Zooplankton Abundance in the Caura River, Venezuela[1]

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ABSTRACT

Zooplankton abundance was studied in the Caura River, which drains 47,500 km² of undisturbed tropical moist forest within Venezuela. During 2 yr of sampling, 72 species were recorded, of which 10 accounted for more than 90 percent of the individuals. Copepods were represented almost exclusively by cyclopoid nauplii. Most of the cladocerans were from planktonic genera; *Bosminopsis* was the most abundant. The rotifer fauna was dominated by the planktonic genera *Filinia, Keratella, Conochilus,* and *Polyarthra*; *Lecane,* a littoral genus, was also common, especially at low water. The mean density of Crustacea was 2.4 organisms per liter (maximum, 10/liter) and the mean for Rotifera was 5.4 per liter (maximum, 35/liter). The annual export of zooplankton biomass from the watershed was 39,270 kg C.

The annual pattern of zooplankton abundance in the Caura River is closely related to hydrologic events. As the river rises early in the wet season and inundates the floodplain, zooplankton densities increase sharply. At peak discharge, densities fall to very low levels. Near the end of the wet season as the river recedes, floodplain lakes drain into the river and zooplankton abundance reaches the annual maximum. Abundance declines when the connection between river and floodplain disappears. There are also small pulses of abundance at minimum flow; these consist chiefly of organisms washed in from channel refuges in response to short-term fluctuations in river level. Reproduction is generally insignificant in the river. Virtually all organisms in the river are swept in from refuges in the channel or the floodplain of the Caura and its lower tributaries. Zooplankton density in the river is regulated by the flow regime and not by biological mechanisms.

RESUMEN

Se estudió la abundancia del zooplankton en el Río Caura durante un período de dos años. La cuenca hidrográfica del Caura abarca una superficie de 47,500 km² de bosque húmedo tropical, libre de perturbación humana. Se registraron 72 especies, de las cuales 10 constituyeron más de un 90 por ciento de los individuos. Los copépodos estaban representados casi exclusivamente por nauplios ciclopoides. La mayoría de los cladoceros pertenecían a géneros planctónicos, *Bosminopsis* siendo el más abundante. La fauna rotífera estaba dominada por los géneros planctónicos *Filinia, Keratella, Conochilus,* y *Polyarthra. Lecane,* un género litoral, también era abundante, particularmente en época de estiaje del río. La densidad media de crustaceos fué de 2.4 organismos/litro (máximo, 10 org./litro) y la media de rotíferos fué de 5.4 org./litro (máximo, 35 org./litro). La exportación anual de biomasa de zooplancton de la cuenca fué de 39,270 kg C.

El régimen anual de abundancia del zooplancton en el Río Caura está íntimamente relacionado con los eventos hidrológicos. Durante el inicio de la estación de lluvias, cuando el rió crece y alimenta las lagunas de inundación, la densidad del zooplancton aumenta pronunciadamente, para luego disminuir a niveles muy bajos, cuando el río alcanza su máxima descarga. Hacia finales de la estación lluviosa cuando el río comienza a receder y las lagunas de inundación drenan sus aguas, el zooplancton alcanza su máxima densidad anual. La abundancia luego disminuye al interrumpirse la comunicación entre las lagunas y el cauce principal. Pequeñas aumentos en la abundancia del zooplancton durante la época de aguas bajas responden a pequeñas fluctuaciones hidrológicas y se deben al lavado y a la incorporación al río de organismos provenientes de refugios de cauce marginales. La reproducción de los organismos en el río es insignificante. Practicamente todo el zooplancton presente en el río proviene de refugios de cauce marginales o de las lagunas de inundación asociados al cauce principal y a sus tributarios inferiores. Se concluye que la densidad del zooplancton en el Río Caura está regulada por el régimen hidrológico del mismo, y no por mecanismos biológicos.

RIVERS OFTEN CONTAIN an abundance of plankton, even though these organisms lack the ability to swim against currents (Hynes 1970, Winner 1975, Rzoska 1978). Factors that influence the abundance of plankton in rivers fall generally into two categories: factors affecting transport of organisms from source areas to the river, and factors affecting growth and reproduction of organisms in the river (Hynes 1970). Standing waters in contact with the channel may supply plankton to the river. Natural lakes and impoundments are obvious examples, but backwaters, oxbows, or braided channels with constant, low flow may be even more important in rivers that have not been extensively altered. The hatching of resting eggs in river sediments may also facilitate the development of zooplankton populations in rivers (Moghraby 1977). Within the river channel itself, the fate of plankton depends largely on the organisms' ability to grow and reproduce. In some large rivers, plankton density increases downstream, implying that the populations are able to reproduce (*e.g.,* Greenberg 1964). However, increases may vary seasonally with flow or may not occur at all (Hynes 1970).
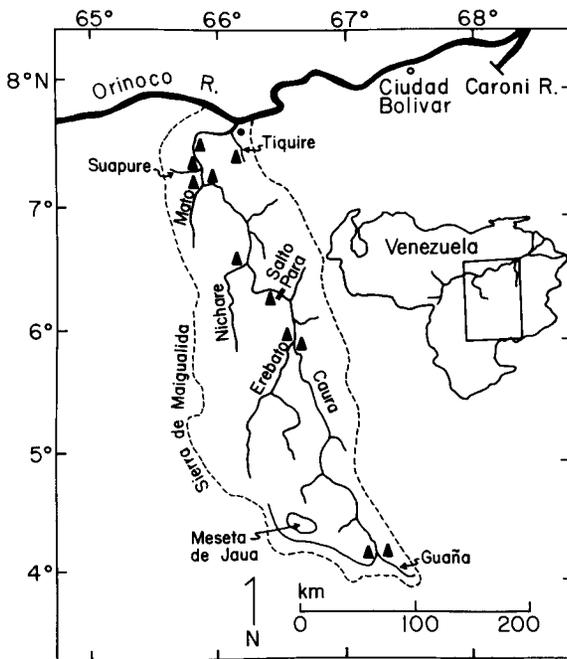
The influence of floodplain on zooplankton abun-

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

dances has seldom been separated from events that occur in the flowing waters of the channel for specific rivers. This is especially true of large tropical rivers, for which even simple documentation of abundance and species com-

position is poor. Ironically these rivers may provide some of the best opportunities for studying natural regulatory mechanisms because they have not been as extensively altered as most temperate rivers. Transit times for zooplankton in large tropical rivers may be very long, and thus would allow significant increases in abundance under conditions favoring reproduction. In addition, numerous tropical rivers have extensive segments of natural floodplain that may be major sources of zooplankton. With these advantages in mind, we determined the abundances and species composition of zooplankton in the Caura River, a majority tributary of the Orinoco River, for two years in an attempt to understand the regulation of zooplankton abundance in the river.

The Caura watershed is not altered, nor is the river impounded. Consequently, the abundances of zooplankton are natural. Furthermore, the Caura is a black-water river; little is known of organismic abundances in such rivers, which are commonly supposed to be virtually sterile because of low pH and high amounts of dissolved organic matter originating from land plants (Janzen 1974).

SITE DESCRIPTION

The Caura River drains a portion of the Pre-Cambrian Guayana Shield in south-central Venezuela (Fig. 1). The basin has an area of 47,500 km², most of which lies at elevations below 1000 m. Annual precipitation varies from 1.3 m in the dry tropical forest near the river mouth to more than 4 m in the rain forests surrounding the headwaters near the Brazilian border (Ewel et al. 1976). Av-
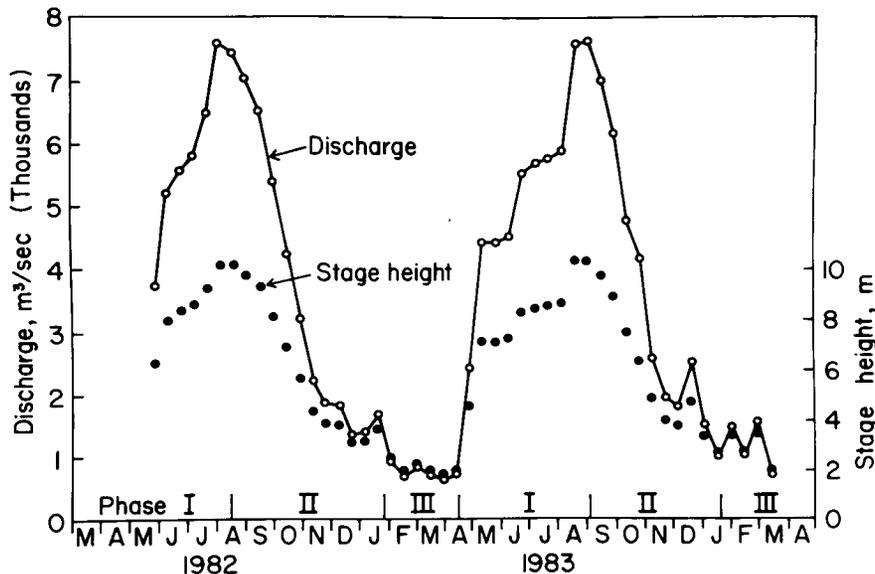

FIGURE 2. Temporal pattern of discharge and stage height at Maripa near the mouth of the Caura River.

erage discharge for the period of study was 3500 m³/sec. Peak discharge occurs in August at the height of the wet season (Fig. 2).

The Caura River originates at the Meseta de Jaua in the southwestern part of the basin and flows southeast near the Brazilian border for about 150 km. Near the confluence with the Guaña, a tributary that is very low in electrolytes and high in color, the Caura turns abruptly north. Over the next 250 km, the gradient of the river is relatively low (0.75 m/km), although there are rapids. In this reach are several tributaries from the western side of the basin, of which the Erebato is the largest. Just below the confluence with the Erebato, the Caura plunges over Salto Para, a spectacular cataract. Tributaries below this point, of which the Nichare and the Mato are the largest, typically have higher conductance and drain areas with vegetation types characteristic of lower elevations.

Undisturbed primary forest covers nearly all of the Caura watershed (NAS 1980), which Ewel et al. (1976) have partitioned into six life zones according to the Hold-ridge system. Dense rain forest (bosque pluvial premontano and bosque pluvial montano bajo) covers about 25 percent of the watershed and is located mostly at higher elevations around the Meseta de Jaua in the south and along the Sierra de Maigualida on the western edge of the basin. Very humid forest (bosque muy humido tropical and bosque muy humido premontano) occupies 37 percent of the basin at intermediate elevations and is mainly concentrated in the south and west. Much of the basin below Salto Para, as well as portions extending upstream along the Caura and the Erebato, are of the humid tropical forest category (bosque humedo tropical, 34%). The remaining 4 percent of the basin, which lies at the mouth of the Caura, is drier (bosque seco tropical) and is the locus of a minor amount of human activity. There has been virtually no development in the rest of the basin. Floodplain lakes occur along the lower reaches.

The waters of the Caura River are very low in electrolytes (mean specific conductance, 15 μS/cm at 25°C; range, 6–22) because of the low ionic yield of the Guayana Shield and the dense vegetation that retains nutrients (Lewis 1986). Although the concentrations of soluble organic carbon are not extraordinarily high (mean, 4.0 mg/liter; range, 1.8–7.4 mg/liter), the water is strongly colored by soluble organic matter (Lewis et al. 1986). The water is slightly acidic (median pH, 6.7; range, 5.9–7.4). Concentrations of total particulate matter are relatively low (mean, 13 mg/liter; range, 5–34) but vary with flow.

METHODS

Zooplankton samples were taken in midchannel near the mouth of the Caura River at biweekly intervals between March 1982 and April 1984. Thirty liters of water were collected with a motorized pump suspended at approxi-

mately 30 percent of the measured depth. 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. Identifications were based on Koste (1972, 1978), Michelangeli et al. (1980), Brandorff et al. (1982), and occasionally on more specialized sources. Species-level discrimination was not always feasible during routine counting. Biomass per individual was estimated from relationships presented in Bottrell et al. (1976). Dry mass is assumed to be 11 percent of body volume (Sitaramaiah 1967), and carbon is assumed to be 44 percent of dry mass.

Samples for a longitudinal profile of the Caura were taken at 5 stations along the river and from the mouths of 6 tributaries in June of 1984 (Fig. 1). Samples above Salto Para were collected at the surface with a rigid sampler; samples below the falls were taken as described above.

Stage height was related to discharge by means of a rating curve (Lewis et al. 1986). Stage height data were available on all sampling dates.

RESULTS

Species composition and relative abundance.—We identified 52 zooplankton species and subspecies in the Caura River (Table 1) and encountered at least 20 more for which species-level identification was not attempted. About half of these species are truly planktonic. Mean and maximum densities are low for all groups, especially the rotifers (Table 2). Much higher densities are reported for the Nile (Rzoska et al. 1955) and for the Illinois River (Kofoid 1908); comparable densities are reported for the River Sokoto (Holden & Green 1960) and the Parana Medio (Paggi & Paggi 1974). Low densities may be characteristic of black-water rivers (Cipolli & Carvalho 1973, Schaden 1978, Vasquez 1984). However, zooplankton densities in the Caura River do not suggest a sterile environment, even though they are lower than those of rivers draining rich agricultural areas. The annual export of zooplankton biomass from the Caura drainage was 39,270 kg C; crustaceans comprised 85 percent of the yield.

A few planktonic species account for the vast majority of individuals present in the Caura River. Adult copepods appeared rarely in our collections, which made the identification of species difficult. We found a few adults of the planktonic genus Tropocyclops, but no adult calanoids

TABLE 1. List of zooplankton taxa from the Caura River, 1982–1984.

Copepoda

Tropocyclops
calanoid
harpacticoid

Cladocera

Bosmina
Bosminopsis deitersi Richard
Bosminopsis sp.
Ceriodaphnia cornuta Sars
Daphnia gessneri Herbst
Diaphanosoma
Graptoleberis testudinaria (Fischer)
Ilyocryptus spinifer Herrick
Moina minuta Hansen
Streblocerus pygmaeus Sars
chydorids

Rotifera

Anuraeopsis
Asplanchna
Beauchampiella eudactylota (Gosse)
Brachionus caudatus Barrois & Daday
B. zahniseri Ahlstrom
B. patulus (O. F. Muller)
B. falcatus Zacharias
B. forficula Wierzejski
B. angularis Gosse
B. havanaensis Rousselet
B. dolobratus Harring
B. quadridentatus (Hermanns)
B. calyciflorus Pallas
B. urceolaris (O. F. Muller)
B. mirus Daday
Cephalodella
Collotheca
Colurella
Conochilus dossuarius var. *coenobasis* (Skorikov)
C. unicornis (Rousselet)
Dipleuchlanis propatula f. *macrodactyla* (Hauer)
Epiphanes macrourus Barrois & Daday
Epiphanes sp.
Euchlanis
Filinia longiseta (Ehrenberg)
F. pejleri Hutchinson
Keratella americana Carlin
K. cochlearis (Gosse)
K. lenzi (Hauer)
K. tropica (Apstein)
Hexarthra intermedia (Wiszniewski)
Lecane melini Thomasson
L. leontina (Turner)
L. obtusa (Murray)
L. bulla bulla (Gosse)
L. ludwigi (Eckstein)
L. proiecta Hauer
Lepadella
Macrochaetus
Monommata
Mytilina macrocera (Jennings)
Notholca
Platyias quadricornis (Ehrenberg)
Platyias quadricornis var. *brevispinus* (Daday)

TABLE 1. *(Continued).*

Ploesoma truncatum (Levander)
Polyarthra vulgaris Carlin
Scaridium longicaudum (O. F. Muller)
Squatinella ? leydigi (Zacharias)
Synchaeta stylata Wierzejski
Testudinella patina (Hermann)
T. mucronata hauerensis (Gillard)
Trichocerca similis (Wierzejski)
T. similis grandis (Hauer)
T. collaris (Rousselet)
T. cylindrica chattoni (de Beauchamp)
Trichotria tetractis (Ehrenberg)
bdelloid

or harpacticoids. Cyclopoid nauplii (*i.e.*, the first 6 of 12 postembryonic developmental stages) account for 85 percent of the copepods. Because cyclopoids lack resting eggs, the prevalence of their early life history stages without adults suggests that the young copepods come to the river from adjacent source areas and that they do not grow rapidly in the river.

Almost all cladocerans in the river are from planktonic taxa. *Bosminopsis* is the most common genus, and most individuals are assignable to *B. deitersi*. Only *Bosminopsis* shows evidence of reproduction in the river; about 20 percent of the individuals carry eggs. Vasquez (1984) also comments on the high relative abundance of *Bosminopsis* in the Caroni, another black-water river.

Although the list of rotifer species is quite long, few were common. Many of the littoral species were recorded only once or a few times in the 43 collections. Planktonic

TABLE 2. *Means and ranges for densities of the most common zooplankton in Caura River, 1982–1984.*

| Taxon	Density, individuals/liter	
	Mean	Range
Copepoda		
Cyclopoid nauplii	1.10	0–4.89
Total	1.30	0–5.18
Cladocera		
Bosminopsis	0.73	0–4.61
Diaphanosoma	0.09	0–1.00
Moina	0.07	0–0.53
Total	1.13	0–5.45
Rotifera		
Brachionus zahniseri	0.39	0–4.44
Conochilus dossuarius	0.14	0–3.33
Filinia pejleri	0.37	0–2.91
Hexarthra intermedia	0.11	0–1.81
Keratella americana	0.62	0–8.17
Keratella tropica	0.14	0–3.87
Lecane proiecta	0.22	0–4.47
Polyarthra vulgaris	2.33	0–17.30
Total	5.38	0.23–35.70
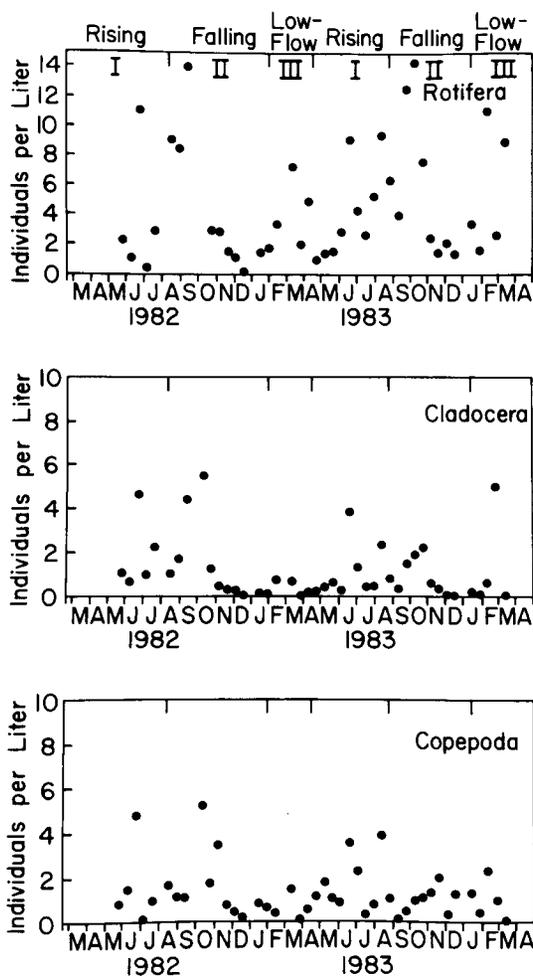
FIGURE 3. Temporal abundance patterns for Rotifera, Cladocera, and Copepoda in the Caura River.

species comprise 80–90 percent of the individuals. The scarcity of rotifer eggs, attached or unattached, implies that rotifers fare poorly in the river.

PATTERNS OF ABUNDANCE.—The annual hydrograph for the Caura can be divided into three parts: rising arm (phase I), falling arm (phase II), and low water (phase III) (Fig. 2). Zooplankton abundance reached peaks of varying magnitude in all three of these phases during 1982–1983 (Fig. 3). The greatest peaks occurred during phase II, at high water, but after peak discharge.

As the river rose during early phase I (April and May), habitat in the channel became more uniform and riverine, and plankton densities fell as the refuges within the channel were flushed. Between May and early June, the river rose above its banks and inundated the surrounding forest and the associated floodplain lakes. The inundation began at

a stage height close to 7 m. As the river continued to rise, it flushed the flooplain lakes and their resident zooplankton populations into the main channel. The effect of the inundation at stage heights above approximately 7 m can be seen clearly in plots of abundance against stage height (Figs. 4, 5).

In 1983, two abundance peaks occurred during phase I prior to maximum discharge. These corresponded to stage height reversals in the vicinity of 7 m. In late June, stage height rose quickly to about 8 m, at which time plankton abundance also rose sharply. River level was then steady, and zooplankton abundance fell. In early August the river rose abruptly again and produced another pulse of zooplankton in the river.

Zooplankton composition in phase I was dominated by planktonic species. Copepods were represented only by cyclopoid nauplii. Bosminopsis, Moina, and Diaphanosoma all increased in 1982. In 1983, Bosminopsis dominated the first peak and Diaphanosoma dominated the second. Filinia and Keratella were common in both years, but Conochilus and Brachionus were also important in 1982.

During phase II, as the river level fell, the floodplain reverted to a lacustrine character. Connections between river and floodplain persisted, however, until the stage height fell below 7 m. The drainage of the floodplain lakes resulted in the phase II maxima, which were also the annual maxima.

Initial increases in density during phase II were due almost entirely to rotifers; crustaceans became important later. Polyarthra, not common during phase I, was very conspicuous during phase II. Filinia and Hexarthra increased in abundance during 1982, but were replaced by Keratella in 1983. Bosminopsis, Diaphanosoma, and Moina lagged behind the rotifers in their abundance peaks. Copepod nauplii appeared near the end of phase II.

During phase III, at minimum stage height, the channel near the mouth became braided, and depressions in the exposed sand held pools of water. Spatial variation in velocity was much greater than at high water, and there was enough calm water to encourage the development of littoral zooplankton species. Short-term fluctuations in stage height, common during the low-water phase, apparently flushed plankton from stagnant channels and low-lying pools. The pulsed density variations and the high proportion of littoral species support this explanation. An increase in habitat diversity within the channel undoubtedly contributed to the greater species diversity at low water.

During phase III, a major portion of the abundance pulse was comprised of nonplanktonic species, of which a littoral rotifer, Lecane proiecta, was the most abundant species in both years. The abundance of L. proiecta seems anomalous, however. Koste (1978) reports that L. proiecta occurs in the floating grass "meadows" of floodplain lakes along the Amazon. Such habitats are rare along the lower
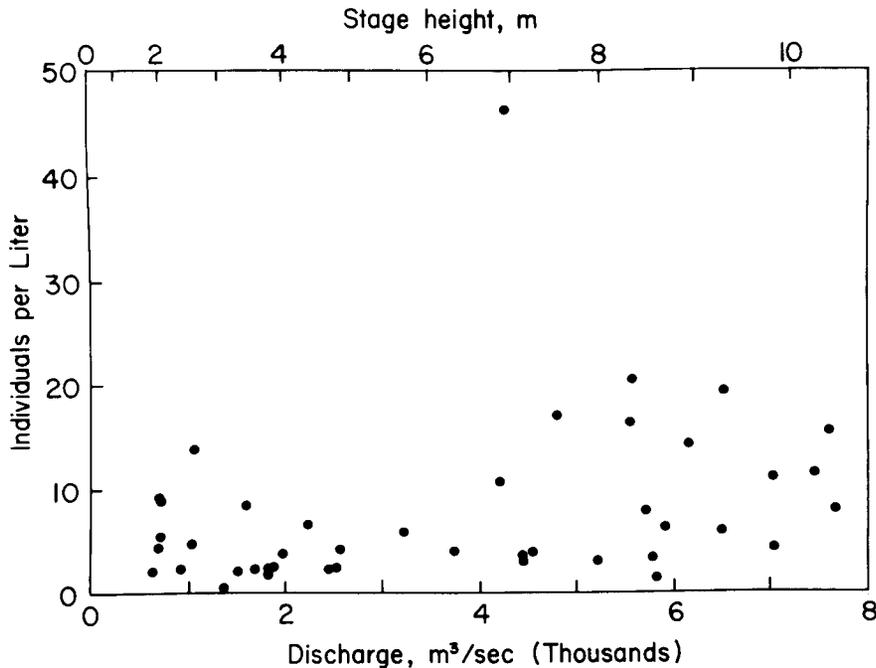
FIGURE 4. Relationship between total zooplankton density and discharge in the Caura River.

Caura, but suitable macrophytes may occur in the lower reaches of low-gradient tributaries such as the Mato or the Suapure. Planktonic genera (*Hexarthra, Keratella*, and *Filinia*) were also common, but less so than *Lecane*. Crustaceans increased less than rotifers at low water. The first year saw virtually no increase, and a modest increase in the second year was restricted to planktonic Cladocera (*Bosminopsis* and *Moina*). In phase III there was also a marked increase in the abundance of larger invertebrates, especially dipteran larvae.

Bosminopsis carried eggs at low water, but also at most other times. The most common rotifer at low water, *L. proiecta*, does not carry extruded eggs and thus yields no information on reproduction.

LONGITUDINAL SURVEY.—We conducted a longitudinal survey of the main stem of the Caura River and several major tributaries during June of 1984 to examine source areas for zooplankton. Stage height at this time was just below 6 m; the river had begun to rise but had not yet inundated the floodplain. Low densities of organisms were thus expected.

During the June survey, densities of copepods, consisting mainly of cyclopoid nauplii, were relatively constant along the river. However, two tributaries, the Erebato and the Mato, had higher densities than the Caura or the other tributaries (Fig. 6). No evidence indicated that copepods were maturing or reproducing in the river. Source areas could not be defined precisely.

Cladocerans were virtually absent in samples from the drainage above Salto Para. Densities below the falls were influenced by contributions from tributaries. More than 90 percent of the cladocerans were *Bosminopsis* and many individuals carried eggs, especially those from the Nichare and the Suapure. Littoral cladocerans such as the Chydoridae were rare (less than 5 percent of all cladocerans).

Rotifer densities followed a spatial pattern similar to that of the cladocerans. Abundances in the Caura were augmented by contributions from tributaries below Salto Para. Above the falls, littoral and benthic forms such as *Lecane, Trichocerca*, and bdelloids were more common than planktonic genera (mainly *Polyarthra*). *Polyarthra* was very abundant in the Nichare and the Mato, which also contained high densities of *Conochilus dossuarius*.

The tributaries below Salto Para, which contained high densities of rotifers and cladocerans, are very sluggish at low water and thus may offer a quasilacustrine habitat. The plankton living in this setting would be flushed out with rising water. Even these areas may not be ultimate sources of plankton inasmuch as reproduction was not evident in June.

DISCUSSION

The proximate factor regulating zooplankton abundance in the Caura River is the flow regime. Changes in water level that cause inundation of source areas augment zooplankton abundance in the main stem. Because discharge
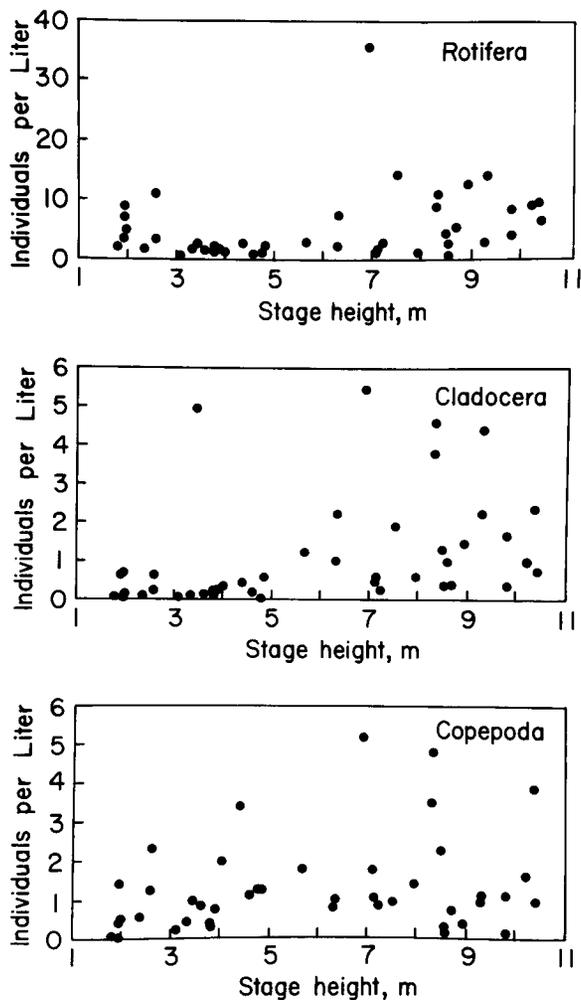
FIGURE 5. Relationship between stage height and density for Rotifera, Cladocera, and Copepoda.
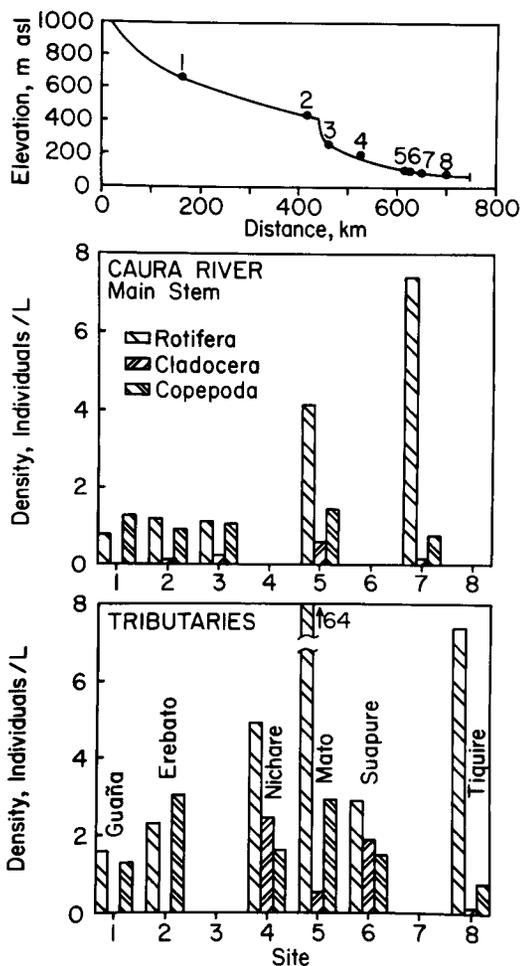

FIGURE 6. Longitudinal profile of Caura drainage showing zooplankton densities at 8 sites. The upper panel shows the elevational profile of the Caura River; the middle panel shows the density of zooplankton along the Caura mainstem; the lower panel shows the density of zooplankton at the mouths of 6 tributaries. Mainstem collections at sites 1, 2, and 5 were taken above the tributary mouth.

follows the same general pattern from year to year, the repeated pattern in zooplankton abundance resembles seasonal trends in many lakes. The similarity is completely superficial, however, because the pattern in the Caura River is based on variations in transport rather than variations in growth.

Water that is not flowing or that is flowing very slowly serves as a refuge and growth area for zooplankton along the Caura River. The quality or quantity of riverside refuges for cladocerans and rotifers improves below Salto Para. Low-water conditions in the channel also appear to increase refuges in close proximity to the river. Rising water first flushes these channel refuges, and subsequently flushes larger refuges in the floodplain further from the river.

Reproduction in the river is restricted to the cladoceran

Bosminopsis; other common species are not reproductive in the flowing water. The mechanisms inhibiting reproduction in the river are not known. The food supply in the Caura, as indicated by phytoplankton abundance, is generally poor, but nonliving particulate organic matter is relatively abundant. Rzoska (1978) has observed that velocities in excess of 0.4 m/sec are not conducive to growth of zooplankton. Velocities in the main channel of the Caura River typically exceed this. Resting eggs probably contribute nothing to the development of populations in the Caura. Only one cladoceran ephippium was recorded in 2 yr of study.

Since zooplankton populations do not grow in the

flowing waters of the river, transport of zooplankton biomass represents production of the floodplain and channel pools. The area of suitable floodplain habitat, which is relatively small in the Caura basin, does not exceed the water surface area of the river (ca 500 km²). The annual zooplankton yield of 39,270 kg C corresponds to a meager 0.08 g C/m²/yr. Zooplankton in oligotrophic lakes and in lakes at high latitudes with short growing seasons produce biomass at comparable rates (Wetzel 1983). Actual production in the floodplain, however, would exceed the yield, because we have not accounted for loss of zooplankton biomass to higher trophic levels within the floodplain.

The most comprehensive work on the zooplankton of tropical rivers deals with the Nile, which has a greatly altered hydrology. The Nile shows considerable seasonal variability in zooplankton abundances, and significant reproduction sometimes occurs in the river (Rzoska 1976). Zooplankton abundance in the River Sokoto, a major tributary of the Niger River, also has been studied; abundance was quite low and reached a maximum at low water (Green 1960, Holden & Green 1960).

A number of recent studies have dealt with zooplankton in rivers of eastern Venezuela. Sanchez et al. (1985) studied four small plains streams over a one-year period, but were unable to discern clear temporal abundance patterns. The highest densities for rotifers (191/liter) occurred in the middle of the wet season. Vasquez and Sanchez (1984) found that rotifer densities in the lower Orinoco River reach a maximum of about 400/liter at low water. *Keratella, Lecane,* and *Brachionus* were the most common genera. In a study of the Caroni River, a large black-water tributary of the Orinoco, Vasquez (1984) encountered maximum rotifer abundances of 5.2/liter at low water. The rotifer community in the Caroni was dominated by littoral and benthic forms, despite the proximity upstream of a very large reservoir. The high-water density maxima in the Caura are thus atypical of rivers in the region.

The relative importance of factors affecting transport and growth provides an explanation for contrasting temporal patterns of abundance. Reproduction is most likely to be successful at low water, when it constitutes the predominant mechanism responsible for abundance peaks. Because transport processes depend on the contact between river and source areas, the timing of abundance peaks produced by this mechanism may vary. Rising water will flush zooplankton from lentic areas into the river, first from low-lying areas and later from the inundated floodplain. Where floodplain source areas are negligible, either naturally or because the floodplain has been altered, rising water will flush adjacent source areas quickly and will probably not produce large abundance peaks. Moreover, without a large floodplain, no mechanism exists to produce abundance peaks during the falling arm of the hydrograph, which was the time of annual abundance maxima in the Caura River.

Transport from source areas along the Caura River results in higher densities of zooplankton in the river than would be suspected from the supposed sterility of black waters. Generally low abundances of zooplankton in black waters are at least partly attributable to high runoff in black-water areas. In standing black waters along the Amazon, Brandorff (1978) found crustacean densities 100 times higher than those of the Caura River. We did not measure the extent of source areas for the Caura, but they are limited and therefore must support high densities of organisms. Although zooplankton densities in the Caura River itself are low, they are not trivial ecologically. Comparable crustacean densities in the Orinoco main stem support fish that rely heavily on zooplankton for food (J. Lundberg, W. M. Lewis, Jr., J. F. Saunders, III, pers. comm.).

ACKNOWLEDGMENTS

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