The macrofauna associated with Eichhornia crassipes roots during the phase of declining eutrophication in the Balbina Reservoir (Presidente Figueiredo, Amazonas, Brasil).

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ABSTRACT: The macrofauna associated with Eichhornia crassipes roots during the phase of declining eutrophication in the Balbina Reservoir (Presidente Figueiredo, Amazonas, Brasil). The closure of the dam across the Uatumã river in 1987 was followed by intense eutrophication of the Balbina Reservoir, Eichhornia crassipes being the dominant aquatic macrophyte. Later, eutrophication declined and between 1991 and 1995/96 E. crassipes surface cover in the research areas diminished from >50% to <1%.During this period, the macrofauna (organisms $\geq$ 3mm, thus excluding smallest insects, such as Chironomidae), colonizing E. crassipes roots, was analysed along the margins of two islands. As a further, possible indicator of declining eutrophication, plankton samples were collected simultaneously in the free water of the same areas. Macrofaunal density varied between 15 - 40 individuals/sample (of 5 roots each), and actually increased along one of the islands, Odonata being the most frequent colonizers, with peak frequencies during the dry season (Aug - Dec). On the level of Order, the patterns were similar along the two islands, but on the level of Families, there were significant differences. No decapod crustaceans were found. Plankton density declined from 12 - 26 individuals / liter in 1991 to < 1 / liter in 1995/96. The different patterns of macrofaunal and of plankton dynamics raise interesting questions as regards resource and space limitation in the marginal ecotones of the Balbina Reservoir.
Key words: Reservoir, Eichhornia, Aquatic macrofauna, Plankton.

RESUMO: A macrofauna associada as raizes de Eichhornia crassipes no reservatório de Balbina (Presidente Figueiredo, Amazonas, Brasil) durante o período de declínio da eutrofização. A construção da barragem do Rio Uatumã em 1987 foi seguido por uma fase de intensa eutrofização no Reservatório de Balbina, sendo a Eichhornia crassipes a macrófita dominante no lago recém - formado. No entanto, após 4 anos começou o declínio de eutrofização, e a cobertura da superfície do lago por E. crassipes nas áreas de investigação diminuí de >50% em 1991 até < 1% em 1995. Durante este período foi investigada a colonização das raizes de E. crassipes pela macrofauna (organismos $\geq$ 3mm; assim excluindo Chironomidae) ao longo das margens de duas ilhas. Também foram coletadas amostras de plancton na água livre, já que a densidade de plancton poderia ser um possível indicador para a redução da eutrofização. A densidade da macrofauna variou entre 15 e 40 indivíduos por amostra (de 5 raizes cada), e atualmente aumentou ao longo de uma das ilhas, sendo os Odonata dominantes nas duas ilhas, particularmente durante a época da seca (agosto - dezembro). A distribuição ao nível de Ordens foi similar nas duas áreas, no entanto, ao nível de Familias houve diferenças significatívas. Não foram encontrados Decapoda. A densidade do plankton mostrou um declínio consistente de 12 - 26 indivíduos / litro em 1991 até < 1 individuo / litro em 1995/96. Discute-se as diferenças da dinâmica populacional entre a macrofauna e o plancton nos ecótonos marginais em relação aos fatores limitantes de seus habitats: nutrientes e espaço.
Palavras-chave: Reservatório, Eichhornia, Macrofauna aquática, Plankton.

Introduction

In 1987 the dam across the River Uatumã (Presidente Figueiredo County, Central Amazonia, Brasil) was closed, and the Balbina Reservoir transformed a hilly landscape under closed Amazonian forest with hundreds of streams into a shallow lake of 2360km^2, excluding the areas of some 2000 - 3000 islands, which - apparently - were never counted. The physico-chemical conditions of the lake are continuously monitored by Eletronorte/

Manaus Energia since the closure of the dam. The slow decomposition of the submerged forest caused relatively mild eutrophication of originally acid waters with low mineral content, this - in turn- resulted in an exuberant growth of aquatic macrophytes, which spread over the surface of the lake during the first years after the closure of the dam, Eichhornia crassipes being the dominant species. Since 1991 eutrophic conditions, i.e. mineral contents and conductivity, declined (Amaral de Melo, 2003), as did surface cover by aquatic macrophytes, and species characteristic of more poor and acid waters, such as Utricularia (Lentibulariaceae) and Cyperaceae appeared. Between 1991 and 1995 aquatic macrophyte distribution in relation to limnological conditions was documented in detail along the edge of two islands (denominated "Ilha das Aranhãs" and "Serra do Chocador"; Walker et al., 1999). During this period, aquatic macrophytes were reduced to ever narrower belts along the forest-covered islands, and - as a consequence of varying water levels - constituted unstable ecotones, the "ecotone" being defined as a narrow belt between neighbouring habitats (Henry, 2003). In the present investigation the ecotone is the habitat of aquatic macrophytes between a narrow strip of sandy/muddy beach along the forested islands and the permanent open water. For the macrophyte evaluation between 1991 and 1995 two zones were distinguished, firstly, a proximal belt being subject to irregular inundation with maximum water depth of 2 - 4 meters, and secondly, a permanently aquatic distal belt with deeper water. The width of both belts varied, depending on wheather conditions and water levels monitored by the management of the Reservoir. Variation of Eichhornia dynamics as a response to local physico-chemical water conditions were also documented in detail for the Jurumim Reservoir (SP) by Luciano & Henry, (1998). In Balbina, Eichhornia crassipes was invariably much denser within the proximal belt along both islands until Sept. 1994, but from Oct. 94 to Dec. 95 it occurred sporadically only and was replaced by Utricularia (Walker et al., 1999; Walker, 2004).

The original objective of the Balbina-Project in 1991 was to investigate these new, artificially created ecotones, because any realistic evaluation of environmental impacts caused by the construction of hydroelectric powerplants must be based on criteria of the changed ecological conditions in the affected areas, including the fauna and flora of the reservoir. As regards the fauna, a first step would be to know the fauna associated with the sub-aquatic parts of the locally dominant waterplants, in the present case the roots of Eichhornia crassipes. In contrast ot Eichhornia azurea, which is primarily rooted in the benthic bottom substrate (Volkmer-Ribeiro et al., 1984), the bulk of E. crassipes roots is freely floating below the water surface, thus providing a niche for the "perizoon, the fauna that colonizes particular submerged surfaces" (Junk & Robertson, 1997). Furthermore, analysis of the collected material led to the unexpected question as regards presence/absence of Decapoda which, in order to be answered, imposed parallel collections in the marginal habitat of submerged plants and forest litter, and to collections in different habitats, such as benthic litter in a nearby forest stream and along its mouth bay.

All collections were confined to the "macrofauna, animals which can be seen by naked eye and collected by hand in the field" (Walker, 1987), a common methodology in aquatic ecology (Junk & Robertson, 1997; Walker, 1994). Collection of the macrofauna colonizing the roots of the then dominant Eichhornia crassipes started in July 1991 and continued until June 1994, including a total of 22 Balbina-excursions, whenever possible at monthly intervals, and for verification of Decapoda presence/absence, additional samples were collected in 1995/96.

In order to get some indication of the more general effects of declining eutrophication on the aquatic ecosystem, plankton samples were taken in the free water along the macrophyte belts, the expectation being, that plankton density should diminish as the result of reduced water fertility. A detailed study of plankton would necessitate diurnal sampling periods, however, all collections and observations were made between 9.00 hours and 16.00 hours.

The results of these macrofauna and plankton collections are presented in the following Tables and Figures. They raise interesting questions as regards the relations between plant and fauna population dynamics in the aquatic habitat during the phase of decreasing eutrophication of an artificial Amazonian lake.

Areas of Collection and Sampling Methods

Areas of collection

The two islands with the respective study areas were described in Walker et al. (1999). The "Serra do Chocador" is a steep range of hills (ca 1 km² area) some 35 km upriver from the dam, and the "Ilha das Aranhas" is a small (ca 20 ha) flat island ca 5 km northeast of the dam. As all islands of Balbina Lake, these two were - and still are - surrounded by the dead forest, trunks with largest branches emerging some 20 - 30 meters above the water surface, while other trees were broken just below the water surface. Near both islands, samples were collected along a 250 - 350m stretch of the southeast shores, and water depth may reach 8 -15m at 15 - 20m distance from the islands' margins. Average surface water temperatures ranged between 29°C and 33°C during the years 1992 - 1994, and mineral content in terms of conductivity had declined by 25 - 50 % between 1989 and 1995 (range in 1995 = 10,6 - 14,9mS.cm^{-1}). Eichhornia cover dropped from 15 - 30% within a belt of 30 - 50m width in 1991 to ca 12% cover within a belt of 10 - 15m in 1994, and finally to < 1% cover within a 20m belt in 1995, while by 1995, floating dead tree trunks had accumulated to >50% surface cover in the respective areas. This accumulation of floating dead trees complicated standardized spatial sampling, because the islands' margins became ever less accessible, and distances between samples varied in relation to open spaces between trunks.

The short and steep forest stream mentioned in Tab.V and Tab.VI originates South-East of the Balbina Village under high-canopy forest and joins the lake via a small, forest-covered bay near the dam. The channel is mostly less than 1m wide and forms shallow pools with submerged litter between the steeper and narrower stretches.

Sampling methods

Periods and frequency of sampling

Weather conditions and time permitting, samples were collected at monthly intervals, always within a single or two sequential days in both areas, the Ilha das Aranhãs and the Serra do Chocador; on 3 occasions, 2 excursions per month were made (see below).

Year 1991: Jul, Sept, Oct, Nov (2 excursions), Dec. Year 1992: Jan (2 excursions), Feb, Mar, Apr (2 excursions), May, Aug, Sept, Oct. Year 1993: May, Aug. Year 1994: Jan, Mar, May, June. (Total = 22 excursions).

Macrofauna colonizing Eichhornia crassipes roots

Number: of samples Ilha das Aranhãs: A total of 28 samples (of 5 roots each) were collected: 10 within a proximal (5 - 10 m) belt, and 18 samples along a more distal belt (up to 50m distance). Serra do Chocador: Total number samples = 30, 10 of which within the 5-10m belt and 20 samples further out (>10 - 50m).

Method: During a given collection period (usually during a single day), samples were taken within the proximal belt, nearer the land, in shallow water with relatively higher plant densities, and within the more distant belt, with deeper water and more dispersed plants. The dangers of navigating through the dead forest, such as hitting trunks provoking branches to break and fall, and submersed obstacles breaking the helix of the motor, imposed strict management of working hours: by 16.00 hours field work stopped so as not to risk getting stuck in the forest after sunset (ca18.00 hours). Fieldwork on the sampling sites began between 9.00 and 10.00 o´clock.

The plants were approached by canoe, rowing very quietly in order to avoid disturbance of the aquatic fauna. A plastic bucket was placed underneath the roots of the chosen plant, and the bucket with the plant carefully lifted out of the water. The animals were then removed by vigorously shaking the roots in the water of the bucket, and the water with the thus extracted fauna was passed through a nylon net (1mm² mesh). The animals visible by bare eye (minimal size ca 3mm) were removed into a sample bottle with 70% alcohol. In addition, after retrieval from the buckets, the roots were carefully examinated for still adherent organisms. The samples thus excluded the youngest larval stages of the colonizing fauna, as well as the larvae of the smallest insects, such as the

Chironomidae. On the first excursion (Jul 91) one sample of 5 plants was removed by hand net and the roots were then shaken within a bucket filled with 70% alcohol. This procedure did not increase the quantity of macrofauna collected, but this sample contained a large number of planktonic organisms. Still, in order not to pollute and disturb the sampling areas with large quantities of alcohol, this method was not repeated. It must also be admitted, that - however careful the approach and root removal - fish may escape. The results in Tab.I are therefore not conclusive as regards fish frequency, they merely document the presence of some species in this habitat. The standardized sample consists of the fauna extracted from five plants, with a distance of one to several meters between single plants.

Table I: The macrofauna collected from E. crassipes roots between 1991 and 1994. Given are the total numbers (Nrs) and % of individuals per category, and number and % of samples colonized. $\bar{X}$ = mean number of individuals per sample (of 5 roots each;). 1) Hirudinea; 2) Stratiomyidae (Diptera); 3) Culicidae; 4) Pulmonata. *Samples colonized do not add up to 100%, because single samples are occupied by several Taxa.

Taxa \ Place	Ilha das Aranhãs				Serra do Chocador			
	Individuals		Samples *		Individuals		Samples *	
	Nrs	%	%	Nrs	Nrs	%	%	Nrs
Odonata	479	65.7	100	28	460	53.36	100	30
Hemiptera	90	12.35	78.6	22	193	22.39	83.3	25
Coleoptera	77	10.55	64.3	18	117	13.37	73.3	22
Ephemeroptera	58	7.96	46.3	13	67	7.77	46.7	14
Trichoptera	12	1.65	17.9	5	1	0.12	3.3	1
Fish	11	1.51	28.6	8	21	2.44	53.3	16
Others [1]	1	0.14	3.6	1	2[3]	0.23	3.3	1
Others [2]	1	0.14	3.6	1	1[4]	0.12	3.3	1
Total	729	100%	100%	28	862	100%	100%	30
$\bar{X}$	26.0				28.7			

Sampling by handnet in other substrates

The marginal habitat of floating plant debris between submerged, rooted Cyperaceae and of submerged litter between stranded trunks along the shallow water edge of the islands, as well as the benthic litter near the water edge in the stream bay and in the stream pools, was sampled by pushing a hand net (1mm² mesh) of ca 8 liter volume underneath the submerged substrate. The animals thus caught were removed by hand and stored in sample bottles with 70% alcohol. Their minimal size was ca 3mm. As a rule two series of 5 nets each were taken during each excursion between 1991 and 1994, adding up to a total of 70 net samples, and for confirmation of these results, a later series of 24 samples was taken in March 1995.

Plankton sampling

One pair of plankton samples was usually collected along both islands on each excursion. The samples were taken within the water depth reached by the roots of the floating water plants, principally of Eichhornia, that is within 10 - 100cm below the water surface, and sampling was done exclusively during day time (between 9.00 hours and 16.00 hours). Thus, vertical diurnal (night/day) plankton dislocation was not considered. The plankton net was dragged horizontally through the water, at speeds not exceeding 80m/min, and over distances of 10 - 100m, depending on the distribution of dead, floating trees and water plants. Plankton samples were taken at the same time and in the same areas as the Eichhornia root samples, adding up to 36 samples along the Ilha das Aranhãs and 37 samples along the Serra do Chocador.

Furthermore, between July and Sept. 1991, 6 samples were collected in the river channel and 5 samples near the dam, and another 3 samples were taken in 1992 in the stream bay near the dam, one in April and 2 in September.

The approximate volume (litres of water that passed through the plankton net) of the samples was calculated from the diameter of the plankton net and the distance of the particular drag. This then permitted the calculation of the approximate number of organisms caught per liter of water that passed through the net, and hence plankton density in the natural environment. The organisms were kept in 70% alcohol until their examination under the microscope. In order to calculate the number of plankton individuals per sample, the animals of a given sample were suspended in a given volume of water, and 1 ml of this suspension was transferred into a petridish with a 1cm² grid. Counting the mean number of organisms settled per cm² then allowed to calculate the number of organisms per 1 ml, and hence, per respective sample, and consequently, per liter of water in the lake (= plankton density). For each field sample, 2 petridish samples of 1 ml suspension were assessed.

Results and Comments

The fauna colonizing the Eichhornia roots

The Macrofauna collected in Eichhornia crassipes roots along the margins of the two islands is presented in Tab. I. There was no quantitative difference of macrofaunal density per root sample between the proximal and distal belts along both islands (Range test, P‹ 0.01, Geigy 1960), for this reason the data of the two belts are not separated in the Tables and Figures. They refer to a total of 140 plants along the Ilha das Aranhãs (28 samples of 5 roots each) and to 150 plants along the Serra do Chocador (30 samples of 5 roots). The mean numbers of organisms per sample (0) are remarkably similar along the two islands, and these numbers indicate that - on the average- the roots of each single plant are colonized by 5 to 6 macrofaunal individuals. The relative frequency of the insect orders is also concordant along the two islands, the Odonata larvae are the most frequent types with more than 50% of individuals, all belonging to the Anisoptera (each Eichhornia plant harbours on the average 3-4 larvae), followed by Hemiptera, Coleoptera and Ephemeroptera, which are relatively well represented, while few Trichoptera occupy this habitat. (It is possible - though- that smallest Trichoptera species were not detected, such as Oxyethira for example, which were recorded from the Rio Paraná; (Poi de Neiff & Carignan, 1997).

Some small- usually juvenile- fish seem to adhere to the roots rather than to escape when disturbed during collection. The ten individuals that were measured ranged from 12-57mm standard length, and included Mesonauta festivum (57mm), Heros severus (20mm), Hoplias malabaricus (Traira, 40mm), and a Tetragonopterine (12mm), among others, not identified.

The complete absence of large crustacea, shrimps and crabs (Decapoda) came as a surprize, considering that palaemonid shrimps in particular are a dominant feature of Amazonian streams and inundation forests (Kensley & Walker, 1982).

Although Tab.I is confined to "Macrofauna", that is, to organisms exceeding ca 3 mm length and easily retrievable by hand, it is important to note that Cyclestheria hislopii (Bair), a large conchostrak with a diameter of up to 3mm, was practically always present, usually in larger numbers, and on one occasion more than 1400 were recorded from a single 5-root-sample. In fact, dominance of these Conchostraka was also shown in later years for the macrofauna colonizing Utricularia mats adhering to floating trunks (Walker, 2004), nor are they confined to Amazonian ecosystems, as documented by Poi de Neiff & Carignan, (1997) for Argentinian lakes. Small organisms frequently mentioned in the field notes are Lumbriculidae (Oligochaeta, mostly ‹ 2mm), Microcrustacea and small chironomid larvae. The almost complete absence of later larval stages of Chironomidae and Chaoborinae, though, is remarkable. It is probable that they adhere to the dead, decomposing leaves nearer the water surface with higher oxygen levels, which contain the resources (algae and microfauna) for their growth and metamorphosis. Nymphs and exuviae of emerged adult chaoborinae floating just below the water surface were - on the other hand - very frequent.

Table II shows that the same taxa, namely Perithemis sp (Libellulidae) and the Belostomatidae are the most frequent types along both islands, while the two islands differed as regards the abundance of the Hemiptera (Corixidae, Notonectidae) and Coleoptera (Hydrophilidae, Noteridae). These few incidental data are a case in point for the basic, hierarchical spatial structure of any ecosystem, in that sample sets of sub-areas (individual islands) have limited predictive value as regards other islands. Sporadic appearance of other Hemiptera Families include Mesoveliidae, Gerrida, Hebridae and Veliida, and of the Coleoptera: Gyrinidae, Dytiscidae and Elmidae. Only 5 species of Odonata larvae (all Anisoptera) were distinguished in the collected material.

The mean faunal density of the root colonizers in the course of the four years of collection is shown in Table III. There are significant differences between the two islands during the same year, and within the same island in consecutive years, thereby the changes between 1991 and 1992 are inverse between the two islands. There is a general tendency of increased faunal density in the later years (1993, 1994), notably in the Eichhornia belt along the Serra do Chocador. Seasonal changes may also occur (Ilha das Aranhãs, 1992). As the Odonata include some 50% of the Eichhornia root fauna (see Tab.I), seasonal differences may be due to seasonality of Odonata emergence, and Table IV supports this suggestion: the number and percentage of Odonata larvae are higher in the later months of the year.

Table II: Frequency (%) of individuals of specific insect Families collected in the E. crassipes roots. 100% = total number of individuals of the respective Order collected. 1) No significant difference between the two Islands (P › 0,15); 2) significant difference (P ‹ 0.01; X^2 - test).

Order / Family \ Place		I. das Aranhãs		S. do Chocador	
		Nrs = 100%	**%**	**Nrs = 100%**	**%**
Odonata	1)	411		378	
Perithemis sp.			84.2		74.3
Hemiptera		89		133	
Belostomtidae	1)		47.2		58.6
Corixidae	2)		49.4		18.8
Notonectidae	2)		2.2		17.3
Coleoptera		48		63	
Hydrophilidae	2)		77.1		22.2
Noteridae	2)		8.3		55.6

Table III: Variation of colonization of E. crassipes roots by the macrofauna from 1991 - 1994, with seasonal differentiation in 1991 and 1992. Dec - July = rainy season; Aug - Nov = dry season; x = mean number of individuals/sample; SD = standard deviation; n = number of samples (of 5 roots each) analysed. * = significant difference between the islands; ! = significant difference between seasons (P ‹ 0.025; X^2 tests).

Period	Ilha das Aranhas				Serra do Chocador			
	$\bar{x}$	±	SD	n	$\bar{x}$	±	SD	n
1991 *	33.0	±	20.8	10	15.7	±	4.6	6
Jul + Dec	37.3	±	27.8	4	16.3	±	6.7	3
Sept - Nov	30.2	±	17.1	6	15.0	±	2.7	3
1992 *	19.6	±	10.0	12	28.5	±	12.1	16
Jan - May !	16.2	±	8.2	9	26.3	±	11.3	11
Aug - Oct !	29.7	±	8.5	3	33.2	±	13.7	5
1993	36.0	±	14.1	2	37.8	±	8.1	4
1994	27.3	±	11.0	3	40.5	±	9.9	4

Table IV: Seasonal difference of colonization of E. crassipes roots by Odonata. % = fraction of Odonata in percent of the total macrofauna collected in the n samples (Other symbols see Tab.III).

Place	**Ilha das Aranhãs**								**Serra do Chocador**							
Period	**Dec. → Jul.**				**Aug. → Nov.**				**Dec. →Jul.**				**Aug. → Nov.**			
	$\bar{x}$	±	SD	n	$\bar{x}$	±	SD	n	$\bar{x}$	±	SD	n	$\bar{x}$	±	SD	n
Nr ind	16,3	±	12.6	18	24.8	±	11.9	9	16.1	±	10.2	17	19.7	±	7.0	7
= %	54,6	±	24.9	18	81.3	±	11.2	9	50.4	+	25.1	17	73.9	±	15.8	7

The question of Decapod absence

Palaemonid shrimps are a dominant feature in Amazonian forest streams and in the inundation forests (Kensley &Walker, 1982), and the three dominant Genera Macrobrachium, Pseudopalaemon and Euryrhynchus colonize the benthic litter habitats. Still, Macrobrachium and Pseudopalaemon were shown to disperse through the open water channel (Irmler & Junk, 1982; Walker, 1994), and were also found between submerged Cyperaceae along the stream edge. Considering that hundreds of forest streams enter the margins of the Balbina Reservoir, the complete absence of shrimps in the Eichhornia roots came therefore as a surprize. Thus, between September 1991 and March 1995 macrofaunal samples were also collected by handnet along the water edge between rooted Cyperaceae and accumulated macrophyte debris, and in the few spots where some submerged litter was accessible, as was the case along the Serra do Chocador. For comparison, submerged litter samples were taken in the small stream entering the reservoir near the dam via a narrow stream bay underneath closed, primary forest. The results of these net-samples are presented in Table V.

Table V: The macrofauna collected by handnet along the islands´ margins."Mouthbay" and "Terra firme" refer to the lower and upper course respectively of the forest stream. Numbers (Nrs) and % = fauna collected in a total of n net samples. x = mean numbers of individuals collected per single net sample.

Taxa \ Place	**I. Aranhas**		**S. Chocador**		**Mouthbay**		**Terra Firme**	
	Nrs	**%**	**Nrs**	**%**	**Nrs**	**%**	**Nrs**	**%**
Odonata	49	62.8	136	43.5	25	53.2	4	7.4
Hemiptera	19	24.4	140	44.7	5	10.6	0	
Coleoptera	0		21	6.7	1	2.1	0	
Ephermeroptera	8	10.2	11	3.5	4	8.5	0	
Trichoptera	0		1	0.3	2	4.3	1	1.9
Díptera	0		4	1.3	1	2.1	0	
Decapada	0		0		2	4.3	42	77.8
Fish	2	2.6	4	1.3	7	14.9	7	12.9
Total	78	100	313	100	47	100	54	100
$\bar{x}$	3.9		15.7		1.2		3.6	
n	20		20		39		15	

The general faunal patterns of these net samples taken along the two islands are similar to the Eichhornia root samples, particularly along the Serra do Chocador. The low number of individuals caught along the Ilha das Aranhãs is due to the difficulty of taking net samples between the very dense, floating tree trunks with few accessible litter leaves below and between them, while low numbers in the stream samples are due to small litter patches in the narrow and relatively steep channel. The fauna of the small stream agrees essentially with earlier data from other Central Amazonian streams, where shrimps were found to be dominant; the number of shrimps per net sample varied between 1.27 and 3.17 in two Central Amazonian stream basins (Walker, 1987), and in later field experiments the most numerous colonizers were the shrimps (22% of individuals), while the Odonata were represented by 3.8 % (Walker, 1994). The mouthbay, connecting the stream with the lake, is evidently a transition zone, the first two shrimps appeared, while the Odonata were still the most frequent type. All the shrimps listed in Tab.V were Macrobrachium sp.

The results of the net samples in Table 5 thus show that the absence of the shrimps in the Eichhornia roots along the margins of the two islands is not a local random effect, but that there must exist a particular reason for shrimps not being able to disperse through the deeper waters between the islands of the lake. A large reduction of the shrimps (Macrobrachium amazonicum) in the Tocantins river within two years after the closure of the dam of the Tucurui Resevoir in 1984 was also documented by Leite & Bittencourt, (1991), and Poi de Neiff & Carignan, (1997) mention a single decapod species in one of the lakes of the Paraná river flood plain (Trichodactylus borellianus, Brachyura), and Junk & Robertson, (1997), do not mention Decapoda in their study of the aquatic macrofauna adhering to macrophytes in the Amazonian várzea.

Plankton

The decline of the eutrophic phase of the reservoir is evident as a drastic decrease of plankton density between 1991 and 1995/96 as shown in Table VI, thereby this decline occurs one year later (in 1992) along the margin of the Serra do Chocador. The exceptionally high densities in September 1991 (and possibly also in Feb. and May 1992) coincided with an intense algal bloom, as verified along the entire

Table VI: Plankton density ($\bar{x}$ = mean number of individuals /liter; n = number of net samples. max = highest density found in the n samples. B = exceptional densities coinciding with algal blooms as recorded on 4 occasions in 1991 (*not included in $\bar{x}$). Other places: Lk = Uatumã river channel and lake near the dam. St = small stream bay near the dam.

Place / Year	I. das Aranhas				S.do Chocador				Other places			
	$\bar{x}$	±	SD	n	$\bar{x}$	±	SD	n	$\bar{x}$	±	SD	n
1991	11.7	±	9.8	8	26.4	±	19.0	11	Lk 12.8	±	18.9	9
max.	28.6				49.0				54,0			
B,Jul	-				167			1				
B,Sept	107*			1	163*			1	St 256*			1
									St 178 *			1
1992	5.9	±	8.1	12	26.9	±	28.9	15	0.24	±	0.13	3
max.	24.6				85.1				0.33			
B,Feb					185*			1				
B,May	197*			1								
1994	0.30	±	0.42	14	0.75	±	1.04	9				
max.	1.30				2.90							
1995/96	0.05	±	0.03	6	0.19	±	0.18	4				
max.	0.08				0.44							

lower part of the Reservoir, from the Serra do Chocador to the open lake near the dam with its stream bays. This bloom appeared to be due to one particular species of planktonic algae - small spherical colonies of single cells without flagella and with one large chloroplast per cell, Chlorococcales being the most probable suggestion (Strasburger et al., 1894), densities of ›5,000 colonies per liter were recorded. This algae bloom was accompanied by high densities of Rotifera (› 1,000 per liter) , which - under normal conditions- were virtually absent in the plankton samples, this in contrast to high rotifer densities in the Jurumim Reservoir (SP), (Melão, 1999, and Panarelli et al., 2003).

Calanoid copepods, with the almost exclusive species Notodiaptomus amazonicus, were clearly dominant during the earlier years, while Cyclopidae and Cladocera seemed to increase in later years (Fig. 1). However, the very low densities (‹ 1 individual per liter) in the later years (1994 - 96) do not allow for valid taxonomic comparisons. Among "other taxa" Sididae, Bosmidae, Macrothricidae and Ostracoda (Tanycypris) were explicitly mentioned, and in a single sample, extracted from pieces of bark removed from a floating trunk with adhering Eichhornia roots, two species of Moina and one Ceriodaphnia species were extracted.

Discussion

The striking discrepancy of population dynamics between the macrofauna colonizing the Eichhornia roots and the zooplankton during the period of 1991 to 1995/96 (Fig. 2) certainly calls one´s attention: the macrofauna per root sample (of 5 roots each) fluctuates between 15 and 40 individuals and actually increases along the Serra do Chocador (Tab. III), while plankton density in the open water shows a consistent and drastic decrease along both islands. This decrease is certainly due to the reversion of former eutrophication: surface conductivity ($mS.cm^{-1}$) fell by 20 % (S. do Chocador) and by 50 % (I. das Aranhãs), and similar reductions refer to NH_4 levels ($mg.L^{-1}$, Walker et al., 1999). The decline of surface water fertility necessarily resulted in the reduction of primary production, i.e. of phytoplankton, thus reducing zooplankton, and of Eichhornia cover along both islands, thus reducing "niche density" for the colonizing micro- and macrofauna.

The relative stability of Odonata larvae colonizing the Eichhornia roots indicates, that this "niche" includes the entire foodweb of these relatively sedentary top predators, which feed primarily on any type of smaller insects. This points to a continuous input to output flow of the smaller, more short-lived prey organisms in Tab.I, mainly plankton, Ephemeroptera and Trichoptera, which are essential inputs of the Odonata-foodweb (Walker, 1987). The data on the macrofauna colonizing Eichhornia crassipes roots in two lakes of the Paraná River floodplain (Poi de Neiff & Carignan, 1997), which include smallest insects (Chironomidae, Ceratopogonidae) support this proposition: a total of 64 species, all categorized in terms of functional feeding groups, suggest an enormous complexity of trophic interactions. Furthermore, the findings that zooplankton within Utricularia mats along the two islands is 10 - 200 times denser than in the neighbouring free water (Walker, 2004) suggests that Eichhornia roots may also be densely occupied by zooplankton, as was actually reported for E. crassipes roots of the Lago Catalão, a river to lake transition zone near Manaus (Antony & Silva, 2001). The spatial restriction of the Eichhornia root volume on the one hand, combined with open input and output flows of biomass on all trophic levels - from microorganisms to top predators on the other hand, explains the relative evenness and long-term stability of the macrofauna associated with E. crassipes roots in the Balbina lake, even during the decline of the Eichhornia density during the 4 years of observation. In short: The macrofauna colonizing Eichhornia roots is space-limited, while the basic input into the foodweb, such as planktonic algae and microfauna, are resource - limited.

The high density of Odonata in E. crassipes roots and in the submerged litter along the islands' margins (Tab. V) is in stark contrast with data on the benthic fauna of other Brasilian reservoirs. In zoobenthos samplings in the Monte Alegre Reservoir (SP) no Odonata were found (Cleto- Filho & Arcifa, 2006), and among the macrobenthic fauna of the Riberão das Anhumas Reservoir (SP) Odonata frequency varied from 2 - 5% (Corbi & Trivinho- Strixino, 2002). The likely explanation is, that Odonata are restricted to very specific habitats, the roots of aquatic macrophytes and benthic litter in the case of the Balbina lake.

As a general conclusion it may be said that, to arrive at an understanding of the ecological changes induced by artificial lakes in Amazonia, necessitates investigations on all structural levels of the involved ecosystems, from specific plants and ecotones to larger areas, as specified by Gosz, (1993), paying special attention to the connectivity between the components on all hierarchical levels (Tundisi, 1999). The few up- to-date studies so far executed in the Balbina Reservoir certainly demonstrate ecological processes of intense dynamic change which, as it may be suggested, will eventually lead to a certain stabilization of a "new natural lake ecosystem" where the intense diversification of emerging ecotones and habitats with their species diversity may balance the losses and modifications caused by forest inundation, provided the forests surrounding the Reservoir remain intact.

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