Variation of planktonic community structure along the Orinoco River Plume

By

Dihalia Fuentes Figueroa

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Approved by:

__________________________ ______________
Julio Morell Rodríguez, M.S. Date
Advisor, Graduate Committee

__________________________ ______________
Jorge Corredor, Ph.D. Date
Member, Graduate Committee

__________________________ ______________
Ernesto Otero-Morales, Ph.D. Date
Member, Graduate Committee

__________________________ ______________
Juan G. González Lagoa, Ph.D. Date
Member, Graduate Comitee

________________________ ______________
Dra. Nilda Aponte Date
Director of Department

________________________________ ______________
Dra. Mónica Alfaro
Representative of Graduate Studies Date

ABSTRACT

The planktonic biomass size structure of tropical and subtropical oceans exerts significant control on the ocean's atmospheric carbon sequestering potential. Understanding the spatial distribution of such structure in the Eastern Caribbean waters, under the influence of the Orinoco River Plume (ORP), may provide further insight on the role of the latter in carbon sequestration. Phytoplankton and zooplankton biomass, size structure and taxonomic composition were estimated in surface waters at stations ranging from near-estuarine conditions, from the Gulf of Paria (GOP) in the southeastern Caribbean, to open ocean conditions off the southern coast of Puerto Rico. Plankton near the Gulf of Paria was dominated by microphytoplankton and mesozooplankton indicating the occurrence of an herbivorous-metazoan food chain; conditions favorable for net carbon flux into the ocean. A sharp decrease in planktonic biomass was observed along the ORP. Such reduction in biomass was followed by changes in predominant planktonic cell sizes with nanozooplankton, largely composed by heterotrophic flagellates, and nanophytoplankton becoming dominant at the northernmost stations farthest removed from riverine influence. Moreover these changes in the planktonic community from large to small cells suggest a continuum in the trophic pathways from an herbivorous food web to a multivorous food web to a microbial food web. Our findings document the spatiotemporal evolution of river-influenced tropical planktonic communities and suggest significant spatial variability of potential carbon sequestration along the ORP.

RESUMEN

La estructura planctónica de los océanos tropicales y subtropicales, en términos de biomasa y tamaño de células, ejerce un control significativo en su potencial para el secuestro de carbono atmosférico. El estudio de la distribución espacial de esa estructura planctónica en el Caribe oriental, influenciado por la pluma de descarga del Rió Orinoco (PRO), puede proveer un mayor conocimiento sobre su rol en el secuestro de carbono. La biomasa de fitoplancton y de zooplancton al igual que su distribución por tamaño y composición taxonómica fueron estimadas en aguas superficiales. Las estaciones consistieron desde condiciones cercanas a las de un estuario, cerca del Golfo de Paria, hasta condiciones oceánicas al sur de Puerto Rico. El plancton cerca del Golfo de Paria estuvo dominado por micro fitoplancton y mesozooplankton indicando la prevalecía de una cadena alimenticia herbívora; condiciones apropiadas para un flujo neto de carbono hacia el océano. Una marcada disminución en la biomasa planctónica a lo largo de la PRO estuvo acompañada por cambios en tamaño de los componentes prevalecientes hasta las estaciones mas hacia el norte donde el nanozooplankton (mayormente compuesto por flagelados heterotróficos), y el nano fitoplancton fueron dominantes. Estos cambios en tamaño de células en la comunidad planctónica de células grandes a células pequeñas sugieren un continuo cambio en la cadena trófica de una cadena herbívora a una multi-herbívora a una microbiana. Estas observaciones documentan la respuesta de comunidades planctónicas tropicales a la influencia masiva de ríos y sugieren una marcada heterogeneidad en la capacidad de secuestro de carbono en la PRO.

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What you must know

Every time I look back
I wonder how I survive
Let me tell you what was like
when I arrived at Magueyes Island

Iguana's chasing me at the dock
and a broom became my ally to fight them all
But when things turn for the worst
I became Forrest Gump

Crazy parties posted on the wall
to be held on Kim, Stacey and Katie's home
One semester I stayed back
when suddenly I saw myself wearing a mustache
it was then I realize
I was far
far from sanity land

Focus in my work
a cruise was coming up
Two days before we go
a piece in the pump just broke

With hysteria I went for help
and seems god answered my prey
Because Noé was sent in my aid
and fixed it en un dos por tres

Strange man he was for me
as he acted so calm
In my mind I was thinking
what its wrong with this man

In the afternoon I returned
to see a no longer broken peace
voilá it was fix and on our way to the sea

My relationship with god became so strong
as a storm was hitting us in our way up
I don't recall how many propositions occurred to me
but it turned out to be a perfect time to do business with him

Then we returned and reality hit us in the face
a lot of samples to process before the next cruise in September
A trip to Connecticut to stay for ten days
in order to receive training for zooplankton knowledge

Once I returned three labs became my home
as counting and measuring were needed to be done
Then writing became my goal
although the muse did not wanted to be so

Alex joined me in the road
to write the thesis once and for all
A sentence was encouraging
a paragraph deserved an ice cream cone

In front of you I am to day
and I bowed to you as you deserve
as you all have more than my respect
This journey of science
turn out to be more
a journey to find myself

To my parents as they are my engine in life and the best alcaguetes that somebody could ask. To my brother (Pumpin) and sisters (Zamara and Karina) for always looking after me and Zamara thanks for all your tips…

To my lab mates (Ramon, Milton, Marla, Elenna, Belitza, Suhey) for
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CHAPTER 1

INTRODUCTION

Background:

Continued increase of atmospheric CO_2 concentration is a global environmental concern (Legendre & Michaud 1998, Rivkin & Legendre 2002). While prior to the industrial revolution atmospheric CO_2 concentration ranged between 190 and 280 ppm, during the past 200 years anthropogenic activities have resulted in an increase to concentrations above 365 ppm (EDOCC 2000). It must be noted that such increase has been significantly mitigated by the oceans through physicochemical and biologically-mediate uptake (Legendre & Michaud 1998, Oschlies 2002, Rivkin & Legendre 2002). The export of organic carbon from the surface into the thermocline has been estimated to represent 11 Gt C per annum, approximately 25% of the total primary production in the world oceans (EDOCC 2000). Major players in such amelioration are primary producers and their grazers (Rivkin & Legendre 2002, Doney 1997, Geomar Report, 2002-2004; Irwin et al. 2006, San Martin et al. 2006, Ducklow & Steinberg 2001). In a simplistic model, phytoplankton removes CO_2 from the water potentially resulting in a decrease in partial pressure that leads to an uptake of CO_2 from the atmosphere. Particles biologically synthesized with such CO_2 could then sink to a depth where it can remain sequestered for a significant amount of time (Doney 1997, Rivkin & Legendre 2002, Ducklow & Steinberg 2001). The potential sequestration for such particles to the deep ocean is determined by the phytoplankton cell capacity to sink (becoming senescent or be vertically transported as aggregates) (Rivkin & Legendre 2002, Richardson & Jackson 2007, Legendre & Rassoulzadegan 1996, Cermeño et al. 2006) or their grazing by herbivores that produce sinking fecal pellets (Rivkin & Legendre 2002, Ducklow & Steinberg 2001, Geomar Report, 2002-2004, Legendre & Rassoulzadegan 1996, Froneman 2004, Cermeño et al. 2006). Other processes include diel vertical migrations by zooplankton or nekton that feed on the surface and metabolize the ingested food at depth as well as deep mixing events in which dissolved organic carbon released by phytoplankton or heterotrophic organisms at the surface is transported downward (Rivkin

& Legendre 2002, Legendre & Rassoulzadegan 1996, Froneman 2004, Ducklow & Steinberg 2001).

In the pelagic environment two contrasting trophic pathways have been identified as predominant, the classical chain (herbivorous food web) and the microbial food web (Teira et al. 2003; Legendre & Rassoulzadegan 1995, Cermeño et al. 2006, Froneman 2004). "The former goes from large phytoplankton and zooplankton to fish" (Legendre & Rassoulzadegan 1995) resulting in a shorter and simpler food web with a high carbon export potential whereas the latter is a complex network of organisms "comprising small eukaryotic algae and cyanobacteria as well as heterotrophic bacteria and protozoa" (Legendre & Rassoulzadegan 1995) which are efficient in recycling organic matter within the euphotic zone and therefore sustaining low carbon sequestration rates (Teira et al. 2003, Cermeño et al. 2006; Froneman 2004). Recent studies by Legendre and Rassoulzadegan (1995) have challenged these two mutually exclusive food webs to propose a continuum of trophic pathways whose extremes are dominated by the classical food chain and the microbial food web. They suggest that such continuum evolves from the herbivorous food web through a "multivorous" food web, to the microbial web, and finally the microbial loop (Legendre & Rassoulzadegan 1995). Moreover, they describe the herbivorous food web and the microbial food web as unstable and therefore transient in nature with the multivorous food web and the microbial loop having higher stability (Legendre & Rassoulzadegan 1995). The typical herbivorous food web is a nitrate-dominated system in which uptake of nitrate by large phytoplankton cells is proportionally higher than that of the smaller phytoplankton size-fractions; while the contrary occurs in systems dominated by the microbial web where ammonium uptake sustains small phytoplankton cells (Legendre & Rassoulzadegan 1995, Liu & Dagg 2003). The multivorous food web is defined as the food web intermediate between the classical food chain and the microbial web in which both herbivorous and microbial grazers have significant roles (Legendre & Rassoulzadegan 1995). In the multivorous food web, large phytoplankton are grazed by large zooplankton (mainly copepods) resulting in an increase in dissolved organic carbon (DOC) from sloppy feeding and ammonium from remineralization processes by bacteria and their protozoan grazers (Legendre & Rassoulzadegan 1995). The microbial loop has been defined as an "almost closed system of heterotrophic bacteria and zooflagellate grazers, with the latter releasing dissolved organic matter used as a substrate by the bacteria (Legendre & Rassoulzadegan 1995). However, this definition was the original one and did not contain autothrophs in it (Nybakken, 1997). Thus, the difference between the microbial food web and the microbial loop strives in that in the microbial food web, "dissolved organic nitrogen is plentiful and recycling of nutrients is occurring" whereas in the microbial loop "dissolved organic nitrogen is scarce and bacteria is competing with phytoplankton for ammonium" (Nybakken, 1997). The microbial loop is typical of areas with limited nutrients influx where large cells account for a small proportion of the phytoplankton biomass and therefore low grazing rates by large zooplankton. Microbial loop conditions are characteristic of oligotrophic waters (subtropical ocean gyres, Doney 1997; Marañon et al. 2003) in which bacterial biomass has been observed to surpass that of phytoplankton (Legendre & Rassoulzadegan 1995, Teira et al. 2003). On the other hand herbivorous food webs are typical of spring phytoplankton blooms, upwelling areas (Teira el al. 2003, Legendre & Rassoulzadegan 1995) and river influenced systems (Hongbin Liu et al. 2005). High nutrient low chlorophyll regions of the North Pacific Ocean are an example of multivorous food web. The microbial food web has also been observed at a retreating ice edge off Antarctica (Legendre & Rassoulzadegan 1995).

In summary, four pathways have been proposed for biogenic carbon transfer from autotrophic to heterotrophic organisms (Legendre & Rassoulzadegan 1995). The type of food web involved is determined by nutrient availability for phytoplankton and the ensued cell size distribution and composition (Legendre & Rassoulzadegan 1995, Cermeño et al. 2006). Observation of the latter serves as a practical parameter for distinguishing the carbon sequestering potential of the ocean (Legendre & Rassoulzadegan 1995, Vargas et al. 2007, Marañon et al. 2001).

Interest in studying food web structures has not only focused on carbon sequestration but carbon transfer among trophic compartments has also been a major concern of fisheries scientist and managers; efficient carbon transfer to upper trophic level is critical for maintenance of fisheries stocks. A study, herein mentioned as an example, is the linear relationship found between phytoplankton, carnivorous fish and squid biomass in open oceans and coastal environments (Iverson 1990).

While size distribution of phytoplankton assemblages generally determines the size of grazers and consequently the type of food web involved (Legendre & Rassoulzadegan 1995, Marañon et al. 2001, Cermeño et al. 2005), phytoplankton size structure itself has been found to be modulated by water column stability conditions and grazing by zooplankton (Cermeño et al. 2006; Rivkin & Legendre, 2002).

Water column stability determines the residence time of planktonic cells within the euphotic layer, favoring losses by passive sinking of large-sized phytoplankton cells or their vertical transport under the effect of vertical motion (Cermeño et al. 2006). Unstable conditions such as upwelling and enhanced eddy diffusion from deep water increases the supply of nutrients to the euphotic zone (Legendre & Gosselin 1989, Ducklow & Steinberg 2001, Williams & Follows 1998), resulting in changes or increase associated to cell size and biomass of the planktonic assemblages (Cermeño et al. 2006, Ducklow & Steinberg 2001). Nitrogen is a controlling factor in pelagic production in aquatic ecosystems (Legendre & Rassoulzadegan 1995). Moreover, the chemical speciation of nitrogen; nitrate (new nitrogen) or ammonium (recycled nutrient) prevailing in an ecosystem can also be determinant of the size of the predominant phytoplankton assemblages (Legendre & Rassoulzadegan 1995). Large size phytoplankton cells have been associated to nitrate-nutrient enriched environments as these can attain higher growth rates than small sized phytoplankton when nutrients, mainly nitrate is in high concentrations (Cermeño et al, 2005, Agawin et al. 2000). On the other hand small size phytoplankters have shown higher uptakes of ammonium than that of nitrate; a physiological constraint for large phytoplankton cells in regenerative systems (Legendre & Rassoulzadegan 1995, Cushing 1989, Marañon et al. 2001). Other sources of nutrients to the euphotic layer are terrestrial (rivers, runoff, sewage) and atmospheric (e.g. nitrate in rain) origin as well as nitrogen fixation by organisms such as *Trichodesmium* sp (Legendre & Rassoulzadegan 1995, Ducklow & Steinberg 2001; Corredor et al. 2001). Studies in the oligotrophic Mediterranean Sea showed that increasing the nutrient supply led to a shift in the biomass distribution, from an inverted pyramid (low autothrophic biomass) to an upright pyramid (broad autotrophic base) (Duarte et al. 2000).

Estimates of zooplankton grazing have been based on food selection by size. A size ratio of 10 is assumed in accordance with plankton classification by logarithmic size fractions (Hansen et al. 1994). In systems dominated by large primary producers, an uncoupled relationship between phytoplankton and its grazers is often seen due to longer generation times for the mesozooplankton (Cermeño 2006, Gasol et al. 1997). Contrastingly, grazing of picophytoplankton by smaller grazers is strongly coupled to its phytoplankton prey as they respond at approximately the same time scale (Liu & Dagg 2003, Gasol et al 1997, Froneman 2004). This strong coupling contributes to less particle flux as there is little carbon available to be exported to greater depths (Froneman 2004). Exception to this generally accepted relationship is where large zooplankton such as microphages (e.g. salps, doliolids, appendicularians and pteropods) becomes abundant (Rivkin & Legendre 2002, Ducklow & Steinberg 2001). These zooplankter, "while ingesting smaller organisms can produce rapidly sinking fecal pellets" (Rivkin & Legendre 2002, Ducklow & Steinberg 2001).

Fertilization processes such as coastal upwelling, river discharge and eddies (mesoscale processes) are recognized for their nutrient input and their enhancement of biomass and dominance of the large size phytoplankton class (>2µm) in the structure of planktonic ecosystems (Legendre & Gosselin 1989, Ducklow & Steinberg 2001, Williams & Follows 1998, Legendre & Rassoulzadegan 1995, Ducklow & Steinberg 2001, Corredor et al. 2001). "Major rivers initially impact the adjacent marine environment in the form of a river plume" (RiOMar 2001). When rivers discharge to the ocean they introduce high concentrations of nutrients and organic matter within the river plume (Green et al. 2006, Jochem 2003, Fasham, M.J.R. 2003). Such a disturbance initially results in elevated phytoplankton biomass typically leading to an "herbivorous food web" which may be expected to be replaced by the microbial web once nutrients are depleted within the river plume, as it is advected out to the ocean (RiO Mar 2001, Liu & Dagg 2003). Common features associated to a river dominated system are light limited conditions in the near-field due to turbid conditions created by suspended sediments which inhibit primary production (Liu & Dagg 2003). As turbidity decreases, due to particle settling and dilution (mid-field), light availability increases and pelagic food webs can be stimulated by-river derived nutrients (Liu & Dagg 2003, Jochem 2003). Far-field plume regions have been characterized for low phytoplankton growth rate resulting from nutrient depletion (Liu & Dagg 2003).

During late winter, spring and early summer, nanophytoplankton represents the most abundant autotrophic component in the Caribbean Sea (Bidigare et al. 1993). During late summer and early fall, the Eastern Caribbean is subject to major freshwater inputs from the Orinoco and Amazon Rivers (Bidigare et al, 1993, Corredor et al. 2001, 2003, Hu et al. 2004). Nonetheless between September and November a reduced inflow of tropical Atlantic waters from the east and enhanced local Ekman circulation into the Caribbean basin results in dominance by the Orinoco River plume (ORP). During this time the ORP extends northwestward over 1000 km from the Orinoco delta; from the Gulf of Paria (GOP) to Northeastern Caribbean (Corredor et al. 2003). Fertilization by the ORP as it enters the Southeastern Caribbean results in a 5-10 fold increase in primary production rates (Bonilla et al. 1993, Morell et al. 2005). As the ORP is advected into the east-central Caribbean and nutrients become depleted, phytoplankton production and biomass are also significantly reduced (Morell et al. 2005). Moreover, phytoplankton pigment data indicates a concomitant reduction of diatoms dominance in the phytoplankton community (Bidigare et al. 1993).

Planktonic Community

A comprehensive review of data available from oceanic and costal estuarine areas (Agawin et al. 2000) showed that picophytoplankton dominated ≥ 50% the biomass and production in oligotrophic, nutrient poor and warm ocean waters but represented <10% of autotrophic biomass and production in cold, nutrient-rich waters. Reduced contribution of picophytoplankton in warm productive waters was suggested to result from increased loss rates, whereas the dominance of picophytoplankton in warm, oligotrophic waters was attributable to the differential capacity to use nutrients as a function of differences in size and growth rates between picophytoplanton and larger cells. Studies in the oligotrophic Atlantic Ocean also showed picophytoplankton as the dominant phytoplankton size fraction (Marañon et al. 2003, Perez et al. 2006).

Fertilization processes have frequently been observed to result in enhanced large diatom-dominated phytoplankton biomass; during upwelling events in the region off Mauritania (Marañon et al. 2001), the Ria Vigo, NW-Spain (Cermeño et al. 2006) and the Humbolt current system off Chile (Vargas et al. 2007). Also, large phytoplankton cells dominate along the salinity gradient in the Mississippi river plume in the near to mid field regions, further to the far field chlorophyll a decreased with a change to smaller cells (Liu & Dagg 2003).

Examination of biomass partitioning shows important differences in food web structure between open-sea and coastal systems. Studies by Gasol et al (1997) have shown that open ocean communities support an order of magnitude more heterotrophic biomass for a given autotrophic biomass in the upper layers than do coastal communities. A revision of reports from the open ocean, coastal and estuarine regions (Gasol et al. 1997) as well as experiments in the euphotic zone in a variety of marine environments (Dortch & Packard 1989) suggest that the high relative heterotrophic biomasses found in unproductive areas results in inverted biomass pyramids, whereas the smaller contribution of heterotrophs to community biomass of productive areas are typical of a normal pyramid with a broad autotrophic base.

Zooplankton dominates the heterotrophic biomass in coastal systems, whereas it is equally partitioned, on the average, between bacteria and protozoa and mesozooplankton in the open ocean (Gasol et al. 1997). These findings suggest a direct carbon flow from phytoplankton to zooplankton, which also would efficiently maintain low protozoan biomass in the coastal zone and a greater importance of flow through microbial webs in the open ocean (Gasol et al. 1997).

Although the bacterioplankton community was not assessed in this study, they are an active component of marine food webs (Cho & Azam 1990). "Heterotrophs co-modulate the net flux of carbon dioxide into the sea by control accumulation of dissolved and particulate organic matter while recycling nutrients for photosynthetic production, " (Van Mooy et al. 2004). Their role has been regarded as more important in the least productive areas of the ocean (Parsons et al. 1984; Del Giorgio & Duarte, 2002). Oligotrophic conditions are characterized by low nutrient concentrations with high proportions of dissolved rather than particulate carbon which favors prokaryotic heterotrophs over phagothrophic heterotrophs (Cotner & Biddanda 2004). In contrast, in eutrophic systems, the high relative concentrations of nutrients and particulate carbon along with increased particle sinking may decrease the importance of prokaryotic heterotrophs (Cotner & Biddanda 2004). Studies by Bird & Kalff (1984) showed a positive relationship between bacterial abundance and chlorophyll a. Extrapolation from a relationship obtained by analysis of a large data set from the literature suggests that bacterial biomass relative to phytoplankton biomass was more significant in oligotrophic waters than in eutrophic waters (Bird & Kalff 1984). Studies done in the Pacific Ocean as well as in the Northwest Atlantic and the Caribbean Sea obtained similar results (Cho & Azam 1990, Uye 1999, Fuhrman et al. 1989, Rath et al. 1993).

CHAPTER 2

Variation of plankton community structure along the Orinoco River Plume

Introduction

Elucidating the role oceans play in ameliorating anthropogenic input of CO_2 to the atmosphere has become a major research topic in oceanography (Legendre & Michaud 1998). One of the keys for constraining the fate of biogenic carbon in the oceans is the understanding of the planktonic biomass size structure dynamics (Cermeño et al. 2006). Two trophic structures with different potentials for carbon sequestration into the deep ocean appear to prevail in the tropical and subtropical oceans: the herbivorous food web and the microbial food web (Teira et al. 2003). The herbivorous food web, characterized by large-sized phytoplankters (2 -200 µm), has been attributed with a large potential for exporting carbon to upper trophic levels (metazoans). This herbivorous food web is also distinguished by its efficient carbon sequestration (mediated by sinking of particulate organic matter). In contrast, the microbial food web, where autotrophic biomass is predominantly composed of smaller phytoplankters (0.2-2.0 µm), has been characterized as highly efficient in recycling organic matter within the euphotic zone and therefore sustaining low carbon sequestration rates (Cermeño et al. 2006). Recent studies by Legendre and Rassoulzadegan (1995) have challenged these two mutually exclusive food webs and propose a continuum of trophic pathways whose extremes are dominated by the classical food chain and the microbial food web. They suggest that such continuum evolves from the herbivorous food web through a "multivorous" food web, to the microbial web, and finally the microbial loop (Legendre & Rassoulzadegan 1995). Moreover, they describe the herbivorous food web and the microbial food web as transient in nature (unstable) but the multivorous food web and the microbial loop as having higher stability (Legendre & Rassoulzadegan 1995). The typical herbivorous food web is a nitrate-dominated system in which uptake of nitrate by large phytoplankton cells is proportionally higher than that of the smaller phytoplankton size-fractions; while the contrary occurs in systems dominated by the microbial web where ammonium uptake sustains small phytoplankton cells (Legendre & Rassoulzadegan 1995, Liu & Dagg 2003). The multivorous food web is defined as the food web intermediate between the classical food chain and the microbial web in which both herbivorous and microbial grazers have significant roles (Legendre & Rassoulzadegan 1995). In the multivorous food web, large phytoplankton are grazed by large zooplankton (mainly copepods) resulting in an increase of dissolved organic carbon (DOC) from sloppy feeding and ammonium from remineralization processes by bacteria and their protozoan grazers (Legendre & Rassoulzadegan 1995). The microbial loop has been defined as an “almost closed system of heterotrophic bacteria and zooflagellate grazers, with the latter releasing dissolved organic matter used as a substrate by the bacteria (Legendre & Rassoulzadegan 1995). However, this definition was the original one and did not contain autothrophs in it (Nybakken, 1997). Thus, the difference between the microbial food web and the microbial loop strives in that in the microbial food web, “dissolved organic nitrogen is plentiful and recycling of nutrients is occurring” whereas in the microbial loop “dissolved organic nitrogen is scarce and bacteria is competing with phytoplankton for ammonium” (Nybakken, 1997). The microbial loop is typical of areas with limited nutrients influx where large cells account for a small proportion of the phytoplankton biomass and therefore low grazing rates by large zooplankton. Microbial loop conditions are characteristic of oligotrophic waters (subtropical ocean gyres, Doney 1997; Marañon et al. 2003) in which bacterial biomass has been observed to surpass that of phytoplankton (Legendre & Rassoulzadegan 1995, Teira et al. 2003). On the other hand herbivorous food webs are typical of spring phytoplankton blooms, upwelling areas (Teira el al. 2003, Legendre & Rassoulzadegan 1995) and river influenced systems (Hongbin Liu et al. 2005). High nutrient low chlorophyll regions of the North Pacific Ocean are an example of multivorous food web. The microbial food web has been observed at a retreating ice edge off Antarctica (Legendre & Rassoulzadegan 1995).

During late winter and spring, nanophytoplankters constitute the most abundant autotrophic component in the Caribbean Sea (Bidigare et al. 1993). During late summer and early fall, the Eastern Caribbean is subject to major freshwater inputs from the Orinoco and Amazon Rivers (Bidigare et al, 1993, Corredor et al. 2001, 2003, Hu et al. 2004). Nonetheless between September and November a reduced inflow of tropical Atlantic waters from the east and enhanced local Ekman circulation into the Caribbean basin results in dominance by the Orinoco River plume (ORP). During this time the ORP extends northwestward over 1000 km from the Orinoco delta; from the Gulf of Paria (GOP) to northeastern Caribbean (Corredor et al. 2003). Fertilization by the ORP as it enters the southeastern Caribbean results in a 5-10 fold increase in primary production rates (Bonilla et al. 1993, Morell et al. 2005). As the ORP is advected into the east-central Caribbean and nutrients become depleted, phytoplankton production and biomass are significantly reduced (Morell et al. 2005). Phytoplankton pigment data indicate a concomitant reduction of diatoms dominance in the phytoplankton community (Bidigare et al. 1993).

We report here on the spatial variability of phytoplankton and zooplankton assemblages along the ORP dispersion axis during its seasonal maximum extension into the Eastern Caribbean. Observations indicate marked changes in total biomass and size class of the large size class microphytoplankton and mesozooplankton. The abundance of mesozooplankton and microphytoplankton at stations close to the GOP indicate dominance by the herbivorous-metazoan food web. Further into the Caribbean, autotrophic biomass in the ORP exhibits an acute decrease. Such decrease is mirrored by an inversion in trophic structure were protozoans become the largest grazer component, a condition consistent with increased predominance of a microbial food web.

Methodology

Study site: A total of eight stations were sampled during two fall cruises (maximum discharge season) along the ORP. Stations one, three and six were sampled during Cruise ORI-VII, in November 2005, and stations two, four, five, seven and eight during Cruise ORI-VIII, in September 2006. Both cruises extended from the Caribbean Time Series Station (CaTS) off the south coast of Puerto Rico to the GOP. Stations positions were obtained using GPS and geo-referenced using near real time ocean color imagery to assure their location within or close to the core of the ORP along its dispersion axis. Station positions, classification (N-nearfield, M-midfield and F-farfield) and salinity are included in Table 1.

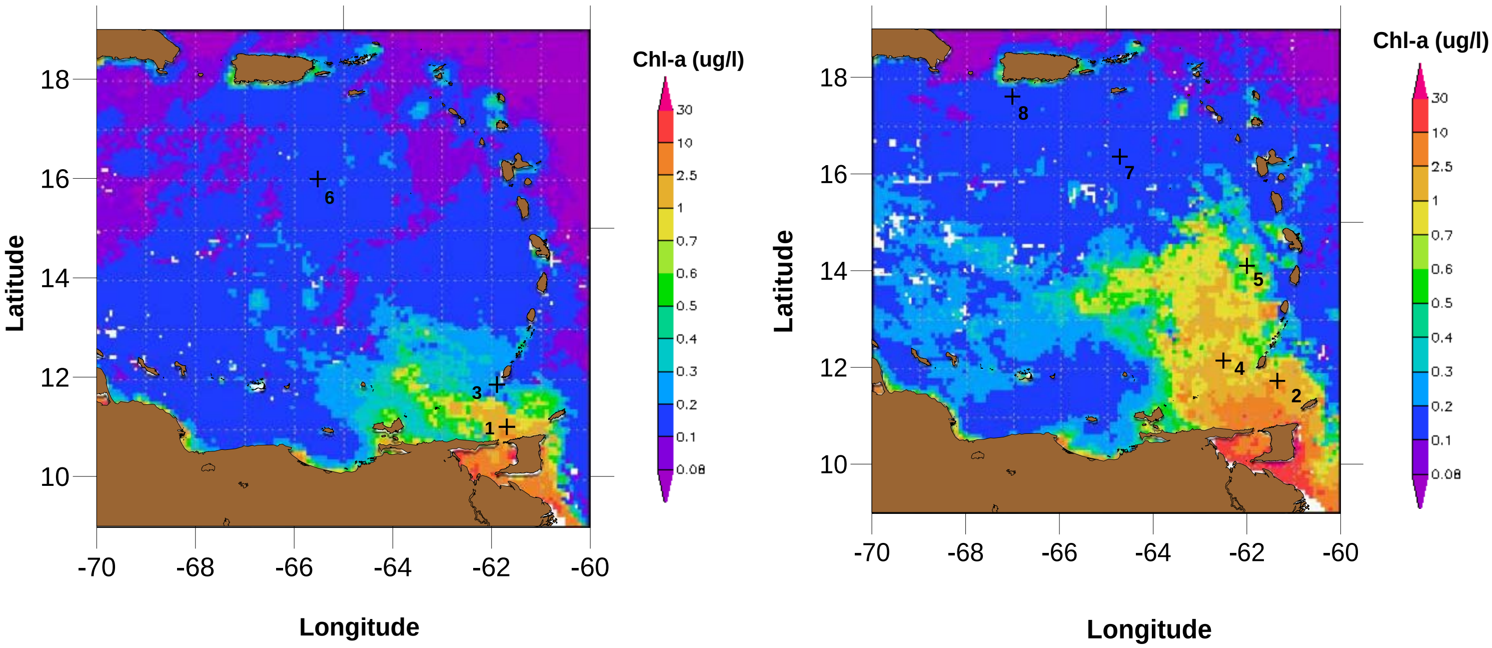

Figure 1. Station locations for R/V Pelican cruises ORI VII (Left) and ORI VIII (Right)

TABLE 1

Station locations and salinity for R/V Pelican cruises ORI VII and ORI VIII

Station	Cruise	Date	Latitude (N)	Longitude (W)	Salinity
(N) 1	ORI VII	November-05	11.00	61.69	25.6
(N) 2	ORI VIII	September-06	11.72	61.35	23.79
(N) 3	ORI VII	November-05	11.85	61.89	33.82
(M) 4	ORI VIII	September-06	12.83	62.50	32.17
(M) 5	ORI VIII	September-06	14.10	62.00	33.29
(M) 6	ORI VII	November-05	15.99	62.52	34.37
(F) 7	ORI VIII	September-06	16.36	64.71	34.95
(F) 8 (CaTS)	ORI VIII	September-06	17.60	67.00	35

Zooplankton sampling and analysis: Three zooplankton size classes were characterized and quantified: nanozooplankton (flagellates: 2 – 20 µm), microzooplankton (ciliates, tintinnids, heterotrophic dinoflagellates, nauplii and copepods: 20 - 200 µm) and mesozooplankton (mainly copepods: >200 μm). Samples for the micro and nano size class were taken at the near surface (0-3m). The nano and micro size fractions were collected using Niskin oceanographic bottles. Heteronanoflagellates were sampled by gently siphoning from the oceanographic bottles into 50 and 15 ml polypropylene centrifuge tubes and fixed in 0.3% glutaraldehyde. After fixation, samples were filtered through black-stained 0.8μm pore size polycarbonate membrane filters and stained with DAPI (4',6-diamidino-2-phenylindole) at 5μg/ml (final concentration), slides were then frozen until analysis by epifluorescence microscopy. Microzooplankton samples were preserved using in 5% Lugol solution and kept in 500 ml polycarbonate bottles. These were sealed and stored at 5º C in the dark until analysis. Mesozooplankton composition at four stations was determined in samples collected in oblique net tows with a cylindrical/conical 200 μm-mesh net with a 0.5 m mouth aperture. One hundred meters of wire were paid out; the net was then held at depth for 30 seconds and retrieved at a constant rate (1 m/s).

Heteronanoflagellates (HNF) were counted using images obtained by a camera mounted in an inverted epifluorecence microscope (Olympus BX 41) with a UV filter set. The area of the image covered was 1600 x 1200 pixels. Sample volume for filter preparation was 15-30 ml depending on abundance, closely related to salinity, and one full diameter of the filter was counted. Only one slide was counted per station. The count was terminated when 100 individuals were reached. HNF were sized using Image J software (Abramoff et al. 2004). Cell volumes were calculated assuming a prolate spheroid shape and biovolume was then converted to biomass (C) using a factor of 0.22 pg C μm -3 (Stelfox-Widicombe et al. 2000). Microzooplankton composition was determined by settling 100 to 500 ml seawater samples. After sedimentation, the sample was concentrated to 5ml and counted at 20x (magnification) using an inverted microscope (Olympus CK 40). Only one sample per station was counted. Counts were terminated when 100 individuals of the dominant taxon were reached. Cell biovolumes were estimated using geometric shapes that were analogous to the shape of the individual taxon. Conversion factors to determine carbon biomass were those characteristic of each group: 0.19 pg C μm -3 for naked ciliates (Putt & Stoecker 1989) , 0.07155 pg C μm -3 for tintinnids (Verity & Langdom 1984) and 0.14 pg C μm-3 for dinoflagellates (Lessard

1991). Copepods were assumed to conform to *Acartia tonsa* stages CI-CVI composition (Berggreen et al. 1988) and nauplii carbon biomass was determined based on a football formula (Godhantaraman & Uye 2003). Water samples for mesozooplankton, were poured into labeled bottles, homogenized by stirring and a 10ml sub sample filtered onto glass fiber filters (GF/F) packed in aluminum foil and refrigerated for CHN determination (Thibault et al. 1999). This procedure was performed in triplicates for each of the four stations sampled. Due to the presence of *Trichodesmium* sp. in some of the samples, 1ml of sample was taken for colony enumeration and CHN determination. This measurement was used for the correction of mesozooplankton CHN measurements.

Biomass differences in the smaller zooplankton assemblages

In order to asses the effect of the ORP on the biomass of micro and nano zooplankton the study area was divided into two regions, 1) one receiving a greater input of river discharge and 2) a region less influenced by the ORP. For this analysis data from lower latitudes (11.00 and 11.85) were pooled comprising one region and from higher latitudes (16.11, 16.36 and 17.6) comprising the second region. Median biomasses were analyzed using Mann-Whitney test after data and none transformation procedures were able to fulfilled the requirements of normal distribution and equal variance.

Phytoplankton abundance and community size structure: Near surface samples (0-3m) for phytoplankton biomass were collected using Niskin bottles and stored in dark polyethylene until sequentially filtered through pore sizes of 20 (nylon), 2 and 0.2 um (polycarbonate membrane) filters. Filters were extracted overnight at room temperature in 90% acetone. Chlorophyll a fluorescence measurements were taken using a 10-AU Turner fluorometer. Phytoplankton carbon biomass was estimated using an 80 g $C.g^{-1}$ Chl a factor reported by (Taguchi et al. 1988) for Caribbean samples under high irradiance regimes. Although literature suggest that the carbon to chlorophyll ratio for oligotrophic environments is higher than the ratio for eutrophic environments , ca. 50 g $C.^{-1}$ Chl a (Buck et al. 1996) (Longhurst 1995 & Barlow et al. 1998), the use of 80 g $C.g^{-1}$ Chl a at all stations did not affect our results.

Profiles of total chlorophyll a fluorescence and salinity were collected using a Sea Bird SBE 25 CTD profiler coupled to a Sea Point fluorometer and a rosette sampler. Discrete whole surface phytoplankton samples were extracted for Chl a and the results used to calibrate the fluorometer.

Phytoplankton and Zooplankton groupings: In order to identify similarities in phytoplankton and zooplankton assemblages between different stations along the latitudinal gradient a Cluster analysis using the Bray Curtis similarity index was performed. Five from the eight stations were used in this analysis due to missing biomass data in some size classes at three stations. The total phytoplankton and zooplankton biomass for each phytoplankton and zooplankton size class was used as the discriminator parameter in the analysis.

Results

Observed salinities and biomass of phytoplankton size fractions across latitudes, as the ORP spreading axis follows a south to north route, are presented in Figure 2. Surface salinity along the ORP ranged from 25.6 in the GOP up to 35.0 in the northeastern Caribbean (Figure 1, Table 1). Total phytoplankton biomass spanned circa an order of magnitude from 191.40 μg $C.l^{-1}$ at the near field off the GOP to 17.80 μg $C.l^{-1}$ at the northernmost station (St.8) off the south coast of Puerto Rico. Biomass for the larger phytoplankton size fractions (>20 μm) ranged from 18.4 μg $C.l^{-1}$ or 66% of the total phytoplankton biomass at latitude 11.72 μg $C.l^{-1}$ gradually diminishing to 22% (3.5 μg $C.l^{-1}$) along the northern section of the ORP. Contrastingly, nanophytoplankton biomass exhibited an increase of the same magnitude from 1.2 μg $C.l^{-1}$ at the GOP to 7.8 μg $C.l^{-1}$ at the far field of total phytoplankton (4.4 μg $C.l^{-1}$ and 44% respectively). Minimum picophytoplankton (<2 μm) biomass were observed in the near field (8 μg $C.l^{-1}$) and the far field (6.0 μg $C.l^{-1}$) with a maximum, 15 μg $C.l^{-1}$, in the mid field near latitude 14 N. This size fraction comprised from 30% to 54% percent of the total phytoplankton biomass.

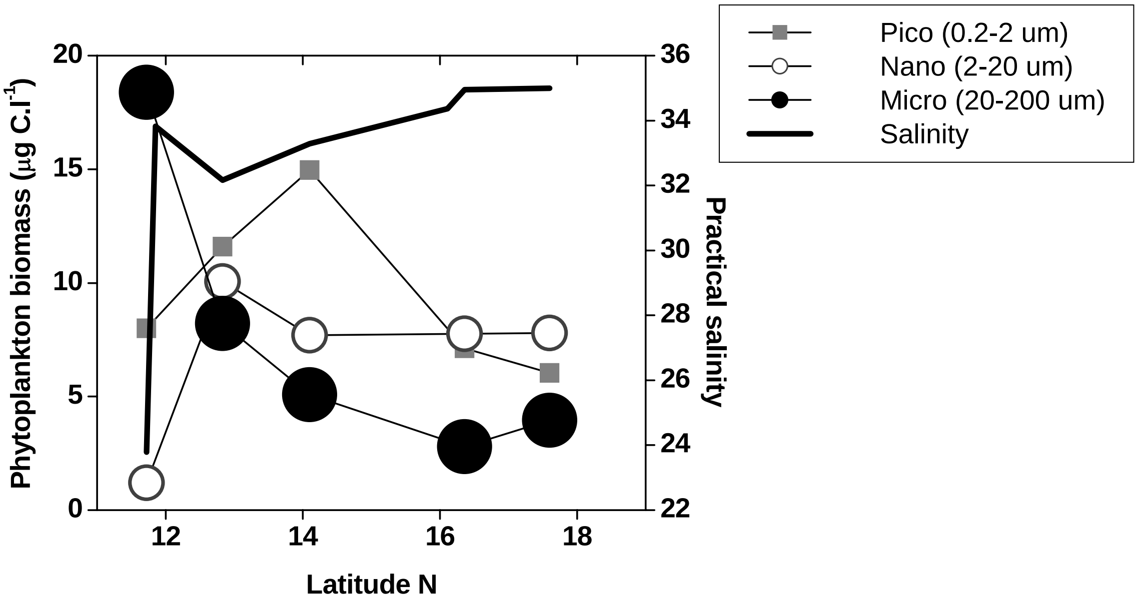

Figure 2. Latitudinal plot for phytoplankton biomass size class and surface salinity.

Total zooplankton biomass, including protozoans, ranged from 17.3 µg C.l^{-1} at station 3, the southernmost station where all zooplankton size fractions were quantified to 7.8 µg C.l^{-1} at station 8 (Fig. 3). Biomass for the mesozooplankton fraction accounted for 75% of the total zooplankton biomass at latitude 11.85 N (13.0 µg C.l^{-1}) and diminished to circa 40 % at the northernmost stations (3.1 µg C.l^{-1}). The microzooplankton component was the least abundant zooplankton size class at all stations; a maximum was observed at the southernmost station with a 2.4 µg C.l^{-1} and remained relatively constant along the ORP with a biomass of ca 1.0 µg C.l^{-1} at the far field stations (Fig. 3). Nanozooplankton biomass remained fairly constant along the ORP with an all station average of 4.5 µg C.l^{-1} and became a dominant zooplankton size class in the mid and far field where its biomass equaled or exceeded that of the mesozooplankton (Fig. 3). Furthermore, when comparing biomass of nano ($T = 5.00$, $p > 0.05$) and micro ($T = 7.00$, $p > 0.05$) zooplankton assemblages from areas most and least influenced by the ORP (Figure 7), results showed no significant differences from one zone to the other.

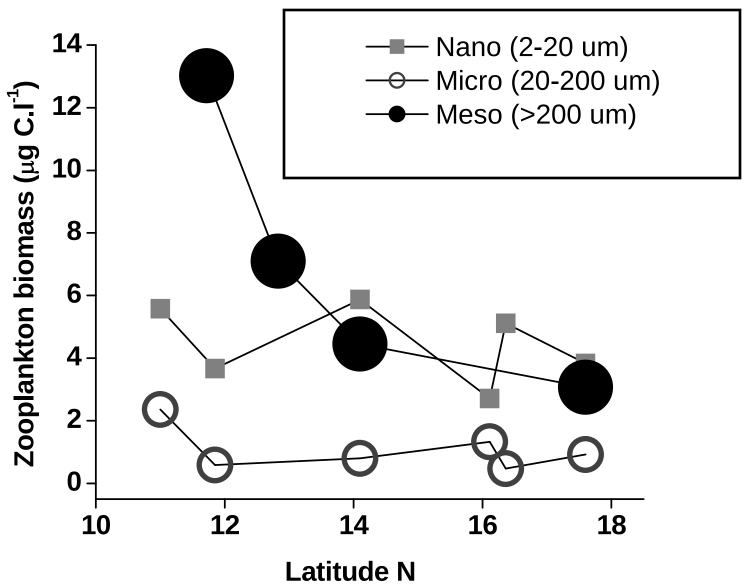

Figure 3. Latitudinal plot for zooplankton biomass size structure along the ORP.

Regression analyses of covariation between zooplankton grazers and phytoplankton prey were based on size ratio preferences (Hansen et al. 1994). Along the latitudinal gradient, the sum of microphytoplankton and microzooplankton biomass were positively correlated to total mesozooplankton biomass ($R = 0.99$, $p = 0.002$, $N=5$). No statistically significant relation was found between the nanophytoplankton plus nanozooplankton and their main grazer, the microzooplankton, or between picophytoplankton and nanozooplankton, its main grazer.

The Cluster analysis of phytoplankton assemblages yields three groupings of phytoplankton size assemblages along the ORP (Fig. 4) with station 2 (lat. 11.72 N) emerging as one, stations 4(lat. 12.83 N) and 5 (lat. 14.1 N) as the second community and stations 7 (lat. 16.36 N) and 8 (lat. 17.6N) constituting the third community. Stations 7 and 8 were the most similar to each other (92%) followed by stations 4 and 5 with 85%. Also this analysis suggests that these two communities are not more than 53% similar to station 2. The Cluster analysis for the zooplankton assemblages also yielded three groupings. Station 3 (lat. 11.85) as one community, station 4 (lat. 12.83) and station 5 (lat. 14.1) as the second community and station 8 (lat. 17.6) as the third community.

Bray Curtis analysis showed that stations 4 and 5 were the most similar to each other (82 %) and had a similarity to station 8 of 77%. The analysis also showed that these two

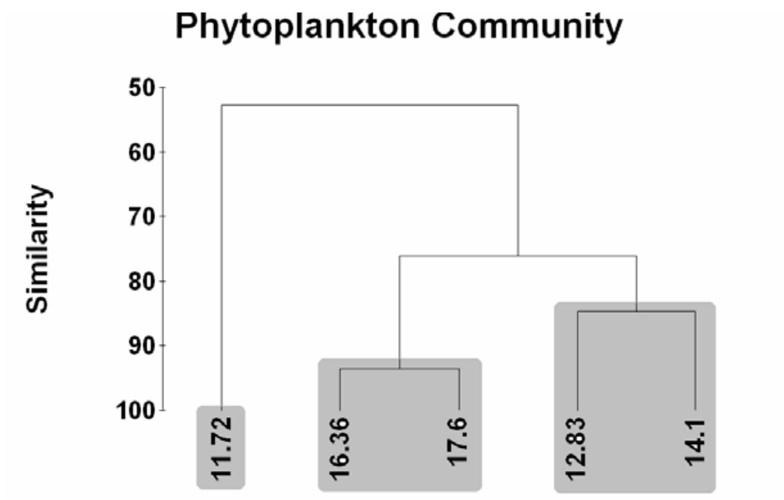

Figure 4. Cluster Analysis of phytoplankton biomass using the Bray Curtis similarity index at 5 stations.

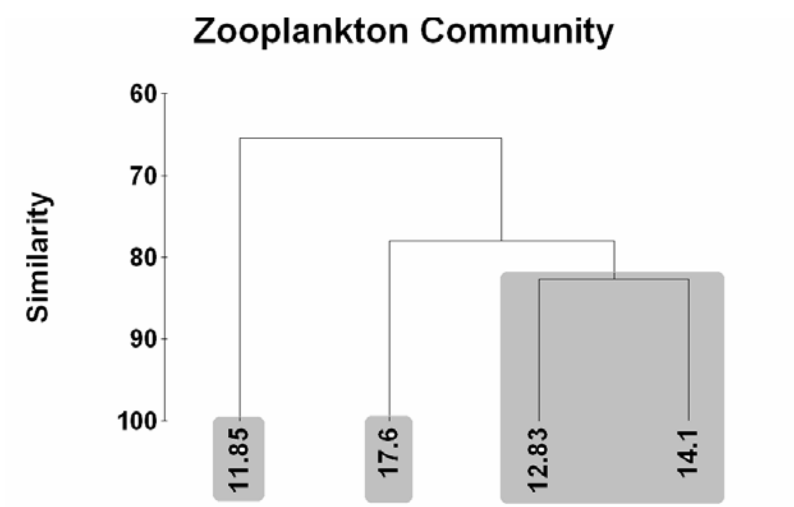

Figure 5. Cluster Analysis of zooplankton biomass using the Bray Curtis similarity index at 5 stations.

communities had a similarity of no more than 65% with station 3.

Discussion

Our observations and statistical analyses indicate the occurrence of three distinct phytoplanktonic and zooplanktonic assemblages in the ORP (Figure 4, 5). In the near field, up to circa latitude 12N, 66% of the autotrophic biomass an order of magnitude higher than typical Eastern Caribbean waters (Corredor et al. 2003) is constituted by large cell phytoplankton, presumably diatoms. Such proportion is significantly higher than the 20% found in the mid and far ORP field. In turn, the latter exceed the 13% reported by Taguchi et al. (1988) for Northeastern Caribbean waters during December and the circa 10% reported for the Tropical Atlantic (<10%) (Marañon et al. 2001). Such autotrophic biomass, reported to sustain high production rates (Bonilla et al. 1993, Morell et al. 2005), results in the development of mesozooplankton biomass (13 μg $C.l^{-1}$) well above that reported by (Finenko et al. 2003) for the Western Tropical Atlantic (8 μg $C.l^{-1}$). The dominance of this large size class in the near field supports the argument attributing to tropical riverine input the development of areas of efficient matter and energy transfer to larger consumers as a result of a shorter food web (Irwin et al. 2006). This simpler and shorter food web dominated by large cells have a significant potential for net atmospheric carbon sequestration into the ocean as large phytoplankton cells have the capacity to sink (becoming senescent or be vertically transported as aggregates) (Richardson & Jackson 2007, Cermeño et al. 2006) and by the production of sinking fecal pellets by large herbivorous zooplankton (Cermeño et al.2006, Froneman 2004).

In the mid field and far field, where salinities between 32 and 35 evidence the ORP dilution in oligotrophic ocean waters, our observations are consistent with a scenario where mesozooplankton grazing has exceeded microphytoplankton growth rates; attributable to physiological constraints (Irwin et al. 2006) and nutrient exhaustion (Bonilla et al. 1993). Such scenario allowed for the development and dominance of smaller phytoplankton (<2um) biomass in the midfield and far field stations. Protozoa to phytoplankton biomass ratios increased from 0.04 at the near field to 0.32 at the far field while mesozooplankton to total phytoplankton biomass ratios ranged from 0.5 and decreased to 0.16 (Figure 6). These results illustrate a shift from large cells to small cells in the zooplankton community. However, results suggest that this shift is not due by the increase in biomass of the smaller assemblages but by the decrease in biomass of the larger assemblage's microphytoplankton and mesozooplankton. This non significant difference in biomass for the smaller zooplankton assemblages (Figure 7) could be as a result of a possible similar magnitude in growth of the prey and grazing pressure by the zooplankton compartment (Strom 2002) and or possible control by other zooplankton assemblages (Froneman et al. 1996). For example, bacterial biomass was found to be constant along the ORP dispersion (L. Kerkhof. pers. comm.) suggesting an equilibrium state with the nanozooplankton. On the other hand studies have reported that "microzooplankton can contribute significantly to the diet of the mesozooplankton even when large diatoms are abundant" (Froneman et al. 1996). Moreover, comparison of results with a truly oligotrophic region such as the Western Tropical gyre in the Atlantic Ocean for the zooplankton assemblages, reinforce our findings that only the mesozooplankton have a higher variability than the nano-micro zooplankton assemblages (Figure 8).

Results showed that from near field to midfield the microphytoplankton biomass decreased gradually and was sustained through the far field. This biomass decrease in microphytoplankton is possibly due to a reduction in dissolved organic carbon (Del Catillo et al. 1999) and the rate of photomineralization (Morell & Corredor 2001) or biomineralization of nutrients as waters become diluted. The latter processes (photomineralization and biomineralization) as well as mesoscale eddy and diazotroph blooms (Corredor et al. 2003) have been identified as sources of new nutrients in the region. Nonetheless, the observed large cell phytoplankton background supported in the far field highlights apparent riverine modulation 1000 km from the river delta and a potential for enhanced carbon drawdown. Hence, none of our stations were in truly oligotrophic conditions like the ones found in the tropical Atlantic ocean which are characterized by heterotrophic components exceeding the biomass of the autotrophic components (Buck 1996). Contrastingly, the decreased in biomass observed in the large zooplankton size class (mesozooplankton) could be as a result of its respond to the decrease in biomass of its main prey (microphytoplankton).

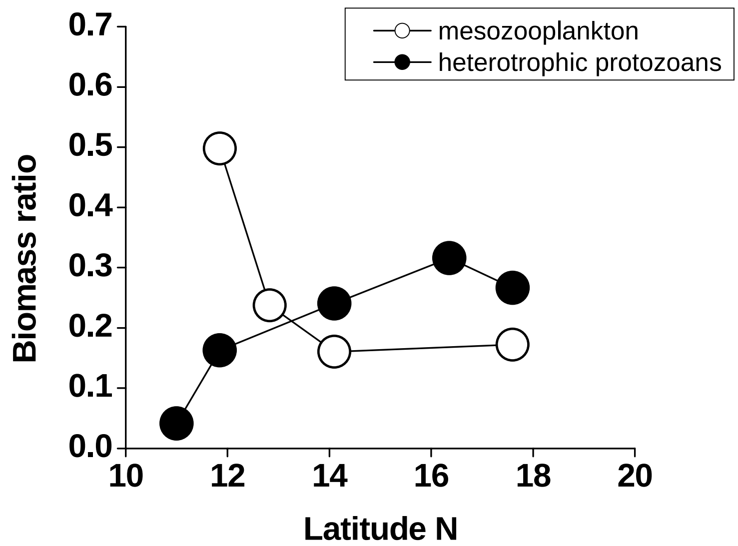

Figure 6. Change of the ratio of meso-and protozooplankton versus total phytoplankton with latitude.

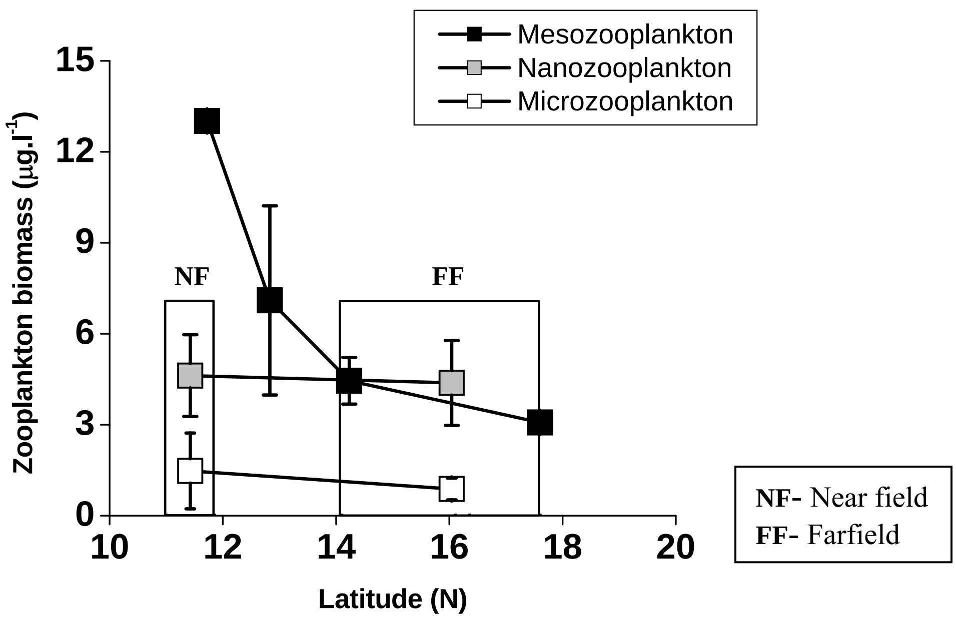

Figure 7. Latitudinal plot for zooplankton biomass size structure (pooling of stations for the micro and nano zooplankton) along the ORP.

Nevertheless, the suggested change in the food web goes from an herbivorous food web in the near field to a multivorous food web in the midfield and a microbial food web in the far field. These observations are sustained by the prevalence of mesozooplankton assemblages over protozoans at the near field suggestive of large cells predominance at this field thus an herbivorous food web, the equivalent biomass of mesozooplankton and protozoan assemblages in the midfield indicating the equivalent contribution of large and small cells (multivorous food web) at the mid field and dominance of protozoan over mesozooplankton at the far field representative of small cell dominated microbial web.

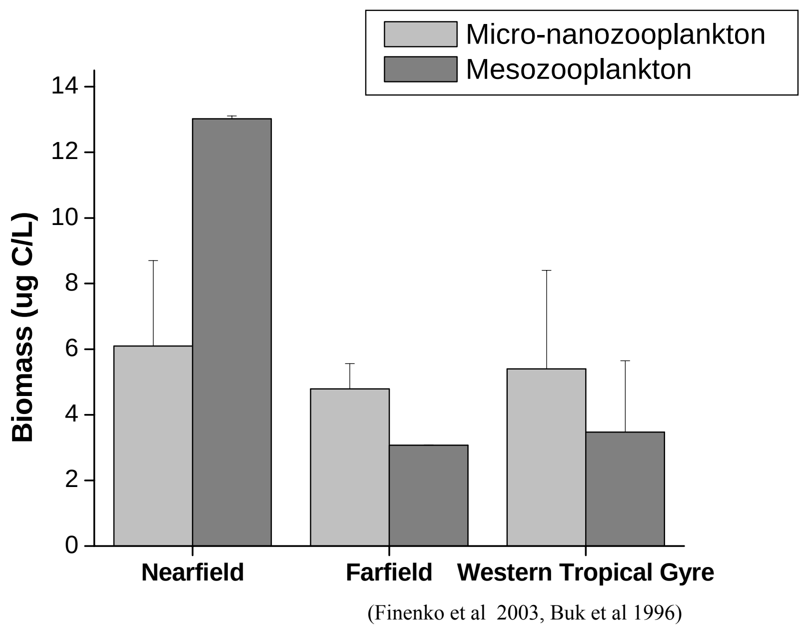

Figure 8. Biomass for the meso and micro-nano size class at the nearfield-farfield compared to the Western Tropical Gyre in the Atlantic Ocean.

CHAPTER 3
CONCLUSIONS

3.1 General Conclusions

This study shows that the Orinoco River plume (ORP) in its maximal discharge season affects the planktonic biomass size structure of an otherwise oligotrophic nanoplanktonic dominated system. However, results suggest that only the larger assemblage's microphytoplankton and mesozooplankton were the only size classes to be affected by the ORP. In addition, results suggest a higher potential in carbon sequestration near the mouth of the river.

Spatial variability in phyto-zooplankton biomass assemblages indicates heterogeneity in carbon sequestration potential along the ORP extension.

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