Trophic interactions within the Utricularia habitat in the reservoir of the Balbina hydroelectric powerplant (Amazonas, Brazil).

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ABSTRACT: Trophic interactions within the Utricularia habitat in the reservoir of the Balbina hydroelectric powerplant, (Amazonas, Brasil). During a project on aquatic macrophyte succession in the lake of the hydroelectric power plant of Balbina (Municipality of Presidente Figueiredo, Amazonas State), the sub-aquatic, carnivorous plant Utricularia (cf. gibba, Lentibulariaceae) was a dominant feature some 7 - 10 years after the closure of the dam in 1987. Examination of the prey of the utriculi and of the macrofauna associated with the Utricularia beds, results in a complex and characteristic foodweb within the Utricularia habitat, grazing by fish on Utricularia plants being one special feature of this foodweb. The wide distribution and frequency of Utricularia in man-made, tropical lakes suggests that this macrophyte may play an important role in the trophic structure of these ecosystems, particularly as regards the management of fish production in nutrient-poor waters.
Key words: Utricularia, prey, foodweb, Amazonas.

RESUMO: Interações tróficas no habitat de Utricularia no reservatório da usina hidrelétrica de Balbina (Amazonas, Brasil). No decorrer de um projeto sobre a sucessão de macrófitas aquáticas no lago da Úsina Hidrelétrica de Balbina (UHE, Município Presidente Figueiredo, Amazonas), Utricularia (cf gibba, Lentibulariaceae), uma espécie sub-aquática e carnívora, apareceu como um fator dominante após 7 - 10 anos do fechamento da barragem, que ocorreu em 1987. A determinação das presas de Utricularia (= conteúdo dos utriculi), bem como da macrofauna associada a esta planta, resultou em uma rede alimentar caraterística e complexa. Uma caraterística especial desta rede alimentar é que peixes tornam-se consumidores de Utricularia, pastando esta planta. A ampla distribuição e altas densidades locais de Utricularia em lagos artificiais nas regiões tropicais indica que esta macrófita pode ter um papel importante na estrutura trófica em lagos pobres em nutrientes, o que mereceria uma avaliação especial no manejo da pesca nestas águas.
Palavras-chave: Utricularia, presa, rede alimentar, Amazonas.

Introduction

Balbina Lake is the reservoir of the hydroelectric power plant of Balbina (Municipality of Presidente Figueiredo, Amazonas State, Brasil), which formed after the closure of the dam across the Uatumã River in 1987.

The elevation of the water level after the closure of the dam transformed the former hilly topography with the hundreds of stream valleys of the Uatuma's drainage system into an inundated area of ca 2,300km², with the trunks of the dead forest emerging within most of this new, mostly shallow lake area, except for the former deep river valleys. Areas of higher elevation transformed into some 1,500 islands, and the total of the thus affected region, including lake and islands, comprizes ca 6,800km². The decomposition of the dead submerged forest induced drastic changes in the hydrological conditions of the Uatuma, which were monitored before, during and after the closure of the dam by "Eletronorte", the government's authority in charge of energy supplies. The physical and chemical parameter changes (temperature, O_2-levels, pH, nutrient concentration, conductivity) followed a pattern of increasing eutrophication, which peaked in 1990/91, and then slowly reverted , approximating the former, more riverine and nutrient-poor conditions by 1995. Nutrient levels fell (conductivity 10 - 15 mS/cm), and the pH reached slightly acid values ($\approx$6,0). These physico- chemical processes induced a succession of aquatic macrophytes: Eichhornia dominated until 1993/94, followed by Utricularia and Salvinia, which were still going strong in 1997/98. The appearance of Utriculara is thus conform to the usual habitat conditions of carnivorous plants, which can maintain themselves in mineral-poor environments (Knight, 1992).

In a joint project between INPA and Eletronorte, data on aquatic macrophyte succession in relation to water quality were collected between 1991 and 1995 (Walker et al., 1999) in the lower reaches of the Balbina Reservoir. In the course of this fieldwork the question arose as regards the possible types of prey organisms of the carnivorous plant Utricularia. Consequently, samples of Utricularia were taken to the laboratory for dissection of their utriculi (i.e. traps or bladders), and the aquatic fauna associated with these Utricularia beds was also sampled. Furthermore, on some occasions, the stomac content of the prevalent animal species in these samples was analized.

The results show some interesting features of trophic interactions within the Utricularia habitat, which might stimulate special research projects as regards the ecological functions of this aquatic macrophyte in natural and in man-made Brazilian waterbodies.

Material and methods

Sampling areas

For the study on plant succession (Walker et al., 1999), two islands were chosen as examples for the more general characteristics of Balbina lake with its islands and dead forests, the "Ilha das Aranhas" (= Spider Island) and the "Serra do Chocador". The Utricularia samples were collected in these same areas of observation. The Ilha das Aranhas is a flat island of ca 20 ha, situated on the left (pre-inundation) bank of the Uatuma River, ca 5 km up-river from the dam. The Serra do Chocador (ca 110 ha) is a range of steep hills in the middle of the former Uatuma river valley, ca 30 km up-river from the dam.

Floating trunks of the dead forest accumulated along the margins of both islands during the years of observation. These trunks were (and still are today) densely colonized by semi-aquatic plants (mostly Cyperaceae), while dense Utricularia mats adhered to the submerged part of the woods. On the average, this belt of floating trunks was some 5-30 m wide, depending on the conditions of winds and water flow. Further out, the water surface was more open, except for the still standing stems of the dead forest and some dispersed, floating trunks.

Utricularia growth in the areas of observation

In the former paper on aquatic macrophytes of the Balbina lake (Walker et al., 1999) the Utricularia species analysed in this study was found to be very similar to U. gibba. However, the INPA Herbarium contains only a single specimen of this species from Mato Grosso State, while U.gibba is also recorded from a hydroelectric lake of São Paulo State (Pompeo & Moschini-Carlos, 1997). Thus, it is certainly one of the ca 50 Utricularia species recorded for Brasil (Fromm-Tinta, 1985), however, its taxonomic position as regards Balbina Lake is uncertain. The species is characterized by thin aereal stems (<1mm in diameter) of ca 5-8cm length, which carry 1-3 yellow flowers, and the morphology of the traps with a pair of large, branched dorsal antennae, agrees with a photograph by Rutishauser & Brugger (1992) of the trap of U. gibba. Part of the traps, notably the larger ones, are of dark, blue-green colour. In the following, only the generic name Uticularia will be used, it will, however, always refer to this one species, which was the only one observed in the areas of observation. The species grows into dense, subaquatic mats which mostly adhere to floating logs which are stranded along the margins of islands, as well as to the underwater parts of the upright dead trees within the areas of the submerged forest.

Sporadic appearance of Utricularia within the areas of observation was first noted in 1992 along the margin of the Ilha das Aranhas. Between the months of July and September of 1994 and 1995, Utricularia covered up to 20% of the area within a ca 5m belt along the margin of the Ilha das Aranhas, and up to 50% along the Serra do Chocador. In the lower lake nearer the dam, Utricularia adhering to the stems of the dead forest was roughly estimated to occupy some 5% of the area. Similar conditions prevailed until November 1997. By December 1998, Utricularia had receeded and Salvinia sp was on the increase.

In the years 1994, 1997 and 1998, a total of twelve Utricularia samples were collected at irregular intervals within a 5 - 50 m wide belt along the two islands Ilha das Aranhas and Serra do Chocador.

Sampling methods

Utricularia sampling: Some branches of Utricularia mats were cut for each sample and immediately introduced into a flask with 70% alcohol, where they remained until their utriculi were analysed in the laboratory.

Macrofauna: On the same places and dates, single hand-net samples of the macrofauna, associated with Utricularia were taken. To this effect, the handnet ($1mm^2$ mesh size) was quietly placed underneath the Utricularia mat, in order to not disturb the fauna, and then quickly lifted out of the water with the thus sequestered plants. The volume of the handnets was 8 - 10 liters, which corresponds to a minimal estimate of the volume of Utricularia habitat sampled. However, as the nets had to be placed below the Utricularia mats at uncertain depth, sample volume, as a rule, exceeds net volume, 10 - 15 liters being a more realistic estimate per sample. The animals were removed from the net by naked eye, and thus, their minimal size is ca 3 mm. Each net sample was preserved in a separate bottle with 70% alcohol.

Plankton: In June 1994 four plankton samples were taken with plankton nets of 12 cm diameter, which were dragged for 50 m at 10 -30 cm depth through the free water, within a belt of 10 - 50 m from the margins of the islands. Hence, the volume of each sample is 565 liters.

Methods of analysis

In the laboratory, the utriculi were dissected and their content analysed under the stereomicroscope (magnifications 5 - 30x). Frequently, fractionation and/or advanced stage of digestion resulted in uncertain identification of the prey organisms; these cases are indicated by a questionmark in Tab.I. In order to establish possible foodweb relations between Utricularia prey and predators on higher trophic levels, the stomac contents of animals caught near or inside the Utricularia habitat were determined via dissection of the digestive tracts under the stereomicroscope.

To get a rough estimate of utriculi density in the Utricularia habitat, 4 net- samples of Utricularia were oven-dried and weighed. Furthermore, in 4 sub-samples of known dry weight, the number of full and empty traps were counted before drying. These data (volume of net sample, dry weight of Utricularia per sample and % full traps) allow to calculate a minimal density of full traps within Utricularia beds in their natural habitat.

Results

Plant biomass, density and size of utriculi

The mean dry weight of Utricularia biomass per net sample was 6.71 ± 4.21g. As a rule about half of all utriculi were empty, because they either were immature or old and no longer functional, or else, because they had not captured any prey within the relevant period before collection. The total number of utriculi in the 4 samples with a total dry weight of 0.09g, was 1,056, the percentage of full traps being 44.27 ± 5.02%. Setting net-sample volume at 15 liters (lowest plant density, see above) these data lead to an estimate of 2,360 full utriculi/liter of Utricularia habitat. However, it is known from research on Utricularia vulgaris (England), that trap number varies with environmental conditions

Table I: Prey types registered in the 618 full utriculi. Questionmarks: owing to fractionation and advanced digestion, identification of the prey is uncertain, but indicates the most probable types.

Algae	Arthropoda
	Microcrustacea
Diatomaceae (=Bacillariophyceae)	
Colonies of Navicularia (?)	Conchostraka
Colonies of Pinnularia (?)	Cichlasteria hislopi
	Cladocera
Xanthophyceae	Daphnidae
Tribonema (?)	Macrothricidae
	Ostracoda
Chlorophyceae, Desmidiaceae	Tanycypris (?)
Micrasterias	Moina (?)
Cosmarium (?)	Copepoda
Closterium	Cyclopidae
	Calanoidae
Chlorococcales	Nauplius larvae
Chlorococcum	
and/or Chlorella	Arachnida
Protozoa	Acari
	Oribatidae
Rhizopoda, Foraminifera	Prostigmata
Arcella (?)	
	Insecta
Nematoda (?)	
(only a single incidence)	Diptera
	Chironomidae
	Chironominae (several species, larvae)
Rotifera	Tanypodinae, Pentaneura (?, Larvae)
	Ceratopogonidae
Lecanidae	Palpomyia or Bezzia (2 larvae)
Bdelloidae	Chaoboridae, 1 larva
	Ephemeroptera
Annelidae	Fragments of small larvae
	Coleoptera
Oligochaeta	Elmidae or Noteridae, 1 larva
Naididae	Hymenoptera
Lumbriculus (?)	Formicidae
Stylaria (?)	Fragments of adult ants

(temperature and luminosity as functions of seasonality, Friday 1992), and while these factors may be comparatively unimportant in an equatorial lake, minimal density may nevertheless fall below this rough estimate of ca 2,000 full traps per liter.

The size of functional utriculi ranges between 0.7-1.5mm length and 0.5 – 1.0mm diameter, hence, the volume per single utriculus ranges between ca 0.2 – 1.7 mm^3.

The prey of Utricularia

Tab.I lists the prey types in the total of 618 dissected, full utriculi, and Fig. 1 shows the relative frequency of ingested prey types. Shown is "prey incidence", that is, the frequency of utriculi catching particular prey, and hence, percent of utriculi containing

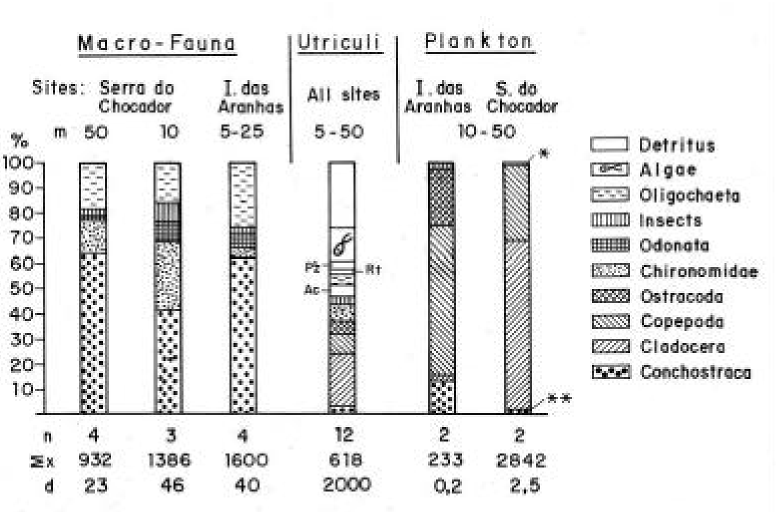

Figure 1: Prey incidence (frequency of Utriculi with respective prey ingestion in %), and composition (relative frequency in %) of the macro-fauna and plankton associated with the Utricularia habitat along the margins of the islands "Serra do Chocador" and "Ilha das Aranhas". m = width of marginal belts sampled. n = number of samples analysed. $\sum x$ = total number organisms registered, and total number of full utriculi analysed. d = estimated density of individuals and of full utriculi per liter. P'z = Protozoa; Rt = Rotifera; Ac = Acari. * Ostracoda; ** Conchostraca; Insects = any types, but excluding Odonata and Chironomidae.

prey organisms of a given taxonomic category. As 12% of utriculi contained more than one prey type, and therefore are counted more than once, addition of prey incidences adds up to a higher number than the total number of dissected utriculi (100% prey incidence = 695).

Predation of microcrustacea (37.7 $\pm$ 5.86%) is significantly more frequent than any other prey incidence ($P \ll 0.01$, X^2-test) followed by algae (13.56 $\pm$ 6.16%) and insects (8.98%, mostly chironomids) with no significant difference between them ($P > 0.3$). Algae ingestion is significantly more intense than ingestion of either Acari, Oligochaeta, Rotifera or Protozoa ($P < 0.025$), prey types that seem to be irrelevant. However, the smallest prey incidence of the Rotifera (1.8 $\pm$ 1.63%) still means that 11 utriculi contained at least one rotifer. Furthermore, Rotifera, Protozoa (Thecamoebae), Acari, Oligochaeta and Conchostraka were found repeatedly in the traps of Utricularia beds near both islands from 1994 to 1998. This indicates that the pattern of Utricularia predation seems to be quite consistent.

The category of Detritus (26.42 $\pm$ 11.58%) probably does not not mean ingestion of detritus particles, although detritus ingestion cannot be excluded by the data. It is more probable, though, that in these utriculi, prey digestion had reached a stage, when identification of prey organisms was no longer possible.

The content of single utriculi is sometimes surprizing. To mention a few examples, a single utriculus containing:

1. four chironomid larvae of 0.7 - 1mm length and one cladocer; as maximum utriculus volume approaches 2mm^3, this prey load is physically possible, but is biologically a rare case;

2.one chironomid larva, one daphnid and one macrothricid (microcrustacea);

3.six cladocera and one daphnid;

4.several utriculi were noted as being "stuffed full" of small algae (mostly Desmidiaceae).

Predation incidence in relation to the fauna colonizing Utricularia

Not surprizingly, the composition of utriculi prey is closely related to the fauna associated with the Utricularia plants (Fig. 1). The larger prey types of the macrofauna, such as the Conchostraka, insects (including chironomids) and oligochaetes, adding up to 16% prey incidence, are heaviliy colonizing Utricularia beds within a marginal belt of 5 - 50m along both islands.The relatively insignificant ingestion of the conchostrak Cichlastheria hislopi is probably due to the size (2 - 3 mm diameter) and sharp edges of its conchs, which may render ingestion unsuccessful in most cases.

The few plankton samples taken in the free water near the two islands do not allow for quantitative assessment; the difference between copepode and cladocera frequency between the two islands may be merely incidental. Still, the total of the four samples shows the prevalence of the microcrustacea that make up maximum prey incidence of the utriculi (37.7%). More informative is the relative density of the prey organisms. The densities of the plankton samples (0.2 – 2.5 organisms/liter) are within the range of zooplankton density found in other Brazilian hydroelectric reservoirs (Reservatório de Corumbá, Goiás, Lansac- Toha et al., 1999; Represa de Curuauna, Pará, Robertson 1980), while 37.7% of microcrustacean prey incidence of ca 2,000 full utriculi per liter add up to some 750 utriculi /liter with ingested microcrustacea. Their live density within the Utricularia habitat was not determined, however, it is reasonable to assume that the density of live organisms is of a similar order of magnitude as the momentary density of killed prey. As recently shown experimentally by Harms (2002), planktonic microcrustacea may prefer to stay and to reproduce within beds of aquatic macrophytes which, in the natural habitats, provide protection against predation by fish. Moreover, macrophytes are filtering out plankton of flowing waters, as reported by Chandler (1937) for a Michigan (USA) river, where 20 meters of thick plant growth filtered out 70% of the plankton from the water flowing through this plant belt. Minimal flows, as they prevail in more or less stagnant waters, have enough force to displace plankton, and the Utricularia beds may accumulate the organisms that are swept back and forth by wind, temperature variation, and by flows resulting from water level regulation by the power plant.

The foodweb of the Utricularia habitat

It is to be expected, that the consumer/resource relationships within the studied habitat of the complexity as shown in Fig.1, is not restricted to ingestion of algae and predation by utriculi. For instance, an average of 5.4% (=1-2 individuals/liter) of the macrofauna collected within Utricularia beds were Odonata larvae of at least 10 species, mostly Anisoptera , which are obligatory predators. Furthermore, small fish were frequently observed to feed along the margins and within Utricularia mats. That is, the fauna colonizing Utricularia essentially contributes to the maintenance of the fish.

Analysis of the stomac contents of 85 supposed predators collected near or inside the Utricularia mats allowed for the construction of the -admittedly rudimentary- foodweb shown in Fig. 2. The dissected animals include:

42 odonata larvae; 23 predatory chironomids (Tanypodinae); 1 coleoptera larva (dytiscid or hydrophilid); 19 fish, including 7 Cichlidae (3 Heros severos, 3 Aequidens sp, 1 Mesonauta festiva) and 12 black piranhas (Serrasalmus rhombeus), which is one of the most frequent species of large fish in Balbina lake. In addition, a group of 11 M. festiva was observed in its natural habitat, feeding along an Utricularia bed.

The trophic relations within the fauna associated with the Utricularia vegetation (Fig. 2) are in tune with the general pattern of freshwater foodwebs, in that smaller fish feed preferably on zooplankton and on insects. Noteworthy is a certain prevalence of the predatory chironomids (Tanypodinae) in this habitat: a relatively larger number (=23) of these were dissected, because they were comparatively frequent in the analysed net samples. A remarkable example is the single analysed coleoptera larva (see above): it was extracted from the stomac of a cichlid fish, and had some 50 chironomid larvae in its own ventricle.

The animal part of the foodweb agrees with the foodweb of Amazonian streams (Walker l987), in that relative size between predator and prey seems to be decisive, larger animals feeding on smaller ones, no matter their species. Thus, large odonata larvae ingest smallest fish and their larvae, while fish catch odonata larvae.

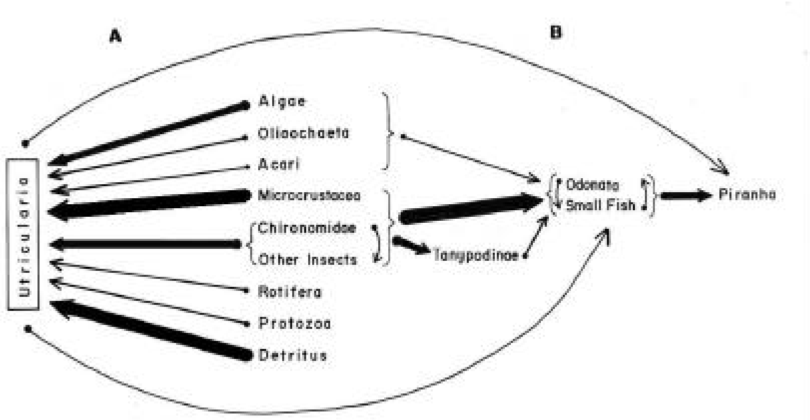

Figure 2: The foodweb of the Utricularia habitat. Arrows lead from prey to predators. A: predation by Utricularia, B: predation by the macro-fauna in the Utricularia habitat. Thickness of lines indicates range of prey incidence (% specific predator/prey interactions, 100% referring to a total of 618 utriculi in A, and to a total of 85 predators in B). Thin lines < 5%; thick lines > 25 %; intermediate lines 7 - 15%.

Rather surprizing is Utricularia grazing by fish. Of the 12 dissected piranhas, one adult and 2 juveniles had sufficient Utricularia in their stomacs to allow for the conclusion that this means ingestion by choice, rather than accidental intake with animal prey caught within an Utricularia bed. The same is true for one Mesonauta festiva. This conclusion is supported by the observation of the group of live M. festiva in their natural habitat, mentioned previously: 3 times the fish were clearly seen to pull out branches of Utricularia, to cut off and to swallow up pieces thereof. It may be added that in a later sample series (Oct 99), 5 of 20 piranhas, 4 of these being juveniles, had Utricularia in their stomacs. As regards small predatory fish, and considering the density of full utriculi (≥2,000/liter), grazing on Utricularia may be a more efficient method to ingest animal protein than hunting for zoo-plankton.

Discussion and conclusions

As noted by Mette et al. (2001), information on the prey species of aquatic Utricularia species is still very scarce. But comparison with their data on predation by three species (U. vulgaris, U. australis, U. macrorhiza) from different German habitats suggests, that there is a general, basic pattern of prey: as U. cf gibba from the Amazonian lake (Balbina Reservoir), the European species ingest primarily copepods, cladocera, ostracods, rotifers and insect larvae associated with the Utricularia habitat. Algae ingestion, however, appears to be insignificant in the European species.

The trophic structure of the Balbina Utricularia habitat is characterized by a considerable degree of bilateral symmetry (Fig. 2), because the Utricularia plant, itself a primary producer, also occupies the same trophic levels as predators. Algae ingestion characterizes it as a herbivore, yet, as a predator of the same prey as caught by fish and odonata, Utricularia also occupies second and third trophic levels. Considering the well-known fact (not shown in this analysis), that zooplankton feeds on phytoplankton, Utricularia as a zooplankton predator actually may occupy still higher trophic levels. A possible example is the foodchain: Algae - copepods - predatory chironomid (Tanypodinae) - Utricularia, which places Utricularia on the 4th trophic level.

Furthermore, Utricularia- grazing by fish roughly doubles the number of different predator-prey interactions within the foodwebs of these fish, because herbivory (= 2nd trophic level) includes the prey organisms of the plant (3rd and higher trophic levels).

These rather playful considerations have nevertheless a more serious aspect , if the enormous complexity of biological interactions is taken into account, which function simultaneously within relatively isolated and limited sub-ecosystems, such as an Utricularia bed of less than one m³ volume surrounding a dead tree, for example. In principle, complexity should reduce stability of foodwebs (May, 1973). However, the data show that the macrofauna within the Utricularia habitats of the Balbina lake is relatively stable and uniform in distant places and in the course of several years. This stability may be the result of different mechanisms. Firstly, water currents distribute the fauna over large areas, which allows for recolonization in case of local extinction. Secondly, aquatic insects with terrestrial winged adults, be they predators or prey, regularly distribute their eggs over large areas, which, again, results in local re-colonization.Thirdly, there is a wide range of omnivory, which allows temporarily declining prey populations to recover, because during these periods, predators switch to alternative prey, ("species redundancy", Naeem, 1998).

Lastly, there are probably a number of cooperative interactions with advantages for all participants. For instance, Utricularia beds may protect more organisms against predation by fish than Utricularia itself is capturing, while predation by Utricularia in turn, is promoting the growth of Utricularia. Furthermore, fish, associated with Utricularia mats, are grazing on these plants, while mineralization during digestion and the resulting excretion of the fish is fertilizing Utricularia growth. Quite generally, species interactions with a net fitness benefit for all interacting species result in mathematically stable multi-species systems, as shown by Eigen and Schuster (1979) on the macromolecular levels, and elaborated by Arrigoni et al. (1993) for cyclic foodwebs, where decomposition of consumers on all trophic levels fertilizes plant growth. The pattern of multiple trophic interactions between plant and animal species within the Utricularia habitats may thus be an example of a stable, complex system.

The expansion of Utricularia sp during the plant succession in Balbina lake (Walker et al., 1999), in combination with the data on food-chain dynamics within these extensive beds of aquatic macrophytes presented in this place, certainly calls for more intensive research on the taxonomy and ecology of Utricularia in Balbina Lake, and more generally, in man-made lakes of mineral-poor waters in tropical regions. Growth and maintenance of Utricularia may play its role in the management of these lakes and of their fisheries industry. Indeed, one may ask, whether ground-up Utricularia plants from managed aqua-cultures might not provide a suitable feed for aquarium-held, ornamental fish.

From a basic, physiological point of view, Utricularia is also specially interesting as regards the interactions between photosynthesis, digestion and respiration, with the resulting phenotype of the plants, as was shown for experimental cultures of U. australis (Adamec, 1995). This knowledge, in turn, would be essential for the conservation of Utricularia in its natural and man-made macro-ecosystems.

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