EL RIO ORINOCO
como ecosistema

THE ORINOCO RIVER
as an ecosystem

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de contaminación, mientras que aguas abajo se observaron aumentos de la DQO y del contenido de coliformes en las proximidades de las ciudades importantes, al igual que un incremento en la concentración de algunos metales en los sedimentos del río en las inmediaciones de las ciudades y de las instalaciones de la industria siderúrgica. Con el conjunto de los resultados obtenidos en este estudio se ha conformado una base de datos que ha sido de utilidad en la industria petrolera para la planificación del uso del agua del río, y para la predicción de los impactos ambientales de los desarrollos petroleros futuros.

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SUSPENDED ORGANISMS AND BIOLOGICAL CARBON FLUX ALONG THE LOWER ORINOCO RIVER

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ABSTRACT

Bacteria, phytoplankton, and zooplankton were sampled between 1982 and 1985 in the main stem and lower tributaries of the Orinoco river, and measurements were made of the rates of photosynthesis and respiration. Organism abundances and metabolic rates are consistently lowest at the time of peak discharge and highest at the time of low discharge or during the early rising phase of the hydrograph. Bacterial abundances are low throughout the system ($<10^6$ cells/cc), and seasonal changes in the abundance of bacteria are less extreme than for other categories of suspended organisms. The abundances of phytoplankton are also low. A small number of species account for a very large proportion of phytoplankton biomass, but the dominant taxa differ significantly among the lower tributaries. The mean algal chlorophyll is below 0.5 ug/l chlorophyll a in the main stem and all three of the lower tributaries. Floodplain accounts for only 37% of the annual transport of suspended algae. Other sources, including stagnant areas within the river channel, account for the remaining 63%. Total annual transport of phytoplankton is 2.4×10^6 kg C/yr, which is less than 1% of the floodplain phytoplankton production. Among the zooplankton, rotifers are dominant numerically, but cladocerans and copepods make important biomass contributions. Dominant species are generally euplanktonic, indicating origin from stagnant pools rather than vegetation mats or substrates. Total annual transport of zooplankton by the river is 0.32×10^6 kg C/yr, which is a small proportion of the floodplain zooplankton productions.

Gross photosynthesis in the Orinoco river and lower tributaries is consistently below 50 mg C/m ^{2} /day. Because of poor light penetration and great water column depth, net photosynthesis by suspended algae is nil. Respiration in the main stem is 80 ug C/l/day, approximately 25% of

which can be accounted for by phytoplankton and the rest by bacteria. The respiration rates, like the photosynthesis rates, are lower for the shield rivers and higher for the Apure than for the main stem. Respiration rates are not high enough to account for significat changes in total organic carbon inventory during transport.

FLUJO DE ORGANISMOS SUSPENDIDOS Y CARBONO ORGANICO EN EL BAJO RIO ORINOCO

RESUMEN

Bacterias, fitoplancton y zooplancton fueron muestreados entre los años de 1982 y 1985 en el cauce principal y los tributarios inferiores del río Orinoco, y se hicieron mediciones de las tasas de fotosíntesis y de respiración. Abundancias de organismos y tasas metabólicas son consistentemente más bajas en la época de descarga máxima y más altas en la época de descargas bajas o durante la primera parte de la fase creciente del hidrograma. Abundancias de bacterias son bajas en todo el sistema ($<10^6$ cells/cc), y cambios estacionales de la abundancia de bacterias son menos extremos que las de otras categorías de organismos suspendidos. La abundancia de fitoplancton es también baja. Un número pequeño de especies representan una proporción muy alta de biomasa de fitoplancton, pero los taxa dominantes se diferencian significativamente de los de tributarios inferiores. El promedio de la clorofila de algas es menor de 0,5 ug/l de clorofila a en el cauce principal y los tres tributarios inferiores. Sólo el 37% del transporte anual de algas suspendidas procede de la llanura inundada. Otras fuentes, incluyendo áreas estancadas en el cauce del río, son responsables del restante 63%. El transporte total anual de fitoplancton es de $2,4 \times 10^6$ kg C/yr, lo cual es menos que el 1% de la producción de fitoplancton de las sabanas inundadas. Entre el zooplancton, los rotíferos son dominantes numéricamente, pero los cladóceros y copépodos aportan una importante biomasa. Las especies dominantes son generalmente euplanctónicas, indicando sus orígenes de charcos estancados en vez de acumulaciones o sustratos de vegetación. El transporte anual total de zooplancton en el río es de $0,32 \times 10^6$ kg C/yr, lo cual representa una proporción pequeña de la producción zooplanctónica de las llanuras inundadas.

La fotosíntesis bruta en el río Orinoco y sus tributarios inferiores es siempre por debajo de 50 mg C/m^2/día. Debido a la pobre penetración de luz y la gran profundidad de la columna de agua, la fotosítesis neta de algas suspendidas es nula. La respiración en el cauce principal es de 80 ug C/l/día, aproximadamente el 25% de ella puede ser debida a la actividad del fitoplancton y el resto a las bacterias. Las tasas de respiración, como las tasas de fotosíntesis, son más bajas para los ríos del Escudo y más altas para el Apure que las del cauce principal. Estas tasas de respiración no son suficientemente altas como para producir cambios significativos en el inventario total de carbono orgánico durante su transporte.

INTRODUCTION

Between 1982 and 1985, Project PECOR (Proyecto Ecosistema Orinoco) obtained quantitative samples of suspended organisms in the Orinoco main stem and lower major tributaries. These samples were processed and counted for bacteria, phytoplankton, and zooplankton. In addition, metabolic rates (photosynthesis, respiration) were measured in river water collected simultaneously with the biotic samples. This information provides the first comprehensive overview of the suspended organisms of the lower Orinoco river. A synopsis of this information will be given here; some subjects have been treated in greater detail elsewhere, as cited below. Samples were taken at four main-stem stations and at the mouths of three major tributaries (Apure, Caura, Caroní) according to the schedule described in the chapter on Orinoco river chemistry (LEWIS & SAUNDERS, this volume). The sampling did not include the floodplain waters, although the effects of extensive areas of floodplain can be estimated by the use of flux models that take into account the addition of suspended organisms from various tributaries as well as the rates of growth and mortality *in situ* (LEWIS, 1987). The principal topics of interest here include: (1) species composition and seasonality of suspended organisms in the main stem, (2) contrasts in species composition and seasonality among major tributaries, (3) the influence of the floodplain on the river with respect to suspended organisms, and (4) metabolic fluxes in relation to transport fluxes.

BACTERIA

Subsamples for counting of bacteria were taken from the integrated samples that were collected for water chemistry analysis. These subsamples were treated in the field with 2% formaldehyde to arrest

growth, and were subsequently counted on a nucleopore filter (0.2 um pore size) after being stained with acridine orange. Further details of the counting methods are as given by Lewis et al. (1986).

Almost all of the bacteria in the Orinoco river and major tributaries are extremely small rod and coccoid forms (median size, ca. 0.5 um). Such small cells are typically dominant numerically in fresh waters (HOBBIE & WRIGHT, 1979). As is frequently the case in lakes, most of the bacteria in the Orinoco river and its major tributaries are unattached, although some are attached to small debris particles.

The numbers of bacteria in the Orinoco main stem, the Caura river, and the Apure river are shown for a seasonal cycle in Figure 1. The abundances for all of the rivers are consistently below 10^6 cells/cc, which is not very high: a median value for total bacterial abundance in fresh waters of moderate productivity would be in the vicinity of 10^6 cells/cc (HOBBIE & WRIGHT, 1979). Comparisons with other rivers are difficult because very few total counts have been done on running waters. However, the lakes of the Amazon system appear to show abundances typically below 10^6 cells/cc (RAI & HILL, 1984).

The abundance of bacteria in the Apure river consistently exceed the abundances of bacteria in the Caura river and in the Orinoco main stem. The Apure river has substantially higher concentrations of nutrients, ionic solids, suspended solids, and dissolved organic carbon. Consequently, the appearance of higher bacterial numbers in the Apure is not surprising. The numbers of bacteria in the Orinoco main stem are similar to those in the Caura river.

The seasonal variation of bacterial abundance in the main stem and tributaries is unexpectedly small. Whereas the abundance of algae vary by more than an order of magnitude (LEWIS, 1987), the abundances of bacteria vary only by a factor of 2 or 3 (Figure 1). In both the Caura river and the Orinoco main stem, the abundances of bacteria are near their highest just as the water level begins to rise. At this time, the concentrations of organic carbon in the river also reach their maximum. The high concentrations of bacteria at this time may reflect terrestrial contributions that are especially strong just as the first portion of seasonal runoff passes through the terrestrial system into the river. In addition, the microbial populations at this time of the year may be better nourished because of the more concentrated and possibly more labile inventory of organic carbon in the water.

Just following the onset of rising water, there is a depression in the abundance of bacteria. This is shared by virtually all suspended organisms in the Orinoco river; it indicates the dilution effect of large volumes of water passing through the system. There is a recovery of

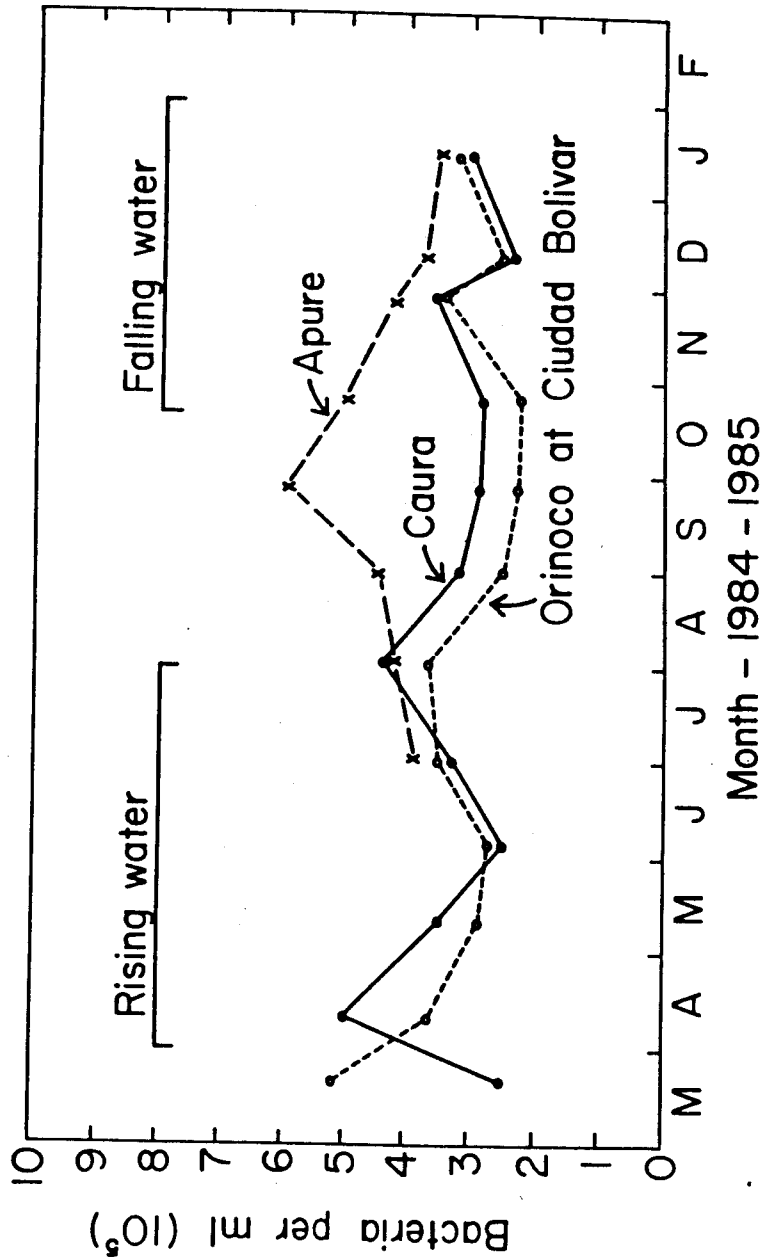

Figure 1 Abundance of bacteria in the Orinoco and in two major tributaries over a 12-month cycle

abundance as the rise in water begins to level off, which is also characteristic of other categories of organisms (LEWIS, 1987; SAUNDERS & LEWIS, 1987b).

During the season of low water, the abundances of bacteria in the Orinoco main stem and in the Caura river are low. This contrasts with the pattern for phytoplankton and zooplankton, which are most abundant when discharge is low. When floodplains are the primary source of bacteria, substantial peaks should be observed during the period of falling water, when the floodplains drain into the river. This is not the case for the Orinoco main stem or for the Caura River. There is an indication of such a drainage peak in the Apure River, but the magnitude of the peak is relatively small.

The abundance data for bacteria suggest that the explanation of bacterial abundances is different from the explanation of zooplankton and phytoplankton abundances. Whereas zooplankton and phytoplankton must originate from stagnant incubation areas either in the upper reaches of the flowing water system or in the side channels or floodplains, bacteria can originate also from terrestrial surfaces. This additional major source of bacteria may explain why the seasonal variability in bacterial abundance is lower than that of phytoplankton and zooplankton.

The relatively low abundances of bacteria suggest minimal effects of bacteria on inventories of organic carbon in the flowing waters of the Orinoco during transit. This conclusion is supported by the high degree of constancy in organic carbon concentrations along the main stem (LEWIS & SAUNDERS, this volume). Because there is no net photosynthesis of algae during transit (LEWIS, 1987), substantial microbial degradation of organic matter would be obvious from the corresponding downstream decrease in concentration of organic carbon. The measured respiration rates also indicate low rates of microbial activity (see below).

PHYTOPLANKTON

Phytoplankton subsamples were taken directly from integrated water chemistry samples at each station. The samples were preserved with Lugol's solution and were counted with an inverted microscope (LEWIS, 1978). Separate diatom slides were prepared to facilitate examination of diatom frustules. Table 1 lists the species that were recorded in quantitative counts for the Orinoco main stem and for the Apure, Caura, and Caroní rivers. The list includes only species that

appeared a number of times. Even so, most of the taxa on the list appear in extremely small quantities.

The Orinoco phytoplankton assemblage is very rich in diatoms. Although many of the diatom species are not euplanktonic (i. e., they are associated with substrates and are unlikely to grow well in suspension), the most abundant diatom taxa are euplanktonic, and most of the taxa of other divisions of algae shown in Table 1 are also euplanktonic. Thus the plankton community is dominated by taxa that are likely to have grown in suspension rather than attached to substrates. Added to this numerically dominant core are other species, particularly of diatoms, that are not euplanktonic and therefore probably originate from substrates supporting algal growth.

The single most important phytoplankton genus in the entire Orinoco system is *Melosira* ; *Melosira granulata* is especially important. *Melosira granulata* is found over a wide range of latitudes on all of the continents (HUBER-PESTALOZZI, 1942). In lakes, it is most prominent during periods of complete mixing, probably because its cells and filaments are large and therefore have high sinking rates in the absence of turbulence. Melosira is capable of perennation, during which cells shrink inside the frustule and remain in the sediments in a dormant condition until they are resuspended (HUTCHINSON, 1967; REYNOLDS, 1973). *Melosira* is also capable of growing well on substrates, provided that the light conditions are appropriate. This combination of adaptations is well suited for river environments, where *Melosira* can grow in quantity in stagnant areas, including floodplains, and leave an inoculum of resting cells from which to begin growth the following year. *Melosira* is a significant component of the phytoplankton in many rivers (e. g., ILTIS, 1982; WHITTON, 1984; DAVIES & WALKER, 1986; UHERKOVICH, 1984).

Melosira shows its strongest dominance in the Apure river, but is also present in quantity in the Orinoco main stem (see also SANCHEZ & VASQUEZ, 1987a), where it shares dominance with other taxa (Figure 2). *Melosira* does not make a large contribution to the phytoplankton communities of the shield waters, however. *Melosira* is often identified with waters that are at least moderately rich in inorganic ions. Thus the failure of *Melosira* to appear in the shield waters may be explained by water chemistry, although any conclusion of this type would as yet be premature because the absence of *Melosira* in the shield rivers may also be explained by factors that have not yet been studied. Melosira may be more important in the Rio Negro (UHERKOVICH, 1976) than in the Venezuelan shield rivers.

Other diatoms that appear in quantity in the Orinoco include *Rhizosolenia* and *Eunotia* .These two genera are identified primarily

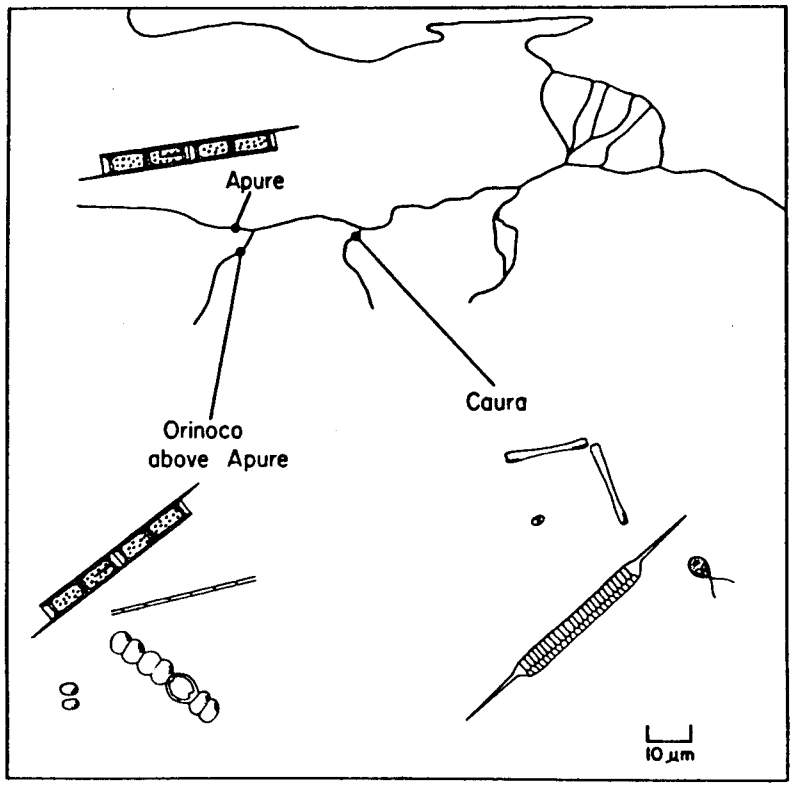

Figure 2. Ilustration of dominant phytoplankton taxa at various points whitin the Orinoco system (draw to escale): Apure, *Melosira granulata;* Orinoco above Apure, *Melosira granulata, Lingbya limnetica, Anabaena sp., Chroococcus spp.*, Caura, *Eunotia, Coccomyxa, Chlamydomonas, Rhizosolenia*

with the shield waters, although they appear in quantity in the main stem as a result of the drainage of the shield waters into the main stem. *Rhizosolenia eriensis* is often associated with oligotrophic conditions, which would suggest chemical control of its dominance in the shield waters, and is widespread in the tropics (HUBER-PESTALOZZI, 1942), including the Amazon System (UHERKOVICH, 1984). *Eunotia asterionelloides* , the dominant *Eunotia* species, is not prominent in lake plankton either at temperate or tropical latitudes; it appears to be mainly associated with rivers. *E. asterionelloides* may be euplanktonic in some of the stagnant waters of the shield, although this remains to be studied directly. In tropical Africa, the genus *Eunotia* is associated with acidic waters of low ionic strength (GASSE et al ., 1983). Thus its occurrence in the shield waters fits the general pattern of its distribution in African waters. Carter and Denny (1982), who found *E. asterionelloides* to be important in the river Jong of Sierra Leone, note that there is considerable confusion in the taxonomy of this species. For this reason, the species may be even more widespread in tropical rivers than would be evident from the literature. Our identification follows Cholnoky (1966) and Hustedt (1952).

The phytoplankton of the Orinoco river above the Apure contains a substantial component of blue-green algae (Table 1; see also BLANCO & SANCHEZ, 1987). Blue-green algae are not found in quantity in the waters of the Apure or in the shield waters draining into the Orinoco. The exact source of the blue-green algae is uncertain; possibly the blue-greens are associated with certain of the upper tributaries. The prominent taxa include both coccoid and filamentous forms. *Lyngbya limnetica* is present in significant quantities. This species is abundant throughout the tropics, especially in lakes (LEWIS, 1978), and indicates stagnant-water origin of the blue-green algae in the Orinoco. *Anabaena* is also present, as is *Chroococcus*.

Chlorophytes are not predominant in any of the major tributaries or in the lower main stem. However, chlorophytes are of notable secondary importance in the shield waters. In particular, significant quantities of microalgae (e.g., *Chlorella*) appear, as do some flagellated forms (*Chlamydomonas*).

The biomass of suspended algae per unit volume of water in the Orinoco river never reaches high levels. Stations along the main stem average 0.11 to 0.19 ug/l chlorophyll a. This corresponds to approximately 10 ug/l of algal carbon. Among the tributaries, the

Table 1. Suspended algae of the Orinoco main stem and lower major tributaries.

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
Cyanophyta						
Chroococcus sp.		R		R	R	
Aphanocapsa delicatissima				I		
A. elachista				R		R
A. sp.				R		
A. sp.				R	R	
Microcystis supersalsa				R	R	C
Synechococcus elongatus	I	C	I	C	R	
S. sigmoidea		R	I	R	R	
Merismopedia tenuissima	R	R	R			R
M. minima	C	I	C			I
Synechocystis sp.	R	R	R			
Coelosphaerium sp.						R
Eucapsa sp.	R					
Oscillatoria limnetica		C	A		R	A
O. tenuis	R				R	C
O. amphigranulata	R		R			
O. subtilissima				R		
O. sp.					R	
Pseudanabaena sp.	R	R		R		R
Anabaena catenula			I		R	I
A. spiroides		R			I	
A. sp.	I			R		R
Lyngbya limnetica	D	A	R	R	R	D
L. sp.					R	R
Aphanizomenon sp.	I	R	R			R
Raphidiopsis curvata	I	I				R
Phormidium sp.	R		R			
Dactylococcopsis fascicularis	R				R	
D. sp.	R		R	R	R	R
D. smithii	R		R	R		

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
Chlorophyta						
Chlamydomonas	R	R		A	R	
Gloeocystis sp.		R			R	
Oocystis marssonii		R				
O. sp.	R					
Ankistrodesmus convolutus	R	I	R	R	R	I
A. falcatus	R	R	R	R	R	
A. densus		R	R		R	
A. gracilis		R		R	R	
Golenkiniopsis solitaria			R			
Schroederia setigera	R	R	R	R	R	R
S. spiralis		R				
Dictyosphaerium pulchellum	I		I		I	
D. sp.		R				
Actinastrum hantzschii	I	I	C			C
Pediastrum duplex			R			
P. tetras			R	R	R	
Scenedesmus brasiliensis	R	R	R		R	R
S. dimorphus		R				R
S. ecornus			R		R	
S. granulatus					R	
S. oahuensis var. clathratus	R	I		R	R	
S. quadricauda	R		R		R	R
S. spinosus var. bicaudatus	R		R			
S. sp. 2				R	R	
S. sp. 3					R	
S. sp. 4						R
S. sp. 5		R			R	
Tetraedron minimum	R	R		R	R	
Coelastrum reticulatum var. polychordum	R	R		R	C	
C. pulchrum			R			
Crucigenia tetrapeda	R	R		R		
Kirchneriella contortum	R			R	R	
K. lunaris		R	R			

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
K. obesa				R		
Coccomyxa minor	R			D	C	
Chlorella vulgaris	R	R	R		R	
Small chlorococcales spp.	I	I	I	A	C	C
Tetrastrum heteracanthum	R	R				
Franceia ovalis	R					
Treubaria triappendiculata	R			R		R
T. sp.				R		
Ankyra judayi		R			R	
Pteromonas limnetica		R				
Closteriopsis longissima	R	R				
Staurastrum asterias	R			R	R	
Gonatozygon kinahani	R	R				
"short filaments" of Van der Heide 1982	R	I				
Eutetramorus planctonius	C	A	I	D	A	C
Staurodeumus coronutus var. minor	R					
S. subulatus				R		
S. sp.			R			
Chlorococcum sp.		I	R	R		R
Pseudosphaerocystis lacustris		I		I	I	
Mesotaenium sp.		R	R	R	C	
Nephrocytium limneticum					R	
Closterium lunata					R	
C. setaceum		R				
Spirogyra sp.	R		R			
Euglenophyta						
Trachelomonas sp.						R
T. ensifera						R
Euglena acus				R		R
Phacus orbicularis			R			

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
A. turgida					R	
Anomoeoneis vitrea	R		R		I	
Cymbella microcephala	R				R	
C. venezuelana		R				
C. lunata						R
C. minuta	R	R		R	R	
Eunotia pectinalis	R	R		R	R	
E. asterionelloides	C	C	I	D	D	
E. rabenhorstii	R		R	R	R	
E. tenella	R		R	R	I	R
E. glacialis	R	R	R	R	R	
E. didyma	R		R	R	R	
E. monodon	R		R			
E. binode	R	R				
E. exigua		I	R			
E. pectinalis var. minor		R	R	R	R	
E. triodon		R	R			
Diploneis oblongella					R	
Fragilaria crotonensis	R	I	R	R		
Frustulia rhomboides	R	I		R	R	
F. vulgaris			R			
Gomphonema angustatum				R		
G. clevei				R	R	
G. parvulum	R			R	R	
G. szabot					R	
G. turris				R		
Gyrosigma spencerii	R	R	R		R	R
Mastogloia smithii var. lacustris					R	
Navicula agrestis	R			R	R	R
N. minuscula		R			R	
N. contenta		R				
N. margaritacea					R	
N. bacillum					R	
N. cincta					R	
N. cryptocephala	R		R	R	R	R

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
Cryptophyta						
Cryptomonas sp.	I	R	I	I	R	R
C. marsonii					R	
C. erosa	R		I	R	R	
Rhodomonas sp.			R	R		
Unid. Cryptophyte sp.		R	R	R		R
Pyrrhophyta						
Peridinium africanum				R		
Unid. Dinoflagellate				I		R
Bacillariophyta						
Cyclotella ferrazae	R	R	I	R	R	C
C. stelligera	R	A	R		R	I
C. stelligera var. tenuis			R			
C. meneghiniana	R	R			R	R
Melosira lirata	I	A	I		R	C
M. distans	I	C	P		I	C
M. granulata	D	D	D	A	A	D
M. roeseana var. epidendron	R	R				
M. italica		R				
M. distans			I			R
M. herzogii		R				I
Stephanodiscus astraea		R	R			I
Rhizosolenia eriensis	C	I	I	D	D	
Actinocyclus sp.		R		R	R	
Coscinodiscus sp.		R		R		
Thalassiosira		R	R			
Achnanthes laterostrata					R	
A. minutissima						R
A. ostrupiri						R
A. submarina				R		
Amphicampa sp.		R				
Actinella brasiliensis	R	R	R	R	R	
Amphora sp.			R			

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
N. ferrazae				R	R	R
N. florinae		R		R		R
N. geitleri	R					R
N. ilopangensis	R		R		R	
N. mucicoloides	R	R	R	R	R	R
N. mutica			R	R		
N. mariposae	R	R	R	R	R	
N. subrhyncocephala					R	
N. densa				R		
N. laticeps				R		
N. pupula var. pupula				R		R
N. pupula var. capitata	R				R	
N. notha				R		
N. teneroides		R				
N. tersa	R	R				
N. seminuloides			R	R	R	
N. venezuelana						R
N. viridula var. rostellata				R		
N. vulpina	R	R	R	R		
N. submolesta	R	R		R		R
N. radiosa	R		R			
N. maculata	R					
Caloneis bacillium					R	
Neidium affine					R	
N. apiculatum		R				
N. affine var. amphirhynchus				R		
Nitzchia aerophila						R
N. filiformis			R		R	R
N. angustecarinata					R	
N. agnewii	I	I	I	C	R	C
N. amphibia				R	R	
N. ferrazae	R	R		R		
N. fonticola	R	R		R	R	
N. frustulum		R		R	R	
N. intermedia			R			

	Main Stem*			Tributaries*		
	1	2	3	1	2	3
N. palea	R	R	R	R	R	I
N. sigma	R				R	
N. subacicularis	R	R				
N. subconfinis	R				R	
N. tryblionella var. victoriae						I
N. obtusa	R					
N. acicularis		R				R
Pinnularia maior						R
P. biceps		R		R		
P. brebissonii	R		R	R	R	
P. viridis	R		R		R	
Stauroneis nana		R		R		
S. phoenicenteron	R	R			R	
Synedra cunningtoni						R
S. inducta					R	
S. sublinearis	R			R	R	
S. tenera		R	R	R	R	
S. radians var. radians		R		R	R	
S. sumpens var. fragilarioides		R	R		R	I
S. ulna var. ulna	R	R		R		R
S. amphicephala		R				
S. sp.						C
Capartograma crucicula		R		R		
Rhopalodia gibberula		R				
Desmogonium rabenhorstianum var. elongatum			R	R		

*Main stem: 1 = above Caura, 2 = Ciudad Bolivar, 3 = Barrancas.
Tributaries: 1 = Caura, 2 = Caroni, 3 = Apure

chlorophyll concentrations are much lower for the shield rivers (0.01-0.04 ug/l chlorophyll a) than for the Apure (mean,0.36ug/l chlorophyll a). Impoundment of the Caronf river by the Guri Dam does not significantly augment the mean abundances of phytoplankton (see also LEWIS & WEIBEZAHN, 1976; SANCHEZ & VASQUEZ, 1987b), in contrast to the effect of impoundment on most rivers (DAVIES, 1979). This may be explained by the low nutrient concentrations that are typical of the shield waters, and by the passage of large volumes of water from the surface of the reservoir. In the main stem of the Orinoco as well as the tributaries, the concentrations of chlorophyll a are comparable to those that would be characteristic of oligotrophic lakes (chlorophyll a<2 ug/l: WELCH, 1980). However, this should not be interpreted as a lack of productive potential for the Orinoco waters in general. In fact, the stagnant floodplain waters along the Orinoco main stem develop very high abundances of algae (up to 10^6 cells/ml: HAMILTON & LEWIS, 1987) that illustrate the productive potential of the main stem waters under stagnant conditions with good light penetration caused by the precipitation of suspended solids.

Suspended algae show marked seasonal cycles of abundance throughout the system. The main stem and all tributaries share a strong tendency to show maximum number of cells per unit volume of water during the period of low discharge. Maxima at the time of low water commonly exceed by a factor of more than ten the minima observed at peak flow (LEWIS, 1987; SANCHEZ & VASQUEZ, 1987a). The maxima at low water are especially interesting because they illustrate the importance of sources of phytoplankton outside the floodplain. Because the rivers are not in contact with floodplain during the period of low water, the algae in the rivers at these times must originate from sources within the channels. Specific sources include headwaters, channel pools, and stagnant side channels. From the irregularity of phytoplankton abundance during low water, it has been postulated that the stagnant areas within channels are especially important sources of phytoplankton (LEWIS, 1987). A proposed mechanism for the appearance of phytoplankton in the flowing waters is based on variations in discharge that are characteristic of these unregulated rivers. The variations, although small in a relative sense, are sufficient to cause irregular flushing of stagnant depressions with the channel. The depressions accumulate biomass while they are isolated from channel flow, and this biomass is subsequently flushed into the channel.

As explained more fully in the section below on primary production, growth of phytoplankton during transit is not posible along the main stem or lower portions of the major tributaries because the light exposure of the cells is too low. Consequently, phytoplankton are affected only by advection and mortality; they are not able to produce

additonal biomass during transit. Experimental evidence and comparisons of upstream and downstream concentrations of suspended algae during the period of low water indicate good survival of phytoplankton during transit, at least for the few days required for water to traverse the lower portion of the Orinoco main stem (LEWIS, 1987).

Transport of phytoplankton reflects both the discharge and the abundance of algae. The patterns of transport differ considerably from the patterns of abundance. Although abundance patterns would suggest maximum transport at the time of low water, the seasonal changes in discharge more than compensate for decreased abundance of algae at high water. Peak transport typically occurs on the falling limb of the hydrograph, and not at the time of low flow, as might be suspected from the abundance patterns (Figure 3).

Because the rates of net growth and mortality of phytoplankton during transit along the main stem are negligible, it is possible to calculate the addition of algal biomass from the floodplain by a simple mass-balance approach (LEWIS, 1987). Application of this approach to the Orinoco

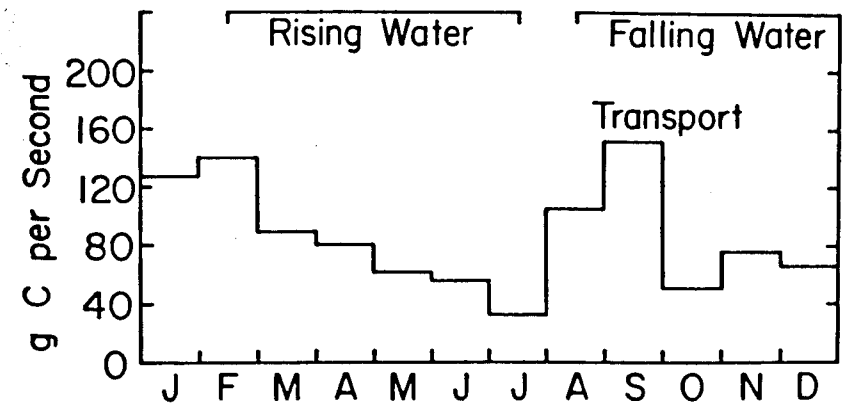

Figure 3. Monthly transport rates for living algal carbon in the Orinoco river lower main stem (averages of the three stations below the Apure river)

main stem indicates that the floodplain accounts for only 37% of the annual transport of suspended algae by the Orinoco. Other sources, including within-channel stagnant areas, account for the reamining 63%. Fifty-eight percent of annual transport occurs when the river is not in contact with the floodplain at all.

The total annual transport of phytoplankton by the Orinoco river is 2.4 x 10^6 kg C. The transport would be much higher if the floodplain were yielding to the river a substantial percentage of its annual plankton production. However, the floodplain yields less than 1% of its total plankton production to the river. Thus, with respect to phytoplankton production, the floodplain functions as a closed unit, even though large amounts of water flow through it. This is accounted for by two features of the floodplain (LEWIS, 1987). First, the internal usage of phytoplankton biomass by the floodplain food webs appears to be rapid and efficient. Second, a large percentage of the annual phytoplankton production of the floodplain occurs after the connection between the river and the floodplain has been broken. Thus the floodplain tends to conserve the phytoplankton biomass that it produces, and consequently has far less effect on the inventory of phytoplankton in the river than might be expected.

ZOOPLANKTON

Zooplankton samples were taken at the same stations and on the same schedule as phytoplankton samples. The zooplankton samples were collected over the full depth of the water column by use of a pump (SAUNDERS & LEWIS 1987a) at several points along the cross-section of the river. The organisms were captured with a net of 35-um mesh and were preserved with a sucrose-formalin solution. Rose bengal was used in separating the organisms from suspended matter. A detailed analysis of the zooplankton in the lower Orinoco main stem and two of the major tributaries (Caura, Apure) is given by Saunders and Lewis (1987a,b,c).

Table 2 lists the zooplankton species that were found between 1982 and 1985 in the main stem of the Orinoco river and the lower major tributaries. As in the case of the phytoplankton species list, Table 2 excludes some rare species. This list is by no means exhaustive for the Orinoco basin; additional lists based on different sampling methods have been published for rotifers (MICHELANGELI et al., 1980; VASQUEZ, 1984a,b), cladocerans (REY & VASQUEZ, 1986), and copepods (DUSSART, 1984).

As shown by Table 2, the rotifers are by far the most diverse group of zooplankton in the lower Orinoco system. Four genera (*Brachionus*,

Copepoda

Diaptomus negrensis
Ergasilidae
Halicyclops
Mesocyclops decipiens
Oithona amazonica
Rhacodiaptomus calatus

Cladocera

Bosmina tubicen
Bosminopsis dietersi
Bosminopsis sp.
Camptocercus ? rectirostris
Ceriodaphnia cornuta
Diaphanosoma brevireme
D. birgei
Daphnia gessneri
Graptoleberis testudinaria
Grimaldina brazzai
Ilyocryptus spinifer
Moina minuta
Simocephalus latirostris
Streblocerus pygmaeus
other chydorids

Rotifera

Anuraeopsis fissa
Ascomorpha
Asplanchna
bdelloids
Beauchampiella eudactylota
eudactylota
Brachionus angularis
B. budapestinensis
B. calyciflorus
B. caudatus
B. dolabratus
B. falcatus
B. mirus
B. patulus
B. havanaensis
B. quadridentatus
B. urceolaris
B. zahniseri
Cephalodella
Collotheca
Colurella
Conochilus dossuarius var.
coenobasis

Rotifera (cont.)

Dipleuchlanis propatula
Epiphanes macrouras
E. sp.
Euchlanis
Filinia longiseta
F. opoliensis
F. pejleri
Hexarthra intermedia brasiliensis
Keratella cochlearis
K. americana
K. lenzi
K. tropica
Lecane bulla bulla
L. leontina
L. ludwigi
L. melini
L. monostyla
L. obtusa
L. proiecta
L. quadridentata
Lepadella
Macrochaetus
Monommata
Mytilina macrocera
Notholca
Polyarthra vulgaris
Platyias quadricornis brevispinus
Platyias q. quadricornis
Ploesoma truncatum
Pompholyx
Rotaria neptunia
Scaridium longicaudum
Sinantherina semibullata
Squatinella ? leydigi
Synchaeta stylata
Testudinella patina
T. mucronata hauerensis
Trichotria tetractis
Trichocerca bicristata mucosa
T. chattoni
T. collaris
T. similis
T. similis grandis

Table 2 Zooplankton of the Orinoco river and adyacent floodplain lakes, 1982 - 1985

Keratella, *Trichocerca*, *Lecane*) are represented by multiple species; the diversity of *Brachionus* is particularly impressive. The diversities of the Cladocera and of the Copepoda are much lower than that of the Rotifera.

The species composition of zooplankton shows some parallel trends to that of the phytoplankton. The species list contains both euplanktonic species and species that are typically associated with substrates. However, the dominant species numerically or in terms of biomass are euplanktonic. This suggests that the principal supply of zooplankton to the rivers is through plankton populations of stagnant waters. The one exceptional species is the rotifer *Lecane proiecta*, which is not euplanktonic but which appears to be common throughout the lower Orinoco basin (SAUNDERS & LEWIS 1987c). Previous studies have shown this species to be associated with aquatic vegetation (HAUER, 1956; KOSTE, 1978). Extremely high densities (10^3 /l) have been found in the open waters of floodplain lakes along the lower Orinoco (S. SIPPEL, unpublished), suggesting a facultative planktonic phase for this species that may lead to its movement into the river.

In the Orinoco main stem, rotifers are numerically dominant; cladocerans and copepods overlap in mean abundance across the main-stem stations (Figure 4). On the basis of biomass, however, cladocerans predominate, while rotifers and copepods overlap in their mean abundance across stations.

In both absolute and relative terms, rotifers are much more abundant in the Apure river than in the main stem (Figures 4 and 5). Rotifers are considerably less abundant in the Caura river than in the Apure, but are still surprisingly abundant in view of the supposed sterility of such dark, ionically-poor waters. The abundances of rotifers in the Caroní river are only one-tenth of those in the Caura river, despite general similarity in the chemistry of the two rivers. The lower rotifer densities of the Caroní River probably reflect the effects of impoundment. The rotifers in the shield water appear to originate from shallow, stagnant water near the river channels. Such areas may be enriched by contact with soil or sediment, or even by rainwater. In the reservoir, without these enriching influences, the river water is apparently not so well suited to sustain rotifers as it is in the small, stagnant pools and side channels.

Cladocerans are notably less abundant in the Apure than in the main stem or in the Caura river even the Caroní river has as many cladocerans per unit volume as the Apure river (Figures 4 and 5). This is a counter-intuitive pattern because the Apure river is notably richer in nutrients, organic matter, and living algae than either the waters of the main stem or the waters draining directly from the Guayana Shield. Because cladocerans are often particularly vulnerable to fish predation, the

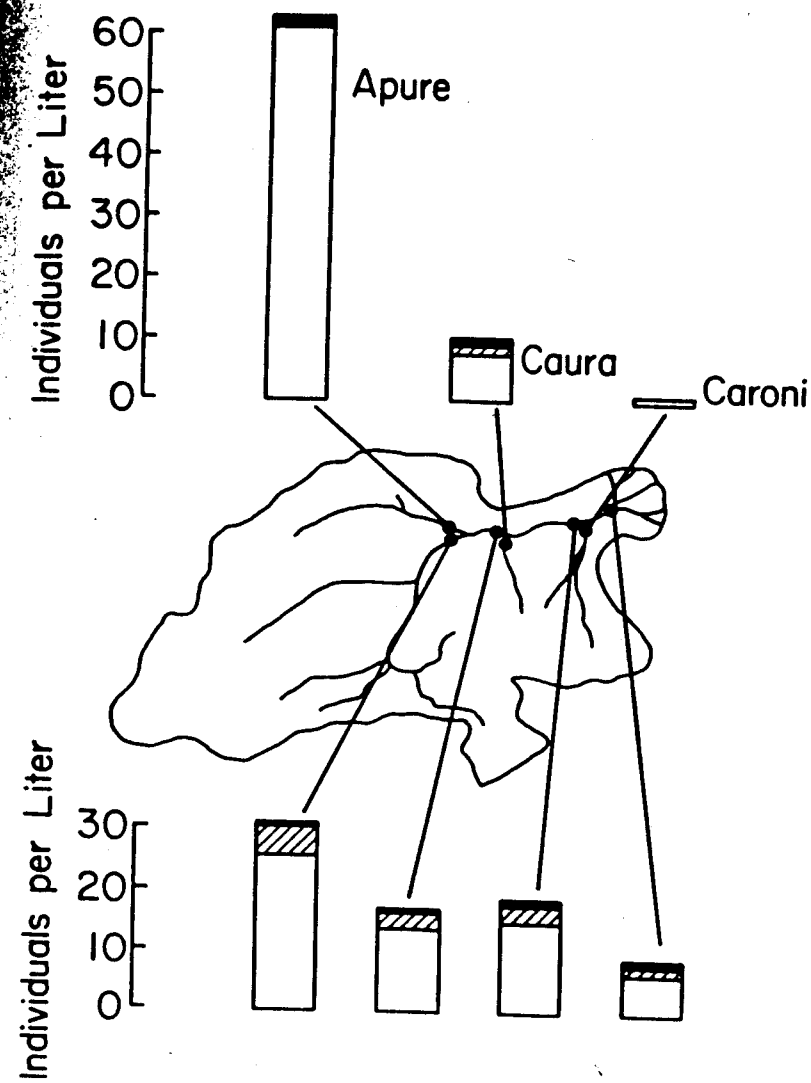

Fig 4. Average abundances of zooplankton in the lower Orinoco river main stem and lower major tributaries. The open portion of each bar indicates rotifers, the hatched portions indicate cladocerans, and the solid portions indicate copepods.

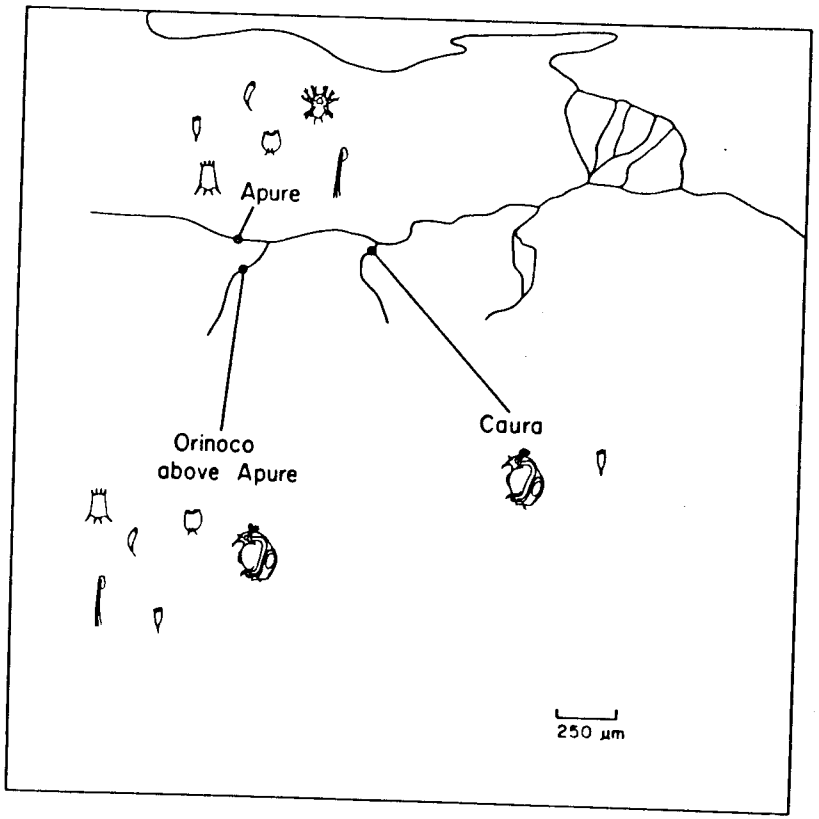

Figure 5. Ilustration of differences in the species composition for dominant zooplankton taxa at various points in the Orinoco system (draw to scale): Apure, *Brachionus, Keratella, Trichocerca, Lecane,* cyclopoid copepod nauplius, *Filinia;* Orinoco above Apure, *Brachionus, Filinia, Trichocerca, Keratella, Lecane, Bosminopsis;* Caura, *Bosminopsis, Keratella.*

smaller numbers of cladocerans in the waters of the Apure may reflect more intense predation pressure on the zooplankton of the source areas of the Apure than of the shield waters or of the main stem. The depletion of cladocerans in the waters of the Apure river is clearly worthy of more intensive study.

The copepods of the Orinoco main stem and of the Apure and shield rivers are primarily early developmental stages; nauplii are by far the most abundant. Copepodid stages are considerably less abundant, and adults are present in extremely small quantities. While the earlier developmental stages dominate numerically in most copepod populations, the bias toward young developmental stages in the river waters of the lower Orinoco system is so extreme that it must be explained either by greater vulnerability of the younger stages to entrainment by the flowing river waters or by selective removal of the older stages during transport.

The absolute abundances of zooplankton in the running waters throughout the lower Orinoco system are very low. Although zooplankton abundances vary widely in lakes, abundances in the range of 20-40 ug/l of zooplankton carbon would not be unusual for oligotrophic lakes (e.g., see the equations of McQUEEN et al., 1986). As shown by Figure 4, the total abundances of zooplankton average considerably less than this. However, during low water, at the time of peak biomass, the abundances may reach the levels that are characteristic of oligotrophic lakes.

Reproduction of zooplankton in transit appears to be trivial. Very few of the organisms in transit carry eggs. High water velocities are known to suppress the growth (RZOSKA, 1978) of euplanktonic zooplankton species.

Zooplankton biomass shows substantial downstream depletion along the main stem (Figure 4). The downstream depletion is far too large to be accounted for by the addition of water from the Caroní and Caura Rivers, which have low zooplankton abundance but insufficient discharge to explain the downstream decline. The downstream decreases in zooplankton abundance suggest mortality in transit. This could occur either by physical mechanisms associated with the high current velocities or by predation. High current velocities, although not compatible with reproduction and growth in many species of euplanktonic zooplankton, still seem an unlikely cause of direct mortality. Studies of the stomach contents of gymnotiform fishes living in the main channel have demonstrated significant zooplankton feeding by some of these fishes (LUNDBERG et al., 1987). The abundance and diversity of this guild of mid-channel fishes were unanticipated. The ability of these fishes to capture individual zooplankton from rapidly moving water in the absence of light near the river bottom is especially surprising. Although

the removal of zooplankton by this particular guild of fishes is not likely to account fully for the decrease in zooplankton abundance downstream within the Orinoco, it suggests the existence of unsuspected food chain components involving zooplankton in the running waters. Thus predation may explain, at least partly, the downstream decreases in zooplankton abundance.

The downstream decreases in overall zooplankton abundance are actually explained by decreases in abundance of rotifers and cladocerans; copepods increase in abundance (Figure 4). Increases in copepod abundance between the Apure river and the delta might be explained by contributions of zooplankton from the floodplain. However, examination of the seasonal data shows that increases in copepod abundance occur even when the river is out of contact with the floodplain. Possible explanations include the addition of copepods from channel vegetation mats or the hatching of detached eggs in transit.

The abundances of individual species and of zooplankton groups vary typically by more than an order of magnitude over the annual discharge cycle. The abundances of all categories of zooplankton are consistently very low during the period of high water. Within the period of low water, individual species and species groups often differ in their abundance patterns.

The persistence of significant quantities of zooplankton through the interval of low water implies that zooplankton, like phytoplankton, must originate from sources other than the floodplain. As in the case of phytoplankton, the origin of zooplankton appears to be associated with stagnant waters within the channel; the proposed mechanism by which these organisms enter the flow of the river is recurrent minor variation in discharge, which is sufficient to cause alternate flushing and stagnation of channel depressions.

As for phytoplankton, zooplankton transport varies less across the seasons than abundance per unit volume. However, in contrast to phytoplankton, transport of zooplankton is highest during the interval of low water, when abundances are highest. Transport during the other major hydrologic phases (rising water, high water, and falling water) is very nearly constant at about one-tenth the rate of transport occurring at the time of low water. Thus a large portion of the total annual transport must be accounted for by mechanisms not involving the floodplain. The total annual transport of living zooplankton biomass is 0.32×10^6 kgC/yr, or 13% of the phytoplankton transport.

The total annual production of zooplankton within the floodplain is very high (TWOMBLY & LEWIS, 1987). Thus the transport figures for zooplankton, as in the case of phytoplankton, suggest that only a very small proportion of the zooplankton production of the floodplain reaches the Orinoco.

METABOLISM

Rivers sometimes support significant amounts of photosynthesis and respiration by suspended organisms (WELCOMME, 1979; WHITTON, 1984; DAVIES & WALKER, 1986). The effects of metabolism by suspended organisms are likely to be greatest given a combination of long transit time, slow water movement, sufficient penetration of light to allow positive net photosynthesis, and a substantial initial inoculum of organisms from which growth can occur. Long transit time is the only one of these conditions that is characteristic of the Orinoco main stem. Consequently, the metabolic rates attributable to suspended organisms in the river are low.

Photosynthesis in the Orinoco river and in the lower major tributaries was studied routinely between 1982 and 1985 by incubation methods (LEWIS, 1987). Among the tributaries, mean annual gross primary production was highest for the Apure river (26 mg C/ m^2/day) and lowest for the shield rivers (Caura, 13 mg C/m^2 day; Caroni 4 mg C/m^2 /day). Along the main stem, mean production varied by station from 19 to 43 mg C/m^2 /day. This level of production is insufficient to offset the maintenance demands of phytoplankton in suspension within the river (LEWIS, 1987). Thus the net production in the flowing waters of the Orinoco main stem and lower tributaries by suspended photosynthetic organisms is zero.

The transparency of the Orinoco waters is quite low. The mean depth at which 1% surface irradiance can be found indicates the approximate vertical extent of positive net photosynthesis in the water column (TALLING, 1971). In the Apure this depth averages 0.46 meters. In the Caura, it is 2.6 meters, and in the Caroni it is 2.9 meters. In the Orinoco main stem, the 1% light level is found between 0.9 and 1.2 meters, depending on the season. Given the great average depth of the water column in the lower tributaries and in the main stem, it is obvious that production exceeds maintenance only in a very small proportion of the total water volume at any given instant during the daylight hours.

Even if the clarity of waters in the lower Orinoco system were greater, or the river depths were smaller and thus allowed light to reach a greater proportion of the water column, the amount of photosynthesis per unit area within the lower Orinoco system could not be very great because of the low abundances of phytoplankton in the flowing waters.

The seasonality of gross production in the lower Orinoco system reflects the seasonality of algal biomass as described above. Superimposed on seasonal changes in abundance are seasonal changes in transparency. Changes in transparency and biomass per unit volume are mutually reinforcing because the lowest transparencies occur at high

water, when dilution reduces the amount of phytoplankton biomass per unit volume. However, the seasonal changes in abundance of algae per unit volume of water are the primary source of variation in gross production.

In the Orinoco main stem, the mean annual respiration rate attributable to suspended organisms is 80 ug C/l/day.Approximately one-quarter of this amount can be accounted for by phytoplankton, and three-quarters by bacteria; the contribution by zooplankton is negligible. The respiration rates for the Caura river are somewhat lower, and are more heavily biased toward bacterial respiration. The respiration rates of the Caroní.waters are even lower, while those of the Apure river are considerably higher than those of the Orinoco main stem. A strong seasonal minimum of respiration occurs during the interval of high water. This is consistent with other biological indicators demonstrating low abundances per unit volume of suspended algae and bacteria during the period of high water. Peaks in respiration occur during low water and just at the beginning of the rising water.

Calculations based on the respiration rates and the transit times demonstrate that the effect of respiration on the carbon inventory of the flowing waters is small. Even at the time of low flow, when the transit times are longest, water passes between the Apure and the delta within about 7 days. This transit time is sufficient to allow a respiratory loss of 0.6 mg/l of organic carbon. Because the carbon concentrations in the main stem are 10 times this amount, the respiratory conversion of carbon is relatively minor in a quantitative sense. However, respiratory conversion is likely to be focused on the most labile of the organic compounds, and thus may have an important qualitative effect on the mean lability of carbon in transit.

CONCLUSIONS

The abundances of suspended organisms of all categories, including bacteria, phytoplankton, and zooplankton, in the lower Orinoco system are lower than might have been expected given the contact of the river with large expanses of undeveloped floodplain that serve as an incubation area for suspended organisms. Even more surprising is the strong tendency of both abundance and transport of all categories of suspended organisms to be sustained or even to reach annual maxima during the interval of low water when there is no contact between the river and the floodplain. Thus the biotic studies demonstrate the great importance of non-floodplain source areas in accounting for the suspended organisms in the Orinoco river main stem and lower tributaries. Alternative source areas include headwaters and, probably most importantly, stagnant areas within the channel that are irregularly

flushed by small changes in water level during the season of low water. Although the floodplains are very productive, their production is largely conserved within the floodplain itself; the transfer of production from the floodplain to the river is almost certainly below 1% for all categories of suspended organisms. Thus while the river influences the floodplain in very drastic and obvious ways, the influence of the floodplain on the river is much smaller than might be expected.

ACKNOWLEDGEMENTS

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ESTUDIOS HIDROBIOLOGICOS Y PISCICULTURA EN ALGUNOS CUERPOS DE AGUA (RIOS, LAGUNAS Y EMBALSES) DE LA CUENCA BAJA DEL RIO ORINOCO

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RESUMEN

Las investigaciones realizadas en el Bajo Orinoco tuvieron como objetivo caracterizar esta parte del río en su estado actual y contribuir a fijar criterios de aprovechamiento y conservación de los recursos acuáticos. Los resultados se refieren a los ríos Orinoco y Caroní, algunas lagunas de inundación, morichales y al Embalse de Macagua (río Caroní). En el Orinoco, la abundancia planctónica se correlaciona inversamente con el caudal. En este río las máximas densidades fitoplanctónicas se deben a las diatomeas, mientras que en el Caroní predominan las Chlorophyta y en las lagunas del Orinoco las Cyanophyta. Más de 400 especies de algas han sido inventariadas hasta la fecha. El zooplancton de estos cuerpos de agua está formado principalmente por rotíferos (más de 136 taxa identificados) con predominio de *Keratella, Brachionus* y *Lecane* en el Orinoco. En el Caroní dominan especies litorales o béntico-perifíticas. 58 taxa de cladóceros han sido identificados (35% formas neotropicales). Datos parciales del perizoo de algunas lagunas del Orinoco señalan que éste se caracteriza por su alta abundancia (larvas de insectos, microcrustáceos, gastrópodos). El bentos de estas lagunas está formado por quironómidos, efemerópteros, anélidos y moluscos bivalvos de escasa abundancia y riqueza. 17 especies de macrofitas acuáticas han sido identificadas en las lagunas del Orinoco con *Eichhornia crassipes, Paspalum repens* y *Oxycaryum cubense* como las más abundantes. La comparación de las comunidades de peces de las lagunas muestran diferencias poblacionales y de distribución de biomasa por niveles tróficos. Los cultivos intensivos de cachama en sistemas modulares de jaulas flotantes en embalses (Macagua, Tumeremo) arrojan buenos resultados: tasas de crecimiento diario e individual de hasta 8 g/día, tasas de conversión del orden de 2:1, densidades del orden de 20 Kg/m^3. La alimentación larval se efectúa con cultivo masivo de cladóceros. Futuras