Limnol. Oceanogr., 34(2), 1989, 397–409
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Zooplankton abundance in the lower Orinoco River, Venezuela

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

Abstract

Zooplankton were sampled quantitatively in the lower Orinoco River and three major tributaries (Apure, Caura, Caroni). Dominant taxa were euplanktonic, which suggests origin from standing waters. In the Orinoco, densities for rotifers (mean, 7.6 ind. liter^{-1}) were greater than those for cladocerans (0.9 ind. liter^{-1}) or copepods (1.2 ind. liter^{-1}), but cladocerans accounted for more than half of total biomass (0.5 μg C liter^{-1}). Average tributary contributions to zooplankton transport in the lower Orinoco (873 kg C d^{-1}) were proportional to their average discharges. Extensive fringing floodplain along the lower Orinoco contributed very little to total transport. At low water in the Orinoco, when there was no contact with the floodplain, the transport of copepods (mainly nauplii) and *Bosmina* increased downstream by more than could be ascribed to additions from the tributaries or to reproduction in transit. These zooplankton appear to originate along the river margin, within the channel, and are probably significant as an energy input for food webs in the channel and as an inoculum to floodplain habitats at the time of inundation.

Zooplankton are often abundant in the main channels of major rivers. The processes regulating their abundance may not be easily discerned, however, because of advection. Growth and mortality processes that are primary regulators of zooplankton populations in lakes also affect zooplankton as they are transported downstream by rivers. Superimposed are advective processes that control the influx of zooplankton to rivers from source areas and the continual loss downstream (Rai 1974; Hynes 1970).

Reservoirs now occupy the main channels of most large rivers and often provide continuous supplies of zooplankton to the rivers downstream. The influence of reservoirs on the development of zooplankton in rivers is well known, especially for highly regulated systems such as the Nile (Rzoska et al. 1955; Talling and Rzoska 1967; Brook and Rzoska 1954; Rzoska 1976) and the Murray (Shiel and Walker 1984; Shiel et al. 1982). Impoundment has altered the original zooplankton dynamics and has obscured the natural sources of zooplankton in rivers.

Natural source areas for river zooplankton must have low flushing rates, i.e. they must be essentially lentic habitats. Lentic source areas exist along the periphery of river channels. They may be divided into three categories on the basis of proximity to the channel: channel habitats, side-channel habitats, and floodplain habitats. Variations in river level govern contact of flowing waters with these source areas (Paggi and Paggi 1974). Channel habitats, which include eddies, channel pools, and river margins, may continuously contribute zooplankton to the flowing waters, or they may contribute zooplankton mainly in response to fluctuations in river level. Spates may cause the elimination of plankton from channel habitats (des Cilleuls 1928), although smaller but repeated fluctuations in river level may be more significant in this respect (Saunders and Lewis 1988*a*).

Side channels (anabranches and backwaters) may support plankton growth because these habitats have little or no flow when river levels are low. Seasonal rises in river level greatly increase flow in these habitats and thereby push resident plankton into the main channel (Osmera 1973; Vranovsky 1974; Saunders and Lewis 1988*b*). The difference between channel and side-channel habitats lies in the frequency with which

Acknowledgments

This study is part of a joint Venezuela–North American ecological investigation of the Orinoco River. Logistical support was provided by the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables. We thank S. Hamilton and S. Sippel for helpful discussions, and Bruce Kimmel and two anonymous reviewers for constructive criticisms.

This work was supported by NSF grants DEB 81-6725, BSR 83-15410, and BSR 86-04655.

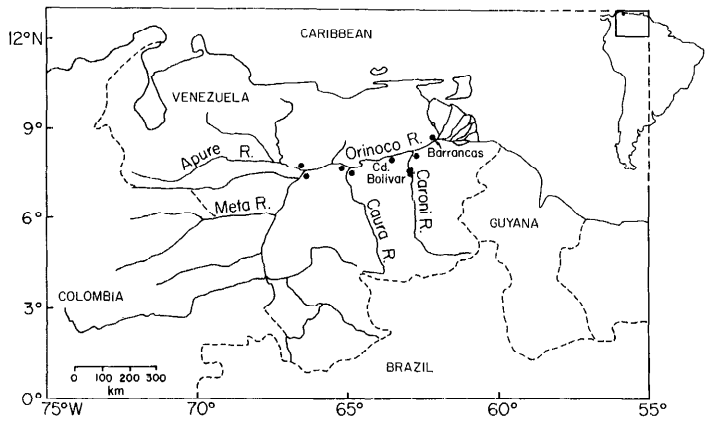

Fig. 1. Map of the Orinoco River watershed in Venezuela and Colombia. Sampling sites—●.

resident plankton are likely to be moved into the main channel. The frequency is more irregular and unpredictable for channel habitats than for side-channel habitats.

Undisturbed floodplain is typically separated from the main channel by a natural levee. Only when river water penetrates the levee will the floodplain be in contact with flowing water. Inundation of the floodplain may increase zooplankton abundance in the main stem by flushing the standing or slowly flowing waters of the floodplain into the river (Saunders and Lewis 1988*a*,*b*; Tait et al. 1984).

Reproduction of zooplankton in the flowing waters can increase plankton abundance (Talling and Rzoska 1967) but typically only at low flow; high current velocities appear to inhibit reproduction (Rzoska 1978). A role for resting stages deposited on the river bottom has also been proposed (Moghraby 1977), but it has not been shown to be of significance in unregulated rivers. The role of the floodplain in providing zooplankton to the main stem of an undisturbed river system is inadequately understood. It is clear that under some circumstances floodplain water bodies may strongly influence the composition of zooplankton in a river (Green 1960; Shiel and Walker 1984; Bonetto 1986; Paggi and Paggi 1974). It is virtually unknown, however, how much biomass comes from floodplains or how it compares to the annual transport of zooplankton biomass. Recent work on phytoplankton in the Orinoco River demonstrated that only 37% of annual transport is derived from the floodplain (Lewis 1988); other biomass originates from headwaters, side channels, or channel habitats. This finding suggests that nonfloodplain habitats may also be important sources of zooplankton.

For the present study, zooplankton abundances and transport in the lower Orinoco River and its main tributaries were quantified for 3 yr. Patterns of transport are used to identify mechanisms and sources regulating zooplankton abundance, and a mass-balance approach is used to estimate the yield of zooplankton biomass from the floodplain. Because the Orinoco River floodplain is relatively undisturbed by human activity, it presents an unusual opportunity to study the natural interaction of a large river and its floodplain. The lack of hydrologic regulation and the negligible influence of impoundments on the Orinoco at present are equally important. These factors, which may have obscured the natural mechanisms controlling zooplankton transport in many large rivers, do not yet influence zooplankton transport in the Orinoco.

Site description

The Orinoco River, which has its headwaters in the southernmost part of Venezuela, drains a watershed of 950,000 km^2 in Venezuela and Colombia (Fig. 1). The Orinoco main stem flows along the northern

edge of the Precambrian Guayana Shield and receives water from geologically and ecologically diverse tributary watersheds. Waters draining the shield, of which the Caura River is representative, are typically of very low ionic strength and are darkly stained by dissolved organic carbon (Lewis et al. 1986). To the north and west of the main stem lies the Llanos, much of which is a vast alluvial plain that supports tropical savanna. As is typical of the waters that drain the Llanos, the Apure River has its headwaters in the Andes and is high in electrolyte and suspended solids (Lewis and Saunders 1988; Saunders and Lewis 1988*c*).

The main stem of the Orinoco is unregulated, and the floodplain is largely undisturbed by human activity. The narrow fringing floodplain along the main stem covers about 6,940 km^2 below the Rio Meta and above the delta (Hamilton et al. unpubl.). The average width of the floodplain (both banks) is ~8 km, within which there are 2,294 lakes that retain water throughout the year (mean area, 21 ha per lake at low water: Hamilton et al. unpubl.).

Three major tributaries enter the lower Orinoco. The varied combinations of chemistry, flow regime, and floodplain among these three tributaries provide very different environments for zooplankton. The Caura is an unregulated, blackwater river with a relatively small floodplain that is confined to an area within 100–200 km of the mouth. The Caroni, which is also a blackwater river, is regulated by the only major impoundment in the Orinoco watershed, the Guri Reservoir, and lacks a well-developed floodplain. The whitewater Apure River is unregulated and has an abundance of aquatic habitats in its floodplain. The flat terrain of the surrounding Llanos is subject to sheet-flooding of pluvial or fluvial origin (Welcomme 1979). As much as 117,000 km^2 of the surrounding Llanos may be inundated by a combination of rainwater and river water, although only a few thousand square kilometers is actually in direct contact with the river. An internal delta of 4,920 km^2 exists between the mouths of the Apure and Capanaparo Rivers, where high water in the Orinoco obstructs tributary flow (Meade et al. 1983). The internal delta contains 1,300 permanent lakes.

Methods

Zooplankton samples were taken at four sites along the Orinoco main stem and from the mouths of three tributaries (Caura, Caroni, and Apure: Fig. 1). Samples were collected biweekly from March 1982 to March 1984 and at 4-week intervals between March 1984 and May 1985. The two uppermost sites (the mouth of the Apure and the Orinoco above the Apure) were not sampled until March 1984.

At each sampling site a composite sample (30 liter) of river water was collected by an electric pump with the intake suspended at ~30% of the maximal depth at each of four points across the channel. A funnel was attached to the intake to minimize avoidance by larger crustaceans (Elster 1958). Pumps are the most practical collection technique for large rivers (Bottrell et al. 1976; Waite and O'Grady 1980). A 35-μm-mesh net was used to capture the zooplankton, which then were preserved with a sucrose-Formalin solution (Haney and Hall 1973). Rose bengal was added to each sample to make it easier to distinguish organisms from other suspended solids.

Subsamples were counted until at least 100 individuals of the most abundant taxon were recorded or until the entire sample had been examined. Rotifers and crustaceans were usually counted separately because they differed greatly in average numerical density. Dead individuals (i.e. empty loricas or exoskeletal remains) were not counted. Biomass per individual was estimated primarily from length–mass or length–volume relationships presented by Bottrell et al. (1976). Lengths were measured for all common species. Dry mass is assumed to be 11% of body volume (Sitaramaiah 1967), and carbon is assumed to be 44% of dry mass (Sverdrup et al. 1942). In most cases, counts and biomass estimates were based on species-level identifications (*see* Lewis et al. 1989). Identification of rotifers was based primarily on Koste (1978); references consulted for crustaceans include Reid (1985),

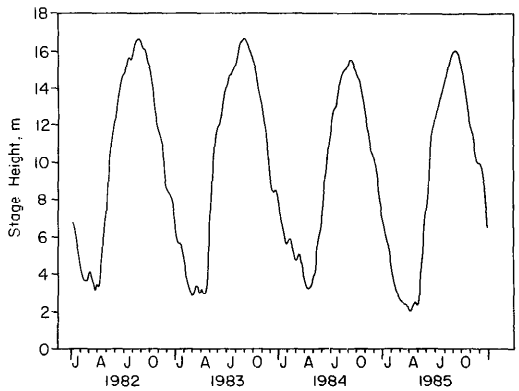

Fig. 2. Stage height of the Orinoco River at Ciudad Bolivar, 1982–1985.

Brandorff et al. (1982), Paggi (1978), and Rey and Vasquez (1986).

Daily stage height readings or discharge were available for the three main tributaries and for the Orinoco at Ciudad Bolivar for the period of study (Lewis 1988). Discharges at the other main stem sites were computed by adjusting the discharge at Ciudad Bolivar for tributary flows.

Results

Hydrologic regime—Major hydrologic features are relatively uniform among the three major tributaries to the lower Orinoco despite great variations in precipitation and physiography within the drainage basin (Lewis 1988). Peak discharge occurred almost simultaneously in the main stem and at the mouths of the major tributaries (except for the Caroni, which is regulated by the Guri Reservoir). Although the hydrograph reflects nearly continuous change in discharge, it is useful to distinguish four phases. The low-water phase, which typically begins in January or February, is characterized by low and slowly changing discharge. In the main stem, stage height during this phase changes <10 cm d^{-1} (Fig. 2). Minimal flow occurs in late April or early May. The rising-water phase is brief and culminates with inundation of the floodplain. Although the river remains within its banks during this phase, it flushes channel and side-channel habitats. The inundation phase begins as the river passes through the natural levee. Peak discharge typically occurs in late August or early September. Inundation brings the river into contact with the many water bodies of the floodplain. High flows typically reduce the residence times of floodplain lakes to a scale of hours or days (Hamilton and Lewis 1987). The falling-water phase begins when the river is back within its banks. The floodplain continues to drain into the river during the early part of this phase.

Most of the flow (73%) reaching the mouth of the Orinoco is derived from parts of the basin above the Apure River. The Caura, the Caroni, and the Apure contribute 9, 11, and 7% of the flow (Lewis 1988).

General patterns of abundance and transport—Planktonic genera dominated the zooplankton of the lower Orinoco and its tributaries (Table 1). Rotifers were present at higher densities than the other two zooplankton groups in all years at all sites. In the Orinoco main stem, average rotifer densities tended to decrease downstream for all major genera except *Trichocerca,* which contains many heleoplanktonic species. Rotifers were least abundant in the Caura and the Caroni Rivers and were most abundant in the whitewater Apure River. Cladocerans were most abundant in the main stem; average densities were lower in the tributaries (Table 1). There were no uniform longitudinal trends for cladoceran densities in the main stem. Copepods increased in density downstream (Table 1). Cyclopoid nauplii were primarily responsible for this pattern; later developmental stages were not abundant. Nauplii are common elements of the plankton in rivers (Welcomme 1979; Saunders and Lewis 1988*a,b*).

Biomass in the main stem was dominated by cladocerans, which comprised $>50\%$ of total zooplankton biomass; rotifers were usually more abundant than copepods (Table 2). In the Caura and Caroni Rivers, where zooplankton biomass was very low, rotifers were typically less abundant than either cladocerans or copepods. In contrast, rotifers comprised nearly 90% of total biomass in the Apure, despite small biomass per individual. The biomass of cladocerans and copepods was surprisingly low in the Apure; it was comparable to that of the two blackwater rivers.

Table 1. Average densities of the major zooplankton genera in the lower Orinoco and its tributaries. Averages are for 3 yr of data at all sites except Orinoco above Apure and Apure mouth, for which only 1 yr of data was available.

	Main stem				Tributaries		
	Above Apure	Above Caura	Ciudad Bolivar	Barrancas	Apure mouth	Caura mouth	Caroni mouth
Rotifera							
Brachionus	1.82	1.40	0.85	0.55	16.04	0.38	0.03
Filinia	2.14	0.94	0.73	0.43	4.29	0.46	0.03
Keratella	8.17	5.32	4.95	2.12	14.34	2.04	0.07
Lecane	2.78	2.34	1.48	0.99	8.49	0.34	0.21
Trichocerca	5.08	1.83	3.32	2.70	7.93	0.66	0.24
Other	6.27	2.51	4.04	0.83	11.10	4.50	0.19
Total	26.26	14.35	15.37	7.62	62.20	8.38	0.77
Cladocera							
Bosmina	0.47	0.26	0.86	0.47	0.04	0.06	0.09
Bosminopsis	2.58	0.78	0.69	0.11	0.04	0.88	0.09
Ceriodaphnia	0.17	0.09	0.18	0.06	0.01	0.04	0.01
Diaphanosoma	0.20	0.31	0.37	0.15	0.04	0.08	0.01
Moina	0.49	0.28	0.20	0.12	0.03	0.07	0.01
Total*	3.97	1.73	2.32	0.92	0.21	1.18	0.22
Copepoda							
Cyclopoid	0.64	0.60	1.06	0.97	2.00	1.03	0.20
Calanoid	0.13	0.10	0.20	0.25	0.10	0.13	0.08
Total*	0.79	0.72	1.26	1.23	2.10	1.20	0.29

* Other taxa present at densities <0.10 ind. liter^{-1}.

The contributions of the tributaries to transport in the Orinoco were proportional to discharge, as shown by discharge-weighted mean biomass, which was comparable at all sites (Table 2). Cladocera were dominant and usually comprised more than half of total annual transport. Interannual variation in transport was low at any given site in the rivers; it varied by less than a factor of two for total biomass transport and usually by less than a factor of three for transport of any one of the three major zooplankton groups.

Seasonal patterns of abundance—Temporal boundaries for phases were defined by river stage height at Ciudad Bolivar, even though the timing of phases varied slightly at other points in the watershed. Water level is an effective indicator of contact between the river and lentic source areas (Hamilton and Lewis 1987; Bonetto 1986; Paggi and Paggi 1974). Rotifer densities in the main stem were inversely related to discharge (Fig. 3); low-water densities were more than an order of magnitude greater than high-water densities. Average cladoceran and copepod densities in the main stem were also at least 10 times greater during the low-water phase than at high water. The lowest densities were not consistently assignable to a specific phase for either the Cladocera or the Copepoda, although the rising-water phase was generally the time of lowest densities.

Temporal density patterns in the tributaries differed from those in the Orinoco. In the Caura River, densities were highest during the inundation phase, despite high discharge. Patterns in the Caura were influenced much more than in the main stem by the flushing of floodplain water bodies during inundation (Saunders and Lewis 1988*a*). Densities in the Caroni were lowest during the falling-water phase and were higher and relatively constant at other times; patterns were controlled by the Guri Reservoir. In the Apure, rotifer and copepod densities were high not only during the low-water phase, but also during the rising-water phase. Cladoceran densities in the Apure were very low in all phases; they did not show the low-water maximum characteristic of the main stem.

Contributions by the tributaries had relatively little effect on longitudinal patterns

Table 2. Annual average biomass and transport of major zooplankton groups in the lower Orinoco and its tributaries. (No data are available for the Orinoco above Apure or the Apure mouth in years 1 and 2.)

	Biomass (μg C liter⁻¹)				Transport (kg C d⁻¹)				Discharge-weighted mean biomass (μg C liter⁻¹)
	Rotifera	Cladocera	Copepoda	Total	Rotifera	Cladocera	Copepoda	Total	
Year 1									
Orinoco above Caura	0.04	0.12	0.05	0.21	119.75	374.14	148.71	642.60	0.25
Orinoco at Ciudad Bolivar	0.16	0.29	0.07	0.53	171.74	535.11	169.18	876.03	0.30
Orinoco at Barrancas	0.04	0.22	0.18	0.45	88.35	431.77	490.05	1,010.17	0.31
Caura mouth	0.06	0.24	0.06	0.36	25.67	102.88	23.46	152.01	0.51
Caroni mouth	0.00	0.10	0.03	0.13	1.11	77.25	7.90	86.26	0.23
Year 2									
Orinoco above Caura	0.19	0.34	0.05	0.58	159.56	348.76	88.59	596.91	0.23
Orinoco at Ciudad Bolivar	0.11	0.45	0.15	0.71	171.37	660.32	347.59	1,179.28	0.40
Orinoco at Barrancas	0.03	0.30	0.15	0.48	57.55	477.48	299.42	834.45	0.26
Caura mouth	0.07	0.15	0.06	0.28	17.34	53.90	16.15	87.39	0.30
Caroni mouth	0.01	0.08	0.07	0.16	2.97	42.13	37.34	82.44	0.25
Year 3									
Orinoco above Apure	0.24	0.59	0.08	0.91	148.69	399.39	96.71	644.79	0.32
Orinoco above Caura	0.20	0.57	0.12	0.89	148.63	487.55	246.18	822.36	0.38
Orinoco at Ciudad Bolivar	0.19	0.85	0.17	1.20	171.46	672.66	477.97	1,322.10	0.54
Orinoco at Barrancas	0.12	0.35	0.13	0.60	141.96	431.58	200.30	773.84	0.27
Apure mouth	0.85	0.06	0.08	0.98	20.66	7.97	4.75	33.37	0.21
Caura mouth	0.04	0.15	0.08	0.28	8.72	52.36	28.20	89.29	0.35
Caroni mouth	0.01	0.04	0.05	0.10	4.02	17.09	37.30	58.42	0.14
Average									
Orinoco above Apure*	0.24	0.59	0.08	0.91	148.69	399.39	96.71	644.79	0.32
Orinoco above Caura	0.14	0.34	0.07	0.56	142.65	403.49	161.16	707.29	0.29
Orinoco at Ciudad Bolivar	0.15	0.53	0.13	0.81	171.53	622.70	331.58	1,125.80	0.41
Orinoco at Barrancas	0.07	0.29	0.16	0.51	95.95	446.94	329.92	872.82	0.28
Apure mouth*	0.85	0.06	0.08	0.98	20.66	7.97	4.75	33.37	0.21
Caura mouth	0.06	0.18	0.07	0.31	17.24	69.71	22.60	109.56	0.39
Caroni mouth	0.01	0.07	0.05	0.13	2.70	45.49	27.51	75.70	0.20

* Year 3 only.

of abundance in the main stem for most of the year. Except during the inundation phase in the Caura, densities in the two blackwater rivers (Caura, Caroni) were less than those observed in the main stem and thus could not have increased densities within the study reach (Fig. 3). In the Apure the densities of rotifers (but not of copepods or cladocerans) typically exceeded those in the main stem, but because discharge in the Apure was <10% of that in the Orinoco, the net effect of additions from the Apure was small. Without significant reproduction in the flowing waters, zooplankton densities in a water mass traveling downstream in the main stem would be expected to remain steady or to decline downstream through mortality, and this pattern was predominant for the three major zooplankton groups. During the inundation phase, when organisms might have been washed from the floodplain into the channel, the average pattern was still one of downstream decline in the lower Orinoco.

Seasonal and longitudinal patterns of transport—If biomass were a conservative substance derived from a single, constant source, its abundance per unit of volume would vary inversely with discharge and its transport would be constant. Although biomass in the Orinoco was inversely related to discharge, transport was not constant (Fig. 4; average for each hydrologic phase computed as in Fig. 3). In the main stem, the low-water phase was typically the time of highest transport for total zooplankton biomass. Transport was also relatively high during the inundation phase, when dis-

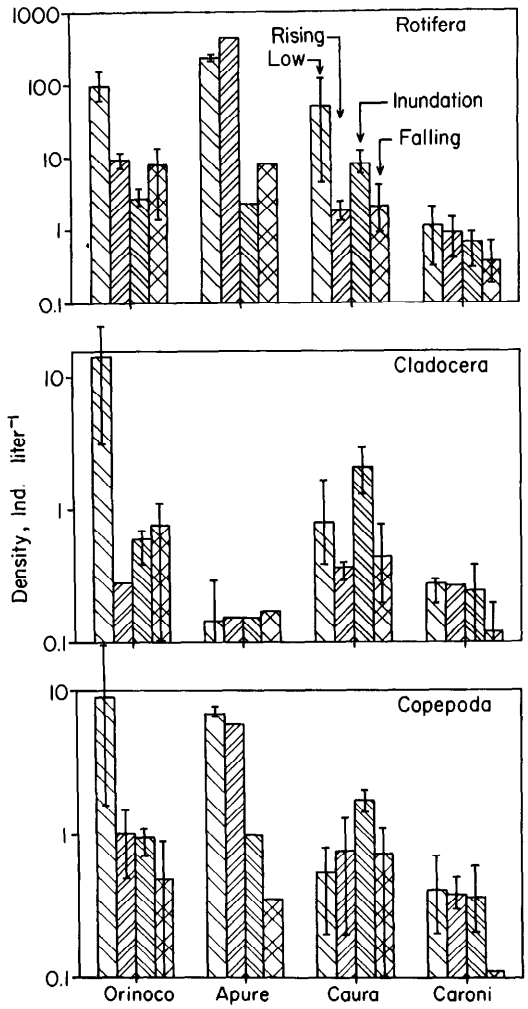

Fig. 3. Average densities during each phase for each group in the Orinoco at Ciudad Bolivar and in three tributaries. Bars indicate range of values for 3 yr except rising-water phase ($N = 2$) and the Apure (1 yr except for low water where $N = 2$).

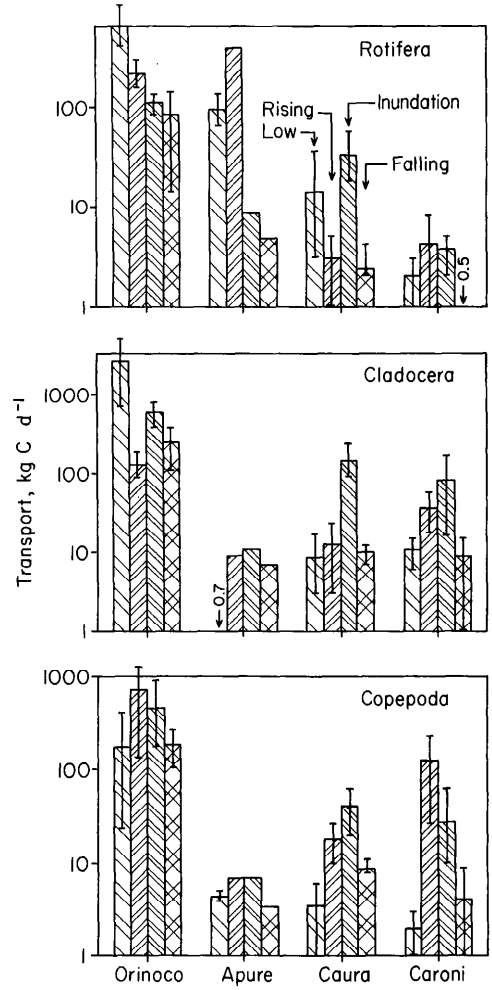

Fig. 4. Average transport during each phase for each group in the Orinoco at Ciudad Bolivar and in three tributaries. Bars indicate range of values for each season. Averages are based on seasonal values for 3 yr except rising-water phase ($N = 2$) and the Apure (1 yr except for low water where $N = 2$).

charge was greatest. For rotifers, peak transport occurred during low water and transport was relatively low during the three other phases. Cladoceran transport also reached a peak at low water, but transport during the inundation phase was almost as high. For the copepods, transport during the inundation phase usually exceeded that of low water. Cladocerans and copepods thus tended to comprise a greater proportion of total transport during the inundation phase than during the other phases (Table 3).

The three tributaries showed superficially similar seasonal patterns of transport (Fig. 4): transport was highest for all three zooplankton groups during rising water or inundation. Zooplankton typically grew poorly, if at all, in the flowing waters of the Caura river (Saunders and Lewis 1988*a*). The annual pattern of transport was determined primarily by the flushing of plankton from floodplain habitats when the river rose above its banks. There was also evidence for the importance of contributions from nonflowing or slowly flowing channel habitats for certain taxa (e.g. *Bosminopsis*). Due to im-

Table 3. Transport of cladoceran and copepod biomass as a percent of total zooplankton transport at each site for each hydrologic phase.

Site	Hydrologic phase			
	Low	Rising	Inundation	Falling
Orinoco above Apure	66	44	87	80
Orinoco above Caura	65	65	88	81
Orinoco at Ciudad Bolivar	81	79	90	83
Orinoco at Barrancas	93	82	92	90
Apure mouth	5	4	67	68
Caura mouth	46	91	85	89
Caroni mouth	86	97	97	96

Table 4. Relative contributions of major sources to total biomass transported within each hydrologic phase and relative importance of each phase to annual total. Data are from March 1984 to May 1985 when all four sites were sampled concurrently. The interval encompasses five hydrologic phases, beginning and ending with low water. Transport for the two low-water phases was averaged before computing the annual composite. The distribution of transport among sources differed little for the two low-water phases if calculated separately (91 and 93% for Orinoco above Apure).

Phase	Phase total as % of annual composite	Source as % of phase total			
		Orinoco above Apure	Apure mouth	Caura mouth	Caroni mouth
Low	43	92	5	2	1
Rising	16	45	31	1	23
Inundation	27	57	4	34	5
Falling	15	93	3	4	<1

poundment, transport in the Caroni was proportional to discharge for all three groups, reflecting the lack of seasonal diversity in sources. In the Apure River, significant reproduction and growth of zooplankton probably occurred in the flowing waters at low discharge, which would explain the high transport at very low discharge (Saunders and Lewis 1988*b*). Even higher transport rates occurred, however, when side-channel habitats were flushed during the rising-water phase.

Discharge-weighted average biomass helps illustrate the relationship between transport and discharge. In the Orinoco main stem, and in the Apure, discharge-weighted average biomass was less than time-weighted average biomass because biomass was high at low discharge (Table 2). For the Caura, where flushing of standing waters was the predominant mechanism of transport, the discharge-weighted biomass exceeded the time-weighted average biomass because there was a positive relationship between biomass and discharge. The same was true of the Caroni, except that the explanation involves export from the Guri Reservoir.

The total biomass that entered the lower Orinoco, either from the upper parts of the basin or from the three tributaries, was not evenly distributed over the hydrologic phases (Table 4). More than 40% of the annual total entered the lower Orinoco during the low-water phase when the tributaries contributed virtually nothing and the river was receiving no water from the floodplain. In contrast, about half of the biomass entering the lower Orinoco during the rising-water and inundation phases came from the tributaries. The flushing of side channels along the Apure during the rising-water phase and the flushing of water bodies on the Caura floodplain during the inundation phase were the principal mechanisms explaining these tributary contributions.

Regulation of biomass transport in the Orinoco main stem—The balance of growth and mortality in transit will affect transport. The proportion of individuals carrying eggs in a population may be taken as an indicator of reproductive activity, but cannot be used to identify where the eggs were produced because the eggs may be carried for up to 2 d at ambient temperatures in the Orinoco (cf. Bottrell et al. 1976). Thus egg ratios set an upper bound on the importance of reproduction in transit. Egg ratios for the major groups were low in the flowing waters of the main stem, even at lowest water. Rotifers carried eggs only at current velocities <1.5 m s^{-1}, and the egg ratio tended to increase with decreasing velocity below 1.5 m s^{-1}. Cladocerans also carried few eggs at velocities >1.5 m s^{-1}, but showed no inverse relationship of egg ratio to velocity <1.5 m s^{-1} (maximal ratio, ~1.0 egg ind.$^{-1}$). Copepod eggs appeared so rarely that reproduction of this group in the flowing waters of the main channel seems to be insignificant. We conclude that reproduction in transit was very limited and had no impor-

Table 5. Seasonal comparison of transport observed at Barrancas with that expected from the sum of transport observed in the Caura, Caroni, and Orinoco above the Caura. Table values are the observed minus the expected expressed as a percent of the expected. (Asterisks: *—$P \leq 0.05$; **—$P \leq 0.01$.)

	Hydrologic phase			
	Low	Rising	Inundation	Falling
Rotifera				
Brachionus	−63.3	26.7	−45.8	−63.4
Filinia	−54.5	17.6	−52.3	−59.4
Keratella	−84.2	301.2	−100.0	−41.2
Lecane	−62.7	95.1	−22.7	−32.9
Trichocerca	89.7	964.5	−88.7	−43.7
Other Rotifera	−67.8	−75.3	−38.5	−55.1
Total Rotifera	−60.4	24.9	−42.5	−49.0
Cladocera				
Bosmina	225.6*	−58.1	−32.9	354.1**
Bosminopsis	−70.3	−85.9	−44.8	−86.8
Ceriodaphnia	−2.4	−100.0	−12.6	−100.0
Diaphanosoma	−2.4	−51.4	−16.0	−75.9
Moina	−25.6	−20.4	29.7	−58.4
Total Cladocera	53.9	−56.4	−27.7	−10.1
Copepoda				
Cyclopoid	111.0	−15.1	−2.8	5.8
Calanoid	1,410.8*	7.3	90.1	87.6
Total Copepoda	577.4*	−1.0	65.8	65.0*
Total	49.4	−19.2	−5.1	1.0

tant effect on the overall abundance of river zooplankton.

Significant population changes in transit would cause changes in transport between two sites along the main stem after adjustments for contributions from tributaries (Table 5). Sites for this comparison were chosen to maximize the transit distance while maintaining an adequate sample size. A *t*-test for paired comparisons was used against the null hypothesis that values observed at Barrancas were less than or equal to those expected. Trends for individual taxa were in some cases completely different than those for other taxa in the same group (Table 5). For example, transport of *Bosmina* increased significantly in the Orinoco as the water mass traveled downstream during falling and low water, but transport declined for all other cladoceran genera. The seasonal pattern for rotifers was quite different from that of cladocerans and copepods. The general pattern for major rotifer taxa was one of downstream decline in transport except during rising water. The significance of the seasonal patterns can be demonstrated by the low probability ($P = 0.03$) that all six rotifer taxa would show, by chance alone, the same sign for change in transport. Cladocerans and copepods that showed increases did so during falling and low water. By examining the hydrologic phases separately, potential source areas can be greatly restricted. Thus it can be inferred that washout of side-channel habitats was an important mechanism of transport for rotifers and that contributions from channel habitats and perhaps floodplain drainage were more important for cladocerans and copepods. Copepods were the main group that showed increases in abundance downstream.

Contributions of the Orinoco floodplain would appear in Table 5 as cases where observed transport exceeded expected transport (positive values) during inundation and perhaps also during falling water. An important role for the floodplain is thus not indicated, despite the floodplain's considerable potential for an important contribution. Preliminary data on zooplankton in the floodplain can be used to produce an estimate of the biomass present at the time of inundation. Mapping of floodplain water bodies between the Caura and Barrancas shows a total surface area at low water of 173 km^2 (Hamilton et al. unpubl.). Al-

though the lakes vary in depth, field experience suggests a mean depth of 1 m. Given a mean low-water biomass of 100 μg C liter^{-1} (S. Sippel unpubl.), there would be ~17,000 kg C as zooplankton in the floodplain between the Caura and Barrancas just before inundation. If all of them were flushed into the Orinoco during inundation, it would increase the total biomass transported in that phase by 10–20%. Dependent on the residence time in the floodplain during the inundation phase, population growth within the floodplain during high water could raise the contribution of the floodplain substantially above 10–20%. Total transport in the lower Orinoco declined, however, between the Caura and Barrancas during inundation (Table 5). Compositional changes along the river and the increased importance of cladocerans and copepods relative to rotifers during inundation suggest that some zooplankton were being flushed out of the floodplain (cf. Shiel et al. 1982; Shiel 1985) but that loss rates were sufficiently high in the main channel to mask these additions for most taxa.

Discussion

Time of travel and current velocity have a major bearing on the biological mechanisms that regulate zooplankton abundance in rivers (Rzoska 1978). For example, a travel time of a few hours would usually preclude major changes in abundance through growth or mortality. In the lower Orinoco between the Caura and Barrancas, transit times for the water mass range from 2 to 10 d in midchannel. At high growth rates, this period is sufficient to allow major changes in abundance. Reproduction did not play an important role in the main stem of the Orinoco, however, as demonstrated by low egg ratios. It appears that current velocity, possibly combined with low food abundance, suppressed growth and reproduction of organisms in transit.

Given that growth in transit is negligible, downstream changes in transport reflect variations in contact with source areas and variations in mortality rates. A high and constant mortality rate would tend to cause the proportion of zooplankton biomass lost from the main stem to be positively related to travel time, which would cause the values in Table 5 to be most negative during low water, least negative during inundation, and intermediate during the other two phases. In fact, there is no consistent pattern in Table 5. This inconsistency indicates wide seasonal variations in mortality or masking of mortality by addition of zooplankton from source areas along the main stem.

Very little is actually known about planktivores in the main stem of the Orinoco. Lundberg et al. (1987) documented the existence of planktivorous fishes in the main channel. Although there is little information concerning their abundance or migrations, their presence in the channel probably varies seasonally. Furthermore, predation may not be the only mechanism resulting in mortality. Mechanical damage may result in the loss of zooplankton (Hynes 1970; Talling and Rzoska 1967), and, in contrast to predation mortality, it is likely to increase with increasing velocity. Seasonal variations in zooplankton mortality rates thus seem likely.

There is considerable seasonal variation in the contact of the river with the lentic source areas. By examining seasonal patterns of transport, it has been possible to assess the contributions of the different source areas. Channel habitats, which include eddies, channel pools, and river margins, make contributions to transport mainly during low water. Physical evidence for the importance of such habitats exists for the Caura (Saunders and Lewis 1988*a*), and the transport patterns for the Caura leave little doubt about the importance of channel habitats in that river. For the Orinoco, the pattern of transport at low water, when the river is not in contact with the floodplain or with side-channel habitats, strongly indicates that channel habitats are also sources of zooplankton for the main stem; in particular they appear to be significant sites of reproduction for copepods. Physical characterization of these channel habitats on the main stem is not yet possible, but they are most likely to lie along the margin of the river channel. The Orinoco, unlike the Caura, moves too swiftly to develop slowly

flowing eddies and pools in the open channel. Circumstantial evidence also supports the existence of significant river margin habitats in the main stem: Dussart (1984) found adult copepods along the margins of the Orinoco, but they were conspicuously absent from our samples taken away from the margin of the channel. During rising water, both the channel and side-channel habitats probably contribute zooplankton to the main stem, as in the Apure River (Saunders and Lewis 1988*b*).

Contributions of the Orinoco floodplain are unexpectedly small. Given the high abundance of zooplankton in the floodplain (Gessner 1955; Twombly and Lewis 1987), the biomass either does not enter the river or is removed rapidly by mortality in transit. Planktivorous fish inhabit the lakes of the Orinoco floodplain (Rodriguez pers. comm.), and there may be an influx of planktivorous fish from the river during inundation as has been observed in the Amazon (Brandorff and Andrade 1978). No quantitative estimate exists for the effect of fish on zooplankton abundance in the Orinoco floodplain, however.

The three lower tributaries of the Orinoco (Caura, Caroni, Apure) make significant contributions to the main stem only during rising water and inundation. The floodplain of the Caura, despite its relatively small size and the generally low productivity of black waters, appears to be very significant for transport during the inundation phase and may constitute 10% of annual zooplankton transport in the lower Orinoco main stem. The vast floodplain of the Apure contributes a strikingly small amount of biomass to the Orinoco main stem. The Apure and the Caroni contribute >50% of the biomass entering the lower Orinoco during the rising-water phase, and the Caura contributes >30% during the inundation phase. Thus the unregulated tributaries (Caura, Apure) make their main contributions only through the seasonal flushing of lentic areas. During falling and low water, the lower tributaries make trivial contributions relative to the biomass already in the Orinoco above the Apure.

The source of biomass in the Orinoco above the Apure remains unknown. Draining the western side of the Orinoco basin are several Llanos rivers that are similar in many respects to the Apure. The Meta, which enters the Orinoco about 200 km above the Apure, is largest. The Orinoco main stem between the Meta and the Apure has a gradient similar to or less than that of the lower Orinoco and may provide conditions suitable for reproduction at low water. The high proportion (40%) of annual transport that is carried into the study reach at low water by the main stem suggests an important role for channel habitats or for reproduction within the upper reaches of the Orinoco because there are few lakes in the upper basin.

The mass-balance approach has made it possible to evaluate the importance of different sources to the transport of zooplankton biomass in the lower Orinoco River and to place these contributions in the context of annual transport. This approach shows that, even during inundation, the fringing floodplain along the lower Orinoco contributes relatively little zooplankton biomass to the flowing waters of the main stem. The three major tributaries to the lower Orinoco make seasonal contributions primarily through the flushing of lentic habitats; on an annual basis, however, their contributions to biomass transport are proportional to their discharge and thus are small. A substantial portion of zooplankton biomass in the lower Orinoco originates in the upper parts of the basin; additional biomass is derived mainly from channel habitats rather than floodplain.

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Submitted: 25 March 1988
Accepted: 23 June 1988
Revised: 7 November 1988