# Long-term patterns of the planktonic cladoceran community of Batata Lake, Amazonia, Brazil.

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ABSTRACT: Long-term patterns of the planktonic cladoceran community of Batata Lake, Amazonia, Brazil. We report results from an eight-year study in Batata Lake, a body of water partly affected by tailings resulting from bauxite mining. Planktonic cladocerans were sampled and certain limnological variables were measured every three months for eight years (1990 through 1997) at a natural station in a part of the lake unaffected by tailings, and at a station in an area of the lake impacted by bauxite tailings. Principal components analysis indicated that the two stations differed in the variables studied, during some periods of falling or low water. The stations were similar mainly during the periods of rising or high water. Our results indicate that low-water samples best identified the difference between the stations, caused by the suspended inorganic matter (tailings). Most of the time, there was no perceptible effect of the bauxite tailings on any aspect of the cladoceran community. The equitability parameter best estimated the influence of the tailings on the cladocerans. The observed changes in equitability indicated that under highly turbid conditions, only those species which have the proper strategies to maintain themselves in a variable and unpredictable environment could persist. The lower equitability values observed during low-water phases may indicate high instability at the impacted station, which may be related to the prevalence of tailings in the water column. In these situations, opportunist species, able to take advantage of the instability, came to dominate.

Key-words: Amazonia, cladocerans, long term, turbidity, flood pulse.

RESUMO: Padrões de longa duração da comunidade de cladóceros planctônicos do lago Batata, Amazônia, Brasil. Nós apresentamos os resultados de um estudo de oito anos no lago Batata, um corpo de água parcialmente afetado por efluente (rejeito) da lavagem de bauxita. Foram amostrados os cladóceros planctônicos e variáveis limnológicas a cada três meses durante oito anos (1990 por 1997) em uma estação natural localizada em uma parte do lago não afetada por rejeito de bauxita, e em uma estação na área do lago alterada pela presença dele.Uma análise de componentes principais indicou que as duas estações diferiram nas variáveis estudadas, durante alguns períodos de vazante e águas baixas. As estações foram semelhantes durante os períodos de enchente e águas altas. Nossos resultados indicaram que as amostras de águas baixas identificaram melhor a diferença causada pelo rejeito entre as estações. Na maior parte do tempo não observamos efeito evidente do rejeito de bauxita em aspectos da comunidade de cladóceros, sendo a equitabilidade a variável que melhor indicou a influência. As mudanças observadas na equitabilidade indicaram que em condições de alta turbidez, só as espécies que têm as estratégias adequadas para se manter em um ambiente variável e imprevisível podem persistir. Os valores de equitabilidade mais baixos observados durante as fases de águas baixas podem indicar instabilidade alta na estação impactada que pode ser relacionada ao predomínio de rejeito na coluna d'água. Nestas situações dominaram espécies oportunistas capazes de tirar proveito da instabilidade.

Palavras-chave: Amazônia, cladóceros, longa duração, turbidez, pulso de inundação.

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## Introduction

The development of the science of limnology mainly in temperate regions has strongly moulded the basic concepts of this discipline. Even today, illustrations of "typical lakes" show mainly those in the Northern Hemisphere, which are waterbodies with well-defined limits and which undergo little fluctuation in water level. In contrast, many tropical lakes are marked by profound and predictable changes in certain intrinsic aspects that are significant in their ecology.

Over the course of a year, the lakes of the Amazon floodplain undergo great changes in shape, depth, macrophyte cover, water chemistry, and primary production, because of the wide fluctuations in water level (Junk et al., 1989). Because the flood pulse modifies the physical and chemical characteristics of the water, this pulse is also the major force structuring the aquatic communities in these environments (Junk et al., 1989).

Studies of the seasonal nature of the effect of water-level fluctuations on zooplankton dynamics have indicated that patterns of variation in species richness, equitability, diversity, and density are strongly influenced by the flood pulse (Koste & Robertson, 1983; Hardy et al., 1984; Garrido & Bozelli, 1997). In contrast to other tropical regions, where there is no evidence of regular seasonality for any zooplankton group (Rajapaksa & Fernando, 1982), there is a marked seasonality in the Amazon floodplain lakes as a result of the hydrological characteristics typical of these environments.

The majority of these studies were, however, done for one year at most. According to Junk & Furch (1985), floodplains must be classified according to the source, amplitude, and predictability of flooding. Therefore, long-term studies are necessary in order to distinguish patterns in the seasonality of the flood pulse, i.e., in order to perceive whether these pulses are identical through the years or whether there are year-to-year differences in the nature of the inundations.

Amazon systems have suffered increasing human impacts, and Batata Lake is a good example. Batata Lake is a clear-water lake as defined by Sioli (1950), but has an artificially turbid compartment because of local bauxite mining activities.

Inorganic turbidity may indirectly affect the zooplankton community by reducing light penetration into the water, leading to a decline in phytoplankton productivity and biomass (Grobbelaar, 1985). Another form of indirect influence is through the coflocculation of algal and mineral particles, possibly affecting the composition and abundance of phytoplankton species (Soballe & Threlkeld, 1988).

High turbidity may also be advantageous to zooplankton, by creating a visual refuge from visual predators (Gardner, 1981) and allowing the coexistence of larger species with planktivorous fishes (Hart, 1986).

The results of previous studies of the zooplankton community of Batata Lake allowed us to evaluate the bauxite tailings as an important factor in the ecology of these animals (Bozelli, 1994; 1996; 1998) and that the magnitude of the influence of bauxite is closely related to the flood pulse. The other key point for the choose of the cladocerans is more related to the biology of the animals. Cladocerans feed by filtering the suspended matter around them. The feeding mechanism is nonselective or poorly selective, which leads to the fact that in highly turbid environments these animals do not succeed in distinguishing between mineral particles and algae, collecting both together (Arruda et al., 1983).

Considering that part of the material ingested by the organisms is of reduced or entirely lacking nutritional value, this certainly will impact on the amount of energy which the organism will have available for metabolic and reproductive functions.

Therefore the aim of the present work was to improve understanding of the seasonal patterns of the cladoceran community in floodplain lakes, and further to determine the role of the bauxite tailings and water-level fluctuations on the planktonic cladoceran community of Batata Lake.

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#### Study Area

Batata Lake is located on the right bank of the Trombetas River ( $1^{0}31'54''$  S and  $56^{0}18'28''$  W) near Porto Trombetas, state of Pará, Brazil. During the low-water phase the lake has a single connection with the river, and during the high water phase, the river water overflows the shoreline dyke which separates the two systems, and they become connected (Fig. 1).

For ten years (1979-89), tailings resulting from bauxite processing were released into the lake. These clay-rich effluents eventually impacted about 30% of the lake's area with a fine silt, causing high local turbidity, especially during the low-water period.



Figure 1: Location of Lake Batata and the collection stations. The hatched line indicates the approximate extent of the layer of bauxite tailings over the natural lake sediments.

# Methods

Samples representing four distinct periods during the year, i.e., rising water (March or April), high water (June or July), falling water (September) and low water (November or December), were collected for eight years (1990 through 1997). Two collecting stations (Fig. 1), both located in the central body of the lake, were termed the "natural station" (NS), without tailings, and the "impacted station" (IS), where tailings were present.

Data on fluctuations in the water level of the Trombetas River were provided by Mineração Rio do Norte S/A.

Water transparency was estimated using a Secchi disk. The quantity of suspended matter was estimated by gravimetry. Chlorophyll-*a* concentration was determined as proposed by Golterman et al. (1978).

The quantitative samples of cladocerans were collected with vertical hauls with a conical net of 68 mm mesh size. The cladocerans were then fixed in 4% formaldehyde. Samples were processed at the laboratory using an optical microscope, and 1-ml subsamples were counted in Sedgwick-Rafter chambers. At least 250 individuals and no fewer than 3 subsamples per sample were counted. If this minimum could not be achieved, the entire sample was counted.

The Shannon and Pielou indices were used to calculate the diversity and equitability, respectively, of the community. Both indices were calculated with the assistance of the SPDIVERS program, in Ludwig & Reynolds (1988).

A principal component analysis was done utilising the environmental variables for extraction of the axes and data were not transformed. Next, the samples were plotted in relation to these axes, with the aim of identifying the differences associated between the natural and impacted stations, associated with the environmental variables. The calculations were done using the Statistica statistical package.

Pearson's correlation was used to relate the parameters of the cladoceran community to the environmental variables. The calculations were done using the Statistix statistical package.

### Results

Principal components analysis explained 76.29% of the total data variation. Axis 1 explained 52.79%, and was strongly correlated with suspended matter, transparency, and water level, composing a turbidity axis. Axis 2 explained the remaining 23.49%, and was more strongly and inversely correlated with chlorophyll-*a* (Fig. 2).

Axis 1 split the samples into those from low- and falling-water periods, which were positioned more negatively, or from rising or high water, which were positioned more positively (Fig. 2). This result was expected, because this axis was highly correlated with the river level. This segregation also showed that, during periods of shallower water, sediment resuspension events are more frequent, forming turbid environments (Fig. 3c and d). This segregation was more evident in the IS samples (Fig. 2), which may indicate the presence of the tailings there.

On axis 2 (Fig. 2), there was a greater concentration of NS samples in the negative set of the axis. This can also be seen in Fig. 3, where many of the NS samples had higher values of chlorophyll-*a* than at the IS; however this appeared more often during the phases of falling or low water (Fig. 3c and d). Especially high values of chlorophyll-*a* were found at the NS in the 1992 low-, 1993 falling-, 1995 falling-, and 1996 low-water phases (Fig. 3). The IS samples were positioned mainly with positive co-ordinates on axis 2, showing that the chlorophyll-*a* values for this station were not especially high. The highest values found were during the falling-and low-water phases (Fig. 2, 3c and d).

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Figure 2: Principal component analysis with environment variables for extraction of the axes. Data for cladocerans at the natural and tailings-impacted stations in Batata Lake during 1990-1997 were plotted (L = low water; F = falling water; R = rising water; H = high water).

Principal components analysis showed that some of the environmental variables differed between the two stations, during certain periods of falling or low waters. The stations were similar mainly during the phases of rising or high water.

The five most abundant planktonic cladoceran species were Bosmina hagmanni, Bosminopsis deitersi, Ceriodaphnia cornuta, Moina minuta, and Diaphanosoma birgei.

With regard to the community parameters analysed (Fig. 4), the NS usually showed higher equitabilities than the IS. Equitability showed no pattern of variation related to the flood cycle in the NS, although higher values were found during rising water, and lower values during low water (Fig. 4a).

Lower values of equitability were recorded in IS samples from low-water phases, especially in 1993, 1994, 1996, and 1997 (Fig. 4d), associated with the extreme dominance of *Diaphanosoma birgei* in 1993, 1994, and 1996, and of *Bosmina hagmanni* in 1997 (Fig. 5).

Species diversity was also generally higher in the NS than in the IS, except during the falling-water phase (Fig. 4). In the NS, rising water was the period of greatest diversities (Fig. 4a). This was also true for the IS, although for the latter high diversities were also found in the falling-water phase (Fig. 4c). Extremely low diversities were recorded in the IS in the 1992 falling-water, influenced by the lower number of species, and in the 1993 low-water, as a consequence of the extreme dominance of *Diaphanosoma birgei* at that time.

Regarding the variation in cladoceran species density, in the NS (Fig. 5), densities of Bosmina hagmanni, Moina minuta, and D. birgei were highest, and were the most variable during the study. Bosminopsis deitersi and Ceriodaphnia cornuta were less abundant. These species showed peaks mainly during periods of rising and falling water. Annual peaks of B. hagmanni and D. birgei coincided during the low-water phases of 1990, 1993, and 1996. The peak of M. minuta preceded peaks of B. hagmanni and D. birgei in the falling-water periods of 1990, 1993, and 1996. This pattern of apparent species replacement from the falling- to the low-water period seemed to repeat every three years (Fig. 5).

In contrast, at the IS the species showed higher peaks and wider fluctuations in abundance. The only exception was *M. minuta. Bosminopsis deitersi* and *C. cornuta* showed the highest relative densities at this station, whilst peaks of *M. minuta* density were less frequent and relatively lower than the corresponding peaks at the NS. *Bosmina hagmanni* was present in high densities more often in this station, and also Acta Limnol. Bras., 15(1):41-53, 2003 **4**5





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Figure 3: Environmental variables at the natural and tailings-impacted stations, measured on four sampling dates per year in Batata Lake during 1990-1997. Units: suspended matter in mg.l<sup>-1</sup>; transparency in meters; chlorophyll in mg.l<sup>-1</sup>.

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Figure 4: Equitability and Shannon diversity (bits. ind.<sup>-1</sup>) at the natural and tailings-impacted stations, measured on four sampling dates per year in Batata Lake during 1990-1997.

appeared three times associated with *D. birgei* in low-water samples, though in the 1990, 1995, and 1996 low waters (Fig. 5). *Diaphanosoma birgei* had extremely high densities in the low-water samples, notably in 1993 and 1996, when this species achieved the highest densities obtained in this study.

The highest peaks in the total density coincided at the two stations. They occurred during the 1990, 1993, and 1996 low-water, and in the 1996 rising-water periods (Fig. 5).

Correlation matrices of cladoceran abundance in relation to selected environment variables, calculated separately for each species and phase of the flood pulse, are given in Tab.I

In the NS, for the samples from rising water, the correlations between transparency and suspended matter, and between suspended matter and chlorophyll-a were significant and understandably indirect (Tab. I). However, the significant correlation between the variables and community parameters is difficult to interpret.

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Figure 5: Densities of the cladoceran species at the natural and tailings-impacted stations, measured on four sampling dates per year in Batata Lake during 1990-1997. (L = low water; F = falling water; R = rising water; H = high water).

During high water, the densities of three species, total density, equitability, and diversity all correlated significantly and positively with transparency. (Tab. I).

For the samples taken during falling water, there was a significant and inverse correlation between suspended matter and *M. minuta*. At this stage, the suspended matter in the water column seems to be highly influenced by the quantity of algal particles, as indicated by their inverse correlation. Water transparency was highly significantly and inversely correlated with suspended matter (Tab. I).

For the samples taken during low water, the algal particles seem to be an essential food resource controlling the increases in density of all the cladoceran species, yet chlorophyll-a was significantly and inversely correlated with equitability and diversity. Transparency seemed to negatively influence the community diversity parameters during the low-water phase, according to the significant high and inverse correlation found between transparency and equitability, and between transparency and diversity (Tab. I).

In the IS, for the samples taken during rising water, transparency seems to be an important variable in structuring the community. Transparency showed a significant and inverse correlation with equitability, diversity, and density of *D. birgei*, reflecting

Table I : Pearson's correlations between the environmental variables (Chlor = chlorophyll a; Trans= transparency; SM = suspended matter) and the community parameters at the naturaland tailings-impacted stations, measured on four sampling dates per year (rising water,high water, falling water; low water) in Batata Lake during 1990-1997. Boldface indicatessignificant correlations at P = 0.05.

NATURAL	Rising			High			Falling			Low		
STATION	Chlor	SM	Trans	Chlor	SM	Trans	Chlor	SM	Trans	Chlor	SM	<u>Trans</u>
B. hagmanni	-0.51	0.26	-0.09	0.06	-0.65	0.76	0.17	0.06	-0.19	0.55	0.13	0.03
B. deitersi	-0.30	0.43	0.09	-0.51	0.23	-0.23	-0.34	0.09	0.15	0.57	0.12	-0.07
C. cornuta	-0.55	0.12	0.10	0.11	-0.60	0.83	0.07	-0.20	-0.01	0.57	-0.04	-0.12
D. birgei	-0.11	-0.03	-0.06	-0.21	-0.35	0.47	0.05	-0.40	0.18	0.63	-0.50	0.59
M. minuta	-0.58	0.27	0.04	-0.28	-0.48	0.17	-0.01	-0.51	0.37	0.43	0.76	-0.34
Total density	-0.33	0.17	0.07	-0.37	-0.49	0.49	-0.03	-0.41	0.26	0.65	-0.04	0.20
Equitability	-0.27	0.24	-0.09	0.12	-0.71	0.58	0.05	0.23	-0.33	-0.45	0.27	-0.68
Shannon diversity	-0.27	0.24	-0.09	0.12	-0.71	0.58	0.05	0.23	-0.34	-0.45	0.27	-0.68
Transparency	0.50	-0.63		0.51	-0.79		-0.62	-0.91		0.20	-0.71	
Sus. material	-0.81			-0.15			0.71		-	0.15		

IMPACTED	Rising			High			Falling			Low		
STATION	Chlor	SM	Trans	Chlor	SM	Trans	Chlor	SM	Trans	Chlor	SM	Trans
B. hagmanni	-0.82	0.05	-0.14	0.61	-0.42	0.35	-0.26	-0.38	0.06	0.17	0.24	-0.31
B. deitersi	0.24	-0.38	0.41	-0.06	0.37	-0.05	0.01	-0.12	0.01	0.47	-0.40	0.35
C. cornuta	0.26	-0.16	0.33	0.66	-0.53	0.18	-0.20	-0.32	0.25	-0.65	0.86	-0.58
D. birgei	0.22	-0.54	-0.44	0.61	-0.69	-0.25	-0.30	-0.43	0.12	-0.47	0.07	-0.30
M. minuta	0.58	0.49	-0.05	0.28	-0.37	0.30	-0.41	-0.35	0.07	0.01	-0.31	-0.14
Total density	0.25	-0.23	0.37	0.69	-0.48	0.13	-0.30	-0.41	0.15	-0.33	0.11	-0.36
Equitability	0.20	0.26	-0.67	-0.07	-0.38	0.49	0.12	-0.02	-0.12	0.62	-0.81	0.61
Shannon diversity	-0.54	0.32	-0.43	0.24	0.04	0.04	0.25	0.05	0.03	0.62	-0.81	0.62
Transparency	0.17	0.45		-0.41	0.27		-0.31	-0.68		0.73	-0.77	
Susp. material	0.04			-0.80			0.83			-0.68		

the increases in these parameters with reduced transparency. Conversely, the abundance of *B. deitersi* correlated significantly with transparency, although directly, indicating an increase in the density of this species when the water is clearer (Tab. I).

At high water, there was a significant, direct correlation among chlorophyll-a, the densities of three species, and total density, suggesting a influence of chlorophyll in the dynamics of the cladoceran community. The significant inverse correlations between chlorophyll-a and suspended matter, and between chlorophyll-a and transparency, reflected increased algal abundance when the water column is relatively free of other suspended particles and transparency is higher (Tab. I).

During falling water, chlorophyll-a probably influences the amount of suspended matter; the correlation between these variables was direct and significant. Chlorophyll-a showed a significant inverse correlation with *M. minuta. Diaphanosoma birgei* seemed to be affected negatively by suspended matter, according to the correlation between them (Tab. I).

For the low-water samples taken at the NS, there were several significant correlations between the parameters of the community and chlorophyll-a. However, chlorophyll-a seemed to act in the opposite way at the IS. High chlorophyll-a concentrations occurred in samples with low densities of *Ceriodaphnia cornuta* and *Diaphanosoma birgei*. Bosminopsis deitersi was the only species that was directly and significantly correlated with chlorophyll-a. The diversity indices were directly and significantly correlated with chlorophyll-a, suggesting the role of this resource in structuring the community; higher chlorophyll-a concentration was associated with higher diversities. The correlation between transparency and chlorophyll-a, transparency and suspended matter, and chlorophyll-a and suspended matter, suggested that, again, other particles than algae are mainly responsible for attenuation of light in the water column. The correlation between suspended matter and *B. deitersi*, equitability, and diversity suggested that these may be the main community parameters and species affected negatively by high concentrations of suspended matter; while *C. cornuta* showed a direct and significant correlation with suspended matter (Tab. I). However it is very important to make clear that we are not talking about causal relationships between the variables.

#### Discussion

The two stations differed mainly in relation to the quantity of suspended matter and in water transparency. The quantities of chlorophyll-a differed between the stations, but this difference was not as marked as the other variables. Water level was another important factor distinguishing the stations, because during shallowwater periods the difference between the two stations became evident.

The variation in total density of the cladoceran community is related to the amount of dilution or concentration according to the total water volume (Brandorff & Andrade, 1978; Bozelli, 1994). This expected variation could not be the same every annual flood pulse. Flood pulses are different in amplitude and duration from year to year. Other factors than those analysed here, which may be acyclic or act in a cycle different from the fluviometric one, may also have affected the observed variations in cladoceran density.

The flood pulse seems to influence the total density of the community, although the degree of its influence is likely to vary with each annual cycle. Usually at both stations, high densities were found during low-water phases, whilst lower densities occurred during high-water phases; however, this pattern was not repeated in every cycle.

The importance of the environmental variables for the cladoceran community seemed to vary according to the moment of the annual water-level cycle. The degree of influence of these variables also differed between the two stations.

The low-water samples seemed to be the most appropriate to identify the difference between the stations, because of the suspended inorganic matter. In the NS, the chlorophyll-a resource directly influenced species density, because its increase benefited some of the cladoceran populations, which also increased. The diversity indices therefore diminished at those times, indicating that opportunistic species increase more rapidly, reaching relatively high densities when the chlorophyll-a concentration increased.

Several experimental investigations have shown that cladocerans can persist under conditions of concentrations of suspended solids up to 20 mg l<sup>1</sup> (Arruda et al., 1983; Scholtz et al., 1988; Kirk & Gilbert, 1990; Kirk, 1991a and b; Bozelli, 1998). Field studies have associated the abundance of some cladoceran species with periods of high turbidity (Hardy, 1992).

Amounts of suspended matter over 20 mg l<sup>1</sup> were rarely measured in this study; such amounts were recorded only three times, at the IS. Food did not appear to be limiting most of the time, considering the amounts of chlorophyll-a present. Roland (2000) concluded that the differences between the impacted and non-impacted areas were less evident from the biomass of the community than from the primary production. Our results suggested that the bauxite tailings influenced the dynamics of the cladoceran community mainly during isolated moments, i.e., as cyclical, very variable events.

Suspended inorganic particles may be an alternate food resource for cladocerans. Arruda et al. (1983) suggested, based on experiments, that "under natural

conditions of low algal productivity and high quantities of suspended particles, the assimilation of organic substrate adsorbed to mineral particles makes this an important nutritional source for the filtering zooplankton, as long as these particles are among the size range of algal particles consumed by these organisms". Lind & Dávalos-Lind (1991) observed that suspended clays form aggregates with DOC, providing a substrate for bacterial colonisation, and most of these aggregates were similar in size to a wide range of edible algae and therefore could also be eaten by microcrustaceans. Lind & Dávalos-Lind (1991) then suggested that this might explain the observed discrepancy between phytoplankton production and fish production in Chapala Lake.

There was no clear seasonal pattern in the influence of bauxite tailings on the planktonic cladoceran community in Batata Lake. Probably most of the time the amount of tailings in the water column was insufficient to reduce the amount of algal particles to the level of starvation for the cladocerans. Nor was the amount of tailings sufficient to reduce directly the fitness of the cladocerans, or interfere in any other manner.

High quantities of suspended inorganic matter occurred mainly during the lowto falling-water phases. Even though the influence of these particles on the zooplankton animals happens at shallow depths, the concentration of this material in the water column depends on stochastic events such as wind speed and frequency, which occur in variable and irregular pulses of intensity (Panosso et al., 1995). The influence of the tailings on the cladoceran community is likely confined to isolated moments, over brief periods of time, in the form of pulses that differ in intensity and depend on water depth and level.

Slobodkin & Sanders (1969, in Putman, 1994) argued that any environment can be characterised by its severity, variability, and predictability. Moreover, according to Putman (1994), no organism can colonise an environment or maintain a stable and persistent population if that environment is severe, variable, and not predictable in space and time. As the severity decreases or predictability increases, the possibilities for successful colonisation improve. This argument seems to be supported by several studies (Arruda et al., 1983; McCabe & O'Brien, 1983, Orcutt & Porter, 1984; Scholtz et al., 1988; Kirk, 1992; Bozelli 1998) which showed that the responses of cladocerans to high quantities of suspended inorganic particles are better expressed through individual and populational parameters such as body size, survivorship and fecunduty than through community parameters. In our study we did not analyse the individual parameters. However, equitability best expressed the influence of the bauxite tailings on the cladocerans. This indicated that under highly turbid conditions, only those few species succeed which use the proper strategies to maintain themselves in a variable and unpredictable environment. Therefore, measured equitabilities at the IS were lower.

Lower equitabilities during low-water phases indicate high instability at the IS. This may be related to the prevalence of tailings in the water column during this time of year. In these situations, opportunist species, able to take advantage of these periods of instability, would spread and dominate. Equitability was higher during periods of rising and falling waters at this station.

The impacted area of Batata Lake, during periods of low water, may provide more severe, stressful conditions. Intermittent processes of re-suspension and sedimentation of tailings bring about considerable temporal variation, making this area unpredictable. However, rising water changes the situation and minimises the presence of the tailings. The IS then becomes more favourable and constant, i.e., more predictable, and the species can then colonise their environment more easily.

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