# INFLUENCE OF HYDROLOGICAL SEASONALITY ON SANDBANK BENTHOS: ALGAL BIOMASS AND SHRIMP ABUNDANCE IN A LARGE NEOTROPICAL RIVER

A Dissertation

by

JOSÉ VICENTE MONTOYA CEBALLOS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2008

Major Subject: Wildlife and Fisheries Sciences

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December 2008

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# ABSTRACT

Influence of Hydrological Seasonality on Sandbank Benthos:
Algal Biomass and Shrimp Abundance in a Large Neotropical River.
(December 2008)
José Vicente Montoya Ceballos, Licenciate in Biology, Universidad Simón Bolívar

Co-Chairs of Advisory Committee: Dr. Daniel L. Roelke
Dr. Kirk O. Winemiller

In this study, I examined the influence of hydrological seasonality on spatiotemporal variation of algal biomass and shrimp abundance on sandbanks of the Cinaruco River in southwestern Venezuela. Seasonal variations of abiotic and biotic variables in the Cinaruco were driven by the hydrological regime. During the high-water periods, river sites in the main channel and lagoon sites were similar in water physicochemical variables and algal biomass. In contrast, physicochemical variables and algal biomass differed between river and lagoon sites during the low-water period. The absence of flow in lagoons and consistently low algal biomass on river sandbanks were the most important features of the spatial variability between main-channel and lagoon sandbanks during low-water phases. Benthic algal biomass was highly uniform at small spatial scales and significantly heterogeneous at large spatial scales. In the second major part of this dissertation, I found a relatively species-rich shrimp assemblage with seven species inhabiting the sandbanks of the Cinaruco. I also observed clear patterns of temporal and spatial variation in shrimp abundance on the Cinaruco sandbanks. Abundance of shrimp on the sandbanks presented remarkable diel variation, showing almost exclusive use of this habitat at nights. Seasonally, shrimp were more abundant during rising- and falling-water periods, when rapid changes of environmental conditions occur. Shrimp abundance was high on those sandbanks with absence of troughs and presence of submerged vegetation. These environmental features presumably promote colonization/establishment and survival/persistence of shrimp in the sandbanks. In a patch-dynamic view of communities, a mobility control model seems to apply to shrimp of the sandbanks in the Cinaruco during the period of rapid changes in hydrology and habitat structure. During low-water periods, when habitat structure of sandbanks is relatively constant, low shrimp abundance appears to be heavily controlled by high fish predation. The annual flood regime of the Cinaruco, which drives the concentrations of dissolved materials, affects material interchanges between aquatic and terrestrial systems, and modifies aquatic habitat structural complexity, is responsible for creating strong patterns of seasonal and spatial variation in benthic algal crops and shrimp abundance on the sandbanks of this large floodplain river.

To my parents, Elizabeth and José Vicente

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# CHAPTER I

# INTRODUCTION: THE CINARUCO, A LARGE FLOODPLAIN RIVER IN THE ORINOCO LLANOS, VENEZUELA

## General features of the Cinaruco

The Cinaruco River is a lowland tributary on the left margin of Orinoco River with an estimated basin area of 11,700 km$^2$ shared between Colombia (11%) and Venezuela (89%). With an approximated length of 505 km, the Cinaruco meanders entirely on the vast tectonic subsidence system of the Orinoco llanos, or plains. The drainage network of all rivers in the western Venezuelan llanos follows the faults system that fractured these plains during the uplift of the Andean Cordillera (Sarmiento and Pinillos 2001). Thus, the Cinaruco extends with an eastward direction for most of its course up to 30 km upstream from its mouth where it changes direction due to the presence of a SW-NE fault (FIG. 1). The Cinaruco has three main tributaries: Rio Juriepe (156 km), Brazo Cinaruco (92 km) and Caño Potrerito (80 km); and hundreds of smaller creeks which drain the surrounding savanna. Some of these creeks correspond to small "morichales". Morichales is a term used to refer to creeks with a riparian forest dominated by *Mauritia* palms.

The Cinaruco basin is located in an extensive aeolian plain containing both fossilized and active dune fields. This aeolian plain is one of the four major regions distinguished by Sarmiento (1983) within the region of the llanos that lies between the

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This dissertation follows the style of Journal of the North American Benthological Society.

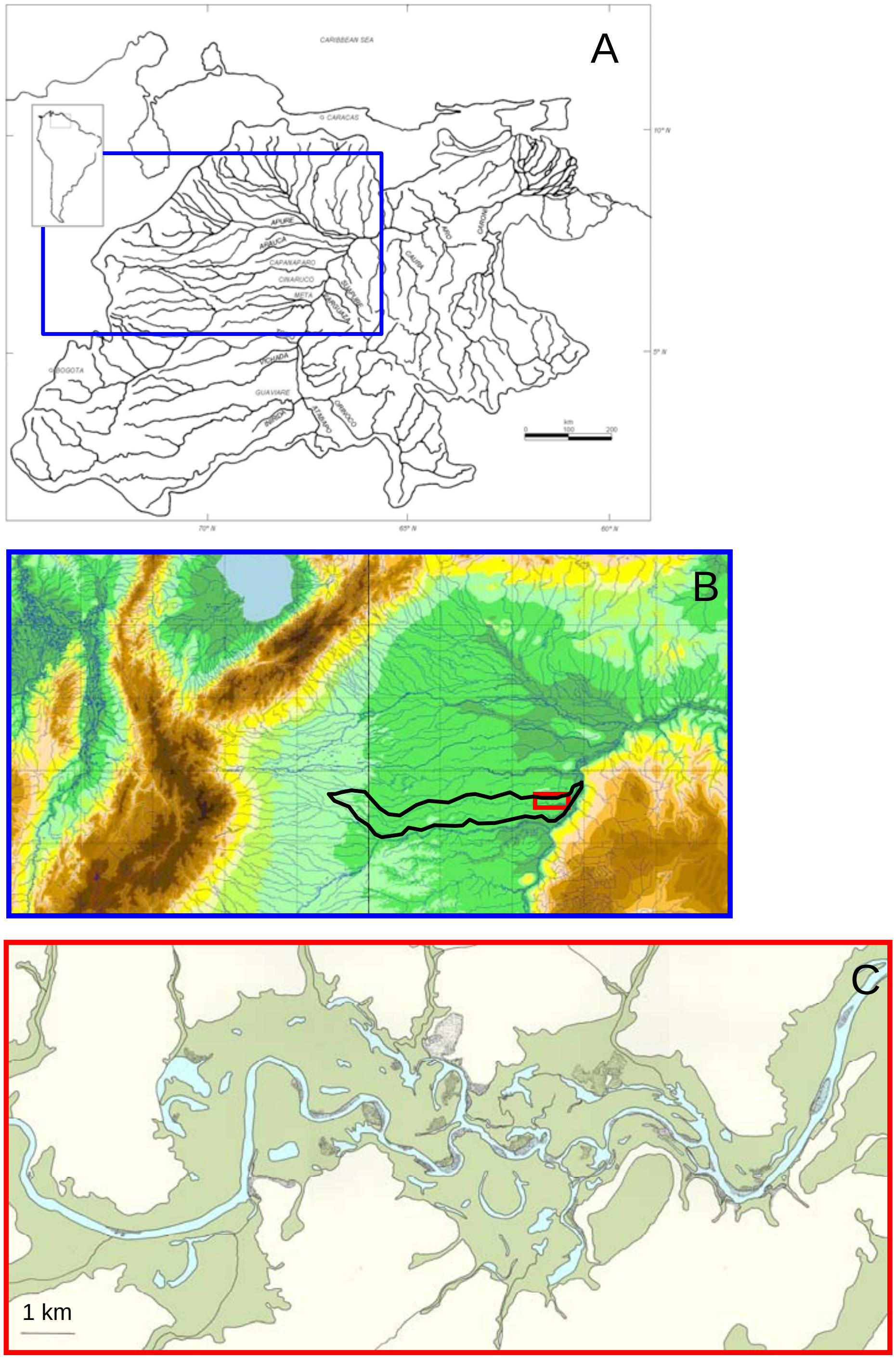

FIG. 1. Location of the Orinoco River basin (A); the Cinaruco River basin (outlined in black) in the llanos of Venezuela and Colombia (B); and the Cinaruco floodplain stretch investigated in this study (C).

lower courses of the Arauca and Meta rivers (Tricart 1974). The presence of dune fields has been considered evidence of past arid conditions during the dry period between the last glacial maximum (Würm) and the late Pleistocene (Tricart 1974, Iriondo 1999). Only a few active dune fields are readily recognizable in the area, whereas the majority of dune fields are fossilized by Holocene alluvium (Tricart 1974). Most of these dunes are currently covered by vegetation, making them only easy to detect using satellite images or aerial photographs (Nordin and Pérez-Hernández 1989).

The present climate in the region is a typical tropical wet/dry climate dominated by the northeast trade winds and the north-south migration of the Intertropical Convection Zone (ITCZ). Annual mean temperature for the Llanos averages around 25-26 ºC, and the amplitude of mean monthly fluctuations is never higher than 3ºC. In contrast, daily temperature amplitudes can be as high as 12 ºC (Sarmiento and Pinillos 2001). Precipitation follows a longitudinal gradient, with lower annual rainfall in the east (around 1300 mm) and higher values (to 2700 mm) in the Andean piedmont in the west (Sarmiento and Pinillos 2001). ITCZ migrations create strongly seasonal precipitation. The wet season spans from May to November (peaking in June - July). The closest meteorological station to the field sites of this study is located in Puerto Carreño, Colombia, located approximately 40 km south of my field site. This station, although not located in the Cinaruco River basin, is sufficiently close to represent the climate at my field site. Mean annual precipitation for Puerto Carreño is 2184 mm. As mentioned above, precipitation is strongly seasonal for this station (FIG. 2A). Another meteorological station located in San Fernando de Apure, ~150 km north of the

Cinaruco, shows the same strong unimodal pattern in precipitation (FIG. 2B), but less precipitation on an annual basis (~1400 mm). Climate data for Puerto Carreño and San Fernando de Apure were obtained from IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia) and INAMEH (Instituto Nacional de Meteorología e Hidrología de Venezuela), respectively.

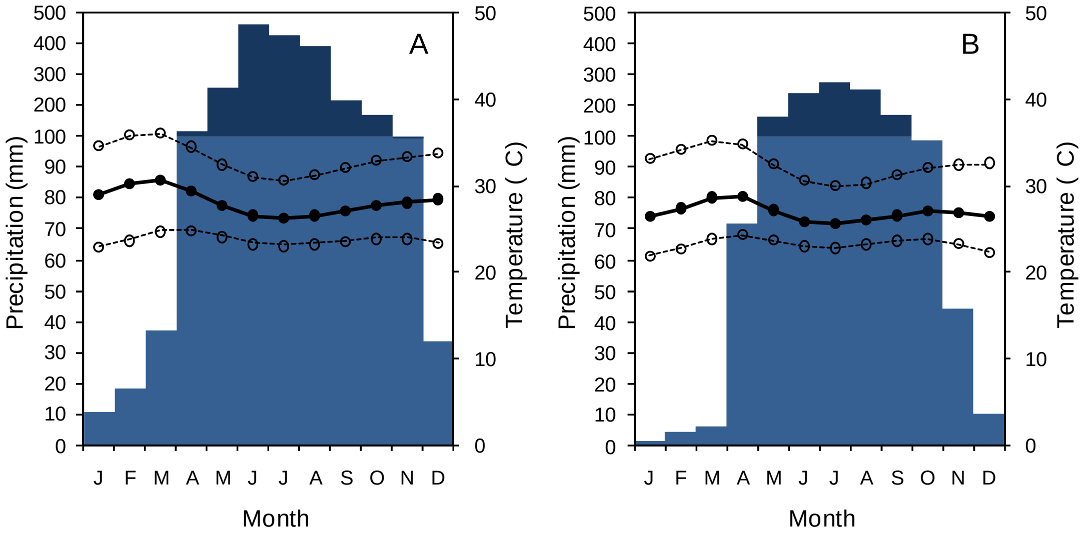

FIG. 2. Climate diagrams of Puerto Carreño (A) and San Fernando de Apure (B), showing cumulative monthly precipitation (in bars) and monthly air temperatures (mean in solid line and mean max. and mean min. temperatures in dashed lines).

This seasonality in precipitation determines the flood dynamics of rivers draining the western llanos. The hydrological seasonality and inundation patterns of the region were assessed by Hamilton et al. (2004), who estimated a long-term mean inundation area of 34,700 km$^2$, with a maximum flooded area of 105,454 km$^2$. The Cinaruco shows a typical unimodal hydrological regime exhibited by large rivers with a dry-wet climate. The average annual discharge of the Cinaruco at its mouth in the Orinoco is 250 m$^3$.s$^{-1}$ (Silva León 2005). For comparison, rivers with similar basin size to the Cinaruco, such as the Atabapo and the Sipapo, which are also Orinoco tributaries that drain forests in southern Venezuela, have discharges that are double that of the Cinaruco. Water level differences between minimum and maximum depths in the Cinaruco are 5-7 m, depending of the year. The low-water season occurs from early January to mid April. The rising-water period extends from mid April to mid June, and high waters persist until early October. The water level gradually declines until the beginning of the next low-water season in January.

The Cinaruco is one of the few large left-margin tributaries of the Orinoco not having its headwaters in the Andes Mountains. Due to the dystrophic character of llanos soils (Medina and Silva 1990), rivers, such as the Cinaruco, that originate entirely or mostly within the llanos have low nutrient and suspended sediment loads. The majority of these rivers can be classified as clear or black-water rivers. In contrast, those having their headwaters in the mountains are rich in nutrients and suspended solids (white-water rivers). Therefore, the landscape of the llanos is a heterogeneous mosaic in which oligotrophic and eutrophic river basins are interspersed allowing for important ecological interactions among them (Winemiller and Jepsen 1998). The Cinaruco basin is bordered on the north by the Capanaparo basin (clear water) and on the south by the Meta basin (white water). The Cinaruco is considered oligotrophic (Roelke et al. 2006, Cotner et al 2006), with low conductivity (4-9 $\mu S\ cm^{-1}$) and moderately low pH (6 – 6.5). Mean water transparency is around 1 m and resembles the values found for other Orinoco tributaries located in the Guayana Shield. Nutrient concentrations (P and N dissolved inorganic fractions) are especially low (Roelke et al. 2006).

The landscape in the Cinaruco River basin consists mostly of savanna vegetation and riparian forests. These savannas, classified as seasonal and hyperseasonal savannas (Sarmiento 1983), are mostly composed of C4 grasses and sedges, and the presence of other type of vegetation in the open savanna is very limited to sparsely distributed small trees and shrubs. These seasonal savannas are controlled by a complex interaction between soil characteristics, water availability and fire. Fire is an important component of this type of ecosystem and occurs annually during the dry season (Medina and Silva 1990).

The Cinaruco drains different ecoregions, from areas with extensive sand dunes to areas more elevated and less prone to inundation. The river, as it can be seen on satellite imagery, presents a meandering course and a variable coverage of riparian forest. In an attempt to characterize the river, I estimated the sinuosity of the main channel as well as the width of the riparian forest for the lower 300 km. Sinuosity was calculated as the ratio between river channel length and valley length on 100 points located randomly in 100 3-km consecutive segments located from the confluence with the Orinoco up to 300 km upstream. Sinuosity values of 1 are indicative of straight river segments. As the number of bends increases, the ratio main channel/valley length also increases. Therefore, higher values of that ratio mean elevated sinuosity. At each of those points, the riparian forest width was measured perpendicular to the river direction on both banks. Those measures where done using Google Earth and were straightforward since the demarcation between savanna and riparian forest is very obvious.

The Cinaruco has sinuosity ratio values that are relatively constant along its last 300 km. Some river segments showed slightly higher sinuosity, such as my study area, but in general, values oscillated between 1.2 and 1.4, which are characteristic values for sinuous channels (Charlton 2008). On the other hand, what was not constant along the lowest 300 km of the Cinaruco was the width of the riparian forest. There was a significant negative relationship between the distance from the river mouth with the width of the riparian forest, as the river approaches Orinoco confluence, the riparian forest gets wider. Satellite imagery shows that in the upper reaches of the river, the influence of sand dunes is much more important than in the lower reaches. FIG. 3 clearly shows that the landscape is very different between two locations situated at lower and upper reaches of the river segment studied. These preliminary findings regarding landscape characteristics could help to formulate research questions aimed at advancing our understanding of ecosystem patterns and processes.

In the second chapter of my dissertation, I present a limnological characterization of the Cinaruco in a segment that is ~50 km from the confluence with the Orinoco. In that chapter I focused on temporal changes in physicochemical variables and sestonic and benthic algal biomass from sites located in floodplain lakes and sites on sandbanks of the main river channel. I found that sites become similar during periods of high hydrological connectivity, and become dissimilar when the flood recedes and connectivity is reduced. Another goal of chapter II was to investigate patchiness of algal biomass in sandy beaches at different spatial scales and in two different seasons. Results from that experimental design, although provocative, opened many more questions.

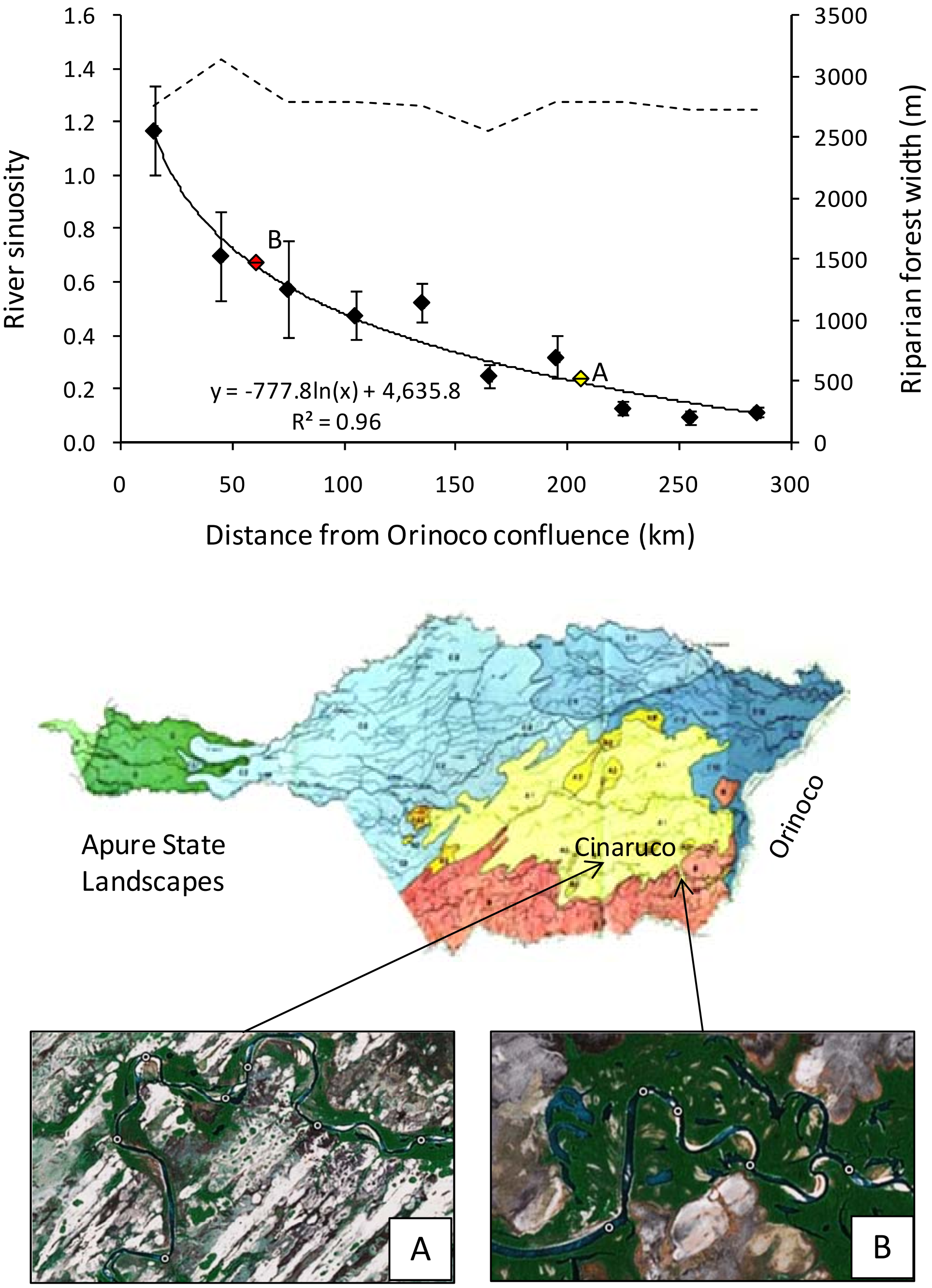

FIG. 3. River sinuosity (dashed line) and riparian forest width (black dots and regression line) for Cinaruco River lower reaches. Points A and B in yellow and red, respectively, correspond to locations at 55 km and 205 km upstream from the confluence with the Orinoco. These two areas are located in different ecoregions of the Apure State. Point A is located at the aeolian plains region with high density of dunes (yellow in the map), and point B is situated on plains that are slightly more elevated and lacking active sand dunes (red). Areas in green correspond to the Andean piedmont ecoregion and in blue to alluvial plains. Map from Comerma & Luque (1971).

Potential top down – bottom up interactions involving benthic algae, grazers, nutrient limitation, and habitat structural complexity, complicate the study of spatio-temporal dynamics of this very important benthic resource. This work is fundamental for answering questions involving those interactions mentioned above. In the Cinaruco, these questions have already started to be experimentally tested (Winemiller et al. 2006, Winemiller et al. *unpubl.*).

## The sandbanks of the Cinaruco near Laguna Larga

The Cinaruco, at my study site shows high heterogeneity due to the presence of a number of different geomorphological units such as sandbanks, oxbow lakes, connected lakes, depressions, back swamps, and creeks, etc. This array of diverse habitat elements and the seasonal changes on hydrological connectivity confers to this area a high potential for lateral exchange of organisms. The occurrence of sandbanks is notable and ubiquitous in the inside of every meander in the river stretch that was studied (FIG. 4). According to the classification of Kellerhals and Church (1989), Cinaruco sandbanks can be classified as point bars in a meandering river. An evident and repetitive profile of runnels and ridges is also present along the shoreline of the point sandbanks. Preliminary observations of sand characteristics of these sand point bars indicated the prevalence of medium size sand (0.5 – 0.25 mm) with moderate uniformity (moderately sorted sediments, i.e., with moderate variation around the median). Due to the presence of wind-blown sand deposits along the Cinaruco River, some sandbanks can show higher uniformity in the distribution of grain size, i.e., poorly to very poorly sorted sediments

(Nordin and Pérez-Hernández 1989). On the other hand, lagoon sediments showed a more variable range in median grain size (towards finer fractions) than sediments from the river shores (Personal Obs.).

FIG. 4. Aerial view of Cinaruco River at its lower reaches during the dry season of 1998. Photographed area shows high habitat heterogeneity. Point sandbars as well as connected floodplain lakes, and savanna – riparian forest borders are readily distinguishable. Orinoco River is shown in the upper part of the picture. Photo taken by María M. Castillo (Universidad Simón Bolívar, Caracas).

One important characteristic of sandbanks in the Cinaruco is the presence of a pattern of ridges and troughs that run diagonal to the flow of the current. This feature is almost ubiquitous in the sandbanks. This type of topography of the sandbanks allows for a differential spatial distribution of resources and microhabitats. Topographic variation also confers this habitat with more heterogeneity for some organisms, and provides refuge for prey (or ambush places for predators), and physical disturbance (Palmer et al. 1995, Rempel et al. 1999, Robinson et al. 2002, Denno et al. 2005).

In the third chapter, I studied shrimp assemblages in the sandbanks of the Cinaruco during a year. In this part of the dissertation, I show that environmental variables that describe sandbanks are important for the abundance of shrimp taxa. Also, I considered the variability in habitat use at different temporal scales, from diel changes in abundance to seasonal patterns. Due to the high mobility of the ecotone between land and water in main channel sandbanks, the unconsolidated nature of the substrate, and variation in the topography of sandbanks, this kind of habitat can be considered as one of the most dynamic on the floodplain of the Cinaruco. Implications for conservation are also discussed regarding sampling strategies for biodiversity surveys and habitat assessment in sandbanks of large floodplain rivers.

# CHAPTER II

# HYDROLOGICAL SEASONALITY AND BENTHIC ALGAL BIOMASS IN A NEOTROPICAL FLOODPLAIN RIVER*

The study of aquatic–terrestrial transition zones in floodplain systems has received greater attention in recent years than in the past, especially given the role of these areas in maintaining biodiversity and mediating interchanges of materials and energy between aquatic and terrestrial habitats (Ward and Standford 1995, McClain and Elsenbeer 2001). The pervasive influence of periodic flood pulses on ecosystem processes within tropical floodplain rivers has been widely recognized (Junk et al. 1989, Lewis et al. 2000). Water-column processes have been examined in several Neotropical rivers, including the Amazon and Orinoco (Lewis et al. 1995). However, ecological dynamics of benthic components in response to seasonal flood pulses remain poorly documented (Lewis et al. 1995). The ecology of the zoobenthos has been studied in several large Neotropical floodplain rivers (e.g., Walker et al. 1991, Junk and Robertson 1997, Ezcurra de Drago et al. 2004), but very little research has examined benthic algae in these systems.

As far as I know, no works have been published on epipelic algae (those living in and on sediments) of large lowland rivers in the Neotropics. Given the much larger surface area of sediments compared to woody debris or other substrates and the

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potential contribution of algal biomass to food webs in river–floodplain ecosystems (Lewis et al. 2001, Thorp and Delong 2002), studies that focus on epipelic algal dynamics are needed to understand better the role of autochthonous C inputs to these systems. Most research thus far has focused on algae that colonize artificial substrates or attach to leaves and roots of submerged or floating vegetation (Engle and Melack 1993, Putz and Junk 1997).

Spatial heterogeneity in natural systems plays a critical role in the maintenance of species diversity and ecosystem processes (Pringle et al. 1988, Levin 1992, Cardinale et al. 2002). Organisms can influence spatial variation in ecosystems via physical disturbance or consumption. For example, spatial heterogeneity of benthic habitats in tropical streams is strongly influenced by grazing fishes that function as ecosystem engineers, and heterogeneity of periphyton communities (over scales of cm–m) is maximized at intermediate grazer densities (Flecker and Taylor 2004). Such findings have broad implications for how we interpret data collected over variable spatial scales. For example, is heterogeneity of benthic algae influenced by changes in the physical environment or activities of grazing fish? How might spatial heterogeneity affect the functioning of benthic algae as an autochthonous C source supporting the food web? These questions are especially pertinent in lowland rivers with extensive floodplains that support large populations of migratory grazing fishes (Winemiller and Jepsen 1998, Winemiller et al. 2006).

Here, I describe the temporal variations of physicochemical parameters and algal biomass of littoral areas of floodplain lakes and the main channel of the Cinaruco River.

I also examined the spatial variability of benthic algal biomass using a nested sampling design that incorporated multiple spatial scales. Seasonal and spatial patterns in physicochemical variables and algal biomass were expected to occur as a result of the annual flood pulse of the Cinaruco, which modulates water retention times and the interchange of materials between terrestrial and aquatic habitats. I expected greater spatial heterogeneity in substrates and benthic algal biomass during high-water periods, when there was increased mobility of the aquatic–terrestrial transition zone, than during low-water periods. My study contributes to our understanding of the ecology of highly dynamic and poorly known aquatic–terrestrial transition zones of tropical floodplain rivers.

## Methods

### Study site

My study area was located in a ~12-km stretch of the lower course of the Cinaruco River with high geomorphological heterogeneity (FIG. 4 & 5). A description of the Cinaruco River is presented in Chapter I. This area is 40 km from the confluence of the Cinaruco with the Orinoco and shows a high degree of meandering. The width of the gallery-forest belt ranges from a few meters to >2 km, with the widest forests located in areas containing many floodplain lakes. A variety of floodplain lakes of diverse origin (oxbows, permanently connected lakes, abandoned channels, and natural depressions) are found in the area.

### Site selection and sampling strategy

The study sites in the channel (R1–R5) were located on exposed point sandbars (FIG. 5). The lagoon sites were located in 4 floodplain lakes that were continuously connected with the main channel. Two sites were located in Laguna Larga (LL1 and LL2), and one each in lagunas Espiñero (EP), Esse (ES), and Ojero (OJ) (FIG. 5). Sites were chosen along sandy shores with a smooth slope and lacking submerged large woody debris or rocks.

Logistical restrictions associated with seasonal variation in water level constrained the placement of sampling sites within the littoral zone of the main channel and floodplain lakes. The land–water margin moved several kilometers along the riparian elevational gradient during the wet season. Monthly sampling occurred from January to May 2002 and from December 2002 to July 2003 (12 sampling dates) for physicochemical variables and sestonic chlorophyll-*a* (S-CHLA) and phaeophytin-*a* (S-PHAE). Seven of my sampling dates corresponded to the low-water period (Jan–Apr 2002, Feb–Apr 2003), and 5 sampling dates corresponded to the high-water period (May and Dec 2002, May–Jul 2003). Benthic samples for chlorophyll-*a* (B-CHLA) and phaeophytin-*a* (B-PHAE) determinations were taken on every sampling date except for July 2003, when the shoreline at many sampling sites had moved a considerable distance landwards and benthic sampling was not possible in riparian forests.

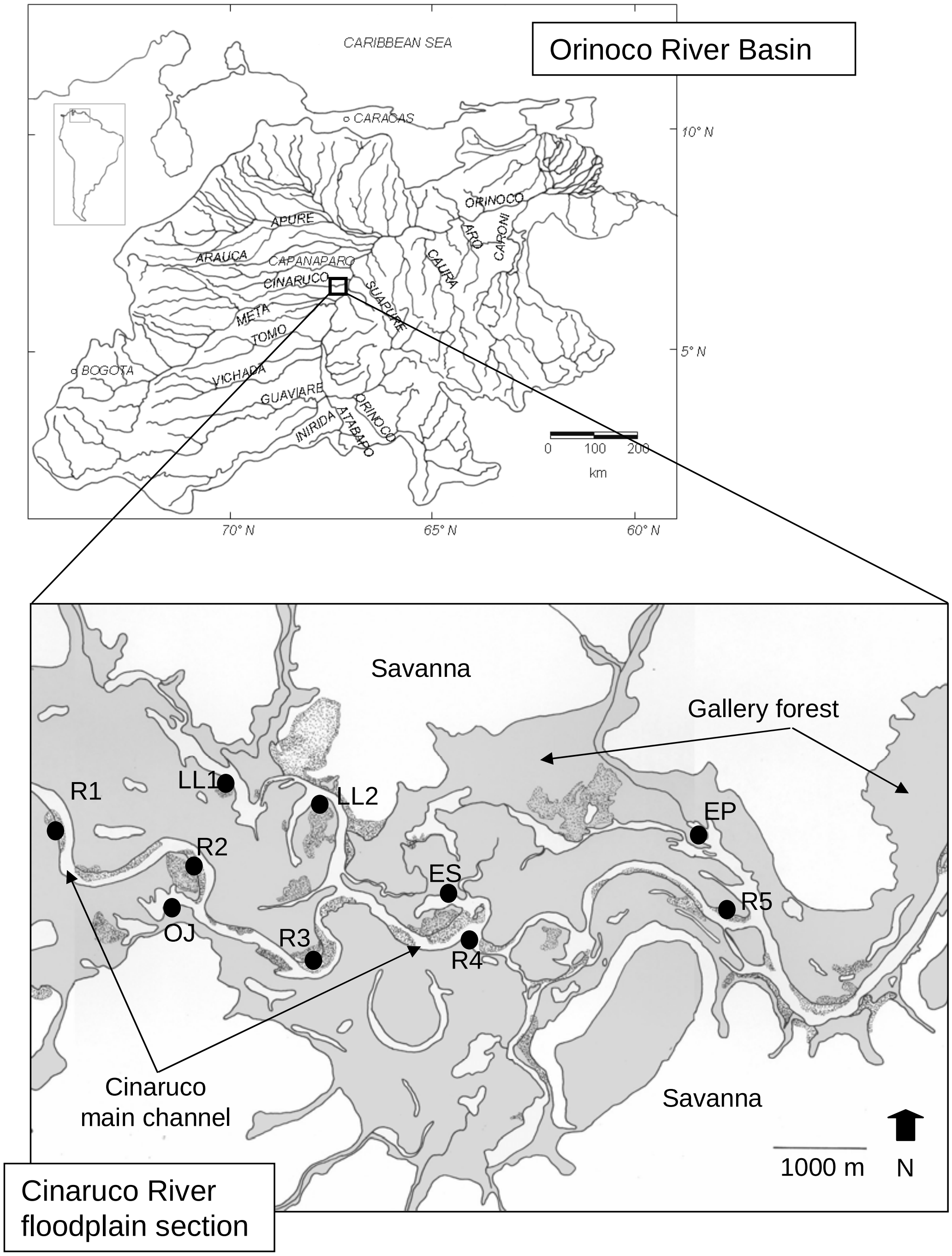

FIG. 5. Study area showing the location of Cinaruco River in the Orinoco River basin and the location of sites for the monthly sampling design. Savanna and the gallery forest are also shown.

Hydrological assessment

A hydrograph of the Cinaruco River was constructed from daily stage-height readings at Laguna Larga (FIG. 6) and 2 natural periods were identified. The low-water period was characterized by low water levels, exposure of point sandbars, and almost no water flow in floodplain lakes, whereas the high-water period was defined by water flow in the floodplain lakes and submergence of point sandbars in the main channel. During the peak of the high-water period (late July), the connection of the river with its floodplain attained its maximum, with extensive areas of savanna inundated. The water-level threshold that discriminated the 2 hydrological periods was 290 to 320 cm (FIG. 6).

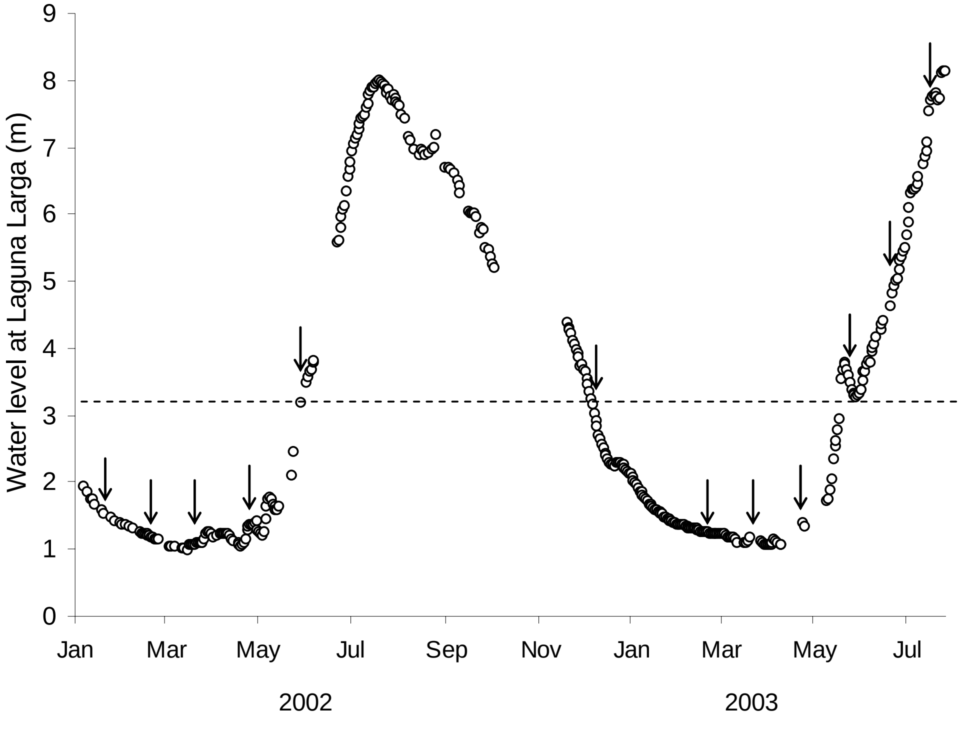

FIG. 6. Hydrograph of Cinaruco River at Laguna Larga during 2002 and 2003. The dashed line shows the approximate depth used to discriminate between the periods of low- and high-water in the floodplain. Arrows mark sampling dates.

Analytical methods

Water samples and in situ water-column measurements were taken at a depth of 30 cm below the water surface in the littoral zone (1-m depth). For every site and sampling date, in situ measurements were made of flow (mechanical flow meter), temperature and dissolved $O_2$ (YSI 95 $O_2$ meter), transparency (Secchi disk), conductivity, and pH (Hydrolab MiniSonde). Water samples were filtered through GF/F Whatman glass fiber filters and $NH_4$, $NO_3$, $NO_2$, urea, soluble reactive P (SRP), and $SiO_3$ concentrations were measured using autoanalyzer technology (Grasshoff et al. 1983). Detection limits achieved with a Technicon II Autoanalyzer were 0.089 µM $NO_3$, 0.009 µM $NO_2$, 0.035 µM $NH_4$, 0.161 µM urea, 0.024 µM $PO_4$, and 0.071 µM $SiO_3$. Triplicate water samples for determinations of S-CHLA and S-PHAE were filtered in situ through Whatman GF/F glass fibers. Triplicate sediment core samples to examine B-CHLA and B-PHAE were taken using a small plastic Petri dish (5-cm diameter and 1.3-cm height) at a depth between 0.7 and 1 m. A Petri dish was pushed into the substrate, and a spatula was placed under the Petri dish to trap the contents during retrieval. The filters and Petri dishes were kept frozen and stored in the dark until analyses were performed. S-CHLA, S-PHAE, B-CHLA, and B-PHAE were determined using the overnight 90% acetone extraction protocol using spectrofluorometric and spectrophotometric methods (APHA 1998). All chlorophyll-*a* values were corrected for phaeophytin-*a*.

I used a hierarchical sampling design to analyze the spatial variation of B-CHLA at different scales within a section of the floodplain of the lower Cinaruco River. My sampling scheme incorporated 4 spatial scales, ranging from the kilometer scale to the decimeter scale.

Selection of survey sites in floodplain habitats (km scale) was not random because of logistic constraints. Thus, macrohabitat was regarded as a fixed variable in the model, and subordinate random factors were nested within it. Subordinate factors included 3 shores within each habitat at the 100-m scale, four 2 × 2 m plots within each shore at the 1- to 10-m scale, and 3 samples (small Petri dishes) within each plot at the 0.1-m scale. This sampling design was carried out during periods of low water (March 2002) and high water (May 2002). A diagram showing graphically the nested design for the study of spatial variability of microphytobenthic biomass in a river stretch of the floodplain of the Cinaruco is presented (FIG. 7).

### Data analyses

Bivariate correlations were run between biotic variables (S-CHLA, S-PHAE, B-CHLA, and B-PHAE) and abiotic parameters for river and lagoon monthly survey data subsets. Pearson product–moment correlation analysis was done using SPSS (version 11.5, SPSS, Chicago, Illinois).

Sampling dates and sites were ordinated based on the measured environmental variables plus sestonic and benthic CHLA and PHAE using correspondence analysis (CA), an indirect gradient technique, in CANOCO (version 4.0; Microcomputer Power, Ithaca, New York). Multivariate normality assumptions were checked using SPSS v. 11.5.

A 3-factor nested analysis of variance (ANOVA) was used to analyze the spatial variation of B-CHLA at different scales. Data were transformed using the $(x + 1)^{0.5}$ transformation to satisfy normality and homocedasticity of variances assumptions. Variance components were calculated for all random factors as described in Underwood (1997). Nested mixed ANOVA was conducted following Sokal and Rohlf (1995), and normality plots were run using SPSS v. 11.5.

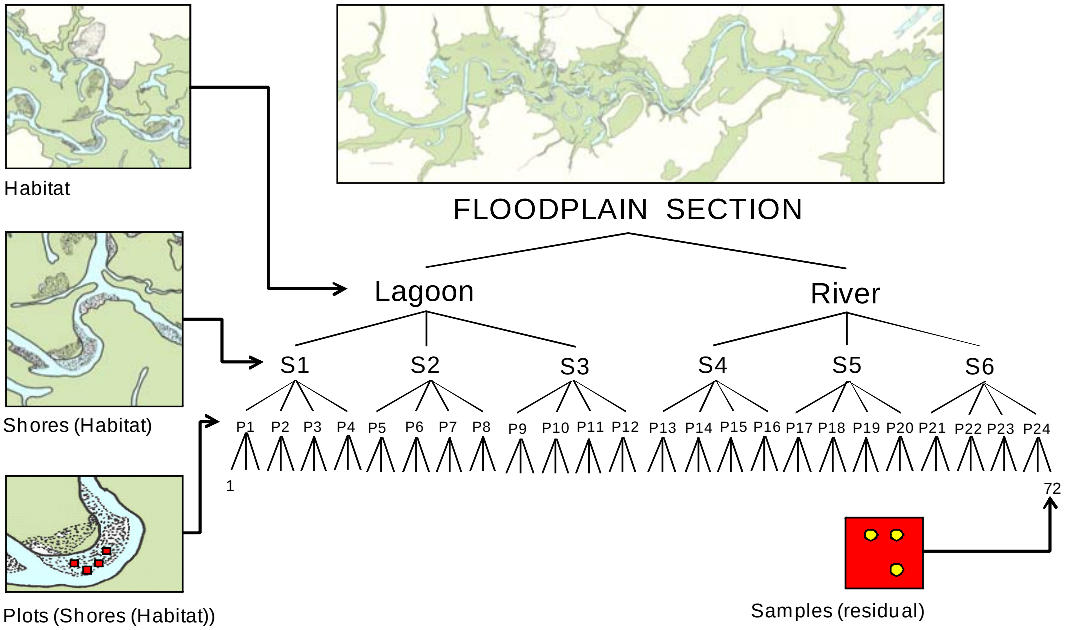

FIG. 7: Hierarchical nested design showing the four spatial scales sampled for the study of variability of microphytobenthic biomass in the floodplain of the Cinaruco.

## Results

### Hydrological and physicochemical variables

The hydrological regime of the Cinaruco showed a typical monomodal pattern exhibited by large rivers with a dry–wet climate (Fig. 6). The water level at Laguna

Larga had a 7-m difference between minimum and maximum depths recorded over the 2 years of sampling. During both years, minimum levels occurred during the first 2 weeks of March, and highest levels occurred during the last 2 weeks of July. From mid January to April of each year, the water level changed little, with values close to the minimum. During May, at the beginning of the rainy season in the area, the water level increased markedly (~2 m in 20–25 d). Striking fluctuations (negative or positive) of >0.3 m in <24 h occurred several times during this period. Water-flow patterns along the margins of the river and inside the lagoons changed as water level rose. Floodwater did not reach the upland savanna until June and remained there until late September. By late October to mid November, the waters had receded enough to expose the sandy beaches in the river's main channel. During this transitional period of descending waters, sudden changes in water level (like those observed during the rising-water phase) were also common. The rate of water-level change was lower for the descending limb of the hydrograph than for the rising limb.

Fluctuations in physicochemical variables in the littoral areas of floodplain lakes and river sites largely reflected the seasonal hydrological regime of the Cinaruco (Figs 8, 9). Water temperature varied inversely with water level, with highest temperatures (~33°C) during the late low-water season and minimum values (~27–28°C) during inundation (Fig. 8A). Temperature was generally lower at river sites than in lagoons. Dissolved $O_2$ ranged from 4.3 to 8.5 mg/L with the highest values during the low-water period and minimum concentrations during the high-water period (Fig. 8B). Water flow varied seasonally in both river channel and lagoon sites (Fig. 8C). Water flow in littoral channel sites averaged 27.3 ± 1.77 cm/s (mean ±1 SE) during low-water phases and 22.4 ± 3.63 cm/s during high-water. Highest values (>40 cm/s) were recorded at the beginning and at the end of the period of high-water (May and December 2002, respectively). A large reduction in flow at river sites was observed starting in June 2003 when flow averaged 6.2 cm/s and again in July 2003 when there was no flow. This reduction does not indicate that water flow stopped in the entire river, but only at the littoral survey sites. I did not detect flow in the lagoons on any of the low-water sampling dates. Throughout the low-water period, Secchi depth averaged between 0.8 to 1.1 m for lagoons, and between 1.1 and 1.4 m for river sites (Fig. 8D). Higher values usually were found during the high-water period. Conductivity and pH also changed with the water level (Fig. 8E, F). At the onset of the high-water period in May, both conductivity and pH declined sharply. Conductivity remained low during the remainder of the high-water season, whereas pH steadily increased after the first month of inundation. Conductivity values were remarkably low in both lagoon and river sites. Maximum values were never >9.4 and 5.2 μS/cm during low and high-water periods, respectively. Recorded pH in the river and lagoons ranged between 5 and 7.

Dissolved nutrients and $SiO_3$ showed large fluctuations, but patterns were not strongly seasonal (Fig. 9A–D). In general, nutrient concentrations in lagoons were similar to values recorded at river sites. Monthly average values for DIN and urea ranged from 0.1 to 0.6 μM (Fig. 9A, B). Particularly notable was the consistent low concentration of $NO_3$ at all sites (data not shown). February 2002 was the only period in which $NO_3$ values were above the detection limit (>0.089 μM). $NH_4$ usually accounted

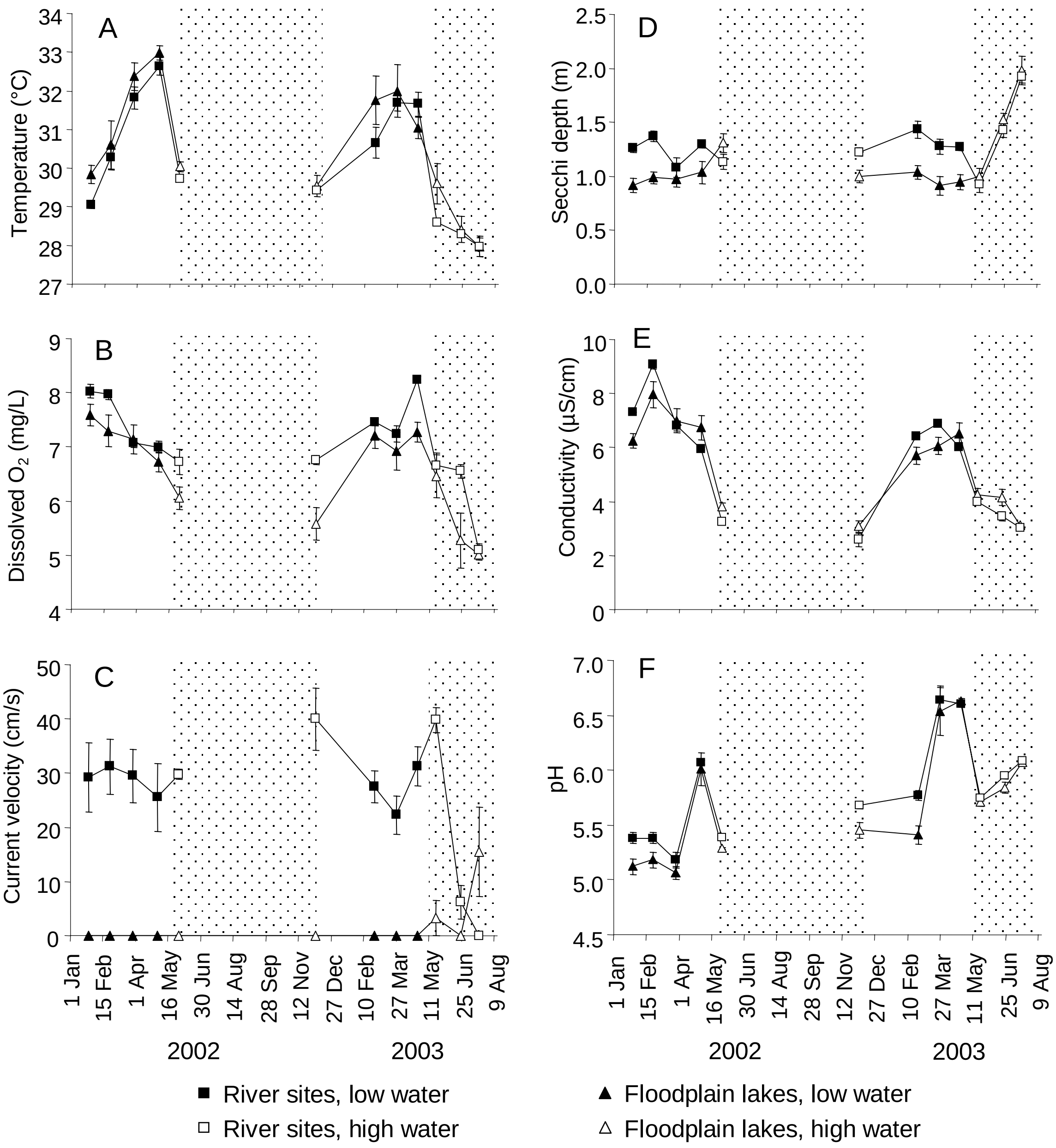

FIG.8. Mean (±1 SE) temperature (A), dissolved $O_2$ (B), water flow (C), Secchi depth (D), conductivity (E), and pH (F) calculated across 20 months for river sites ($n = 5$) and floodplain lakes ($n = 5$). Shaded areas indicate high-water periods.

for >50% of DIN. Around 30% of the measured values for $NH_4$ and urea fell below their detection limits (data not shown). An increase in DIN concentrations at the beginning of the flood period was observed during the 2nd year, but not during the 1st year. Another DIN peak was observed in February 2002 (middle of the dry season).

SRP concentrations were similar between river and lagoon sites as well as hydrological periods (Fig. 9C). Dissolved $SiO_3$ was more dynamic, with peaks during low-water periods, and very low concentrations during inundation periods (Fig. 9D).

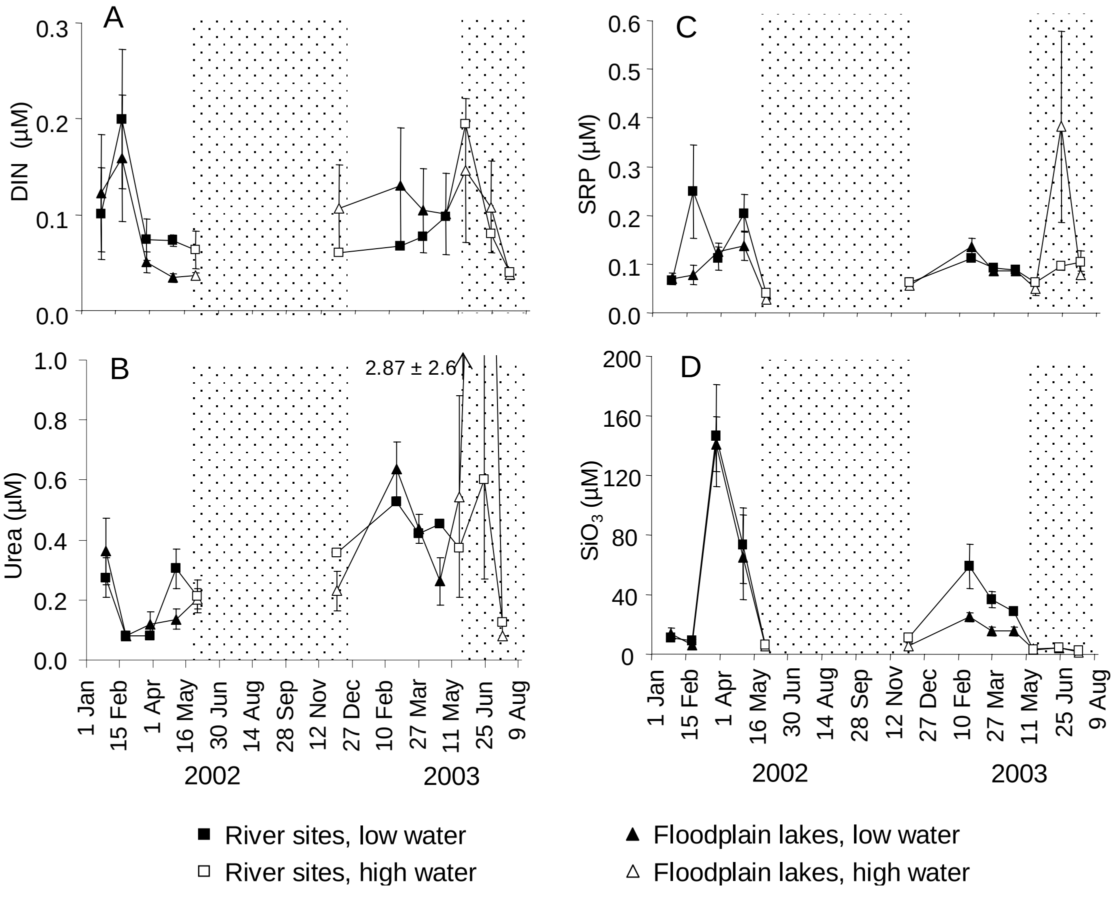

FIG. 9. Mean (±1 SE) dissolved inorganic N (DIN) (A), urea (B), soluble reactive P (SRP) (C), and dissolved $SiO_3$ calculated across 20 months for river sites ($n$ = 5) and floodplain lakes ($n$ = 5). Shaded areas as in FIG. 8.

The $SiO_3$ peak in both lagoon and river sites during late March 2002 coincided with the first local rainstorm. $SiO_3$ values increased by two orders of magnitude, from values as low as 3 µM in February 2002 (average values of 6.03 and 8.72 µM for lagoons and river, respectively) to concentrations >210 µM at one of the river sites (average values of 141.02 and 146.78 µM for lagoons and river, respectively). None of the recorded values for $SiO_3$ fell below the method detection limit, and only <5% of the values for $NO_2$ and $PO_4$ were below detection limits.

Sestonic and benthic CHLA and PHAE

S-CHLA and S-PHAE concentrations in lagoons were always higher than those in river sites (sometimes 3x differences; FIG. 10A, B), with the exception being the period of high-water when concentrations in the river and lagoons were similar. S-CHLA was inversely correlated with the water level in both river and lagoon sites ($\underline{r}_{river}= -0.781$, $\underline{r}_{lagoons}= -0.868$, $\underline{p} < 0.001$). S-CHLA was positively correlated with temperature, dissolved $O_2$, conductivity, and dissolved $SiO_3$ in river and lagoon sites (range of $\underline{r}$ values between 0.55 and 0.73 with all $p < 0.001$).

B-CHLA also was higher in lagoons than in river sites (Fig. 10C, D). Like S-CHLA, B-CHLA declined rapidly at the beginning of the high-water period. B-PHAE was always higher than B-CHLA. B-CHLA in river and lagoons showed the same significant relationships with abiotic variables observed for S-CHLA. However, B-CHLA was negatively correlated with flow in the river sites ($\underline{r} = -0.470$, $p < 0.001$), but not in lagoons. S-PHAE and B-PHAE correlations with abiotic variables were similar to those of S-CHLA and B-CHLA, respectively, except that relationships were weaker.

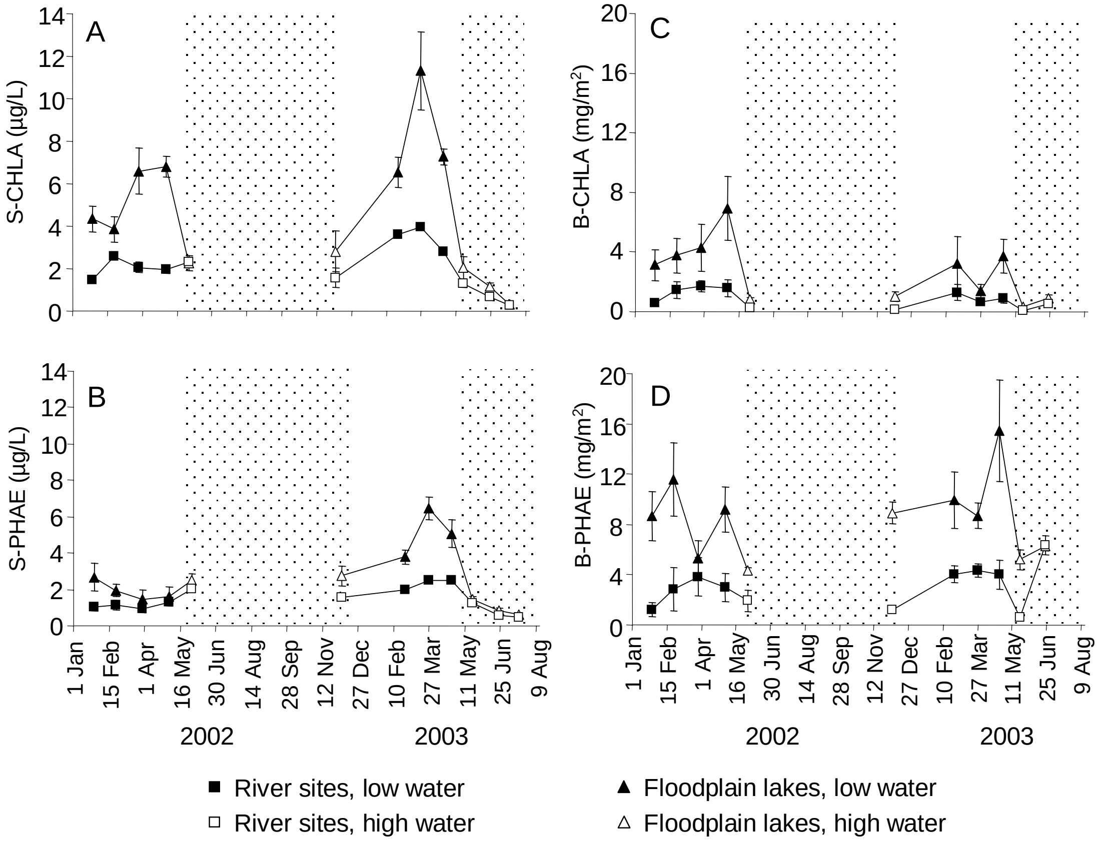

FIG. 10. Mean (±1 SE) of seston chlorophyll-*a* (S-CHLA) (A), seston phaeophytin-*a* (S-PHAE) (B), benthos chlorophyll-*a* (B-CHLA) (C), and benthos phaeophytin-*a* (B-PHAE) (D) calculated across 20 months for river sites ($n$ = 5) and floodplain lakes ($n$ = 5). Shaded areas as in FIG. 8.

## Ordination

CA based on physicochemical variables plus sestonic and benthic CHLA and PHAE revealed 2 strong environmental gradients (FIG. 11). Eigenvalues for the first 2 CA axes were 0.246 and 0.073 (total inertia = 0.402), indicating the 1st and 2nd axes of the CA accounted for 61.3% and 18.2% of total variation among sampling dates and sites, respectively. Axis 1 was positively correlated with concentrations of $SiO_3$ and B-CHLA and negatively correlated with water level. The 2nd axis was positively correlated with water flow, and negatively correlated with B-CHLA, B-PHAE, and S-CHLA.

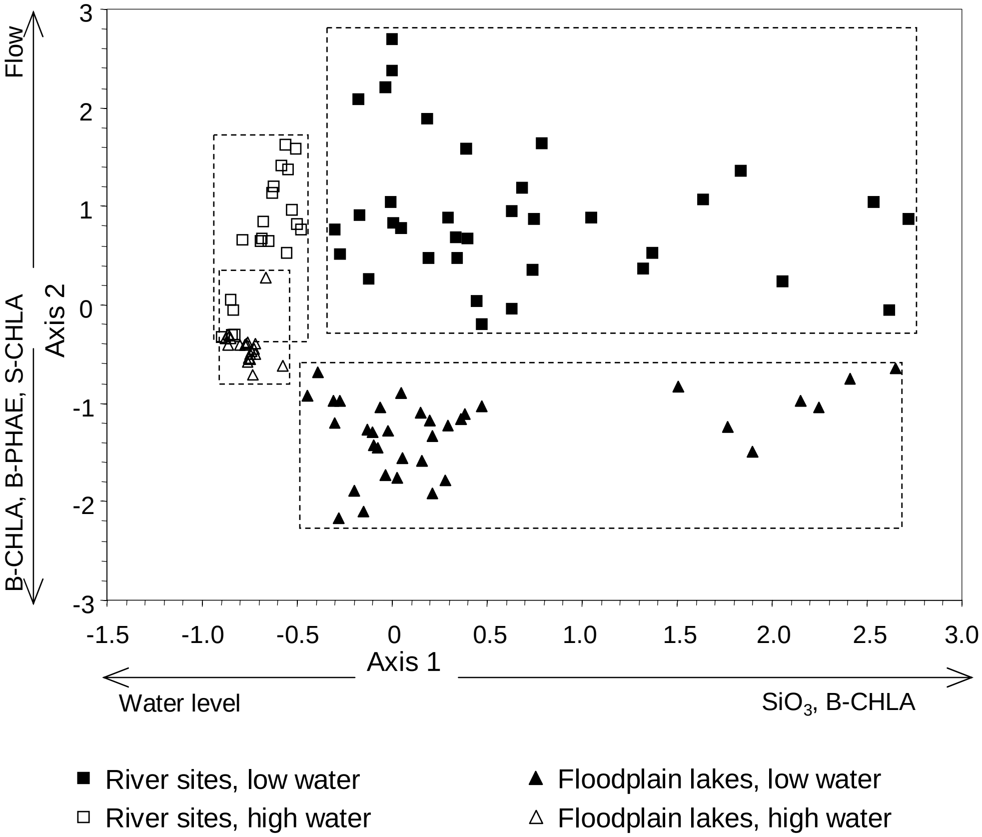

FIG. 11. Correspondence analysis ordination plot of the sampling sites and dates, based on physicochemical variables, seston chlorophyll-*a* (S-CHLA), seston phaeophytin-*a* (S-PHAE), benthos chlorophyll-*a* (B-CHLA), and benthos phaeophytin-*a* (B-PHAE). Subgroups based on habitat (floodplain lakes or river) and sampling periods (during low or high water) are enclosed with dashed lines. The first 2 axes explained 79.5% of the variation among sampling dates and sites. The most important variables contributing each axis appear next to the arrows.

Hydrological periods were well separated along the 1st axis, and habitats (lagoon vs river) were separated along the 2nd axis (FIG. 11). Thus, I was able to distinguish four groups based on attributes of physicochemistry and chlorophyll concentrations: lagoons at low water, lagoons at high water, river sites at low water, and river sites at high waters. Among chemical variables, dissolved $SiO_3$ was particularly important in separating sites into high-water and low-water groups along the 1st axis. Samples with the highest positive axis-1 scores corresponded to late March 2002 (following the first storm of the year). B-CHLA had a large influence on both multivariate gradients that separated sites and sampling dates according to hydrological seasons and habitats.

Spatial variability of B-CHLA

Significant variation in B-CHLA was found at the within-habitat, between-site level (shores) in hierarchical samples collected during both March and May 2002 ($p < 0.001$; Table 1, Fig. 12A). Within-habitat variation accounted for >95% of total variance. There was no significant effect of between-plot variation on B-CHLA during March. However, May samples revealed significant variation of B-CHLA between plots

TABLE 1. Summary of nested mixed analysis of variance for benthic chlorophyll a (B-CHLA). Data were transformed before analysis as $(x+1)^{0.5}$. *** = $p < 0.001$, % variance = variance components estimates.

| Source | df | MS | F | % variance |
|---|---|---|---|---|
| B-CHLA (March 2002) | | | | |
| Habitat | 1 | 20.59 | 10.57 | – |
| Shore (habitat) | 4 | 1.947 | 12.53*** | 95.5 |
| Plots (shore[habitat]) | 18 | 0.155 | 1.70 | 0.9 |
| Samples/residual | 48 | 0.091 | | 3.6 |
| B-CHLA (May 2002) | | | | |
| Habitat | 1 | 9.11 | 1.56 | – |
| Shore (habitat) | 4 | 5.853 | 27.49*** | 98.7 |
| Plots (shore[habitat]) | 18 | 0.213 | 4.89*** | 0.7 |
| Samples/residual | 48 | 0.043 | | 0.6 |

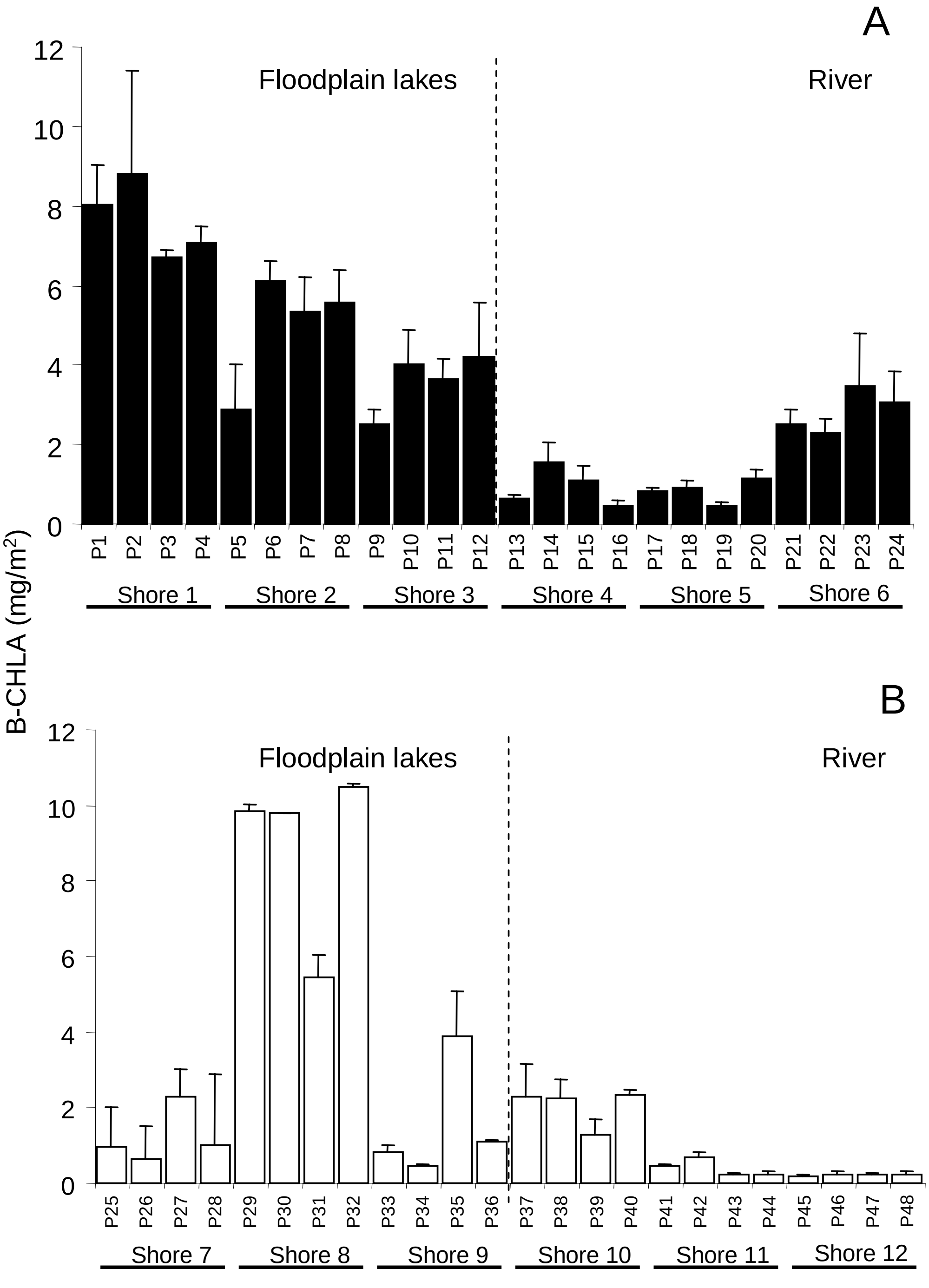

FIG. 12. Mean (±1 SE) benthic chlorophyll-*a* (B-CHLA) per plot (P1 to P48) in each shore (shore 1 to 12) during March (A) and May (B) 2002. There were 3 samples (Petri dishes) in each of 4 plots in each of 3 shores in each habitat of the floodplain section. Vertical dashed lines separate floodplain lake and river shores.

within habitats ($p < 0.001$; Table 1, Fig. 12B), although the proportion of total variance explained by between-plot variation was only 0.7%. The size of the residual variance was unexpectedly small for both months (3.6% and 0.6% for March and May, respectively), suggesting that patchiness at the smallest scale (Petri dishes) was negligible. March results imply that during the period of low-water, processes controlling the distribution of algal biomass on substrates were spatially uniform at intermediate and small scales (at plot and Petri dish level), but were not uniform across larger scales (among shores).

## Discussion

### Variability in physicochemical variables

Hydrologic seasonality was strongly associated with variation in all of the physicochemical variables I measured as well as with algal biomass in littoral zones of the main channel and floodplain lagoons of the Cinaruco River. Major limnological shifts associated with seasonal changes in water level have been documented for other floodplain systems in the Neotropics (e.g., Hamilton and Lewis 1987, Forsberg et al. 1988). In the Cinaruco, seasonal variability in physicochemical parameters was consistent with effects of dilution with increasing water level and concentration effects during water recession. Conductivity values in the Cinaruco were among the lowest values recorded for rivers draining large watersheds in the Neotropical region. Among the left-bank tributaries of the Orinoco, the Cinaruco has the lowest reported values for conductivity, alkalinity, turbidity, and concentration of total suspended solids (Depetris and Paolini 1991).

The Cinaruco showed conditions characteristic of an oligotrophic river, and the ecosystem probably is strongly N limited (Cotner et al. 2006, Roelke et al. 2006). Values for DIN and SRP fell within the lower ranges reported for clearwater and blackwater tributaries of the Amazon (Forsberg et al. 1988, Furch and Junk 1997) and Orinoco (Hamilton and Lewis 1990, Vegas-Villarubia and Herrera 1993). However, sestonic chlorophyll concentrations were high during the low-water period. I did not measure total N and P, and it is possible that nutrients associated with a dynamic labile pool of dissolved organic compounds or with the particulate fraction were important for growth of phytoplankton, a phenomenon that has been observed previously (Forsberg et al. 1988, Melack and Forsberg 2001).

I expected DIN and SRP to increase as water level rose, a response that would have reflected decomposition and release of organic matter in flooded areas. Instead, these nutrients peaked ~1 month after floodwaters had begun to enter riparian forests and savannas. Allochthonous input from the floodplain probably did increase during flooding, but I probably did not detect changes in dissolved nutrients in the water column, in part, because of a strong dilution effect and strong biological demands. Allochthonous inputs appeared to be of great importance for the variability of $SiO_3$ in my study. Sponges were very abundant on trees (personal observation), so biological demand for dissolved $SiO_3$ should have increased during the high-water period. In blackwater streams of the Amazon basin, Chauvel et al. (1996) found a strong biological control of $SiO_3$ in the system. $SiO_3$ dynamics in blackwaters seems to be controlled by biogenic processes (Konhauser et al. 1992, Chauvel et al. 1996).

Stormflow-type peaks in $SiO_3$ concentration were observed after the first rain storm in the vicinity of the study area. These peaks could have been the result of the transport of high quantities of $SiO_3$-rich ashes to the water via overland and subsurface flow (McClain and Elsenbeer 2001). Large areas of savanna burn annually during the low-water period, and large inputs of ashes can enrich the water with $SiO_3$. *Trachypogon* sp., the dominant grass species in Cinaruco savannas, has a high $SiO_3$ content (7–14%; Mata et al. 1985). Phytoliths are sometimes abundant in sediment samples from lagoons and main channel of Cinaruco (personal observation). A similar situation has been documented for streams draining grasslands and maize cultivars in tropical Africa, and for some of these streams, phytolithic grasses serve as one of the main transport paths of $SiO_3$ (Bootsma et al. 2003).

### Variability in biological variables

Concentrations of both B-CHLA and S-CHLA varied up to one order of magnitude on an annual basis. Phaeophytin-*a* concentrations were greater than chlorophyll-*a* in the sediments, but not in the water column. Accumulation of senescent benthic algae in the sediment as well as the potentially important deposition of senescent phytoplankton could explain why B-PHAE concentrations were high relative to B-CHLA. I was not able to enumerate benthic algal assemblages at a detailed taxonomic level, but preliminary examination of samples revealed a high proportion of small pennate diatoms and green algae. Microscopic examination of sandy sediments (grain size >63 μm) did not reveal filamentous algae (either Cyanobacteria or Chlorophyta).

This sediment fraction retained an unusually high number of large planktonic algal cells, such as *Micrasterias* spp. and *Staurastrum* sp.

Most limnological studies in Neotropical rivers have been conducted in the open-water areas within main channels and floodplain lakes. Interactions among terrestrial and aquatic systems should be greatly magnified at the littoral areas where ecotones between open water and the shore are formed (Ward et al. 1999). Studies on benthic algal biomass in temperate lakes have demonstrated small-scale patchiness (Downing and Rath 1988, Cyr 1998, Kahlert et al. 2002). My results showed the opposite pattern, with high uniformity at small scales (i.e., within and between plots at the decimeter and meter scale), and larger heterogeneity at large spatial scales. This high level of uniformity observed at smaller spatial scales was unexpected. Two potential factors could be responsible for spatial uniformity of B-CHLA within shores but not among shores. First, water flow and sediment dynamics at a given shore may generate homogeneity in substrate composition and other physical characteristics, which creates relatively large patches of resources required by the benthic algae. I found little evidence of small-scale patches on sandy substrates within the littoral zone of the Cinaruco during the low-water period. However, during the high-water period small-scale heterogeneity was greater than during the low-water period, probably because littoral areas had been inundated only for a short period. During May, scattered shaded areas were interspersed with open areas along the same shore, and littoral zone topography generally was not as uniform as it was during the low-water periods. In addition, higher benthic algal biomass turnover rates during May (Cotner et al. 2006) may have reflected the early succession stage of an algal assemblage dominated by species with higher growth rates and resilience. Autotrophic C inputs from highly productive benthic algal assemblages during early stages of succession would have the potential to affect the entire food web.

A second potential factor that could explain spatial heterogeneity at larger scales, but not at smaller scales, is grazing pressure by detritivorous fishes, especially by *Semaprochilodus kneri*. This species is the most abundant large grazer of organic sediments in the Cinaruco (Winemiller et al. 2006). Strong grazing pressure on benthic algae could override effects of basal resources, such as substrate composition, nutrients, or light, on benthic algal abundance and spatial distribution (Pringle 1996, Flecker and Taylor 2004). Flecker and Taylor (2004) found a parabolic, density-dependent relationship between substrate heterogeneity and a grazer fish in an Andean piedmont stream in Venezuela. According to this relationship, intermediate fish densities accounted for maximum substrate heterogeneity, whereas low and high densities were associated with lower heterogeneity in the distribution of organic matter and benthic algal biomass.

Field observations have shown that not all locations within my study region show the same grazing intensity by detritivorous fishes. In experiments with artificial substrates that were retrieved on a daily basis, I observed grazing activity after only 1 day at some sites, but little grazing activity after as many as 4 days at other locations (unpublished data). Moreover, relatively high within-treatment, between-location variation was observed in controlled field experiments designed to test fish effects on substrates (Winemiller et al. 2006). Thus, the abundance and feeding behavior of *S. kneri* and other grazing fishes may be influencing seasonal variation in the spatial distribution of benthic algal biomass at intermediate scales within shallow regions of this oligotrophic but species-rich ecosystem.

In conclusion, my study revealed how the spatial and temporal patterns of variation in limnological attributes and algal biomass in the Cinaruco River and its floodplain lagoons are associated with seasonal hydrology. My analysis of the spatial distribution of epipelic algal biomass suggests a potential interaction between bottom–up and top–down effects on this system, dynamics that have been demonstrated to be complex in other systems (Hillebrand 2002). Patterns revealed by my descriptive study stress the importance of scale for future research on heterogeneous aquatic ecosystems.

# CHAPTER III

# ABUNDANCE OF SHRIMP TAXA IN RELATION TO ENVIRONMENTAL VARIATION OF SANDBANK HABITATS IN A LARGE FLOODPLAIN RIVER

Freshwater shrimp are important components, in terms of numbers and biomass, of the stream fauna in large floodplain rivers (Odinetz-Collard 1987, Nessimian et al. 1998, Dudgeon 1999, Richardson and Cook 2006, Collins et al. 2007). Shrimp play an important role in foodwebs where they are present (Covich et al. 1999, Dudgeon 1999, Collins et al. 2007) and are also pivotal at maintaining heterogeneity in resources distribution and biomass in tropical streams (Pringle 1996). Additionally, shrimp link food webs of different habitats due to their temporal migrations or passive transportation downstream (Moreira and Odinetz-Collard 1993, March et al. 1998, Montoya 2003).

In this chapter, I studied patterns of distribution and abundance of an assemblage of shrimp during a hydrological season in several sandbanks of the Cinaruco River, a large meandering floodplain river of the Orinoco River basin. Because of mobility of shrimp and their potential to freely move within the river, they serve as an ideal subject to evaluate if there is any habitat preference for sandbanks at spatial and temporal scales and if habitat preference (if any) is related to changing environmental factors of the sandbanks. Shrimp (like most floodplain organisms) possess behavioral traits and life histories that promote population persistence in rivers with seasonal patterns of inundation (Walker 1992, Odinetz-Collard and Magalhães 1994, Lytle and Poff 2004).

The study of species-habitat associations in benthic habitats of the main channel of large floodplain rivers have been limited mostly to littoral ecotonal areas due to logistical difficulties of sampling deeper areas of main channels (but see Dettmers et al. 2001, Marchese et al. 2002, Ezcurra de Drago et al. 2004, Strayer et al. 2006).

Large floodplain rivers are dynamic and ecologically complex. Large rivers typically are characterized by high biodiversity and productivity in a heterogeneous landscape mosaic. The high spatial heterogeneity of floodplains is easily evidenced by the presence of numerous distinctive habitats with varied degrees of connectivity among them (Junk et al. 1989, Winemiller 1996, Amoros and Bornette 2002). Hydrological connectivity, which is influenced by fluvial geomorphology and human activities, is of utmost importance for the maintenance of ecological integrity of floodplains (Ward and Stanford 1995, Pringle 2003). The relationship between high habitat heterogeneity and hydrological connectivity in floodplains governs the spatial and temporal dynamics of organisms, particulate organic matter, sediments, and nutrients (Power et al. 1995, Poff et al. 1997, Amoros and Bornette 2002, Charlton 2008). Hydrologic and hydraulic variability in large rivers helps to maintain a series of structural (habitat) elements in the floodplain landscape over time. Reconfiguration of habitat patches in active mosaics (*sensu* “shifting habitat mosaic” of Stanford et al. 2005) helps to maintain a great heterogeneity at the landscape level. This persistence of habitats over time is not static but very dynamic, in which the constant change of physical features of habitat patches (i.e., their location, shape, and size) is largely mediated by the interplay between hydraulics and hydrology.

One of the most prominent features of meandering floodplain rivers is the presence of sandbanks that are formed on channel bends (point) or on its sides (lateral). Sandbanks can be seen as a dynamic habitat and, although they can be considered homogeneous at large scales, sandbanks have characteristics at small scales that make them structured habitats for certain small fishes and invertebrates. Sandbanks are considered functional landscape patches because they act as natural bioreactors that transform different forms of nitrogen as water moves through the interstices (Fisher et al 2001). Apart from their role as biogeochemical patches, sandbanks are also patches from the point of view of community ecology. Contrary to what is usually assumed, open-sand substrates are not undisrupted, continuous large uniform spaces covering all the bottom of rivers and lakes. Especially in rivers, sedimentary environments reflect stream's hydrologic and hydraulics processes. Distinct sedimentary facies (patches) intersperse throughout river beds and shores in 3-dimensions. The unconsolidated nature and high mobility of sandbanks, combined with the constant formation of stream bedforms as ripples, dunes, and sand waves, increases the complexity of this habitat (Kellerhals and Church 1989, Howard 1992, Gordon et al. 2004, Strayer et al. 2006, Charlton 2008).

This study reveals how shrimp assemblages from seven contiguous sandbanks of a large river varied over spatial and temporal scales (seasonal and diel) in their abundance patterns and composition. Then, I investigated shrimp habitat use as mediated by seasonal hydrological changes in the main channel.

## Methods

### Study site

This study was performed in the Cinaruco River, a lowland clear-water tributary of the Orinoco, located in Apure State, southwestern Venezuela. A detailed description of the physical features of the Cinaruco River is presented in Chapter I. Samples were collected in a ~8 km river segment of the main channel of the Cinaruco River located approximately 55 km upstream of the confluence with the Orinoco. This segment of the Cinaruco has high geomorphologic heterogeneity, including a pronounced river sinuosity and the presence of ubiquitous sand point bars at each river turn. Sandbanks in the Cinaruco occur in a variety of shapes and sizes, and are continually changing. In the Cinaruco, point sandbars tend to be larger than lateral sandbars, and they usually hold important slack-water zones in the main channel of the river (personal observation). Heterogeneity in this area is also enhanced by the presence of a diverse array of water bodies, such as isolated and connected floodplain lagoons, isolated pools, creeks, backwaters, and side channels.

### Sampling

Shrimp assemblages on the sandbanks of the Cinaruco River were studied using a field collection made by D. A. Arrington in 1999. Also, a few samples collected by the author between 2002 and 2003 were used to complement the information on species assemblage composition. These samples were collected as part of a project in which fishes were the primary focus. Although all specimens were preserved from this collection effort, they were not a focus of the data analyses in Arrington (2002) and Arrington and Winemiller (2003).

Methods used to obtain samples were described by Arrington (2002) and Arrington and Winemiller (2003), however, I briefly describe how samples and accompanying environmental data were collected in the field. The sampling strategy consisted of paired diurnal and nocturnal samples that were collected on a monthly basis from February to June and from November to December of 1999. No samples were collected between July and October, because sandbanks were inundated. Samples were collected by seining on seven main-channel sandbars using a 6.4 m x 1.8 m seine (4 mm mesh). These seven sandbanks were located in a river segment centered at approximately 6°33' N and 67°24' W (FIG. 13).

FIG. 13. Location of sampling sites on Cinaruco River near Laguna Larga. Sampled sandbanks are shown with numbers from 1 to 7. Laguna Larga connects to the main channel near sandbank # 5. This NASA LandSat image was taken during the dry season of 2000.

At each sandbank, three contiguous, non-overlapping 10-m length hauls, taken parallel to the shore, were pooled together to make a sample. During each month, diurnal samples (between 09:00 and 16:00 h) were taken from seven sandbars over a 2-day period. Nocturnal sampling (between 21:30 and 02:00 h) was performed on a single night within 3 to 6 days of the corresponding diurnal sampling in the same area. No samples were taken at sandbar # 3 during November 1999.

Environmental variables, such as depth, current velocity (measured with a mechanical flowmeter), temperature, and dissolved oxygen (measured with a YSI 85 meter) were determined *in situ* at each sampling site and date. Percentage substrate coverage of leaf litter was estimated visually. Presence/absence of troughs, fine particulate organic matter (FPOM), and submerged vegetation were recorded qualitatively by assigning a value of zero for absence and a value of one or two for sparse/moderate or abundant presence, respectively, of those features in the sampled area.

Additionally, the fraction of the moon illuminated (at midnight) for each of the sampling dates was included as a variable to characterize the habitat for nocturnal samplings. The fraction of the moon that is illuminated at new moon is 0, at first and last quarter it is 0.5, and at full moon is 1.0. This variable was extracted for each sampling night from the Astronomical Applications Department of the U.S. Naval Observatory (USNO) website at http://aa.usno.navy.mil/data/docs/MoonFraction.php

Shrimp specimens were fixed in 10% formalin and later preserved in 70% ethanol. Based on obvious morphological differences, shrimp were separated and counted in the field as palaemonids or sergestids (*Acetes paraguayensis*). Samples from June, November and December of 1999 were deposited in the Texas Cooperative Wildlife Collection (TCWC) by D.A. Arrington. Those samples were retrieved from the collection in their entirety and studied. Samples from February to May 1999 were not found in the TCWC and their whereabouts are unknown. However, information from counts done in the field was used to establish patterns of abundance at a coarse taxonomic scale (i.e., palaemonids vs. *A. paraguayensis*) for the full dataset. It means that the records of abundance for *A. paraguayensis* are complete for the entire period of study. There were 118 missing palaemonid shrimp (3% of total shrimp sampled) from February to May 1999 that could not be identified and quantified at species level.

### Data analyses

Diel variation in abundance of shrimps was compared for palaemonids and *A. paraguayensis*. Wilcoxon signed-rank test was used to investigate for differences between diurnal and nocturnal abundances of palaemonids. A test was not needed for *A. paraguayensis* since that species was not collected at all during daylight surveys. Due to the reduced number of organisms collected during the day and to the highly contagious distribution of the diurnal set of samples, only nocturnal samples were further used in any statistical tests performed to investigate for patterns and relationships between habitat variables and shrimp abundances.

Spatio-temporal (seasonal) variation of shrimp assemblages (palaemonids and *A. paraguayensis*) in the Cinaruco River sandbanks (i.e. variability among sandbanks and among seasons) was assessed using a permutation-based non-parametric multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001, McCune and Grace 2002). PERMANOVA is a nonparametric method for multivariate analysis of variance which is especially applicable for ecological data sets where response variables (such as abundance or biomass of different species in an assemblage) are potentially not independent and not conforming to the assumption of multivariate normal distribution. To test for the multivariate hypothesis of differences among abundance of different species (variables) in samples from different groups or treatments, PERMANOVA calculates p-values using permutation procedures.

The effects of location (sandbank) and date (month) were tested with an experimental design based on an unreplicated two-factor crossed PERMANOVA where experimental units (sandbanks as subjects) are sampled repeatedly through time (months). Under this design (similar to a randomized complete block design), in which there is only one replicate in every treatment-block combination (any sandbank-month combination), there is no formal test for the interaction term (sandbank x month). In fact, this model assumes that there is no interaction between factors. However, there are several ways to investigate for the presence of factor interaction in this type of experimental design. One of these is graphical, using interaction plots (Quinn and Keough 2002). For each of the two response variables in the present design (*A. paraguayensis* and palaemonids), I graphically determined that there was no interaction (sandbank x month) using interaction plots (plots not shown). PERMANOVA was run using the software PC-Ord (version 5.10, MjM software, Gleneden Beach, Oregon) (McCune and Mefford 2006).

Ordination methods model a set of observations associated with multiple variables as a reduced space with few dimensions, while maintaining the distance relationships among the observations. Nonmetric Multi Dimensional Scaling (NMDS) is an ordination method that is based on preservation of the ordering relationships among the objects (Legendre and Legendre 1998, McCune and Grace 2002). In NMDS, a stress value is generated every time a new configuration is produced. That stress value indicates the goodness-of-fit between the original multivariate space and the new reduced space that is being generated. When searching for an optimal solution of reduced in dimensionality, the objects (and the distances among them) in the original *k*-dimension multivariate space are reconfigurated by an iterative procedure.

This procedure occurs in a step down fashion and serves to accommodate the original multivariate space into a reduced space ranging from 6 to 1 dimension or ordination axes. At each step, a stress value is obtained. By reducing dimensions, the objects go through a reconfiguration that imposes distributional limitations in the new space. As it can be expected, stress rises as dimensions (or axes) are removed from the solution. For example, an ordination solution of $k$-1 axes, or dimensions, will be better fitted than a solution of $k$-2 axes; and one of $k$-2 axes will be better fitted than one of $k$-3 and so on, being $k$ the dimension of the distance matrix from the original multivariate space. This is because the reconfigurations that are necessary to be completed to fit the objects every time the dimensional space gets reduced, involve progressive distortions thus producing a subsequent and monotonic lack of fit. The lower the stress value, the better the fit. So, it can be assumed that the best solution is the one with the least stress;

but that it is not necessarily the case, especially for practical reasons. Solutions with more than three dimensions are usually avoided since their interpretation can become very complex and difficult. The statistical part of choosing the “best” or most adequate number of dimensions is plotting stress values as a function of dimensionality of the solutions. As mentioned above, stress decreases as dimensionality increases and the “best” or most adequate solution is that where the change in stress shows the greatest decline in the graph (scree plot), i.e. the point of inflection (elbow) in the curve (Kruskal and Wish 1978, McCune and Grace 2002).

A NMDS based on Euclidean distances was conducted on the environmental data to characterize sandbars and sampling dates in a reduced spatio-temporal multivariate space. Eleven habitat variables were included: depth, current velocity, temperature, dissolved oxygen, leaf litter percentage cover, FPOM, troughs, submerged vegetation, and fraction of illuminated moon. Given the disparate nature of their measurement units, all variables were standardized according to their maximum values. Thus, each variable contributed equally to the calculated dissimilarity matrix.

The NMDS procedure was run using PC-Ord v. 5.10. A final solution was achieved based on the lowest stress obtained using a Monte-Carlo test based on 100 runs in a cascade procedure from six axes to one and using a stability criterion of 0.0001 (McCune and Grace 2002). Since NMDS dimensions provide insight regarding the environmental variables that make sandbanks distinct, the dimensions or axes were labeled according to the variables that correlated significantly with axes scores. Kendall ($\tau$) correlation coefficients between axes and environmental variables were calculated.

Bubble plots (where graphed points were weighted according to their relative importance of a chosen variable) were generated for the variables responsible for driving distributional patterns of points or objects in the reduced multidimensional space.

To identify the relationships between the two shrimp taxa (*A. paraguayensis* vs. palaemonids) and the ordination axes (revealing the habitat variables accounting for variation in shrimp abundance across space and time), I used a joint plot. In a joint plot, vectors representing the two shrimp taxa were assembled onto the NMDS ordination. They were drawn using the regression determination coefficients derived by regressing each of the ordination axes (scores) with each shrimp abundance vector as explained in McCune and Grace (2002).

## Results

### Shrimp species of the Cinaruco

A total of 3,730 shrimps from seven different species were collected. One sergestid and six palaemonid shrimp species were identified. The planktonic shrimp *Acetes paraguayensis* Hansen 1919 (Sergestidae) was only present in nocturnal samples. The six palaemonid species were present in both, day and night samples. The palaemonid species identified were: *Macrobrachium dierythrum* Pereira 1986, *Palaemonetes carteri* Gordon 1935, *Pseudopalaemon amazonensis* Ramos-Porto 1979, *Pseudopalaemon chryseus* Kensley & Walker 1982, *Pseudopalaemon gouldingi* Kensley & Walker 1982, and an undescribed species, *Pseudopalaemon* “sp1” (TABLE 2).

Species accumulation curves from June, November and December show asymptotes at 6 species for diurnal samples (13 samples) and 7 species for nocturnal samples (8 samples) (FIG. 14). Further sampling conducted by the author and collaborators on Cinaruco sandbars between 2002 and 2003 did not produce additional species.

Spatio-temporal variation of shrimp abundance in river sandbars

The sergestid *A. paraguayensis* occurred on the sandbanks exclusively at nights. Palaemonids were present in both diurnal and nocturnal samples, but were more abundant during the night. Results of a non-parametric Wilcoxon signed-rank test (*Z*= -3.51, n= 48, p< 0.001) indicated that there was a significant diel difference in palaemonid abundance, with greater numbers at night (FIG. 15).

TABLE 2. Checklist of freshwater shrimps (Crustacea, Decapoda)[1] found in Cinaruco River sandbanks.

Suborder **Dendrobranchiata**
  Family Sergestidae
    *Acetes paraguayensis* Hansen, 1919

Suborder **Pleocyemata**
  Infraorder **Caridea**
  Family Palaemonidae
    *Macrobrachium dierythrum* Pereira, 1986
    *Palaemonetes carteri* Gordon, 1935
    *Pseudopalaemon amazonensis* Ramos Porto, 1979
    *Ps. chryseus* Kensley & Walker, 1982
    *Ps. gouldingi* Kensley & Walker, 1982
    *Ps.* sp1.[2]

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[1] Classification based on Martin and Davis (2001).

[2] Undescribed species.

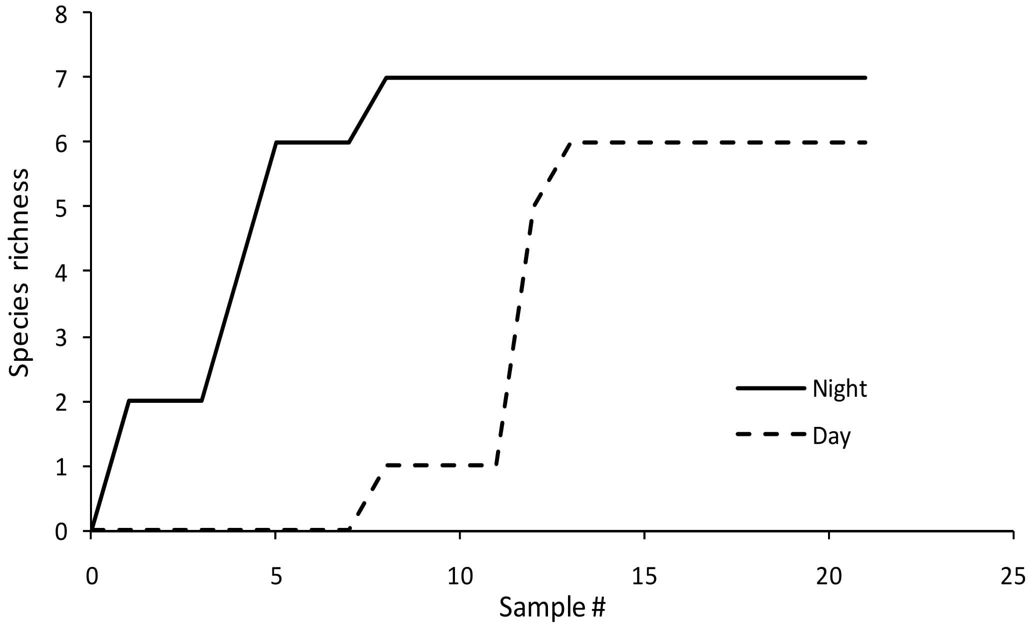

FIG. 14. Shrimp species cumulative curve for samples from June, November and December 1999. Diurnal samples retrieved the same number of species obtained during night, with the exception of the sergestid *Acetes paraguayensis*.

PERMANOVA showed that shrimp abundance on sandbanks was significantly associated with location (among sandbars) and season (among months) (TABLE 3). Shrimp abundance peaked in May-June for the sergestid *A. paraguayensis*. Palaemonid abundance peaked in November-December. During low-water months (from February to April), shrimp were less abundant (FIG. 15). In the Cinaruco, May and June are the months when the water level rises due to the annual flood pulse. During the rising-water period, littoral areas, such as main channel sandbanks, are rapidly inundated. During November and December, when the water level is falling, the landscape changes more gradually than in May and June. During the falling-water period, sandbanks start to emerge after four months of submergence.

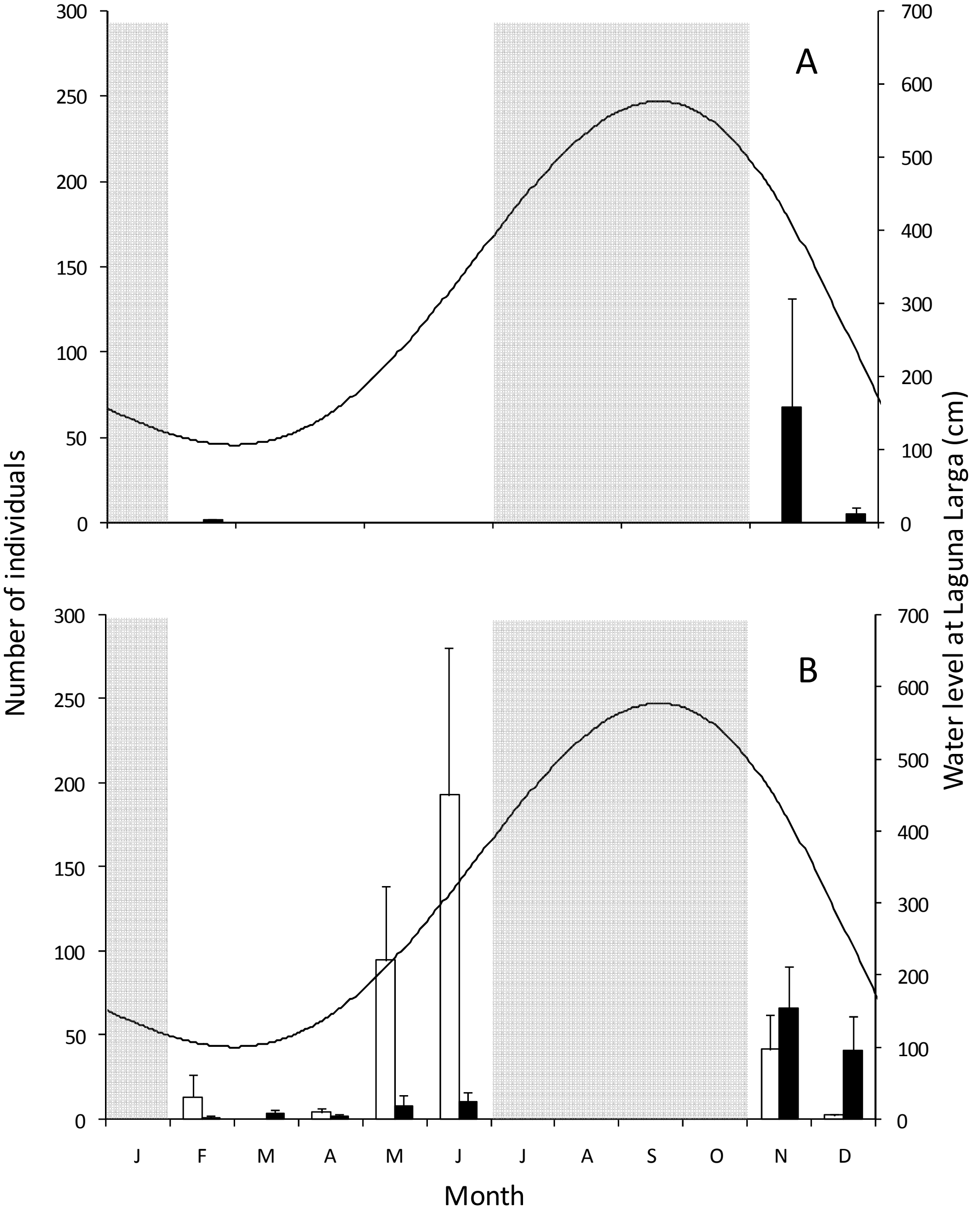

FIG. 15. Seasonal variation of mean number of sergestid (empty bars) and palaemonid (filled bars) shrimp per sandbank collected in diurnal (A) and nocturnal (B) samples in the Cinaruco River during 1999 (mean + SE). N=7, except in November when only 6 sandbars were sampled. No samples were taken on January and from July to October (shaded areas). A smoothed hydrograph of the Cinaruco River was superimposed on each bar plot to show water level variation during 1999.

TABLE 3. Two-factor crossed permutation-based nonparametric multivariate analysis of variance (PERMANOVA). Evaluation of differences in taxa (*Acetes paraguayensis* and palaemonids) abundances between groups (sandbanks and months). This design is similar to a randomized complete block configuration in which each combination of factors is unreplicated.

| Source | d.f. | SS | MS | F | p* |
|---|---|---|---|---|---|
| Sandbar | 6 | 158100 | 26349 | 3.04 | 0.0002 |
| Month | 6 | 237420 | 39570 | 4.56 | 0.0002 |
| Residual | 36 | 312230 | 8673.1 | | |
| Total | 48 | 707750 | | | |

* Randomization test of significance of pseudo F values based on 4999 randomizations

When all sampling dates were pooled together, shrimp abundance varied significantly among individual sandbanks (FIG. 16). *Acetes paraguayensis* was most abundant on sandbanks 2, 4, and 5, whereas palaemonids were more abundant on sandbanks 1 and 5. Sandbanks 3, 6, and 7 had low shrimp abundance.

Shrimp – habitat relationships

To characterize sandbanks and establish relationships between shrimp abundance with habitat features, an NMDS was run for the environmental multivariate space. The final NMDS solution contained three ordination axes that accounted for 87.9% of the variation in the original *k*-dimensional space. The proportion of the original variation represented by each of the dimensions ($r^2$) was (1) 0.11, (2) 0.26, and (3) 0.51. Orthogonality of axes ranged from 96.4 to 99.8%. The NMDS solution had a stress value of 0.13 and a final instability of 0.0001. Since dimensions 2 and 3 represented most of the variation, a bidimensional NMDS ordination plot was drawn based on those two axes (FIG. 17). Troughs and vegetation (plus FPOM and leaf litter to lesser extents) influenced most the configuration of sampling sites/dates in the bidimensional space.

High scores on dimension 2 were associated with the presence of troughs and the absence of vegetation and FPOM. High scores on dimension 3 were associated with presence of troughs and FPOM and absence of vegetation and lower percentages of leaf litter coverage (FIG. 17, TABLE 4). Although dimensions 2 and 3 both correlated significantly with vegetation and troughs, axis 2 had a stronger relationship with vegetation, and axis 3 had a stronger relationship with troughs (TABLE 4).

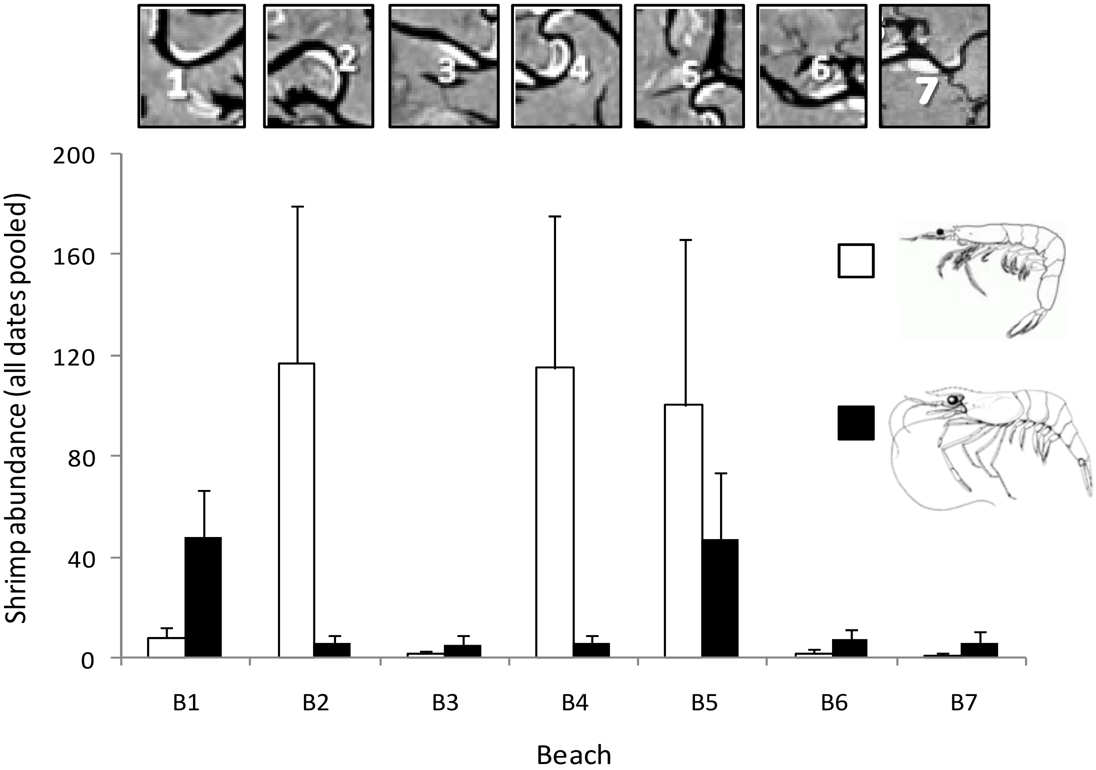

FIG. 16. Abundance (mean + SE) of *Acetes paraguayensis* (empty bars) and palaemonids (filled bars) per sandbank in 1999 (pooling all sampling dates together) n = 7, except B3 (sampled only 6 times). Satellite images of the seven sandbars are shown in the upper panel.

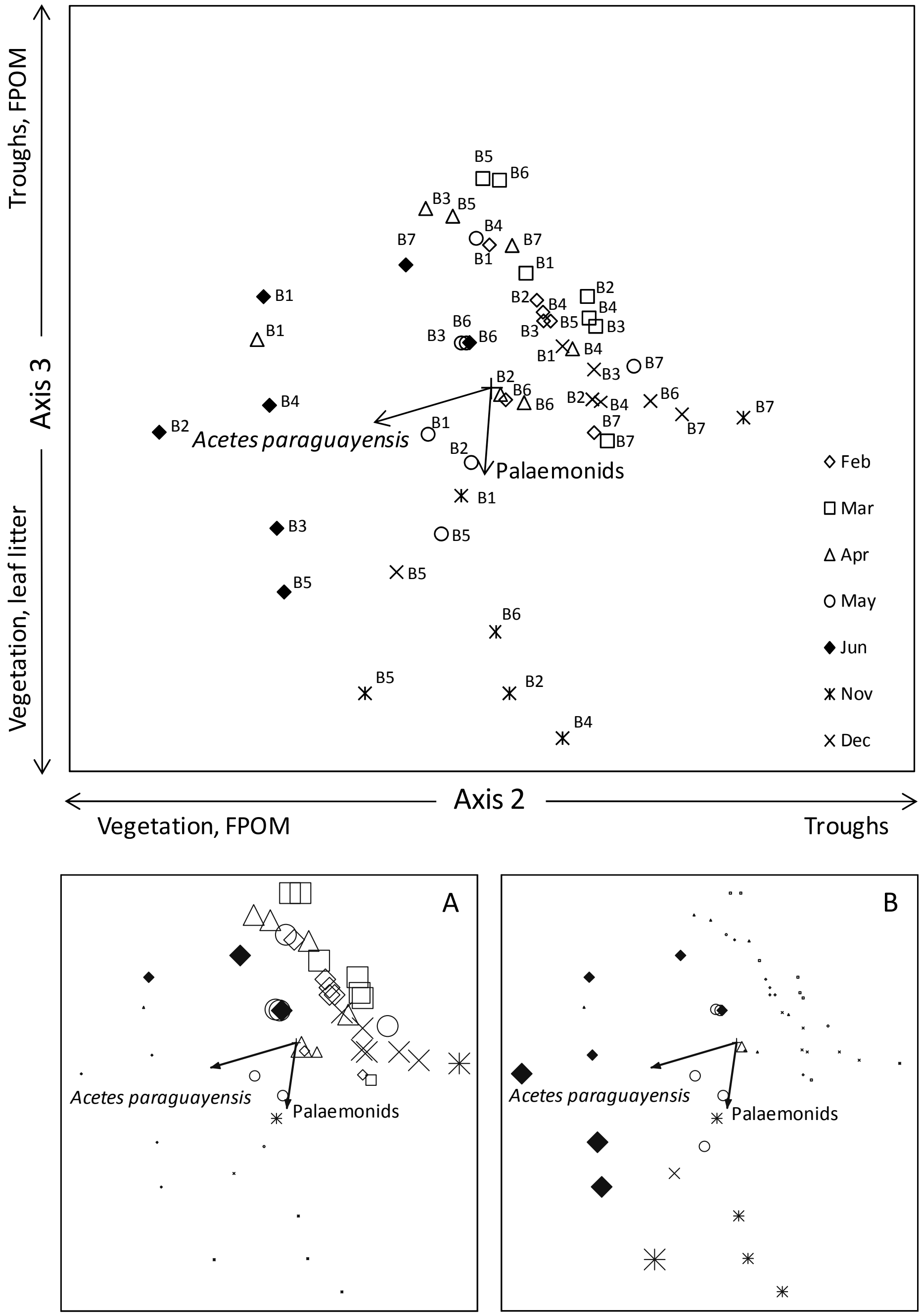

FIG. 17. Ordination plot based on nonmetric multidimensional scaling (NMDS) using Euclidean distances of environmental variables (upper large panel). Each point represents a site and sampling date. Sandbanks are labeled with the letter B and a number. Sampling dates are depicted as with different symbols. Plots in the lower panel show objects (sites and sampling dates) weighted by relative importance of troughs (subplot A), and vegetation (subplot B). Vectors radiate from the centroid of the ordination scores and show the relationship between shrimp taxa (*A. paraguayensis* vs. palaemonids) and ordination axes.

TABLE 4. Kendall's rank correlation coefficients (τ) of habitat variables with NMDS ordination axes, (N=48). Significant correlation coefficient values (p< 0.05 and p< 0.01), are shown as underlined and double underlined, respectively.

| Axis | 1 | 2 | 3 |
|---|---|---|---|
| Depth | -0.071 | -0.083 | -0.013 |
| Current velocity | 0.176 | 0.178 | -0.246 |
| Temperature | 0.010 | 0.195 | 0.077 |
| Dissolved oxygen | 0.184 | 0.090 | 0.353 |
| Leaf litter | -0.120 | -0.047 | -0.213 |
| Troughs | -0.230 | 0.411 | 0.618 |
| Illuminated moon | 0.281 | 0.159 | 0.057 |
| Vegetation | -0.035 | -0.570 | -0.461 |
| FPOM | 0.533 | -0.409 | 0.424 |

Samples were clearly separated in NMDS ordination space according to sites/dates, with samples having troughs and no vegetation, centered on the first Cartesian quadrant of the plot with high scores on dimensions 2 and 3, and those samples with vegetation but lacking troughs, centered on the third Cartesian quadrant with low scores on dimensions 2 and 3. This interaction between submerged vegetation and troughs is shown unambiguously in subplots A and B of FIG. 17.

Vectors show relationships between abundances of shrimp taxa (*A. paraguayensis* vs. palaemonids) and the two axes in a bidimensional representation of the habitat (FIG. 17). *Acetes paraguayensis* abundance vector was significantly correlated with axes 2 and 3 (TABLE 5, p<0.01 and p<0.05, respectively) meaning that abundance of this pelagic shrimp is related to the presence of vegetation and absence of troughs. Palaemonids, on the other hand, had a significant correlation only with axis 3 (TABLE 5, p<0.01), which was associated strongly with presence-absence of troughs.

TABLE 5. Kendall's rank correlation coefficients (τ) of shrimp taxa with NMDS ordination axes, (N=48). Significant correlation coefficient values underlined as in Table 4.

| Axis | 1 | 2 | 3 |
|---|---|---|---|
| *Acetes paraguayensis* | 0.005 | -0.317 | -0.232 |
| Palaemonids | -0.151 | -0.092 | -0.379 |

Pooling together shrimp abundance raw data and categorizing it onto the three levels of vegetation and troughs (absence, sparse, and abundant), FIG. 18 reveals the strong interaction between these two factors in shaping patterns of shrimp abundance on the sandbanks.

## Discussion

Shrimp assemblages of Cinaruco sandbanks showed temporal and spatial patterns of distribution and abundance. Diel variation in shrimp abundance showed that *A. paraguayensis* was present exclusively at nights, whereas palaemonids, although present occasionally at daytime, were clearly more abundant during nights. Seasonally, shrimpwere more abundant during rising-water and falling-water periods when environmental conditions of the sandbanks change rapidly. Shrimp occupation of certain sandbanks and not others was related to habitat characteristics that presumably promoted colonization/establishment and survival/persistence. Potentially favorable environmental features include the absence of troughs and presence of submerged vegetation.

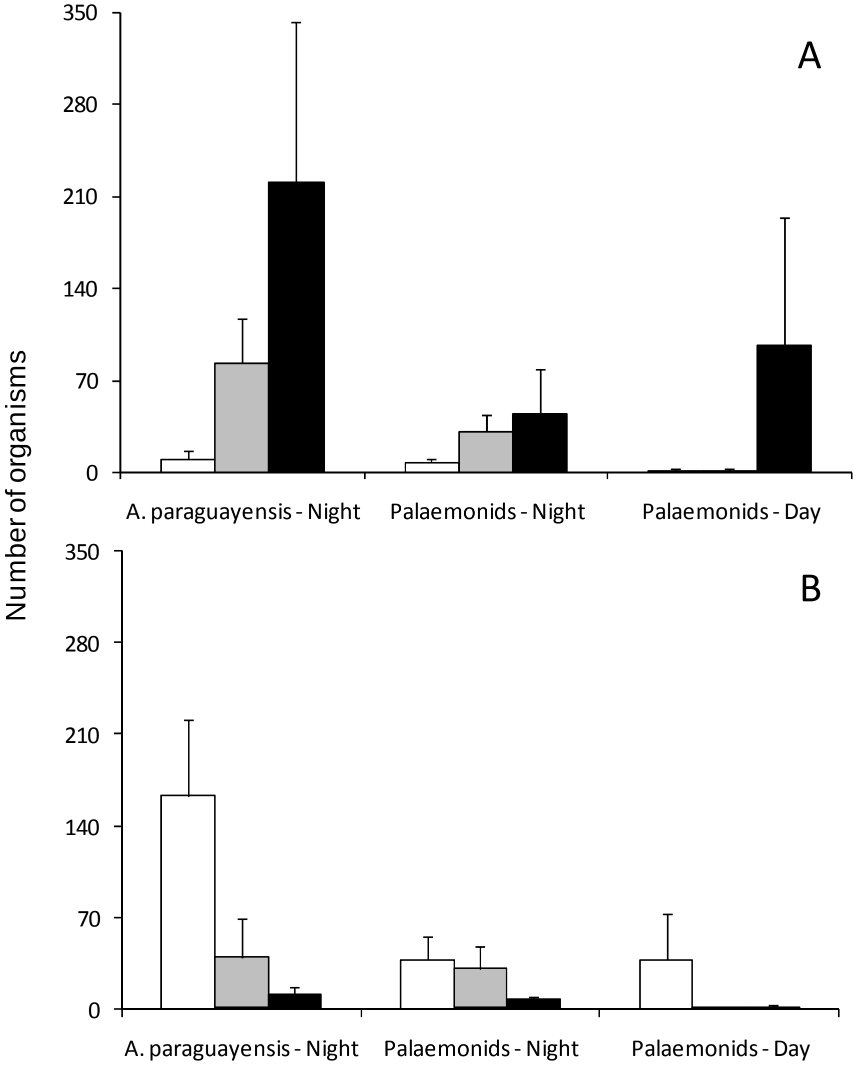

FIG. 18. Abundance (mean + SE) of *Acetes paraguayensis* and palaemonids during day and night for variable levels of troughs (A) and submerged vegetation (B) estimated in this study. Absence, sparce/moderate, and abundant presence of troughs and submerged vegetation in the sandbanks are represented by empty, grey and black bars, respectively. Plots were generated by pooling all sampling dates and sandbanks together.

The pattern of ridges and troughs observed in almost all sandbanks under low-water conditions is lost in some of them during rising and falling-waters. Sandbanks #3, #6, and #7 retained the ridge and trough topography, yet they did not develop vegetation during the rising and falling-water periods, and they never had high shrimp abundance.

These three sandbanks are lateral sand bars; whereas the other four are well-developed point sand bars (see FIG. 13). Therefore, shrimp abundance in sandbanks is likely to be associated with the fluvial morphology of the channel, specifically through sandbank topography and location (on bends or not).

It is well known that interplay between river hydrology and hydraulics is responsible for the creation and dynamics of habitat patches in riverine landscapes (Poff et al. 1997, Pitlick and Van Steeter 1998, Stanford et al. 2005). This "shifting habitat mosaic" (*sensu* Stanford et al. 2005) of a river is achieved by the interaction of hydrology and hydraulics through processes such as suspension and transport of sediments, debris and snags, scour-and-fill alluviation (erosion and deposition of sediments), channel avulsion, formation and maintenance of submerged sand dunes and waves (bottom topography), and removal/regeneration of aquatic vegetation and riparian forest. All of these processes are constrained by fluvial geomorphology which, in essence, delineates the basic habitat template of any river.

Organisms of fluvial ecosystems are adapted to exploit and survive in dynamic habitats, and the population persistence for some if not most of these organisms may even depend on recurrent disturbances (Humphries et al. 1999, Rempel et al. 1999, Robinson et al. 2002, Jenkins and Boulton 2003, Lytle and Poff 2004, Walks 2007). In a patch-dynamic view of communities (in this case seeing sandbanks as habitat patches distributed along a river), disturbance and patch colonization are the two main factors driving community structure in patches (Townsend 1989). According to the patch dynamics concept, spatio-temporal variation in habitat conditions drive assembly of communities under different models of community structure, from a niche model where there is a high spatial variation that allows different species to partition resources under constant conditions; to a model in which the temporal and spatial variability is high such that competition is of little importance (mobility control). The latter model seems to apply to shrimp assemblages of sandbanks in the Cinaruco River. Fish assemblages of these same sandbanks studied by Arrington (2002) disassembled and re-assembled in a deterministic manner, but were more influenced by unexplained factors (stochastic factors) when colonization rates were low, such as in newly created patches (recently flooded areas).

Due to rapid changes in water level during rising and falling- water periods, organisms are continuously forced to abandon patches and colonize others (community assembly dynamics under mobility control). But during the low-water period, changes in water level are less influential, and there is less structural complexity in sandbank habitats. Biotic interactions, such as competition and predation may become stronger during this period. Predation by fishes is expected to be more intense under low-water conditions on the sandbanks of the Cinaruco (Arrington 2002). Thus shrimp numbers are presumed to be reduced due to direct or indirect (perceived threat) effects of predation during low-water conditions. My subsequent surveys revealed that the density of palaemonid shrimps is high throughout the year in other habitats of the Cinaruco (leaf litter areas in lagoons). Therefore, the low numbers of shrimp on sandbanks during the four months of the dry season could be due to the high density of predatory fish on sandbanks, the limited availability of refugia, and the relatively constant environmental conditions.

Submerged vegetation on sandbanks probably functions as a refuge from predation for shrimp on the sandbanks. Several fish species on the Cinaruco sandbanks fed upon shrimp, some of them almost exclusively. However, shrimp species of Cinaruco sandbanks present a number of characteristics that may be of significant importance as defensive traits against fish predation. *Pseudopalaemon chryseus, Ps. amazonensis, Ps. gouldingi*, and *Palaemonetes carteri* are of small size, transparent and, although bottom dwellers, also can swim occasionally in open water (Kensley and Walker 1982, Carvalho et al. 2006). The other palaemonid species on the Cinaruco sandbanks, *Macrobrachium dierythrum*, is also small, transparent and bears red dots which may provide better camouflage against the orange sands of the Cinaruco. *Acetes paraguayensis* not only is transparent, but moves in swarms when performing lateral and vertical diurnal migrations. Being small, transparent, and moving in swarms are not only beneficial traits for shrimp on the sandbanks but also for some species of fishes. Small and transparent fishes, such as *Amazonsprattus scintilla* (Clupeiformes, Engraulidae), may reduce predation from fishes by aggregating among huge numbers of *A. paraguayensis* in open water areas along the banks of clear- and black-water rivers in Brazil (Carvalho et al. 2006).

The biology of *A. paraguayensis* is poorly documented; however, other species of the genus *Acetes* are known to form swarms of thousands of individuals that perform vertical and lateral migrations to avoid predators and to access resources on a diel basis.

Data from the Cinaruco River are consistent with a migration pattern in which individuals occupy littoral areas during night and migrate to open, deeper waters during the day. This species has not been sampled in any other habitat of the Cinaruco River other than sandbanks in the main channel. This migratory pattern implies that *A. paraguayensis* could provide an important trophic link between littoral and pelagic habitats (Collins and Williner 2003).

The swarming and the diel vertical migrations in *Acetes* have been well documented. Several species of *Acetes* occupy areas near or at the bottom during daylight and move up to surface waters at night (Xiao and Greenwood 1992, 1993). In neritic waters, diel vertical migration in pelagic shrimp, such as *Acetes*, is also believed to be synchronized with tidal currents to achieve landward transport (Omori 1974). The use of light and tidal currents as stimuli allows maintenance of local populations via migration involving both horizontal and vertical pathways (Xiao and Greenwood 1993). The habitat occupied by *A. paraguayensis* during the daylight time in the Cinaruco remains undocumented. The bottom of the main channel is assumed to have a strong flow velocity. However, as mentioned by Kellerhals and Church (1989), there are several bedforms that can provide refuge to organisms in that type of habitat. Additionally, bottom profiles of river channels at bends show a gradient in current velocity and the presence of eddies with counter flows and/or areas with reduced velocity (Lagasse et al. 2004, Charlton 2008). Some knifefishes (Gymnotiforms) are adapted to live in the bottom of large rivers, such as the Orinoco, and maintain populations over time without being swept downstream (Lundberg et al. 1987). Other vertebrates, such as turtles, crocodilians, and even freshwater dolphins, prefer areas close to sandbanks on river bends (point bars) instead of lateral bars (Smith 1993, Leatherwood et al. 2000). In the case of crocodilians, the presence of deep pools adjacent to point sandbars is a determinant for selecting nesting and feeding habitats (Thorbjarnarson and Hernández 1993, Muñoz and Thorbjarnarson 2000). In contrast to point sandbars, lateral bars usually are not adjacent to deep pools. Availability of potential refugia and connectedness to other patches is greater at point sandbanks than in lateral sandbanks.

This study shows preliminary evidence that *A. paraguayensis* prefers sandbars that are known to be adjacent to deep pools (point bars) instead of side or lateral bars. I presume that this specific geomorphological configuration of patches in the main channel of large rivers favors the migration of this sergestid shrimp between day and night habitats. According to Kirk Winemiller (pers. communication) the presence of large groups of piranhas in those deep pools could act as a filter for fishes that are known to prey on shrimp, facilitating therefore the presence of shrimp during day-time in this kind of habitat.

### Shrimp richness and assemblage composition

Seven species of shrimps would be considered a relatively high species richness for a habitat patch in a Neotropical river. Is this a reflection of an extraordinarily species-rich system, or is it a function of my extensive sampling effort throughout different hydrological periods? For comparison, the Caura River, an Orinoco tributary in the Guayana shield, which is four times larger than the Cinaruco, only has five shrimp species and has been subjected to more extensive surveys than the Cinaruco, including multiple river reaches and habitats (Magalhães and Pereira 2001). A recent AquaRap survey near the confluence of the Ventuari and Orinoco rivers produced ten species of freshwater shrimps, and the authors attributed this elevated richness to the confluence of three major biogeographical regions –the Orinoco Llanos, the Guayana shield, and Amazon (Pereira and García 2006).

Most of the shrimp species found on the sandbars of the Cinaruco River are not common. The Cinaruco is the second locality in the Orinoco basin for reported occurrences of *Pseudopalaemon chryseus* and *Ps. gouldingi*. An apparent undescribed *Pseudopalaemon* species was also collected in the Cinaruco River. All shrimp species of the Cinaruco sandbars are small and transparent or semi-transparent. *Macrobrachium dierythrum* is one of the smallest species in a genus with more than 200 species, and all *Pseudopalemon* species are small. Life history traits common to the palaemonids found in this study include low fecundity, small clutch size, large eggs, and reduced number of larval stages (1 to 3 larval stages compared to 8 to 11 in other palaemonids from more rich waters in the Orinoco basin). This kind of life history strategy probably is adaptive when resources availability is low in unproductive ecosystems (Walker 1992, Odinetz-Collard and Magalhaes 1994).

The only non-palaemonid shrimp in the Cinaruco, the sergestid *A. paraguayensis*, is a poorly-known, pelagic species. Field records of *A. paraguayensis* are sporadic, which has hindered systematic study (but see Collins and Williner 2003).

One or possibly two additional species of caridean shrimps are present in the Cinaruco River. A few samples taken from submerged wood in small creeks in Laguna Larga produced three juvenile specimens of *Euryrhynchus* spp. (Decapoda: Euryrhynchidae). This genus of small freshwater shrimps, common in blackwaters and clearwaters of the Amazon and Orinoco basins, is usually overlooked due to its tiny size and preference for cryptic habitats. With the additional one or two species of *Euryrhynchus*, the number of identified shrimp species for the Cinaruco increases to 8 or possibly even 9.

# CHAPTER IV

# SUMMARY

## The patch dynamics view of sandbanks along large rivers

Floodplains of large rivers are very diverse and exhibit complex spatial and temporal variability acting at different scales. In chapters II and III, I showed how benthic algal biomass and freshwater shrimp abundance varied spatially and temporally among sandbanks in the Cinaruco, and how the sandbanks can be seen as patches along a large river.

Patch-scale field experiments conducted by Arrington et al. (2005) showed that the relative importance of biotic interactions for community assembly of fish and macroinvertebrates in littoral habitats of the Cinaruco River are modulated by both, the physical characteristics of the habitat, and the location of those habitats on the landscape. Here, in this study, sandbanks could be seen as patches in a shifting mosaic (*sensu* Stanford et al. 2005) along the main channel of a large lowland river, the Cinaruco. During low-water periods, when environmental conditions are relatively constant on sandbanks, abundance of shrimp is likely to be kept low by a high fish predation pressure and limited availability of refugia. On the other hand, hydrologically-driven spatio-temporal variation of sandbanks physical characteristics showed the high dynamism of this riverine habitat of large rivers, especially during periods of rapid water level changes (i.e., rising and falling water periods). During those periods is when physical disturbances of sandbanks are more striking and sandbanks really differ from each other especially in habitat structure (presence/absence of vegetation and troughs). The presence of vegetation as potential refuge areas seems to be important for shrimp presence at seasonal scales; and the presence of adjacent deep pools to sandbanks is likely favoring the diel movements of swarming pelagic shrimps between patches.

These results basically support Arrington et al. (2005) findings on the factors that determine community assembly at patch scale in littoral areas of the Cinaruco. Further studies are required to elucidate the relative importance of habitat complexity, and the topology and functioning of the network of habitat patches along the main channel of large rivers (connectedness of habitat patch types, environmental filters, biotic filters, etc) in determining the presence and persistence of shrimp species among the sandbanks of the Cinaruco.

Physical descriptors of sandbanks, such as size (shrinking or expansion due to floods or water recession), location (laterally on the main channel or on the convex side of a bend), shape (i.e., edge/area ratio, radius of curvature), topography (i.e, elevational gradients, presence of troughs and ridges), sedimentary characteristics, presence or absence of buried organic material between consecutive deposited sand layers are just some of the most important variables that could help to identify discrete sediment facies as habitat patches in the benthic realm of large rivers at large scales. This large-scale descriptors approach seems to be appropriate to more effectively study relationships between distribution and abundance of invertebrates and environmental variables in large rivers (Bartsch et al. 1998, Thomson et al. 2001, Strayer et al. 2006).

## Studying main channel habitats in large rivers: Conservation implications

The importance of studying river main channels as a network of interconnected meso-habitats (or hydraulic units/facies) as well as considering the effects that adjacent-nearby habitats could have on patterns and processes in one determined site has been highlighted considerably during the last years (Palmer et al. 2000, Thomson et al. 2001, Amoros and Bornette 2002, Robinson et al. 2002, Montoya et al. 2006, Strayer et al.2006).

The dynamics of benthic algal biomass and shrimp abundance in the sandbanks of the Cinaruco showed that their seasonal patterns are intimately linked to the annual hydrological regime. Shrimp were scarce during low water periods, more abundant at nights, and relatively species-rich when considering overall sampling effort. With respect to algae, benthic algal biomass presented distinct spatial patterns of heterogeneity depending upon the season, and although algal biomass was higher at low-water periods, the absolute benthic algal biomass on the floodplain at inundation could be several times higher due to the increased availability of substrate. These results, although essentially descriptive, are of utmost importance for the understanding of the functioning of the Cinaruco River. They also make obvious the need for a comprehensive sampling design across different temporal and spatial scales when the objective is to describe how the system functions. For example, to generate a simple shrimp species list, there is imperative to consider their diel variation as well as seasonality of the system. This has been highlighted by several authors, especially recently and in relation with shrimp and fish assemblages (Johnson and Covich 2000, Arrington and Winemiller 2003).

Also, a lack of information on benthic processes in benthic systems of tropical rivers make imperative the need for more studies that consider dynamics of patterns and processes at different spatio-temporal scales. This knowledge would be of utmost importance for future plans of habitat management or restoration in tropical developing countries. Sandbanks are especially imperiled among riverine habitats when developing projects are conducted in large rivers. Habitat degradation and destruction is one of the main causes of biodiversity losses (Allan and Flecker 1993, Bayley 1995), but also of functionality and ecosystem services to the society (Covich et al. 2004). When a sandbank is obliterated by the construction of a dam, such as many sandbanks in the lower reaches of the Caroni River in Venezuela, there are several aspects to consider when there is a need to restore those ecosystems. Currently, there are plans to restore some sandbars in the lower Caroni River but the monitoring study only takes into account recreational use aspects for the success of that restoration plan.

The importance of sandbanks for instream processes, such as transport of carbon and nutrients, can be very important because sandbanks can provide adequate areas for accumulation of biomass that later are purged out downstream due to river spates (Walks 2007). Also, differential distribution of resources due to the presence of sandbanks creates heterogeneity that facilitates the interaction of a larger number of species.

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