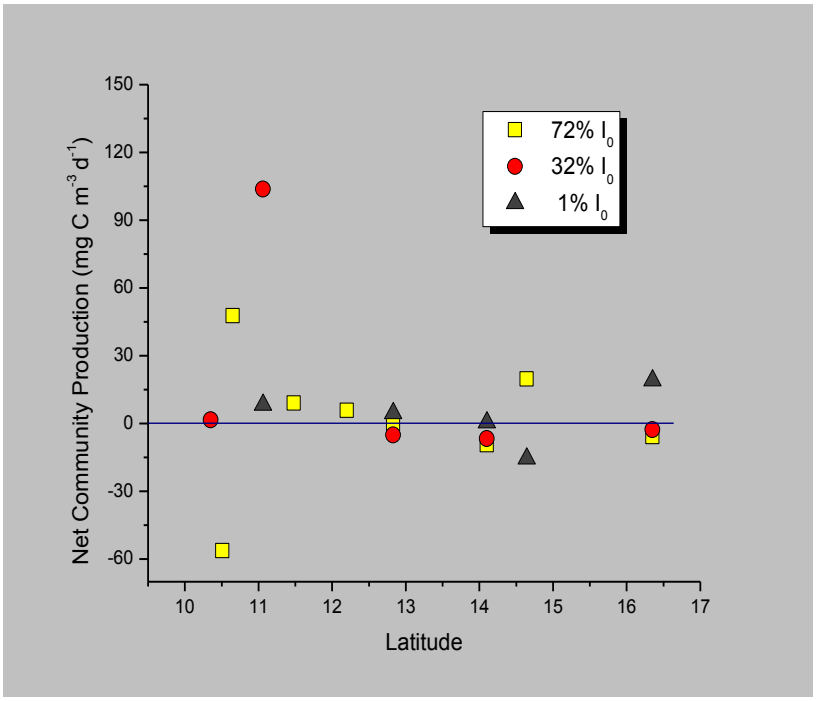

Figure 10. Net Community Production estimates for samples incubated at 72, 32 and 1 % irradiance along the ORP plume during ORI-VIII, fall 2006.

V. Discussion

Metabolic balance of ORP waters:

Given 1) the limited impact of the OPR on planktonic GPP and CR rates at low irradiance depths (see above results), 2) the average ORP plume depth and 3) the relative abundance of measurements of near surface samples, estimation and discussion of the metabolic balance of the plume will be based on samples collected at 72 % irradiance depth (Z_{PW}). Figure 11 below depicts estimates of NCP, CR and computed GPP rates for samples from such solar irradiance regime.

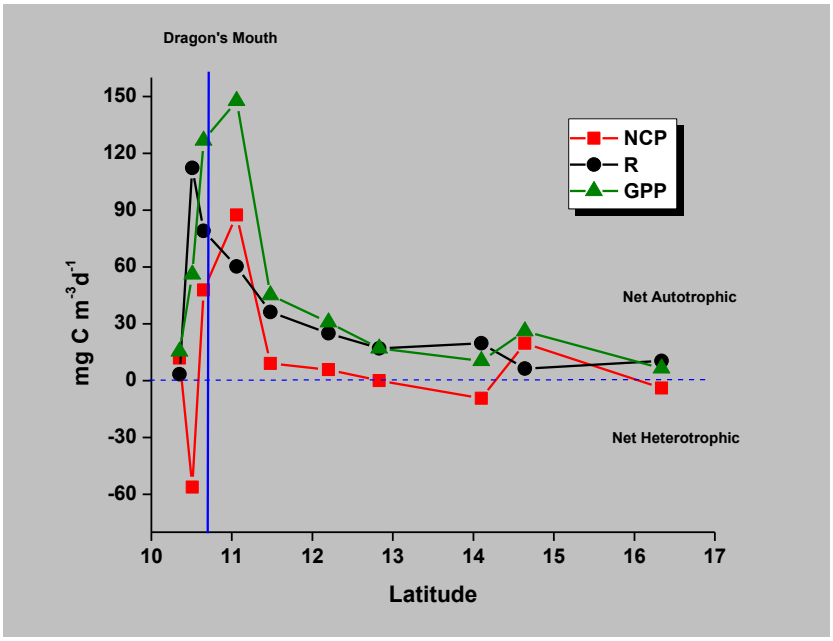

Figure 11. Sea surface (72 % irradiance) gross primary production (GPP), net community production (NCP) and respiration (R) using light-dark bottle oxygen technique along the latitudinal gradient across the ORP during ORI-VIII, fall 2006.

In waters outside the Boca de Dragón (just north of latitude 11°N), which connects the Gulf of Paria with the Southeastern Caribbean, a frontal structure dividing outflow from the Gulf of Paria from Caribbean waters results in a concurrent increase in

salinity and decrease in chlorophyll and Kd_{PAR}. Such observations imply dilution of riverine dissolved and particulate carbon which could 1) explain the observed diminution of CR and 2) result in an increase in GPP responding to higher irradiances allowed by a lower $Kd_{PAR.}$ Dissolved Organic Carbon (DOC) measurements in the region by Del Castillo et al. (1999) indicate a decrease from 270 uM within the GOP to 175.9 just outside the frontal region. Previous studies in the area have reported dominance of large phytoplanktonic cells (Fuentes, 2007) and high fucoxanthin concentrations, indicative of diatom populations (Antoun, 2009). Between 11.06 and 11.5 ºN, a steep increase in salinity (27.67 to 31.38), accompanied by an analogous depression in Chl *a* (0.85 to 0.44 $mg.l^{-1}$) evidenced further dilution of the plume consistent with the observed proportional decrease in primary production and respiration (NCP=9.03 $mg.C.m^{-3}.d^{-1}$)

Northward of the above described gradient (from 12.15 to 16.35 ºN), both CR and GPP show limited variability with averages CR = 18.9 (sd = 10.9) and GPP = 22.10 (sd = 15.11). These observations indicate neutral to autotrophy conditions thus differing from Morell and colleagues (unpublished results) who reported net heterotrophy for the ORP mid to far field.

Metabolic balance of the ORP, contrasting with global observations:

The metabolic balance of the tropical and subtropical Atlantic has become a driver for intense debate. Characterization of the relationship between gross primary production and community respiration for different provinces of the Atlantic Ocean (Serret et al., 2001 and Serret et al., 2002) have resulted in arguments indicating

widespread occurrence of heterotrophic plankton metabolic balance and implying the advection of “imported” carbon to sustain the implicit deficit.

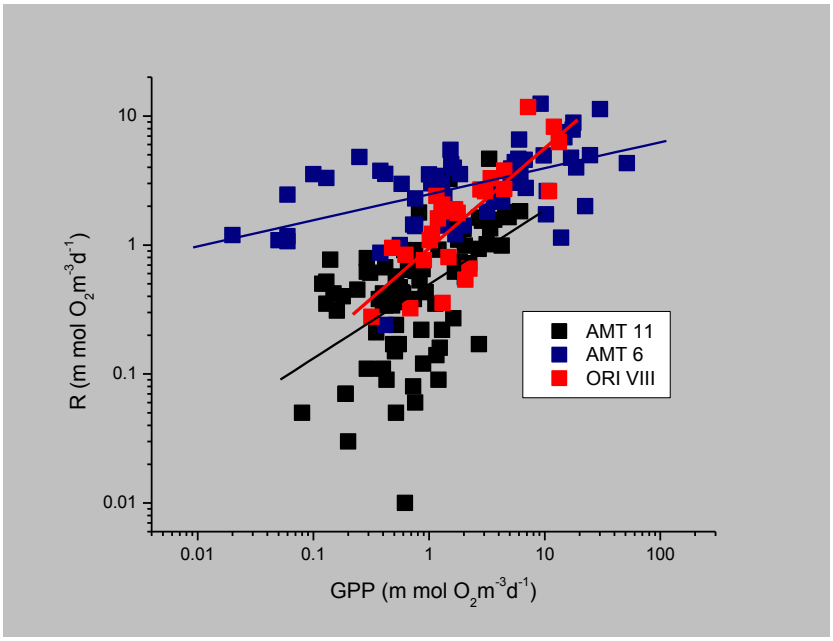

Figure 12. Relationship between gross primary production and respiration (GPP:R) in AMT6, AMT11 and ORI-VIII. Blue and black lines represent the fitted regression (R =0.39 + 0.20 GPP, and R =-0.30 + 0.57GPP) for AMT6 and AMT11 respectively. Red line represents the fitted regression (R =-0.02 + 0.77GPP) for ORI-VIII.

The above figure depicts GPP and CR data from Atlantic Meridional Transects 6 and 11 (Serret et al., 2001, 2002) as well as our results (ORI-VIII). Data from AMT11 represents regions characterized by the author as under an unproductive and isolated regime (central South Atlantic) with AMT6 representing an unproductive but “subsidized” regimes in the Eastern Tropical Atlantic and the Subtropical North Atlantic Subtropical Gyre. Interestingly our observations do not follow either of the regressions by Serret’s but connect both. Observations at the highly productive southern ORP region fit well into the regression for a subsidized region while observations at the mid to far field exhibit a metabolic balance of isolated unproductive regions. These results

suggest the remaining riverine DOC (Del Castillo et al., 1999) to be refractive to planktonic respiration.

Community Respiratory Efficiency:

ETS:R relationship indicates that community respiration exceeds the potential respiration. This discrepancy can be attributed to 1) problems in the dark incubation bottles, such as change in physical factors (e.g. temperature), and biological factors (i.e. bacterial growth) (Hernández-León and Ikeda, 2005), 2) problems with the GF/F filters. Arístegui and Montero (1995) indicate that the use of GF/F for filtering small amounts of water generates an underestimation of ETS activity because many bacteria will pass through the filter. Figure 13 shows observed (ORI-VIII, fall) and historical (Ori-III, IV) ETS data for the region.

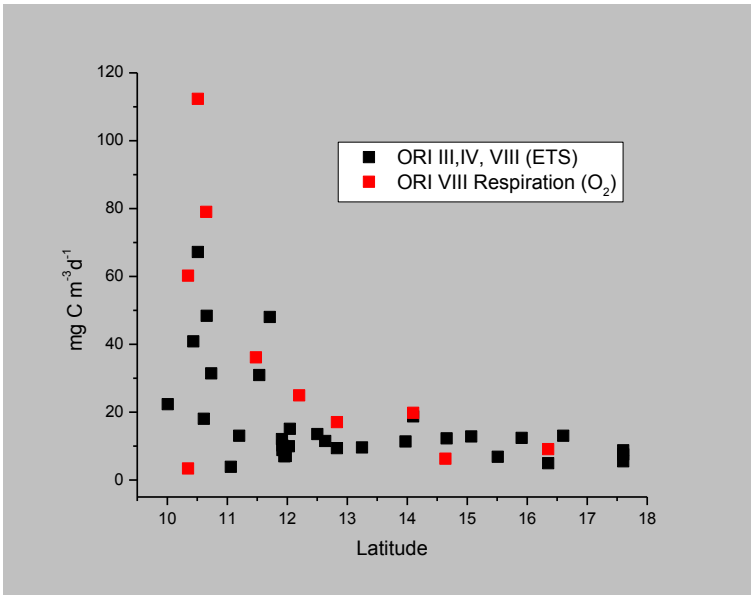

Figure 13. Comparison between electron transport system activity during ORI III, IV and VIII with community respiration (oxygen consumption) during ORI VIII along the ORP.

Covariation of GPP and POCP in the ORP

The GPP and $PO^{14}CP$ relationship, along the ORP, indicates that ~72 % of the gross primary production was measured using P-I curve produced by ^{14}C uptake in the eastern Caribbean Sea. This percentage was lower than that presented by Marañón et al. (2005), who estimated that ~80 % of the variability could be explained by the changes in the rate of POCP. When only data from low production regions was included in the regression (values lower than 40 mg c $m^{-3}d^{-1}$) (Figure 15), the relationship was described by GPP= 2.53 $PO^{14}CP$ + 7.65. These results indicate major underestimation of production when estimated from the PI curve production model, especially at low production rates.

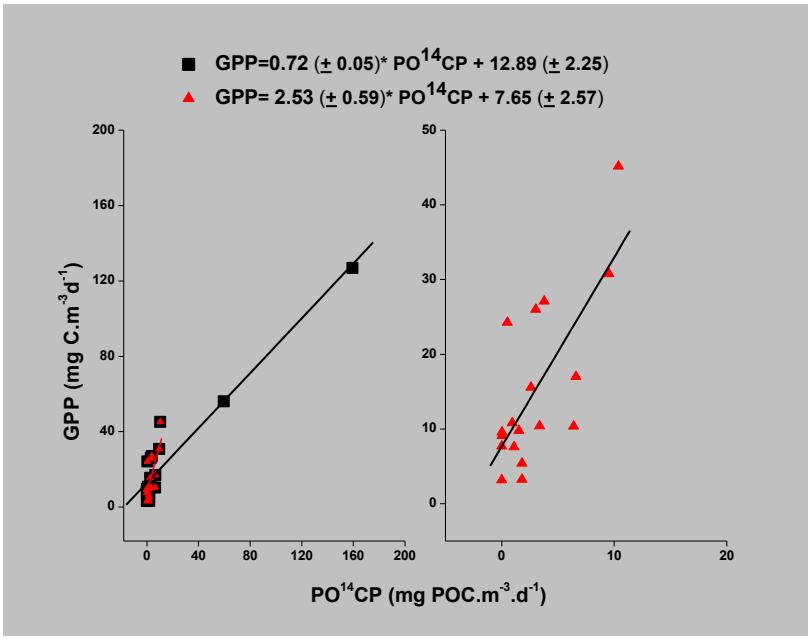

Figure 14. Relationship between particulate organic carbon production ($PO^{14}P$) and gross primary production (GPP) during ORI-VIII. Squares show all data along the plume. Red triangles show data from low production in the Caribbean.

VI. Conclusions

- The ORP has an outstanding impact on near surface plankton abundance and metabolism particularly off the GOP (near field). A lesser influence was observed in samples from depth exposed to low irradiance regimes. While metabolic processes in the ORP near field are largely dominated by dilution processes, the observed plume exhibits a net autotrophic balance.

- The dissolved organic carbon in the mid and far field does not result in a sustained enhancement of community respiration as observed by Serret in the Atlantic Meridional Transects cruises. A change in regime from subsidized to isolated regions was observed along the river plume. At the highly productive southern ORP region fits well into the regression for a subsidized region, at the mid to far field exhibit a metabolic balance of isolated unproductive regions.

- Community respiration determined by oxygen consumption indicates that ETS underestimates the respiration rates in the ORP.

- Estimation of GPP by determining oxygen evolution rates in simulated *in situ* incubations results in GPP estimates significantly higher than $PO^{14}CP$ fixation rates estimated from PI curves. This is particularly noticeable in waters with low phytoplankton concentrations suggesting POC leakage in the latter method.

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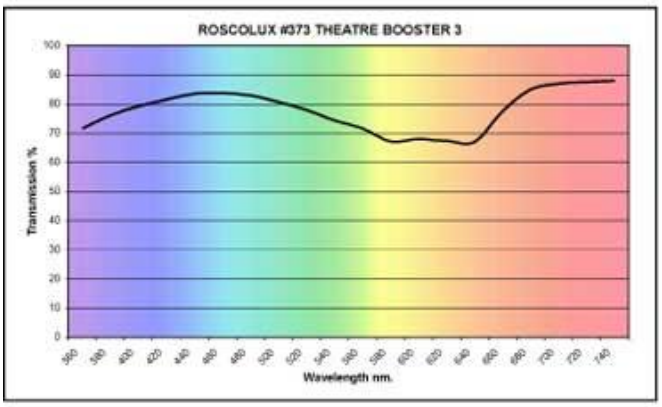
VIII. Appendices

Appendix 1. Roscolux color filter technical data sheet for 72 % light transmission.
http://www.rosco.com/us/filters/roscolux.cfm?sortOrder=no#colors

rosco **COLOR FILTER TECHNICAL DATA SHEET**

SWATCHBOOK:	ROSCOLUX
COLOR FILTER:	#373 THEATRE BOOSTER 3
DESCRIPTION:	Color Effects Lighting Filter.
TRANSMISSION =	72% or -0.5 stop loss
MIRED SHIFT =	Not Applicable.
CC EQUIVALENT =	Not Applicable.

COLORIMETRIC DATA
OBSERVER: CIE 1964 10°
SOURCE: • 'A' (tungsten)
° 'D65' (daylight)

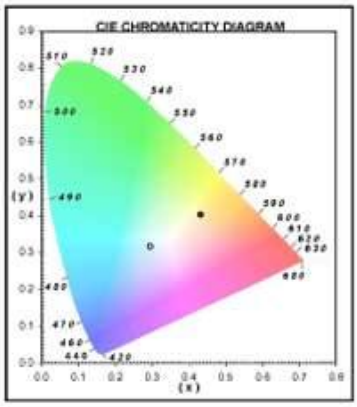


HUNTER LAB SOURCE A	
L*	87.817
A*	-3.729
B*	-8.912

HUNTER LAB SOURCE D65	
L*	88.697
A*	-2.98
B*	-7.471

CIE 1964 SOURCE A	
Y	71.606
(x)	0.431
(y)	0.403

CIE 1964 SOURCE D65	
Y	73.524
(x)	0.295
(y)	0.316



nm.	360	380	400	420	440	460	480	500	520	540	560	580	600	620	640	660	680	700	720	740
trans %	72	76	79	82	84	84	83	81	78	74	72	67	68	67	67	78	85	87	88	88

MATERIAL SPECIFICATIONS:

General Description:	Co-extruded Polycarbonate Film
Substrate:	PC (Polycarbonate)
Thickness:	3.0 mil (.003" or 76.2 micron)
Manufactured in:	U.S.A.

AVAILABLE SIZES:

- √ 20 in. x 24 in. sheets (50cm x 60cm)
- √ 24 in. x 25 ft. rolls (60cm x 7.62m)
- 48 in. x 25 ft. rolls (121cm x 7.62m)
- 60 in. x 20 ft. rolls (152.4cm x 6.10m)
- 13.5 in. Diameter Glass (34.3cm) - Cut to order

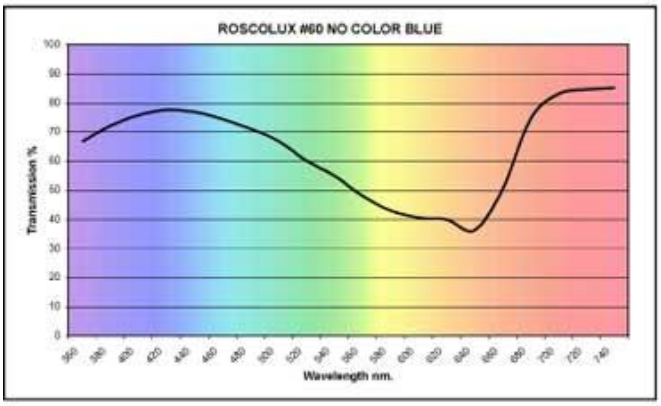
Appendix 2. Roscolux color filter technical data sheet for 62 % light transmission.
http://www.rosco.com/us/filters/roscolux.cfm?sortOrder=no#colors

rosco COLOR FILTER TECHNICAL DATA SHEET

SWATCHBOOK:	ROSCOLUX
COLOR FILTER:	#60 NO COLOR BLUE
DESCRIPTION:	Color Effects Lighting Filter.
TRANSMISSION =	62% or -0.7 stop loss
MIRED SHIFT =	Not Applicable.
CC EQUIVALENT =	Not Applicable.

COLORIMETRIC DATA

OBSERVER:	CIE 1964 10°
SOURCE:	• 'A' (tungsten)
	° 'D65' (daylight)

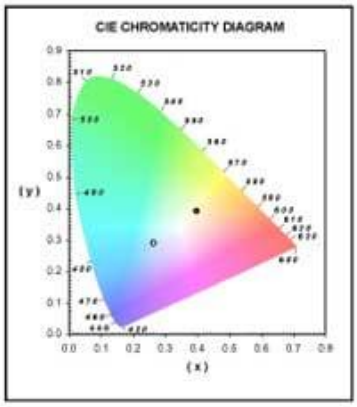


HUNTER LAB SOURCE A	
L*	75.360
A*	-10.606
B*	-23.362

HUNTER LAB SOURCE D65	
L*	77.698
A*	-6.315
B*	-19.993

CIE 1964 SOURCE A	
Y	48.853
(x)	0.397
(y)	0.392

CIE 1964 SOURCE D65	
Y	52.701
(x)	0.263
(y)	0.290



nm.	360	380	400	420	440	460	480	500	520	540	560	580	600	620	640	660	680	700	720	740
trans %	67	72	76	78	77	75	71	67	60	55	48	43	41	40	38	50	75	83	85	85

MATERIAL SPECIFICATIONS:

General Description:	Deep-Dyed Polyester Film
Substrate:	PET (Polyethylene Terephthalate)
Thickness:	1.5 mil (.0015" or 38 micron)
Manufactured in:	U.S.A.

AVAILABLE SIZES:

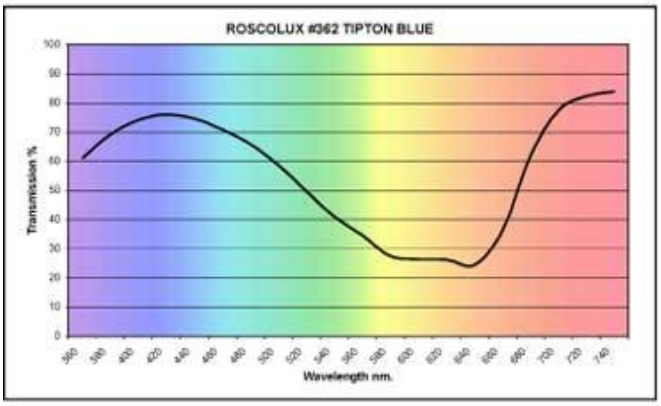
- √ 20 in. x 24 in. sheets (50cm x 60cm)
- √ 24 in. x 25 ft. rolls (60cm x 7.62m)
- √ 48 in. x 25 ft. rolls (121cm x 7.62m)
- 60 in. x 20 ft. rolls (152.4cm x 6.10m)
- 13.5 in. Diameter Glass (34.3cm) - Cut to order

Appendix 3. Roscolux color filter technical data sheet for 32 % light transmission.
http://www.rosco.com/us/filters/roscolux.cfm?sortOrder=no#colors

rosco **COLOR FILTER TECHNICAL DATA SHEET**

SWATCHBOOK:	ROSCOLUX
COLOR FILTER:	#362 TIPTON BLUE
DESCRIPTION:	Color Effects Lighting Filter.
TRANSMISSION =	32% or -1.6 stop loss
MIRED SHIFT =	Not Applicable.
CC EQUIVALENT =	Not Applicable.

COLORIMETRIC DATA
OBSERVER: CIE 1964 10°
SOURCE: • 'A' (tungsten)
° 'D65' (daylight)

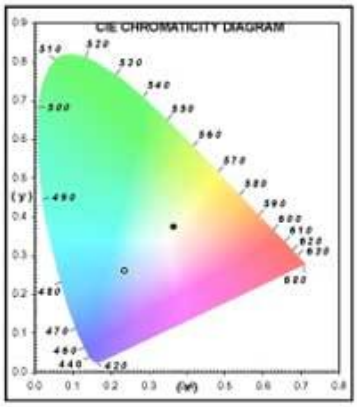


HUNTER LAB SOURCE A	
L*	66.357
A*	-14.003
B*	-35.712

HUNTER LAB SOURCE D65	
L*	69.847
A*	-6.097
B*	-30.77

CIE 1964 SOURCE A	
Y	35.787
(x)	0.365
(y)	0.374

CIE 1964 SOURCE D65	
Y	40.532
(x)	0.236
(y)	0.262



nm.	360	380	400	420	440	460	480	500	520	540	560	580	600	620	640	660	680	700	720	740
trans %	61	69	74	76	75	71	66	59	50	41	35	28	27	26	25	37	62	78	82	84

MATERIAL SPECIFICATIONS:

General Description:	Deep-Dyed Polyester Film
Substrate:	PET (Polyethylene Terephthalate)
Thickness:	1.5 mil (.0015" or 38 micron)
Manufactured in:	U.S.A.

AVAILABLE SIZES:

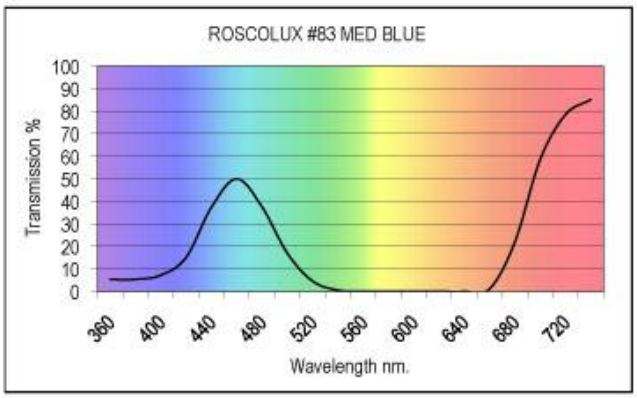
- √ 20 in. x 24 in. sheets (50cm x 60cm)
- √ 24 in. x 25 ft. rolls (60cm x 7.62m)
- √ 48 in. x 25 ft. rolls (121cm x 7.62m)
- 60 in. x 20 ft. rolls (152.4cm x 6.10m)
- 13.5 in. Diameter Glass (34.3cm) - Cut to order

Appendix 4. Roscolux color filter technical data sheet for 4 % light transmission.
http://www.rosco.com/us/filters/roscolux.cfm?sortOrder=no#colors

rosco **COLOR FILTER TECHNICAL DATA SHEET**

SWATCHBOOK: ROSCOLUX
COLOR FILTER: #83 MED BLUE
DESCRIPTION: Color Effects Lighting Filter.
TRANSMISSION = 4% or -4.7 stop loss
MIRED SHIFT = Not Applicable.
CC EQUIVALENT = Not Applicable.

COLORIMETRIC DATA
OBSERVER: CIE 1964 10°
SOURCE: • 'A' (tungsten)
° 'D65' (daylight)

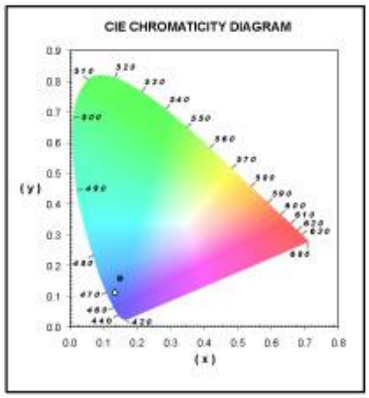


HUNTER LAB SOURCE A	
L*	19.944
A*	-7.724
B*	-81.263

HUNTER LAB SOURCE D65	
L*	29.263
A*	15.465
B*	-65.311

CIE 1964 10° SOURCE A	
Y	2.975
(x)	0.149
(y)	0.158

CIE 1964 10° SOURCE D65	
Y	5.941
(x)	0.134
(y)	0.112



nm.	360	380	400	420	440	460	480	500	520	540	560	580	600	620	640	660	680	700	720	740
trans %	5	5	7	15	37	50	38	17	5	1	0	0	0	0	0	1	22	59	78	85

MATERIAL SPECIFICATIONS:
General Description: Deep-Dyed Polyester Film
Substrate: PET (Polyethylene Terephthalate)
Thickness: 1.5 mil (.0015" or 38 micron)

Manufactured in: U.S.A.

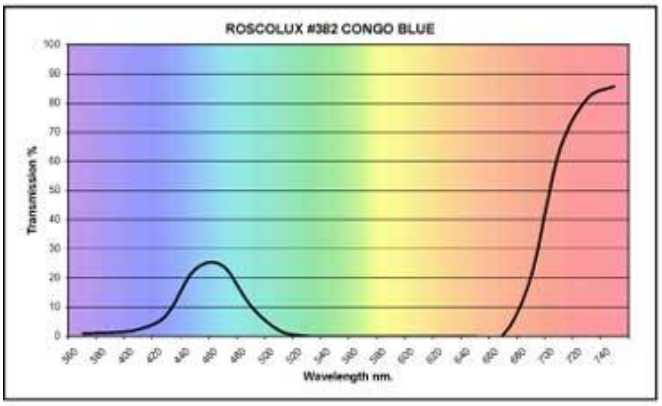
AVAILABLE SIZES:
√ 20 in. x 24 in. sheets (50cm x 60cm)
21 in. x 24 in. sheets (53 x 60cm)
√ 24 in. x 25 ft. rolls (60cm x 7.62m)
√ 48 in. x 25 ft. rolls (121cm x 7.62m)
60 in. x 20 ft. rolls (152.4cm x 6.10m)
13.5 in. Diameter Glass (34.3cm) - Cut to order
Consult Rosco

Appendix 5. Roscolux color filter technical data sheet for 0.56 % light transmission.
http://www.rosco.com/us/filters/roscolux.cfm?sortOrder=no#colors

rosco **COLOR FILTER TECHNICAL DATA SHEET**

SWATCHBOOK:	ROSCOLUX
COLOR FILTER:	#382 CONGO BLUE
DESCRIPTION:	Color Effects Lighting Filter.
TRANSMISSION =	1% or -7.5 stop loss
MIRED SHIFT =	Not Applicable.
CC EQUIVALENT =	Not Applicable.

COLORIMETRIC DATA
OBSERVER: CIE 1964 10°
SOURCE: • 'A' (tungsten)
° 'D65' (daylight)

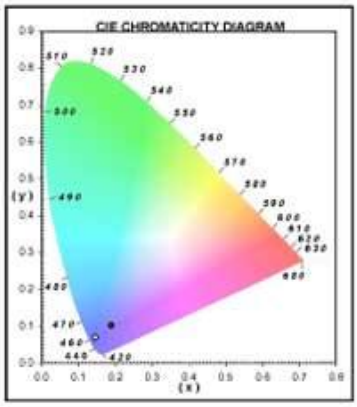


HUNTER LAB SOURCE A	
L*	8.040
A*	19.628
B*	-69.961

HUNTER LAB SOURCE D65	
L*	14.216
A*	38.922
B*	-60.93

CIE 1964 SOURCE A	
Y	0.890
(x)	0.189
(y)	0.103

CIE 1964 SOURCE D65	
Y	1.767
(x)	0.147
(y)	0.070



nm.	360	380	400	420	440	460	480	500	520	540	560	580	600	620	640	660	680	700	720	740
trans %	1	1	2	7	23	24	11	2	0	0	0	0	0	0	0	0	20	63	81	86

MATERIAL SPECIFICATIONS:

General Description:	Co-extruded Polycarbonate Film
Substrate:	PC (Polycarbonate)
Thickness:	3.0 mil (.003" or 76.2 micron)
Manufactured in:	U.S.A.

AVAILABLE SIZES:

- √ 20 in. x 24 in. sheets (50cm x 60cm)
- √ 24 in. x 25 ft. rolls (60cm x 7.62m)
- 48 in. x 25 ft. rolls (121cm x 7.62m)
- 60 in. x 20 ft. rolls (152.4cm x 6.10m)
- 13.5 in. Diameter Glass (34.3cm) - Cut to order