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Zooplankton abundance and transport in a tropical white-water river

James F. Saunders, III & William M. Lewis, Jr.
University of Colorado Center for Limnology, Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, CO 80309-0334, USA

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Abstract

Zooplankton abundance and transport were studied in the Apure River of western Venuzuela over a 15-month period. Much of the lower portion of the drainage basin, which is an extensive savanna of low relief, is subject to seasonal flooding. Although more than 50 zooplankton species were recorded during the study, nine rotifer species accounted for more than 90% of total density (mean, 138 individuals $\cdot L^{-1}$). Copepods were represented primarily by *Mesocyclops decipiens*. Most cladocerans were planktonic, but cladocerans were not abundant. Crustaceans comprised 46% of annual mean zooplankton biomass (1.9 $\mu gC \cdot L^{-1}$) but only 2% of zooplankton numbers. The annual transport of zooplankton biomass from the watershed was 29300 kgC. Zooplankton abundance showed a strong, inverse relationship to discharge. Secondary branches (caños) of the braided channel appeared to be the primary source areas, but populations of some species also reproduced in the main channel at low water. As the river began to rise, caños were flushed and thus abruptly ceased to serve as source areas. Zooplankton transport fell sharply and remained low until the river inundated the floodplain. Secondary production in the floodplain was exported to the river as long as a connection existed. After drainage ceased from the floodplain, transport fell to very low levels until caños again became suitable habitat. Seasonal fluctuations in river level regulate the development of source areas suitable for zooplankton growth and control the export of plankton from the source areas. Plankton in the running waters reproduce only at low water.

Introduction

The abundance of zooplankton in rivers is controlled by variations in transport and variations in growth. The physical interaction of flow regime and source areas regulates transport by determining the rate at which plankton are added to the main channel of the river. A rise in river level, for example, may bring the river into contact with floodplain water bodies and flush plankton into the river, as we have documented for the Caura River of Venezuela (Saunders & Lewis, 1987). This phenomenon is probably common in unregulated rivers with well-developed floodplains.

Changes in the abundance of zooplankton populations in the main channel depend on the balance of growth and mortality. Zooplankton populations can expand in rivers by growth of the suspended organisms (Talling & Rzoska, 1967) or by the hatching of resting eggs in river sediments (Moghraby, 1977). Resting eggs are typically derived from lentic source areas but spend a period of dormancy in the river. However, increases do not always occur. Losses to predators (e.g., Lundberg *et al.*, 1987) or through physical injury in the lotic environment (Hynes, 1970; Talling & Rzoska, 1967) may result in population decline. Rzoska (1978) found that reproduction of zooplankton in rivers is rarely observed at velocities in excess of 0.4 $m \cdot s^{-1}$.

Plankton densities in unregulated tropical rivers are often low. Of the three kinds of waters described by Sioli (1984: black, clear, and white), black-water rivers appear to support the lowest densities. Vasquez (1984) found maximum rotifer densities of $5.2 \cdot L^{-1}$ in the Caroni River, and Saunders & Lewis (1987) encountered rotifer densities up to $36 \cdot L^{-1}$ in the Caura River. Recent work on white-water rivers in eastern Venezuela suggests a higher capacity to support zooplankton; Sanchez *et al.* (1985) report rotifer densities as high as $191 \cdot L^{-1}$. Higher zooplankton densities in white waters are consistent with the belief that white waters are the most productive of the three neotropical water types (Fittkau *et al.*, 1975).

We present data here on the composition and abundance of zooplankton in the Apure River, a major, white-water tributary of the Orinoco River. Although the watershed reflects some human influence, the river is not regulated. Thus conditions are natural for zooplankton and we have an opportunity to examine the influence of an extensive floodplain on zooplankton abundance and transport.

Site description

The Apure River drains an area of 167000 km^2 in western Venezuela (Zinck, 1977; Fig. 1). Headwaters of the Apure are on the eastern flank of the Andes approximately 800 km by river from the Orinoco. The river descends rapidly over a distance of about 100 km to the Llanos, a savanna region that has very low relief and where much of the drainage area is below 100 m asl. Transit time across the Llanos varies seasonally in the range of 1–4 weeks. The low gradient and flat terrain result in extensive braiding of the river channel. At low water, many of the anabranches, which are known locally as caños, remain connected to the main channel, but have greatly reduced flows. During the wet season, heavy rain and flooding by rivers produce sheet flooding that may cover a large portion of the watershed. The Apure floodplain differs from the typical fringing floodplain in its extent of coverage and pattern of flooding (Welcomme, 1979). An internal delta is formed by the Apure and Arauca rivers where these low-gradient tributaries flow into the Orinoco River. Within this internal delta is a network of channels and lagoons that have formed by erosion. Throughout the lower Llanos, there are broad shallow depressions (esteros) in irregular terrain that hold water after rains or floods. Those that are deep enough to hold water on a permanent basis are called lagunas. In addition, borrow-pits from road construction (prestamos) provide a variety of aquatic habitats, some of which are permanent (Mago, 1970).

Population density in the basin is relatively low; San Cristobal in the Andes is the only city with a population greater than 150000. Only 5 other towns have populations in excess of 25000. Seasonal extremes of water availability make the lower Llanos region suited mainly for grazing cattle at relatively low densities and for crops with short growth cycles. Although there are a few water-storage reservoirs in the northern part of the basin, they have no capacity to control flooding in the Llanos. Recently, water storage has been attempted by means of dikes in the floodplain (Michelangeli *et al.*, 1980). Bank stabilization and flood control levees are used near larger towns to prevent damage. In general, however, human influence is not extensive in the lower part of the drainage and the intimate relationship between river and floodplain is essentially undisturbed.

The relatively high sediment load (median, 233 mg$\cdot L^{-1}$; range, 64–644) and conductance (median, 123 $\mu S \cdot cm^{-1}$; range 88–225) characterize the Apure as a white-water river. Strong seasonal trends are evident for dissolved and particulate matter.

Methods

Zooplankton samples were taken near the mouth of the Apure River at approximately 4-week intervals between March 1984 and May 1985. A composite sample (30 L) of river water was collected with a motorized pump suspended at approximately 30% of the measured depth at each of 4 points across the channel. Although reports vary concerning the efficacy of pumps for sampling zooplankton (de Bernardi, 1984), the method has no clear biases and is the most practical collection technique for large rivers (Bottrell *et al.*, 1976; Waite & O'Grady, 1980). The organisms were retained with a 35-μm mesh net and preserved with a sucrose-formalin solution (Haney & Hall, 1973). Rose bengal was added to facilitate separation of organisms from suspended matter. Subsamples were scanned until at least 100 of the most abundant taxon had been counted, or until the entire sample had been examined. Rotifers and crustaceans were counted separately. Biomass per individual was estimated from relationships presented in Bottrell *et al.* (1976). Dry mass is assumed to be 11% of body volume (Sitaramaiah, 1967), and carbon is assumed to be 44% of dry mass. Samples for a longitudinal profile of the Apure were taken at 5 stations along the river and from 3 sites on tributaries in June of 1984 (Fig. 1).

Means for density, biomass, and daily transport reflect appropriate adjustment for months sampled in both years. Mean daily transport is computed with discharge reported on the day of sampling. Annual transport, which is also adjusted to account for months sampled in both years, is computed with time-weighted discharge means for each sampling interval.

Stage height and discharge data for the Apure River at San Fernando de Apure were obtained from the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables. The use of a standard rating curve was found to be impracticable due to changes in channel characteristics at high water. Smooth curves were fit by eye to calibration data (N = 34) that were available over the range 37.4–45.0 m. Daily stage height readings were available for the period of study.

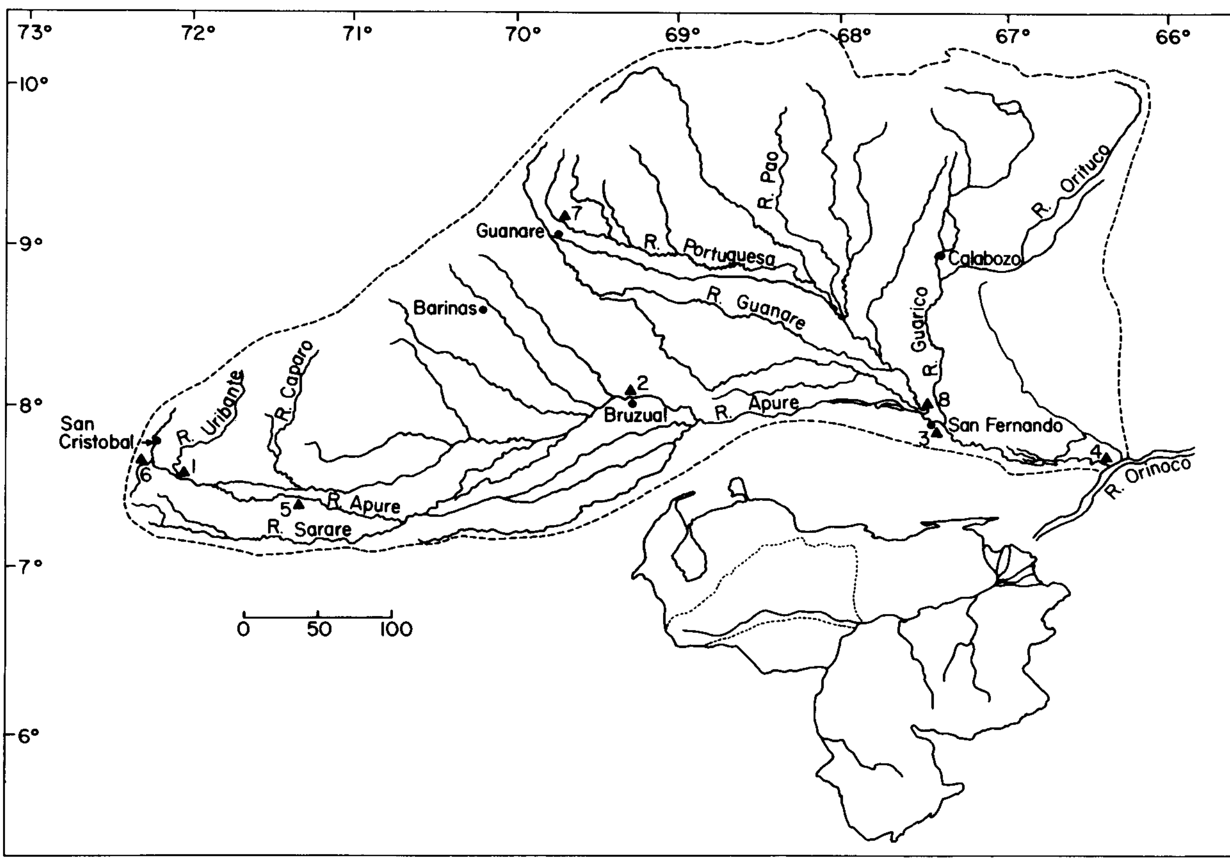

Fig. 1. Map of the Apure River drainage. The dot indicates location of the routine sampling site; the triangles indicate sites sampled in the longitudinal survey.

Results

More than 50 zooplankton species were encountered in the Apure River samples. Nearly all of the genera were planktonic. Although mean densities were relatively low for all groups (Table 1), maximum densities for the rotifers are comparable to those found in productive lakes. Densities are also comparable to those found in large rivers draining rich agricultural areas (Kofoid, 1908; Rzoska *et al.*, 1955). The annual export of zooplankton biomass from the Apure River was 29300 kgC. Copepods and rotifers contributed nearly equal amounts (46 and 42%, respectively) to annual export.

All of the common zooplankton species were planktonic except *Lecane proiecta*. Copepods of all stages were present, but nauplii comprised about 2/3 of the individuals. Despite the presence of adult copepods, which were mainly of the cyclopoid *Mesocyclops decipiens*, no eggs were observed. The absence of eggs argues against reproduction in the main channel, although somatic growth could have occurred. The predominance of younger developmental stages may reflect either the composition in source areas or more efficient transport of smaller stages that are more easily carried by currents (Brook & Woodward, 1956).

Nearly all of the Cladocera were planktonic species, of which *Moina minuta* was the most common. *Moina* was also the only cladoceran that carried eggs in the river. *Ceriodaphnia cornuta* and *Diaphanosoma birgei* were often present but were never abundant. *Bosminopsis deitersi*, which is the most common cladoceran in some Venezuelan black-water rivers (Vasquez, 1984; Saunders & Lewis, 1987), was rare in the Apure River. Because ephippia were never observed, we have no indication that resting eggs played any role in determining cladoceran abun-

Table 1. Annual densities, biomass, and transport of common zooplankton taxa in the Apure River.

Taxon	Density, individuals · L^{-1}		Biomass, $\mu gC \cdot L^{-1}$		Transport, $kgC \cdot d^{-1}$	
	Mean	Range	Mean	Range	Mean	Range
Copepoda						
Cyclopoid nauplii	1.29	0.1 – 5.6	0.02	0 – 0.09	1.85	0.05 – 6.96
Calanoid nauplii	0.31	0 – 3.3	0.02	0 – 0.26	2.24	0 – 10.41
Cyclopoid copepodids and adults	1.53	0 – 9.4	0.85	0 – 4.68	36.10	0 – 275.00
Total	3.13	0.2 – 11.1	0.89	0.02 – 4.69	40.20	3.19 – 275.80
Cladocera						
Moina minuta	0.20	0 – 4.4	0.01	0 – 1.17	2.44	0 – 35.26
Total	0.50	0 – 4.5	0.09	0 – 1.21	10.81	0 – 42.03
Rotifera						
Brachionus budapestinensis	10.40	0 – 153.0	0.02	0 – 0.61	1.37	0 – 18.41
B. calyciflorus	6.47	0 – 73.3	0.26	0 – 4.54	11.55	0 – 136.70
B. caudatus	20.65	0 – 231.0	0.09	0 – 1.16	3.24	0 – 45.69
B. urceolaris	4.19	0 – 37.8	0.11	0 – 1.02	2.74	0 – 30.70
Keratella americana	4.25	0 – 44.4	0.00	0 – 0.04	0.13	0 – 1.41
K. cochlearis	1.79	0 – 12.2	0.00	0 – 0.01	0.04	0 – 0.37
K. tropica	29.64	0 – 248.0	0.14	0 – 1.49	5.81	0 – 58.86
Lecane proiecta	19.52	0 – 274.0	0.09	0 – 2.47	4.90	0 – 74.18
Polyarthra vulgaris	13.62	0 – 94.0	0.07	0 – 0.56	2.63	0.07 – 10.67
Trichocerca spp.	14.54	0 – 106.0	0.05	0 – 0.42	1.79	0 – 12.75
Filinia spp.	4.15	0 – 40.0	0.02	0 – 0.20	0.48	0 – 3.37
Total	134.65	0.5 – 1089.2	0.94	0 – 15.88	42.18	0.29 – 477.73
Total	138.29		1.92		93.19	

dance in the main channel. In general, crustaceans were not numerically abundant in the Apure and did not seem to be reproducing to any significant extent in the main channel.

Sixty percent of the rotifers belonged to the planktonic family Brachionidae, which is often associated with relatively hard waters. Rotifers almost certainly reproduced in the main channel because up to 20% of the individuals were carrying eggs. Most littoral rotifers were rare in our samples. The abundance of *Lecana proiecta*, which is known to be associated with floating-grass meadows (Hauer, 1956; Koste, 1978), suggests strongly that off-channel habitats were important sources for the plankton found in the main channel, because the main channel is generally a poor habitat for macrophytes.

Patterns of abundance

The hydrograph of the Apure River follows a regular pattern that entails nearly constant change (Fig. 2). Water rises in early summer as the wet season brings rain to the drainage basin. Discharge increases rapidly and an extensive area is flooded. Discharge declines rapidly after reaching a peak in August. Although the rate of decline slows by December or January, the decline does not cease completely; low water is not a time of constant flows. High zooplankton abundance occurs during the low-water period (Feb–Apr: Fig. 3). Rising waters reduce zooplankton populations to very low levels. The relationship between abundance and discharge is thus strongly inverse and suggests a simple dilution effect.

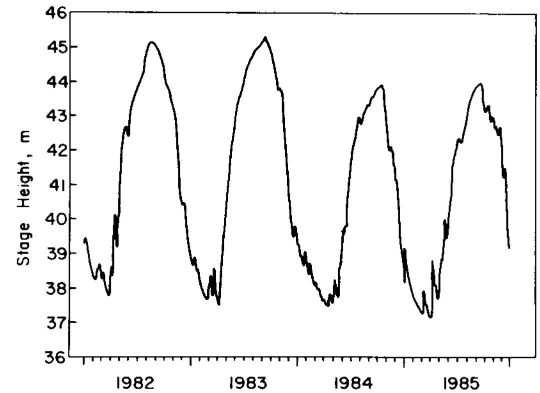

Fig. 2. Temporal pattern of stage height in the Apure River at San Fernando de Apure, 1982–1985.

Transport of biomass was highest during the low-water period and declined sharply as the river began to rise (Fig. 4). Transport rose again during peak dis-

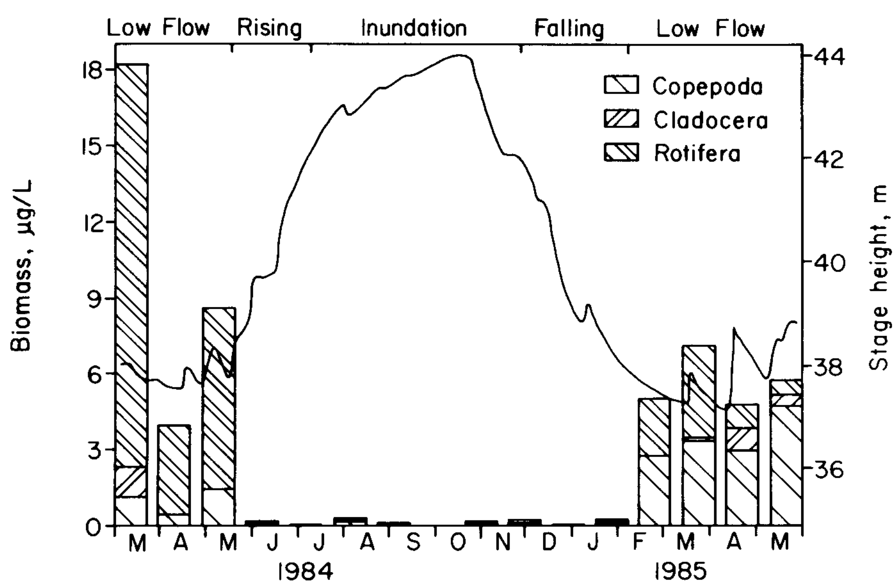

Fig. 3. Zooplankton biomass and stage height in the Apure River, 1984–1985.

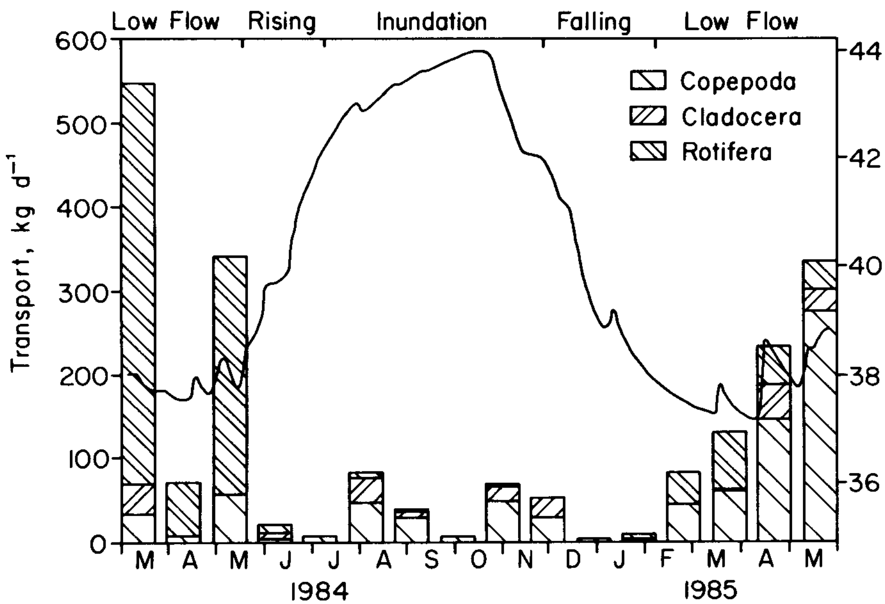

Fig. 4. Transport of zooplankton biomass and stage height in the Apure River, 1984–1985.

charge, but declined as river level fell. High transport at high discharge would not be expected if densities were responding only to dilution. The relationship between transport and discharge in the Apure River shows instead that high water level incorporates additional source areas (Fig. 5). At low water, zooplankton are derived mainly from caños or other water bodies confluent with the main channel. At high water, the river inundates the floodplain and engulfs the lakes on it.

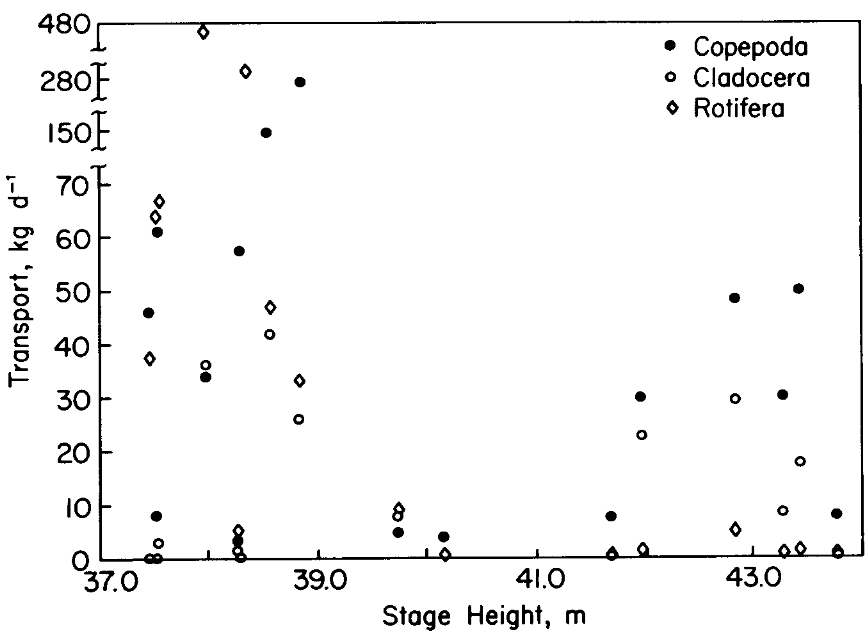

Fig. 5. Relationship between transport of zooplankton biomass and stage height for the Apure River, 1984–1985.

Table 2. Zooplankton densities (individuals · L^{-1}) from a longitudinal survey of the Apure River, June, 1984. See Figure 1 for the station locations.

	Main Stem				Caño	Tributaries		
	1	2	3	4	5	6	7	8
Brachionus spp	0.0	0.3	0.6	2.0	0.7	0.0	0.0	0.5
Keratella spp	0.0	0.3	1.8	12.6	1.1	0.0	0.0	1.2
Lecane spp	0.4	0.7	1.6	0.7	12.7	2.5	0.6	0.6
Other rotifers	2.0	0.7	2.6	1.7	6.1	5.1	2.6	6.7
Cladocera	0.0	0.3	0.0	0.3	0.6	0.0	0.0	0.0
Cyclopoid nauplii	0.0	0.0	1.8	0.4	1.7	2.5	0.0	2.1
Cyclopoid C1–C6	0.0	0.0	0.9	0.1	0.3	0.3	0.0	1.0
Total	2.4	2.6	15.3	17.8	23.5	10.4	3.2	12.1

Longitudinal survey

Samples were taken from the main stem of the Apure River (sites 1–4) and from two tributaries (sites 6–8). Site 4, which is at the mouth of the Apure, was sampled on 5 June. Site 5 is located in a large caño that is not part of the main channel, but that had detectable flow in June. At the time of sampling, the Apure had just begun to rise.

The caño site contained the highest zooplankton densities and was the most diverse site for the Cladocera (Table 2). Densities and species number in the Apure main stem increased markedly over the 600-km segment that was sampled. A similar increase in density and species number occurred between sites 7 and 8, which are 300 km apart on a major tributary, the Portuguesa. Some zooplankton populations in both rivers appear able to grow and reproduce in the flowing waters under low-flow conditions.

Discussion

Rotifer densities in the Apure River (mean, 135 L^{-1}) were high relative to other values reported for unregulated rivers in Venezuela. The difference is especially great when the Apure is compared to black-water rivers such as the Caura (5.4 L^{-1}; Saunders & Lewis, 1987), and supports the contention that white waters are more productive. At least part of the difference is attributable to reproduction of rotifers in the main channel of the Apure; zooplankton abundance in the Caura was controlled almost entirely by advective mechanisms.

Crustacean densities in the Apure (3.6 L^{-1}) do not differ greatly from those reported for the Caura (2.4 L^{-1}). Reproduction by copepods was not observed in either river, and reproduction by cladocerans was quite limited in both cases. Travel times in the Llanos (1–4 weeks) are sufficient to permit somatic growth of crustaceans in the Apure, but the data do not show the extent to which this potential may be realized. Advective mechanisms appear to regulate crustacean densities in the Apure.

Transport of zooplankton biomass in the Apure is the result of currents that carry organisms into the main channel and growth of populations in stagnant waters, principally at times of low discharge. Zooplankton biomass represents a relatively minor component (0.2%) of the total particulate carbon transported annually.

We can identify four hydrologic phases that have significant bearing on zooplankton transport in the Apure River. River level at San Fernando de Apure allows us to set temporal boundaries for the phases. The low-water phase is characterized by discharges below 350 $m^3 \cdot s^{-1}$, which is less than 20% of the annual mean discharge. During this phase, which lasts from February to April, zooplankton abundance is high, especially for the rotifers, and there is evidence of reproduction in the river. Caños and other water bodies confluent with the main channel probably comprise the principal source areas.

The river begins rising with the advent of the wet season in May or June. Early in the rising-water phase, the contents of caños and other low-lying source areas are flushed into the main stem, thereby augmenting transport. Flushing depletes these sources quickly and transport drops sharply as the river continues to rise. Additional source areas of any size are on the floodplain and make no contribution to transport in the main channel until the river rises above the natural levee along the riverbank.

A third phase corresponds to inundation of the floodplain. Zooplankton transport rises after the river inundates the floodplain because the numerous small lakes lose zooplankton to the flow. Other characteristics of the floodplain may also be important determinants of biomass transport during the inundation phase. By sheet flooding, the Apure creates an extensive area of low flow suitable for the development of zooplankton populations. Transport can thus be enhanced and sustained by growth during the high-water period. In contrast, when the Caura River inundates its narrow, fringing floodplain, the contents of suitable habitats are simply flushed into the river and transport cannot be sustained due to the continued rapid flushing (Saunders & Lewis, 1987).

During the inundation phase, copepods comprise proportionately more of transport than do rotifers or cladocerans. Rotifers are more important at low water. It is not clear whether this difference is attributable to compositional differences in the primary source areas (caños vs. floodplain lakes) or to the ability of copepods to grow well on the inundated floodplain. The inundated floodplain appears to be a highly productive environment that exports biomass to the river over a period of months. Transport of zooplankton biomass during the inundation phase represents export from the floodplain because river velocity is too high to permit reproduction. The observed export of zooplankton biomass probably represents only a fraction of actual production because most zooplankton biomass is undoubtedly lost to higher trophic levels (predators) within the floodplain habitat. Not all of the portion that is exported from the floodplain travels to the Orinoco via the mouth of the Apure River. The path of flow at times of sheet flooding causes part of the floodplain to drain directly into the Orinoco. Thus a portion of zooplankton biomass may bypass the main channel of the Apure.

The fourth and final phase begins as the river falls and loses contact with the floodplain. Because the main channel has been cut off from source areas in the floodplain, and conditions are not yet suitable for the development of zooplankton populations in caños, transport falls to very low levels. When the falling-water phase ends, we see a rise in transport as low-flow conditions allow the development of zooplankton populations in caños.

Seasonal fluctuations in river level regulate the development of source areas suitable for zooplankton growth, and control the export of plankton from these areas. At high water, plankton growth occurs only on the floodplain and not in the main channel. At low water, growth and reproduction in the main channel augment the transport of zooplankton biomass by the Apure River.

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