

## THE BENTHIC ZOOCOENOSSES OF CENTRAL AMAZON VARZEA LAKES AND THEIR ADAPTATIONS TO THE ANNUAL WATER LEVEL FLUCTUATIONS \*

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### RÉSUMÉ

Les zoocénoses benthiques des lacs varzea de l'Amazonie centrale et leurs adaptations aux variations annuelles du niveau de l'eau.

L'auteur met en évidence l'existence de deux phases distinctes dans le fonctionnement des lacs varzea de l'Amazonie centrale, à savoir une phase de basses eaux et une phase de hautes eaux. Les sédiments argilo-limoneux mous des lacs sont colonisés par une faune benthique typique.

Pendant la période de basses eaux, quelques macrophytes émergés se développent selon une bande étroite tandis que des prairies flottantes de *Paspalum repens* s'observent pendant la montée des eaux, ils sont colonisés par des faunes tant « limnokaniques » que benthiques.

Enfin l'évolution de la faune benthique en fonction des phases et leurs adaptations aux variations annuelles du niveau de l'eau sont discutées.

### ABSTRACT

The author points out that varzea lakes show two distinct phases, a high- and a low-water phase. Soft silty-clay lake sediments are colonized by true benthic fauna. Few emergent macrophytes growth in the low water phase in a narrow band, while floating meadows of *Paspalum repens* are observed at rising water, they are colonized by both, limnokinal and benthic fauna.

Evolution of benthic fauna is followed up according to the phases and their adaptations to the annual water level fluctuations discussed.

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Varzea lakes cannot strictly be considered as lakes according to the classical limnological definition, but occupy a position intermediate between river and lake; thus they exhibit the hydrographic properties of both types of water body. Whether the characteristics of a standing or running water body predominate depends on the basin morphology, the underlying geological structure and the topographical position in relation to both river and terra firme.

This feature is the result of the extremely large annual water level fluctuations of the rivers, which on average are 10 m in the Central Amazon but can be as high as 14 m and are never less than 5,5 m. River water can either reach varzea lakes directly through canals or by overflowing the river banks at rising water. In this way the hydrography of the lakes is determined for all or part of the year by the water regime of the rivers. At times of exceptionally high water level, the whole varzea area is inundated to a depth of several meters, causing single lakes to lose their individuality for a time. When the water level in the rivers is very low, however, the lakes can dry out completely. These extremes occur relatively seldom, but with apparent regularity, in the Central Amazon. Water level data of the past 70 years for the Rio Negro at Manaus show that at intervals of 10 to 20 years exceptionally high water level maxima and low minima can be expected (Fig. 1). These data are applicable to the lower Rio Solimoes (REISS 1977) are therefore valid for the varzea lakes of this area.

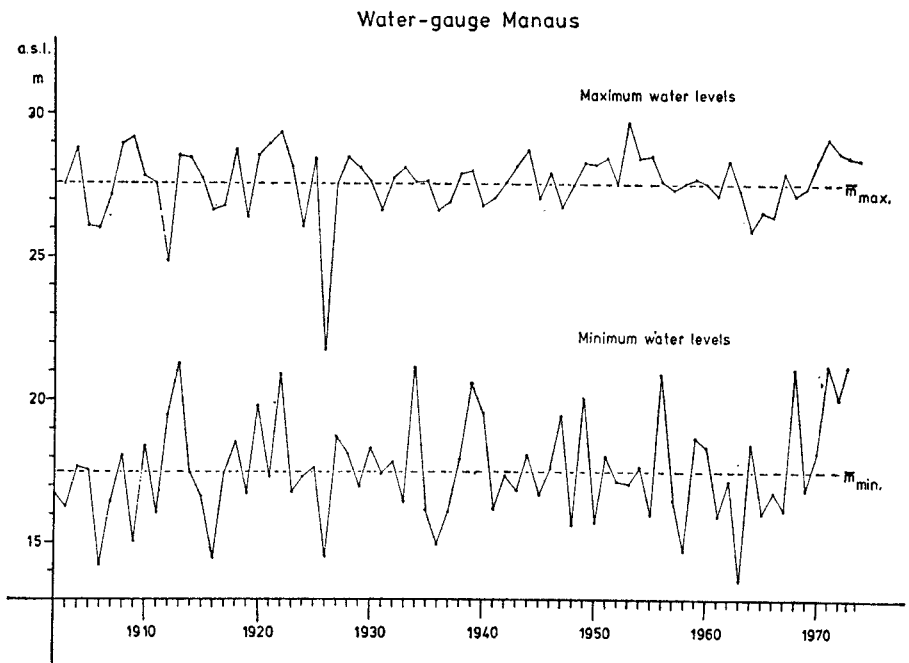


Fig. 1. Annual water level maxima and minima in the Rio Negro at Manaus for the period 1902-1974.

The large annual water level fluctuations together with these regular extremes of water level are more important than any other abiotic factor complex in determining the structure of the benthic biocoenoses of a varzea lake. The objective of this paper is to illustrate the main methods of adaptation by the benthos to these conditions, and to the prevailing thermal stratification characteristics and seston content of the varzea lakes. These latter two abiotic factor complexes do not have as large an influence as the water level fluctuations, however.

The Central Amazon varzeas lakes are generally shallow, maximum depth being about 15 m, and the water has a relatively high content of suspended matter. This is a result of the inflow of inorganic suspensoids with the rivers during the annual high water phase and resuspension of the lake sediments in the lake water at low water. A second, purely autochthonous components is present in the form phyto— and zooplankton. According to SCHMIDT (1973) phytoplankton production is highest when the levels of inorganic suspensoids are lowest and the prevailing optimum light conditions allow maximum rates of photosynthesis. This occurs during the phase of falling water level when a varzea lake is cut off from the river, its inorganic suspensoids have settled out, and resuspension has not yet started. These two factors, plus the fairly high detritus content result in low transparency values for the water body throughout the year. This is illustrated by the Secchi disc readings, which in Central Amazon varzea lakes range between 0,1 m (at minimum water level) and 3 m. Values between 2 and 3 m, however, are found only in those lakes which receive substantial inflows of black and clear water from the terra firme i.e. in mixed water lakes. When inflow from the terra firme is negligible, as in white water lakes, the Secchi transparency remains less than 2 m.

The second important limnological factor complex is the thermal stratification and the related concentration of dissolved oxygen. During the low water period (normally at water levels less than 5 m) all varzea lakes are thermally homogeneous except for periods of a few hours or days when there is weak surface stratification, so there is therefore a plentiful supply of oxygen in the whole water body. At rising water, however, the critical depth of 5 m is exceeded, and stratification is more prolonged; this can result in stagnation of the bottom water layers lasting several months during the high water phase. At such times the oxygen content here decreases to a few per cent of saturation or is not detectable. In addition, concentrations of  $H_2S$  are considerable (1,5 mg/l; MENEZES SANTES 1973). Even the water nearer the surface is often poor in oxygen and values of less than 30 % of saturation can be found at depths of only 2 m. Usually, however, full circulation also occurs in the high water phase; this results in oxygen entering the deeper layers and the consequent oxidation of the  $H_2S$ . Full circulation occurs when heavy rains or cold air from the Antarctic (so-called « friagem ») cool the surface water layers to the same temperature as the deeper layers. During the period of maximum water level there is always a slight increase in the oxygen content of the bottom waters, since the water flow through a varzea lake is stronger at this time when the water is rising or falling.

On the basis of abiotic factors, therefore, it seems that varzea lakes show two distinct phases, a high— and a low— water phase. Optimal conditions for the qualitative and quantitative development of true benthic fauna occur in the low water phase (water depths less than 5 m), when there is full circulation of the water body and a plentiful supply of oxygen to the whole of the lake bottom. Colonisation of the bottom is uniform since the soft silty-clay lake sediments are structurally homogeneous between the shore and central regions of the lakes. Except for a few stenobathic species in the shore regions, the biocoenose cannot be divided into littoral and profundal zones. Because of the low transparency of the water and the resulting unfavourable light conditions, there are no submerged aquatic plants except for local occurrences of *Utricularia* sp. Light also limits the development of a sessile algal flora in the shore regions, as does the lack of a firm substrate such as stones, twigs, etc. Thus the only substrate available for colonisation by true benthic fauna in a varzea lake is the soft silty-clay lake sediment.

Growths of emergent macrophytes in the low water phase are reduced to a narrow band of free floating aquatic plants such as *Eichhornia crassipes*, *Pistia stratiotes* or *Salvinia auriculata* which, together with their animal colonies form the biocoenose of the limnokinon. This term is discussed later in more detail. A « floating meadows » zone is completely absent or reduced to a few remnants at this period (Fig. 2).

At rising water, the lake surface area and depth increase rapidly, and the predominantly grass-covered terrestrial areas of the varzea are flooded. The plants thus submerged are almost certainly colonised by aquatic organisms, but there is no further information on the course of events. At the same time an ever-widening band of floating Gramineae develops, which in the Central Amazon consists mainly of three species *Paspalum repens*, *Echinochloa polystachya* and *Paspalum fasciculatum* (JUNK 1970). The two latter species remain rooted in the substrate but *Paspalum repens* can form free-floating colonies. These floating meadows (Fig. 2) offer optimum substrate and nutrient conditions to an « Aufwuchs » fauna which is rich, both qualitatively and quantitatively (JUNK 1973). The thickly interwoven texture of the grass shoots and root bunches, which hang freely in the water, acts as a mechanical filter for planktonic organisms, which in this way become available as a food source for the Aufwuchs fauna. In addition, on the under sides of the grass shoots immediately below the water surface a substantial periphyton community develops where light conditions are favourable. This community can also be grazed on by the fauna (FITTKAU, personal communication).

On the lake side extending in front of the floating meadows, there is a much narrower belt of the free floating plants mentioned above. Its structure is basically the same as it was at low water. Submerged aquatic plants can naturally not grow during high water.

As the water level rises, the forest surrounding the lakes is flooded to a depth of several meters, but at mean maximum water level the higher parts of the river

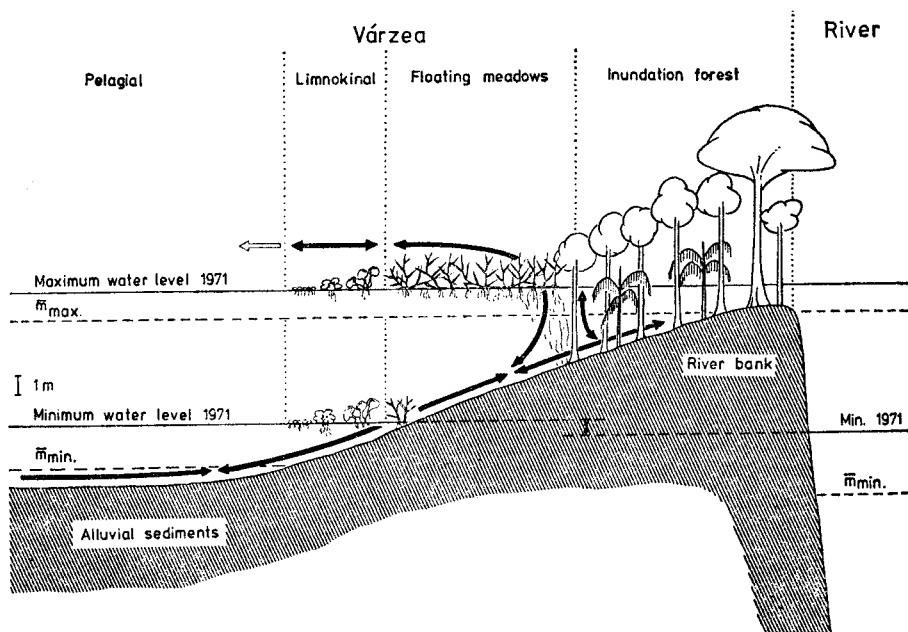


Fig. 2. Diagrammatic representation of the changes in the benthic biotopes of Central Amazon várzea lakes which depend on the annual water level fluctuations. As well as the mean maximum ( $\bar{m}_{max}$ ) and minimum ( $\bar{m}_{min}$ ) water levels, the extreme maximum and minimum water levels of 1971 are given. The arrows symbolise the water level dependent partial or total migration of macrobenthic species into the biotopes which are optimum for them at the time. The degree of independence of the large water level fluctuations shown by the illustrated biocoenoses can be graded from the least to the most in the order lake benthos, inundated forest, floating meadows, limnokinal.

bank remain dry. Connections to the rivers over extensive areas of the bank only occur in times of extreme maximum water level, such as in 1971 (Fig. 2). Among the benthic fauna of the inundated forest (IRMLER 1974) are many species peculiar to this biotope as well as some which occur in the floating meadows and (or) make up part of the lake benthos (Table 1).

At rising water there are rapid changes in the composition of the lake bottom fauna. As already mentioned, the bottom waters become thermally stratified and at high water this results in a marked qualitative and quantitative impoverishment of the bottom fauna in the central parts of the lake. The zoocoenological structure strongly resembles that of the profundal bottom fauna of eutrophic lakes in temperate latitudes. In an extreme situation the macrozoobenthos of the profundal zone of a várzea lake consists at high water of only the prey animal and one predatory species; these are the chironomids *Chironomus gigas* and *Ablabesmyia* sp. AR 1 (Table 1).

The shallow water near the lake banks also stagnates, since the overlying floating meadows prevent any circulation in their vicinity. This results in deple-



tion of oxygen. Thus even in the littoral areas the development of a characteristic littoral benthic zoocenose is limited at high water.

When the water level falls, the inundated forest dries out rapidly. The floating meadows dry out hanging in the crowns of trees, or on the dried out lake bed. Some of the plants pass into a terrestrial vegetation phase.

Both the floating meadows with their numerous grass species which endure the changing water levels in various ways, and the many floating plants of the Amazon (*Ceratopteris thalictroides*, *Salvinia auricularia*, *Azolla* sp., *Eichhornia crassipes*, *Reussia rotundifolia*, *Jussiaea natans*, *Pistia stratiotes*) must be considered as effective adaptations to the large annual level fluctuation in the várzea water body. According to JUNK (1970) the grass *Paspalum fasciculatum* is submerged during the high water phase, but dies if submerged for longer than the average length of time. *Echinochloa polystachya* increases rapidly in length during rising water and the distal parts of the shoots float. *Paspalum repens* has a floating stage lasting 4-5 months during which there is no contact with the substrate. This grass does, however, always need a terrestrial vegetative phase, even if very short. The floating plants show a very high degree of adaptation to fluctuating water levels and their existence in only threatement when the water body dries out, and then only locally.

We now consider the way in which the benthic fauna has adapted to these conditions. As well as high reproduction rates (IRMLER 1974) and short development times necessitated by the high tropical water temperatures, migration is an important factor in this respect. At rising or falling water, partial or entire populations of animals migrate into the biotope which temporarily offers them optimal living conditions. The larvae of the chironomid *Goeldichironomus pictus* (Table 1) for example, occurs at low water with an abundance of about 100 individuals/m<sup>2</sup> in the lake sediment in a water depth of 1 m. The whole population follows rising water and colonises the floating meadows when they appear. This is their true biotope. In a short space of time, by successive generations, individual densities of 9000 individuals/m<sup>2</sup> can be attained. As the water level falls, part of the population migrates again into the lake sediments where it forms a « reservoir » for the recolonisation of the floating meadows for the next high water period, (REISS 1974).

*Goeldichironomus natans* undergoes a similar migration ; it develops in massive numbers in floating meadows (REISS 1974), and small populations are also found in the lake sediments and limnokinal.

A third chironomid species, Chironomini gen. A2 sp. A2, has often been recorded in all the cited benthic biotopes of Central Amazon várzea lakes (Table 1) and is a typical member of the zoocenose of floating meadows where it can occur in very large numbers. The rapid colonisation of floating meadows at rising water therefore occurs by migration both from the limnokinal and from the benthic of the lake bottom or from the inundated forest.

*Campsurus notatus* apparently migrates more extensively ; its larvae colonise the silty-clay sediments of white water lakes and the adjoining inundated forests and follow the changing water levels.

IRMLER (1974) recorded a water level dependent migration for *Euryrhynchus burchelli* in the inundated forest. This species occurs also in the floating meadows and lake benthos, so it can be assumed that the migrations extend to both these biotopes.

There are indications that both horizontal and vertical faunal movements occur in the inundated forests (IRMLER 1974), especially with the Bivalve *Eupera simoni*. This species can colonise not only the inundated forest floors but also the trunks of the submerged forest trees to a height of several meters. By contrast, *Eupera bahiensis* occurs also in the floating meadows outside the inundated forests, and migrations to and from these biotopes can also be assumed to take place.

It is clear, then, that there is a partial faunal exchange in the form of migrations between all the benthos biotopes of a várzea lake. These biotopes are considered to be the lake plus the inundated forest which is joined to it, and the two form a functional unit and part of the lacustrine ecosystem during the high water phase. The faunal migrations are shown in Fig. 2 as black double-headed arrows, symbolising the reversibility of faunal movements.

Such an adaptation allows at least some of the members of a zoocoenose to exist relatively independently of water level fluctuations. The members of the limnokinon, however, are so highly adapted that they remain unaffected by water levels, and their existence is only locally threatened (like that of the floating plants) when the water body dries out completely. As already mentioned, this happens every 10-20 years in Central Amazon lakes and therefore cannot be regarded as catastrophic. Since the várzea lakes of any particular area differ considerably in water regime and do not all dry out to the same degree or at the same time, it is always possible that the dry lakes can be recolonised from the hydrologically more stable lakes.

The kinon is a biocoenose which up to now has received little attention ; FITTKAU (1977), with special reference to the Amazon, points out its importance in running waters, especially streams (rhitrokinon) and rivers (potamokinon). In Amazonian lakes there is another kinon (called here limnokinon) which is a unique community ; it is defined as the biocoenose of the lake surface which floats there freely or consists of organisms which feed mainly or exclusively in this biotope (the limnokinal). All Neuston and Pleuston organisms belong to this biocoenose.

As in running waters, the extent of the kinal in standing waters also depends on variations in the state of the lake ; these, however, are comparatively smaller in standing water. The position of the limnokinal varies according to surface and wind, but it normally extends as a band of variable width in front of the floating meadows. In the Central Amazon the limnokinal is normally much broader on the windward (west) side of a várzea lake than on the leeward (east) side. The whole open lake surface of very small várzea lakes can be covered with floating plants.



In addition to the floating plants in the limnokinin, and the Aufwuchs of which will not be discussed in detail in this paper, the limnokinal offers another substrate for the fauna. This consists of free floating particles of dead vegetation of allochthonous or autochthonous origin, such as pieces of twig, branch or wood from the adjacent forests, and leaf and shoot fragments torn from the floating meadows or from floating plants. These particles are often only a few millimeters long and they serve as substrate for the larvae of several chironomid species ; the entire larval and pupal development take place on these. At this stage, nine species have been identified : *Parachironomus* sp., *Stenochironomus* sp., *Polypedilum* (3 species), Chironomini gen. A2 sp. A2, Chironomini gen. A6, *Goeldichironomus natans* and *Goeldichironomus fluctuans*. All these species except the last occur also in the floating meadows where they can occur in very large numbers. *Goeldichironomus fluctuans* (Table 1), however, appears to be a limnokinobionthic species (REISS 1974). Other limnokinobiontic species are the two waterbugs *Rheumatobates klagei* and *Rh. crassifemur esakii* (Gerridae), which live on large amounts of animal matter floating on the free water surfaces of the limnokinal. Among these are water insects which occur by chance in the limnokinal itself or come from the pelagic region. The conspicuous absence of adult water insects from the surface drift of Amazon lakes could be a result of their consumption by water bugs in the kinal as well as consumption by fish.

While the two species of Gerridae control the water surface from above, Notonectid species do this from below ; two species which are frequently found in the limnokinin are *Marterega membranacea* and *Lueno platycnemis*. They also occur in the potamo—and rhitrokinon (FITTKAU 1977) and therefore belong to a general kinobiont faunal stock, to which the free-moving casedwelling members of the Naididas also belong (Table 1).

This description of the zoocoenological structure of the limnokinin of Central Amazon várzea lakes is not based on long-term investigations, and much more information is needed, especially on the mesofauna and microflora which could be the most important food component of this ecosystem.

The distribution of floating plants in standing water is pantropical ; therefore one would expect there to be a limnokinal both in the New World and the Old World tropics. The only occurrence outside the tropics known to me is cited by LENZ (1952) who describes the occurrence of larvae of several chironomid species (*Metriocnemus*, *Dyscamptocladus*, *Limnophyes*) in fragments of dead *Phragmites* shoots floating on the water surface of the Great Plön lake in East Holstein. The animals occur in large numbers in early Spring from the end of February to the middle of April. The pupae lie on the reed fragments in gelatinous casings which project freely up into the air. According to LENZ, this is so that pupation and final development into the adult can occur under direct insolation and in warm air even when the water temperatures are still very low.

As shown in Fig. 3, four benthic biotopes can be distinguished in a Central Amazon lake ; these are the limnokinal, the inundated forests, the lakes, and the

	Low water period	High water period
Limnokinal		
Floating vegetation		
Inundation forest		
Lake sediments without submerged waterplants	Littoral	Profundal

Fig. 3. Schematic diagram of the seasonal occurrence of the benthic biotopes in Central Amazon várzea lakes in relation to water level.

floating meadows. These are all littoral in character except for the lacustrine deep sediments which have a profundal zoocenose during the high water phase. These biotopes all show considerable seasonal changes in character and area, caused by the annual water level fluctuations of the rivers. The structure of their zoocenoses shows corresponding rhythmic changes, the most important feature being partial migration of the fauna into an area which offers it optimum conditions at the time. In addition there is at least one unique taxon in each zoocenose which has not yet been found in other benthic zoocenoses. The limnokinal is independent of water level fluctuations and is temporally and structurally the most stable biotope. Production of phyto- and zoomass is greatest in the floating meadowd, which probably also have more species than any other benthal zoocenose. A subdivision of the benthal biocenoses mentioned above into chorio-coenoses will certainly be necessary. It must also be determined to what extent the biocenological concept obtained from the study of Central Amazon várzea lakes is applicable to the várzea of other parts of the Amazon.

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