

Large rivers of South America: toward the new approach

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Introduction

It is likely that water consumption for life maintenance is the most important of the multiple uses of water. In most of the biosphere, water is very scanty, or even unattainable, and, even more serious, a progressively smaller amount of water can be devoted to direct consumption because of increasing pollution. Therefore, an increasing number of people depend on a smaller amount of water.

Of equal concern is that the loss of water quality also affects all forms of life in the biosphere. A decrease in the biodiversity at the continental level is now expected, with an impact on human populations that is even more difficult to measure. Surface waters are the most accessible, but only continental fresh waters allow direct use for human, plant and animal consumption. The accessibility of surface water at the continental level depends a positive water balance involving rainfall, and landscape physiography to retain, accumulate, or allow its runoff towards the sea. Continents have different portions of standing water (bodies of lentic water) and running water (lotic environment).

South America is in a privileged situation since it has a greater volume than other continents of surface running waters. This fact provides possibilities for access to "new" and clean water in the future, providing that the proper use of ecosystems prevents erosion, and that pollution from toxic substances or the effect of acid rains is also prevented. Equally important is the design and adequate monitoring of various programs of urban flood control, hydroelectric generation, navigation, and other possible alterations of hydrological regime.

As Morletto (1984) describes in his South American ecological profile, the area of the South American continent is double that of Europe, and extends to the southern latitudes of the biosphere. However, owing to its triangular shape, with its southerly apex, its climate is greatly influenced by the ocean, and

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Table 2 shows some characteristics that enable comparison of rivers with mountain vectorial landscapes to rivers with floodplain landscapes (equipotential) according to the concepts of GONZALEZ BER- NALDEZ (1981).

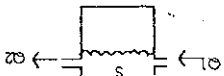
Consequences of the movement of water in large rivers

The main difference from lakes is that in rivers the movement of water is horizontal; moreover, between small and large rivers, the main difference is that in the former, water moves only temporarily while in large rivers flow is permanent and determines the distribution and abundance of organisms. Rivers, therefore, are systems of macrosystems in which water, nutrients, sediments and organisms pass through a certain section at a certain speed.

To understand better the functioning of fluvial macrosystem variability, a typical lake (for example the Mascarell lake, Rio Negro, Argentina) can be compared to a dammed lake (for example, Yacireta dam on Parana River at Argentina).

A very simple example, made with a glass (for the lake volume, relatively constant) and two tubes (one is the input of water, the other is the outlet of surface water) is illustrative.

Volume (V) in the glass is the standing amount of information (generally speaking) in a certain time (t). If water were not renewed (upto), the internal organization would depend on the amount and quality of elements in the glass (nutrient, species, etc.), on the energy fluctuations that our 'glass' (or water body) seasonally receives, and on interactions of elements within the system.



Total internal change: $TTRI = (P - E)S + Q_1 - Q_2$ where:

- P = Energy inflow (precipitation, solar energy)
- E = Energy outflow (runoff, thermal advection, etc.)
- S = Surface area
- Q₁ = Inflow of information (water, sediments, spp.)
- Q₂ = Outflow of information (water, sediments, spp.)
- t = time

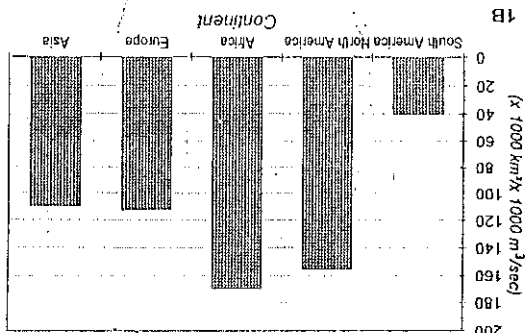
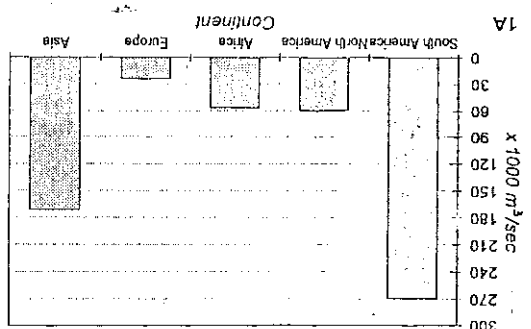


Fig. 1. Large rivers of the world. 1A: Mean discharges; 1B: Arc discharges.

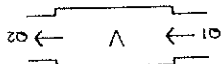
seasonal periods, and the extent of circulation essentially depends on physical attributes, especially in temperature. The periodic circulation of water is determined largely by the amount of solar energy that the water mass receives locally. Lakes, therefore, can be considered as systems with great potential energy and low kinetic energy. From an energetic point of view, they can be considered as 'cumulators' with a slow active volume: the hypolimnion.

In South America, although large rivers include small and large lakes in their basins, as well as wetlands and other lotic environments, the greatest volume of water is temporarily or permanently moving in a horizontal direction. Water renewal rate in any given section is high compared to that in standing waters. The concentration of elements (nutrients, or organisms, sediments) must be expressed in relation to discharge values, not volume.

The greatest amount of energy that goes through the system is kinetic, and this is of great importance when analyzing nutrient flows, temporal distribution patterns of organisms, and the use and management of rivers. Physiographical differences, particularly gradients, can determine the presence or absence of tributaries, and the presence of rapid or slow runoff sectors. These latter do not have the characteristics typical of vectorial flow (typical of rivers) since they can move in different directions during different periods of the year, depending on the flow volume of the collector stream.

Table 2. Brief comparison of lowland and mountain rivers of South America.

Characteristic	Subtropical lowland rivers	Mountain rivers with temperate climate
Vectoriality	Minimum (equipotentials)	Vectorials
Physiography	Complete basin is reception-discharge	Zone of head-waters - transport - delta
Time of water concentration	High	Low
Kinetic energy	Low	High
Hydroelectric regime	Bimodal: maxima in summer and autumn	Commonly unimodal spring-summer
Suspended load	Low	Variable
Bedload	Low and fine	Commonly high, coarse
Water flow	Meanly vertical	Meanly horizontal
Hydraulic effects of vegetation	High	Moderate-low
Organic matter	High Production	Moderate-low
CPOM (a)	Low	High
FPOM (b)	High	Moderate-low
DOM (c)	High	Low
Biotic structure	Continuum	Communities or continuum
(a) Coarse particulate organic matter, (b) Fine particulate organic matter, (c) Dissolved organic matter		



But in rivers:

Then:
 Total turnover rate $\rightarrow TTR = (1 - Q_2/V) + TTR!$
 Total turnover time $TTr = 1/TTR$

We should now place the input from the water tube (nutrients, sediments, organisms) Q_1 in the graphic, and the outlet tube that will bear the Q_2 symbol. In this second example, there is, besides the internal metabolism of the system, an inflow of information (nutrients, sediments, organisms) per unit of time.

Normally, in lakes and rivers, the volume is relatively constant, and the input and outlet volume of flow vary in an analogous way. The turnover rate (TTR) is the percentage of the total water within the glass that comes enters or leaves in a certain time. The turnover time is the reciprocal of the turnover rate and states the time necessary for a complete renewal of water in the glass.

If the glass has a 1 litre capacity and 100 mL income per day, the turnover rate will be $100/1000$, or 0.1 or 10 percent per day.

Both rates are of significant use in determining the value of the exchange of information of the system under analysis. In practice, the turnover time rate is generally used. The TTR would be different along river sections. Values of nutrient concentration in rivers offer only a small amount of information if not discussed in

relation to the volume of flow crossing this point or section.

Turnover time for the Yacyreta dam (situated on the watercourse of the Alto Parana) is about 3 weeks. Turnover time for the Mascardi lake has an approximate value of five years. Water renewal in large rivers (and in other elements of the system) is quite high in relation to the information volume comprised in the system. For this reason, indices used in describing the system status cannot be the same as those used in the study of systems of low turnover (as happens in most lakes).

Bioecologic analysis, using indices of dominance, abundance, equitability, diversity and other features used in ecosystems with low turnover times (HURLBERT 1971), are of little use to indicate organization complexity and the functioning of communities that live in large rivers. Most indices express the organisms distribution between a number of species. The disadvantage is that they do not incorporate the magnitude of turnover-time and turnover-rate. Returning to our example of the glass, an increase of 10 individuals (or species or information units, generally speaking) gives the same result even when the flow rate in the system varied greatly. If the outlet rate (death, emigration) were 0, the change rate would be 10. But it would also be 10 if 200 individuals were incorporated, with 190 leaving, or if 1,000 were incorporated and 990 were to exit.

These indices are not sufficiently sensitive to explain changes to systems with a high population turnover due to horizontal movement of

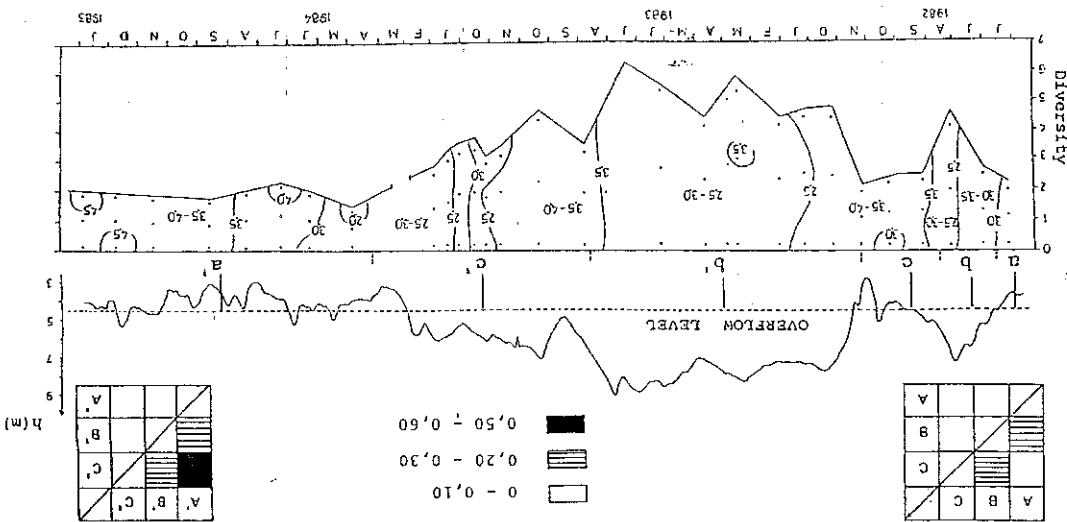


Fig. 2. Comparison of phytoplankton diversity and similarity index before and after flood in a pond of Parana river floodplain. Adapted from Zaloccar (1993).

many as the different elements that form the community), each represented in a different color. Therefore, our perception would have a different color according to the number of colors (species, elements) forming the blade, and the speed of the fan.

The problem becomes yet more complex since, in the case of rivers, changes do not occur in the form of cycles (biogeochemical cycles are not cyclic within the system) and because flows occur as energy and matter pulses, representing flood phases and dry phases.

Both phases form the 'hydro-sedimentologic pulse' (or simply 'pulse'). The nature of these pulses is variable over a century, and even over a decade. Variability throughout a long time series shows regularities that may be profitably studied by the use of a rescaled range analysis; this enables determination of hydrological variability tendencies (ARMENGO *et al.* 1991).

In rivers, the amount of water that goes through a certain section and within a certain unit of time varies generally in a sinusoidal way as a consequence of rainfall distribution, phy-

geography and basin soils.

Frequency, scale and duration of dry and flood phases depend on the topographical position of river islands and on the nature of co- systems on the floodplain, and with a greater or less frequency on the hydrological events that take place during summer or winter. Each river

water during floods in the river valleys. They can also provide misleading conclusions since on several occasions diversity shows only small change despite a 60% renewal of species within the community between high and low water phases (FRUTOS 1993, ZALOCAR DE DOMITROVIC 1993). Even when comparing the extreme situation of low water and extraordinary flood, specific diversity does not reflect significant contrasts. The use of the simplest similarity index (e.g. SÖRBERG'S) to different situations of extreme high and low waters indicate that the similarity is less than 30% for phytoplankton

In riverine biological systems, particularly those of high change rate - such as planktonic groups or invertebrate groups that live in plants - the complexity analysis requires knowledge of change rates, response times, and the possibility of a population or community repeating its structure throughout time (POI DE NEIFF & BRUGNATTAS 1989, IUSZAR 1994).

To represent this idea graphically, consider a fan: perception is completely different when the blades of a fan which is not working (that is to say, without performing its essential function) are observed and when the blades move at different revolutions per minute.

In our example of the fan, now consider each blade as a species (or population or biotom) and our fan as having 'X' number of blades (as

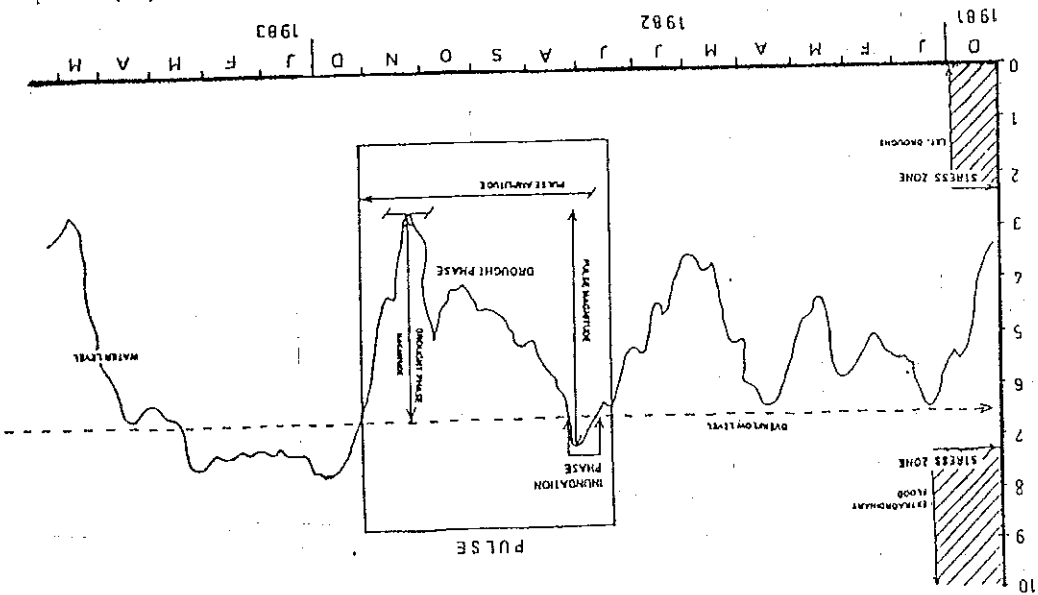


Fig. 3. Lowland of Chou Island (Parana River, 58°55'W; 27°30'S). Attributes of the one pulse in one phase of the floodplain. (After Neire et al. 1994).

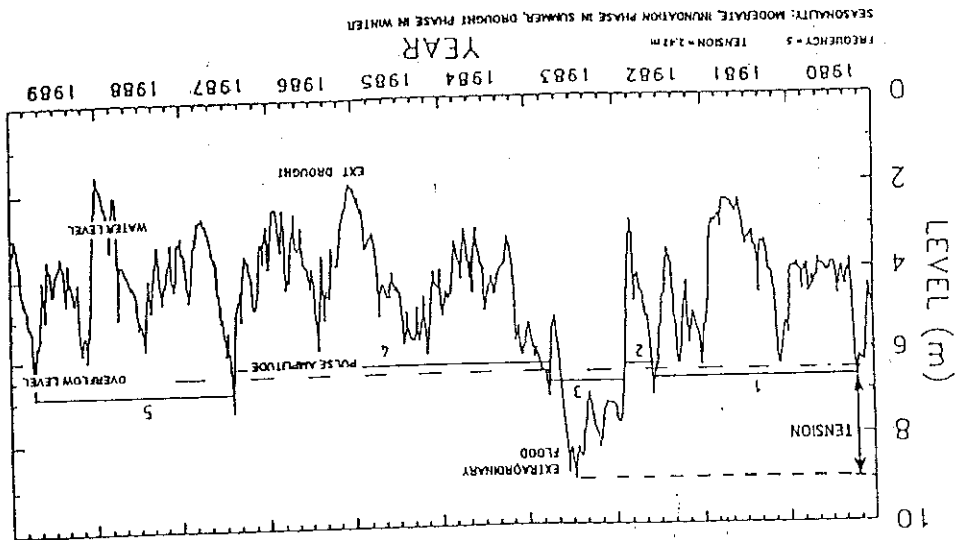


Fig. 4. Hydrometric level of the Parana River at Corrientes during the 1980-1990 decade. Sequence of the pulses in the same topographic position of the Chou island along the decade. (After Neire et al. 1994).

or river section receives, with greater or less regularity, a flood phase or a dry phase of certain magnitude. This group of hydrological attributes defines the characteristics of the pulse system or 'FIT-RAS' function (Frequency, Intensity, Tension, and rain magnitude). NEIRE et al. (1994). In Figs 3 and 4, the FIT-RAS function is graphically described, and its different according to different topographical levels of the floodplain.

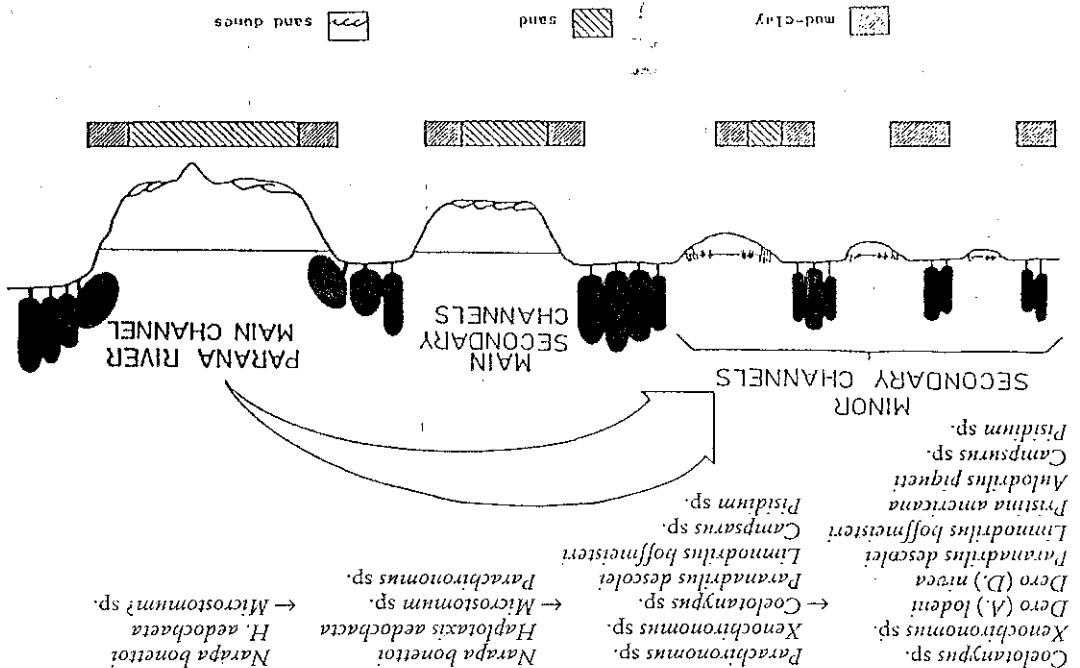


Fig. 5. Alluvial valley of the Lower Parana River: transverse zonation of the benthos in lotic environment. (Adapted from Marchese & Ezcurra de Drago 1992).

Table 3. Parana river cross-section. Species richness in lotic and lentic environments near of the confluence of the Parana and Paraguay rivers.

Channel	Island water bodies	Fringe floodplain
(1)	(2)	(3)
19	13	12
Cyanophyta	91	68
Chlorophyta	83	43
Bacillariophyceae	57	4
Chrysophyceae	8	16
Xanthophyceae	2	85
Euglenophyta	24	7
Cryptophyceae	4	8
Dinophyceae	2	6
Total no. of species	207	242

(1) Zalocar de Domitrovic & Vallejos (1982).

(2) Zalocar de Domitrovic (1990).

(3) Zalocar de Domitrovic (1992).

(4) Zalocar de Domitrovic (1993).

JUNK et al. (1989) explained a significant part of the biological organization of rivers with floodplains as the result of 'flood pulses', and noted that periodic flood events produce stress situations for biota, reflected in system 'resetting'. BONETTO (1975, 1976) explained that

Ecologic consequences of the pulse system

It is generally known that the floodplain landscape of large South American rivers is very different from the high land ecosystems limiting the river. It is also known that there are biological differences between the different sectors of the watercourse and floodplain. In large rivers with laterally located floodplains (fringe-floodplains, sensu WELCOMME 1985), it is possible to find a growing complexity of organization in communities transverse to the actual watercourse of the river. MARCHESI & EZCURRA DE DRAGO (1992) described a typical zonation with an increase in complexity (amount of species, specific diversity, trophic niches) from the main watercourse to the minor tributaries (Fig. 5). This increase in species richness in a section transverse to the Low Parana was related to modifications in the physical and chemical properties of the environment (discharge, sediment texture, organic substances, dissolved oxygen).

For phytoplankton and zooplankton (ZALOCAR 1990, 1992, 1993), the trends are similar (Table 3).

The water temperature regime of South America large rivers is little known and requires high variability of large rivers

Some tools to elucidate the biotic

Rooted vegetation with floating leaves growing in floodplain lakes has ecophenes of its own during flood and dry phases (JUNK 1970, NEIFF 1978). When covered by flood water, they accelerate growth and modify their anatomy and morphology (NEIFF 1978), thus attaining - during this stress phase - productivities up to five times greater than average annual productivity (NEIFF 1990 a), as shown in Table 4. This productivity response has not been noticed during the flood phase in the Amazonian floodplain (JUNK 1986).

Floods represent a major change in the biological structure. However, there are trees with adaptations which enable them to photosynthesize even when immersed (JOY & CRAWFORD 1982, FERNANDES CORREA & FURCH 1992, NEIFF & REBORATTI 1989, TUNDISI 1994). Some trees exist for nine months with the soil flooded without noticeable modifications in growth, even in cases of long-term floods that cause the death of great numbers of trees of the gallery forest in one year (NEIFF et al. 1985). The phenology of some species of the Amazon varzeas would not be affected by floods (CITIVERIA 1995).

I emphasize that the dry phase is a powerful selection factor on the distribution and abundance of animals and plants. Most fish populations cannot survive, or suffer important losses during extended droughts (MERKON et al. 1993).

Vertebrates find fewer and lower quality environments during this dry phase; this leads to a concentration (overload of individuals) in an area (up to 5 to 10 times smaller than the one in the flood period) and individuals are more vulnerable.

The biocoenoses of large rivers are regulated by the hydrodynamics of pulses. But low water phases are as important as flood periods (NEIFF 1990b, NEIFF et al. 1994). This is not just a semantic problem concerning the 'flood pulse' concept given by JUNK et al. (1989). During this dry phase, plants suffer from stress (NEIFF & POI DE NEIFF 1990) due to leaf abscission and the cessation of growth.

Floods produce 'rejuvenation' processes in ecosystems that form part of the river.

Table 4. Net primary productivity (on dry weight base) (N.P.P.) in Parana River floodplain, downstream of Parana-Paraguay confluence. (After NEIFF 1990 b).

Species	Stress Period Long. (days)	N.P.P. Stress Period (Tn. Ha ⁻¹)	N.P.P. Annual Period (Tn. Ha ⁻¹)	Production Rate (g.m ⁻² .d ⁻¹)	N.P.P. Effective Annual (Tn. Ha ⁻¹ .yr ⁻¹)	Production Rate (g.m ⁻² .d ⁻¹)	Site*	Year
<i>Polygonum ferrugineum</i>	14	2.50	65.18	17.85	18.30	5.10	El Gato (IS)	1987
<i>Ludwigia peploides</i>	11	1.96	65.04	17.81	6.7	1.84	La Guardia (Sta. Fe) (BW)	1971
<i>Victoria cruziana</i>	10	0.29	10.58	2.90	0.89	0.24	Baúpe (Chaco) (P)	1976
<i>Nymphoides indica</i>	10	0.85	31.02	8.50	2.20	0.60	Don Felipe (Sta. Fe) (P)	1971
<i>Echinochloa polystachya</i>	12	1.72	52.31	14.33	14.10	3.86	La Cacerola (Sta. Fe) (P)	1971
			Flood Period				Low-Water Period	
			Potamophase				Limmophase	

* P = Pond, BW = Backswamp, IS = Island.

mass are useful indicators of the system's complexity (Fig. 5). It is useful to analyze the biological variability of pulsatile systems, employing rates that combine population abundance according to ranges with respect to frequency values in the community (McNAUGHTON & WOLF 1984). The shape of these curves provides information on stress situations during long floods (Fig. 6) in different biological groups (POI DE NEIFF & BRUGUETAS 1989). During the critical periods, the diversity decrease and the distribution of relative abundance shows a geometric curve. We could use an index that combines three biological parameters: *abundance*, as mean density (or individual numbers in each hydrological phase) or better, moment within the phase); *frequency*, i.e. the number of phases (or moments within the phase) occupied, as an expression of the niche amplitude; and *the mean weighted* or barycentre, i.e. the mean weighted by the density of population in each hydrological phase, to evaluate the position of a population or populations for a given hydrological curve.

Finally:

$$P_i = \sum_h (N_h \bar{X}_h)$$

where:

- P_i = Population position in a hydrosedimentological pulse;
- \bar{X}_h = Mean coordinate weighted by density of population in each pulse h.
- N_h = Population density in the hydrological phase (or date) h.

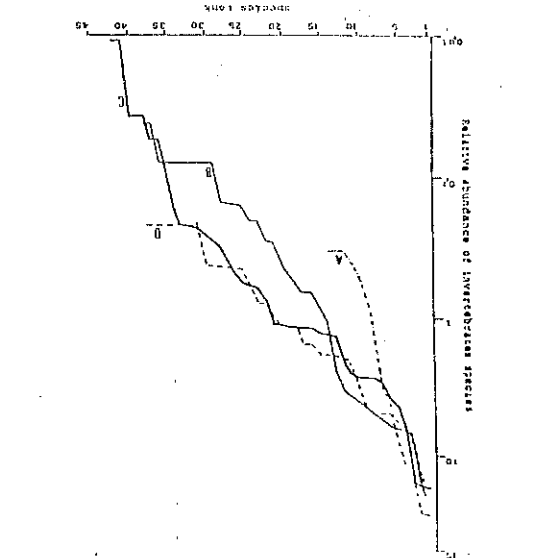
The 'abc method' (abundance/biomass comparison) was proposed by WARWICK (1986) as a means of detecting pollution effects on macrobenthic communities. Subsequently, MEYER & DERBN (1990) proposed the ABC index:

$$ABC = \frac{B_1 - A_1}{B_1 - A_1} \frac{N}{N}$$

where:

- B_1 = % dominance of species i (ranked from the highest to the lowest biomass)
- B_i = % dominance of species i (ranked from the most to the least abundant species)
- N = total number of species.

The index is negative in heavily stressed conditions and positive in unstressed conditions. The number of times for cumulative percentage.



Sampling date	Hydrological phases	Distribution of abundance	Species diversity
January 1983	High water	Geometric	2.7
January 1982	Low water	Log-normal	3.7
September 1982	Low water	Log-normal	3.8
July 1982	Normal flood	Log-normal	4.1

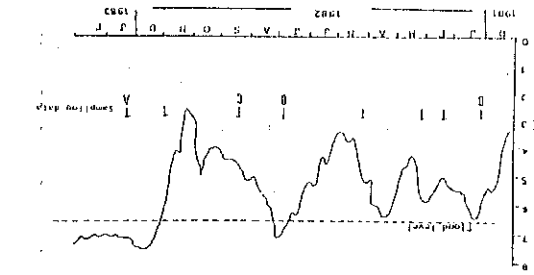


Fig. 6. Distribution of the relative abundance of invertebrate species associated with aquatic vegetation. The mean monthly water level of Paraná River are given for Puerto Corrientes. No more Paraná water enters the floodplain below the level indicated by the horizontal dotted line. (Adapted from POI DE NEIFF 1989).

priority as a tool within the Global Change Program. Interactions among physical, chemical and biological factors at regional and local level need be incorporated in the thermal study of these rivers (BUDKO et al. 1994, DRACO 1994). Species richness in a given environment or river section and the use of productivity bio-

hypobionism. Most of the trophic net is based on the phytoplankton. Magnitudes can vary in different lakes, but the productivity gradients overall are vertical.

In large rivers of South America, productivity is generally greater when the basin is considered as the unit of analysis. The greatest amount of energy is captured by macrophytes and by floodplain forests (NEIRE 1990a).

Efficiency in the accumulation of energy displays differences in areas that are transversal to the watercourse, with higher values towards the floodplain. Assessments for the potamo-phytoplankton are 3-6 in ha⁻¹ year⁻¹ (GARCIA DE EMIGIANI & ANSELMI DE MANUELA 1983, PEROTTI DE JORDA 1980, RAI & HILL 1984), while vegetated lakes with *Fichbornia crassipes* attain values from 12 to 16 in ha⁻¹ year⁻¹ (PEREZ DEL VISO et al. 1968, LAJAVANA 1980, NEIRE & POI DE NEIRE 1984, JUNK 1986), and the gallery forest of the islands of some rivers frequently have values of 20-36 in ha⁻¹ year⁻¹ (NEIRE 1990a, NEIRE & KERBOVATTI 1989).

Utilization of phytomass and necromass (non-living biomass)

Currently, the percentage of this primary production transferred to consumers is not known and even less known is the efficiency of transfer throughout trophic nets. The direct consumption of plants is low, due partly to the low amount of herbivorous tissue produced and partly to the large amount of tissue produced that is almost inaccessible as a source of food.

A large portion of the incoming energy from plant productivity is captured by consumers in the organic form of detritus in different grades of processing. This is not exclusive to large South American rivers (VANNOIRE et al. 1980, CUSHING et al. 1983). The main difference in South American rivers with large floodplains is that the organic debris does not come from terrestrial ecosystems, but from vegetation growing in the river itself, and its thus autochthonous, as is the detritus from the river.

The amount of organic matter produced is always high, mainly because of the contribution of wetland vegetation on the floodplain. Respiration is low, since the oxygen in the water is quickly exhausted and gives rise to the formation of intermediate organic components that characterize 'clear waters' and 'black waters',

dominance is the percentage of the total number of species minus one (cumulative biomass dominance).

COCKE et al. (1993) concluded that the method gives information about both pollution and physical disturbance. I think that the ABC index can be used to analyze the fluctuations in communities induced by the river regime (pulses).

For certain studies, it is necessary to know which population/s is/are the one/s which constantly occupies/ an important space or volume within the system throughout a series of time in relation to other biotic components of the system.

For such purposes, I suggest the use of the prevalence index:

$$P = \int_0^1 \sum (U_i/N)^{1-t} \cdot t^{t-1} \cdot n \text{ spp}$$

where:
 U_i = Unit of importance (Productivity, Density, N = Importance value magnitude (Other)

This index can be used in attempts to explain the dynamics of groups in ecosystems regulated by pulses, and particularly in those with a high change rate due to marginal flows (in LEWIS et al. 1990) such as the plankton of floodplain lakes exchanging water with the river. As in other indices, it can also be of use in analyzing the biotic variability in long time series since it includes ideas of prevalence and persistence of populations in environments of great variability. One generally accepted idea is that biological complexity, mainly species richness, increases downstream, towards the river mouth. This does not occur in rivers such as the Paraguay-Parana (NEIRE 1990b), where the greatest biological complexity is found in the high basin of Parana (NEIRE 1990b), where the greatest biological complexity relates to the extension and spatial variability of wetlands within the basins of these large rivers, and with the PIFRASAS hydrological function along the river (NEIRE 1990b). Additionally, fluctuations in temperature are one of the most important causes of biological complexity in tropical rivers.

Production of organic matter

In Patagonian lakes of South America, greater productivity is generally concentrated in the top of the water column, with low values in the

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BRUGUETAS & NEHR 1991).

time of the necromass of the same plant doubles During winter, the necromass that decomposes in the water experiences 15-18°C temperatures while, during summer, the process occurs between 22 and 32°C.

Finally, the production of organic matter (NEHR 1990a) is equal to, or higher than, its decomposition (POI DE NEHR 1991, 1993) in a river with floodplain such as the Low Parana. The P/R rate is closely related to the pulse function (FTTRAS).

The hydrosedimentological regulation of the river, and the additive effects of dams in particular, can alter the FTTRAS function in some or all floodplain ecosystems. From this alteration, changes in the P/R quotient, and in the quality and quantity of organic debris available for consumers, can be expected. The chain effects deserve special investigations.

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