Trap size and prey selection of two coexisting bladderwort (*Utricularia*) species in a pristine tropical pond (French Guiana) at different trophic levels

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    An analysis of the morphology and the prey consumed by two carnivorous species of bladderworts (*Utricularia gibba* and *U*. sp.2) from a pond (Annie pond) in the heart of the Kaw swamp (French Guiana) has allowed a comparison of the preferential prey of: 1) a single species over two different periods (the end of the rainy season and the beginning of the dry season during an oligotrophic phase); and 2) the two coexistent species within a single period (the beginning of the dry season, during a temporary mesotrophic phase). Among the immediately adjacent planktonic and periphytic animals, and despite their low prevalence relative to smaller organisms such as Gastrotricha and Rotifera, cladocerans and copepods (particularly large individuals) appeared to be strongly predated. The differing organization and size-class distributions of the traps, as well as the extent of epiphytic colonization, had a probable defining effect on the alimentary regime of the two species of *Utricularia*. These more or less adaptive characteristics allowed the bladderworts to take advantage of the distinct preferences of various potential prey in terms of nutrition behaviour and habitat so to limit the feeding competition between the two sympatric species. The impact of this selective zooplankton predation by bladderworts on the trophic organization and the ecological functions of this pond are also addressed.

Keywords: *Utricularia*, Carnivorous plants, Tropical swamp food webs, French Guiana.

Introduction

Carnivory, a strategy adopted by certain floating, root-less aquatic species, appears to be particularly well-adapted to nutrient-poor bodies of water (Knight & Frost 1991 and Guisande et al. 2000). More generally, it is adapted to unfavorable conditions, particularly those involving low nutrient availability (Adamec 1997). Carnivory is based upon the assumption that the capture and breakdown of prey in traps enhances plant performance in terms of growth, reproduction and competitive ability (Givinish et al. 1984) by uptake and translocation of prey-derived nutrients (Friday & Quarmby 1994). At the same time, producing and maintaining the organs involved in attracting, capturing, and digesting prey is energetically costly and consumes nutritive elements (Englund & Harms 2003). In addition, because traps are less photosynthetically efficient than conventional foliage (Benzing 1987 & Knight 1992), investing in carnivory comes at the expense of the production of photosynthetic cells. Therefore, as the plant grows, this strategy leads to a reduction in its photosyn-

thetic capacity, a function that has been thought to be stimulated by the input of nutritive elements coming from the digestion of prey. Given these conditions, carnivory appears to be particularly advantageous in waters that are simultaneously low in nutritive elements and in which photosynthesis is hampered by limitations in the amount of available energy due to strong coloration of the water and/or to shade created by other floating macrophytes.

Utricularia, the bladderwort, is a widespread genus of carnivorous plants whose species range from the tropics to the arctic region (Taylor 1989). This genus encompasses aquatic, sub-aquatic, and terrestrial epiphytic species. Thirty-three species have been identified to date in French Guiana, including 9 aquatic species (Jeremy, pers. comm.), out of a total of about 214 species (including more than about 50 aquatic species) identified worldwide (Taylor 1989). Both comparative studies, in which single species are examined in different environmental contexts, and transplantation experiments have demonstrated that the amount of investment towards carnivory within a given species (defined as the proportion of the total biomass that is made up by the trap biomass) is not genetically determined (Knight & Frost 1991). Instead, the allo-

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cation is adaptive, with the number and size of the traps varying according to the prevailing conditions of the habitat (Guisande et al. 2000). Two parameters have been particularly well analyzed, either alone or together, and have yielded conflicting results: (i) prey density, with a positive effect (Sorenson & Jackson 1968, Jobson et al. 2000), negative effect (Guisande et al. 2000), or no effect (Knight et Frost 1991); and (ii) conductivity, which is thought of as reflecting the richness in nutritive elements, with a positive effect (Knight & Frost 1991, Guisande et al. 2000, 2004) or no effect (Jobson et al. 2000). More integrated studies on *Utricularia vulgaris* (Englund & Harms 2003) involving the combined experimental modification of the amount of light and the prey density have shown that investment in carnivory should be considered as a product of the trophic relationship between *Utricularia*, its prey, and the epiphytic algae that colonize it. By contributing to the nourishment of prey immediately adjacent to the traps, these algae indirectly provide bladderworts with nutritive elements necessary for their growth (Ulanowicz 1995). This involvement of *Utricularia* in a closed feedback loop (Englund & Harms 2003) seems particularly well justified because 75% of the zooplanktonic prey found in its bladders belong to populations that have been linked to the presence of macrophytes and their epiphytes which are used for their habitats or for their resources (Guisande et al. 2000).

In this study, we present a description of the morphology of *Utricularia* bladders and a study of the prey consumed by *Utricularia gibba*, a perennial species, during two hydroclimatic seasons in a pond within the Kaw swamp in French Guiana. In addition, we have used the same criteria to compare *U. gibba* (U1) with *U. sp.2* (U2, a species that was sterile during the study but which had a general morphology similar to that of *U. breviscapa*) in order to determine whether these two coexisting species have developed distinct strategies (trap size and alimentary regime) to limit their competition over resources.

Materials and methods

Study area

Annie pond (04° 38' N – 52° 09' W) is situated in the heart of the Kaw swamp, a humid littoral zone of more than 110,000 hectares in French Guiana. This pond, which was discovered in 1998, is only accessible by helicopter. The present study was enabled by the introduction of a floating platform in December of 2001. This three hectare stretch of water, with a depth of between 1.00 to 1.75 m at the end of the rainy season, is a permanent body of open water situated amidst the characteristic vegetation of the entire Kaw swamp: very dense vegetation developed on a continuous bed of floating peat. The vegetation is dominated by two fern species (*Thelypteris interrupta* and *Blechnum serrulatum*), associated with herbaceous plants (*Sagittaria lancifolia, Ludwigia nervosa*, and *L. torulosa*). The pond's open water is locally colonized by highly-abundant macrophytic vegetation that is either floating (*Pontederia rotundifolia, Pistia sp., Salvinia auriculata*) or submerged (*Cabomba aquatica*), with two rooted species dominating (*Nymphaea rudgeana* and *Eleocharis interstincta*). Accumulations of gas maintain the presence of more than one meter thick islets of uprooted peat on the surface, forming rafts on the water. At least three species of bladderworts are found in the pond: *U. gibba*, which grows partially attached to the roots of *N. rudgeana* and to the sedges that colonize the rafts; and *U. sp.2* (*U. breviscapa* ?) and *U. foliosa*, which form free colonies located in the subsurface or deep in the pelagic zone, respectively.

The open acid (pH=5.6±0.2, N=21 in rainy season ; pH=6.2±0.4, N=11 in dry season) water of the pond is delimited by a shrubby vegetation formation that is adapted to permanently hydromorphic soils and to long periods of submersion. This vegetation is used during the rainy season (from January to July) as a support for the nest building of diverse water bird species (*Nycticorax nycticorax, Egretta alba, Cochlearius cochlearius, Ardea cocoi, Phalacrocorax brasilianus* and *Agamia agami*).

Water chemistry

Global incident energy (LI-COR pyranometer) and subsurface water temperature (Pt sensor) were measured using an automated datalogger (LI-COR LI 1400, powered by a solar panel) every 30 minutes (with a measurement every minute) from a floating platform anchored at the southern part of the pond. Conductivity (WTW 187-S conductometer) and dissolved oxygen concentration (YSI 58) were measured *in situ* below the surface at the location of the bladderworts under study. The measurements were carried out at both the beginning and the end of the photosynthetic cycle, with additional midday measurements performed in August. Filtration was performed *in situ* using Whatman GF/F glass fiber filters to estimate the chlorophyll concentration and the percentage of active chlorophyll by fluorescence measurements (Turner Design TD 700). In the laboratory, concentrations of nutritive elements (water filtered at 0.7 μm for (NO_2+NO_3)-N and PO_4-P measurements and acidified unfiltered water for SiO_4-Si measurements) were determined using a Technicon auto analyzer. In August, measurements were also performed in situ to determine NH_4-N concentrations (colorimetric method). The respiration and gross

photosynthetic production of subsurface (-20 cm) phytoplanktonic communities were estimated using the oxygen method. Incubations in light (between 10:00 a.m. and 2:00 p.m.) were carried out in situ below the surface, while incubations in the dark were performed on the platform (flasks kept in a cooler filled with locally-obtained water).

Zooplankton populations present near the *Utricularia*

The micro-fauna was sampled immediately adjacent to the sites of plant collection. In June, water samples of from 500 ml to 1 l were obtained with a bucket from within dense colonies of *U. gibba*. The different samples were combined to form a 13 l sample that was then concentrated (to about 50 ml) alive by slowly siphoning the water through a 40 μm mesh net. In August, a simpler method was used that permitted a greater number of organisms to be collected. Specifically, the two samples were collected using a submerged pump moving through the plant mass. The pumped water flowed through two filtering nets for meso- (sizes greater than 150 μm) and micro-zooplankton (between 40 μm and 150 μm). The volumes of water filtered (180 l for U1 (*U. gibba*) and 90 l for U2 (*U. sp*.2)) were determined based on the amount of particulate matter present in the water. The animals (zooplankton and periphyton) were preserved in a neutral formalin solution. After screening and identification of the organisms, their densities and biomasses were estimated using an image analysis technique (Lam Hoai *et al*., 1997).

Study and preparation of trap samples

In June of 2004, at the end of the rainy season, a sample was taken from a single dense colony of U1 that was discovered at that time. In August of 2004 (at the beginning of the dry season), the analyzed samples were collections of multiple individual samples taken randomly at different sites within the pond that had been colonized by mono-specific colonies of U1 or U2. The samples were fixed in a neutral formalin solution. Branches were randomly selected for analysis in the laboratory. For U1 traps, individually dispersed along the stem without any visible structural hierarchy, 10 traps were randomly selected and removed, from 10 and 5 branches, in June and August respectively. The U2 traps (from 6 shoots), which are organized into whorls, were isolated and grouped according to their positions relative to the shoot tip (e.g. apex plus immature leaves) for their morphological analysis and pooled for the study of the prey predation.

The diameter (L) and volume (V) of the traps (Fig. 1b and 2b), and the height (TDH) and width (TDW) of the trapdoors (Fig. 1c and 2c), were measured using an image analyzer. A subsample of the measured traps was saved in order to study their contents. To do this, each trap from each subsample was opened under a binocular loupe, and all of the complete or partially-digested organisms were individually examined under the microscope. In the tables and figures: 1) copepods and cladocerans are grouped into families because their more or less partial digestion often precluded a more precise determination; 2) the large number of rotifer families present were grouped into a single taxon; and 3) all the gastrotrich species were grouped into a single taxon. Still, the text provides additional information regarding the specific composition of these various groups. The relative levels of the various food items (i) found in the bladderworts are expressed both in terms of frequency of occurrence (FOi: number of traps with the item i versus the total number of traps containing at least one prey) and relative abundance (RAi: number of prey i versus the total number of captured prey). Preferences in the diets of U1 and U2 were evaluated using the Liner Food Selection Index (L) (Strauss, 1979). L was calculated for the principal prey as L=ri-pi, where ri is the RA of prey item i in the bladder and pi is the RA of the same prey item i among the overall zooplankton community.

The traps from the two species were subdivided according to volume, and also, for U2, into four classes as a function of the extent of epiphytic colonization: Type 1 (low or not colonized (Fig. 2b) ; Type 2 (partly colonized) ; Type 3 (regularly colonized) ; and Type 4 (luxuriant colonization).

Results

Climatic context (Fig. 3)

The average daily subsurface water temperatures in June (Fig. 3A) and August (Fig. 3B) 2004 were 26.3° and 26.2°C, respectively, with daily thermal amplitudes of 3°C and 4°C. This amount of variation occurring on individual days was greater than the monthly variation that occurs during the year (annual amplitude of 2.9°C between the average minimum in February and the maximum in June). In June, the total incident irradiance averaged 1474 J d^{-1}, with maximum values of 600 W m^{-2} and strong daily variability (CV 24%). In August, the light was significantly greater (1974 J d^{-1}) and less variable (CV 14%), with maximum values exceeding 800 W m^{-2}. Due to the proximity of the equator, the duration of light was identical for the two periods.
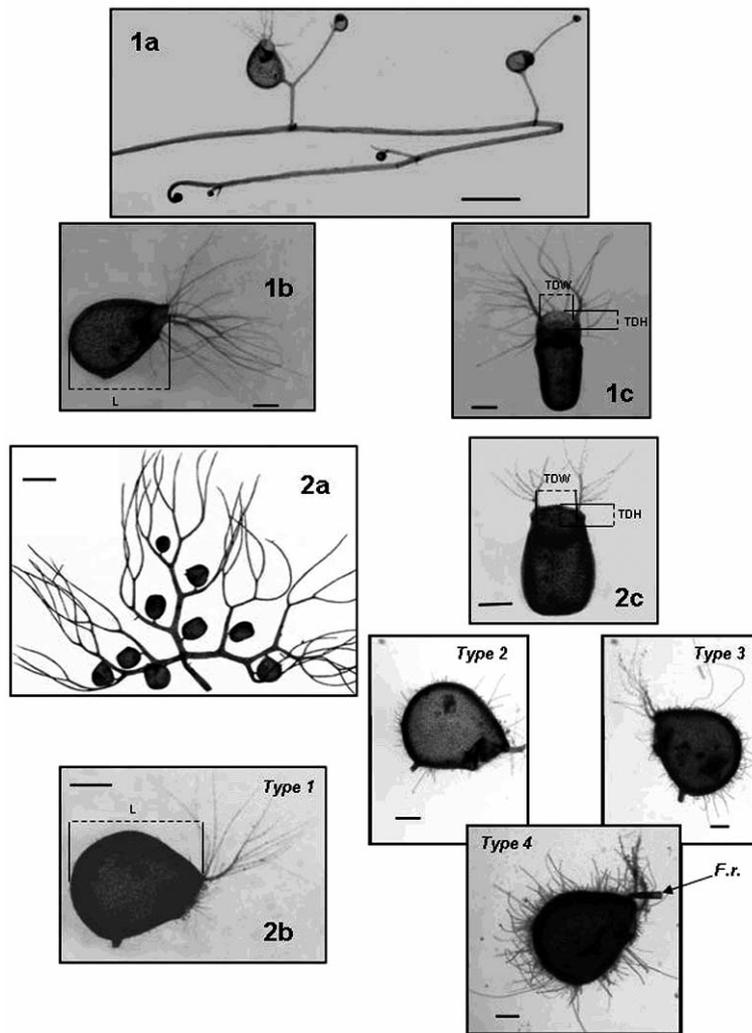
Fig. 1-2. *Utricularia gibba* (Fig. 1): a, stolon, b, lateral and c, ventral bladder views. (Abbreviations: L=trap length, TDW=trap-door width, TDH=trap-door height). Scale bars: 1a=2.5mm, 1b and 1c=0.4mm. *Utricularia* sp.2 (Fig. 2) : a, whorl of the three lobes of the leaf, b, lateral and c, ventral bladder views. Type 1 to 4 degrees of bladder colonization by epibiont community. Arrow corresponds to *Floscularia ringens* (epiphytic rotifer). See Fig. 3 for abbreviations. Scale bars : 2a=2mm, 2b (type 1-4) and 2c=0.4mm.

Table 1. Water chemistry during two surveys in Annie pond. Conductivity (Cond., μS cm^{-1}); nutrient concentrations, NH$_4$-N, (NO$_2$+NO$_3$)-N, PO$_4$-P, SiO$_4$-Si (μM); chlorophyll *a* concentrations Chla (mg m^{-3}) and active chlorophyll *a* percentage (%). (n.d.: no data; in brackets : number of analyses).

	Cond μs cm^{-1}	NH$_4$-N μM	(NO$_2$+NO$_3$)-N μM	PO$_4$-P μM	SiO$_4$-Si μM	Chla mg m^{-3}	active Chla %
9-14 June	48 (1)	n.d.	0.36(2)	0.03(2)	15.01(4)	1.0 (4)	27 (4)
24-26 August	88 (5)	0.82 (5)	0.15 (5)	0.12 (5)	23.7 (5)	9.4 (15)	66 (15)

Table 2. Dissolved oxygen (D.O.) and saturation rate of O$_2$ (Sat.). Overall respiration (R) - Parameters of phytoplanktonic activity: - Percentage of total daily photosynthetically available radiation (PAR) - Photosynthetic productivity (A) -Efficiency of gross primary productivity (GPP).

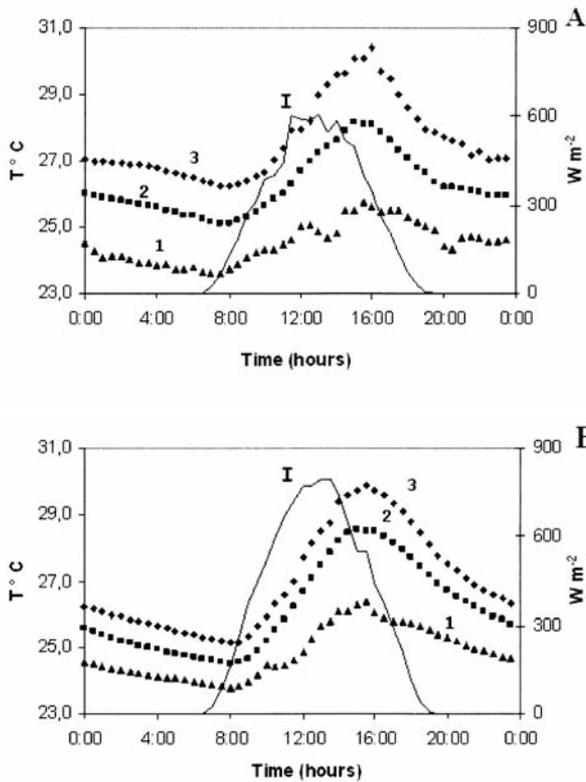|	9-14 June		24-26 August		
	8 AM	4 PM	6 AM	12 AM	4 PM
D.O. (mg l^{-1})	3.00 (5)	2.96 (5)	2.03 (2)	3.54 (3)	5.62 (3)
Sat (%)	39 (5)	39 (5)	25 (2)	59 (3)	77 (3)
PAR (%)	2	93	0	39	89
R (mgO$_2$ m^{-3} h^{-1})	17 (15)		39 (5)		
A (mgC m^{-3} h^{-1})	3.7 (14)		111.8 (5)		
GPP (mgC mgChla^{-1} h^{-1})	n.d.		20.8 (5)		

Fig. 3. Water temperatures (°C) and total incident irradiance (W m^{-2}) at 15 mn intervals. Daily means of total incident irradiance (I, continuous line) and absolute minima (**1**), maxima (**3**), and mean (**2**) of temperature. A - June 2004, B - August 2004.
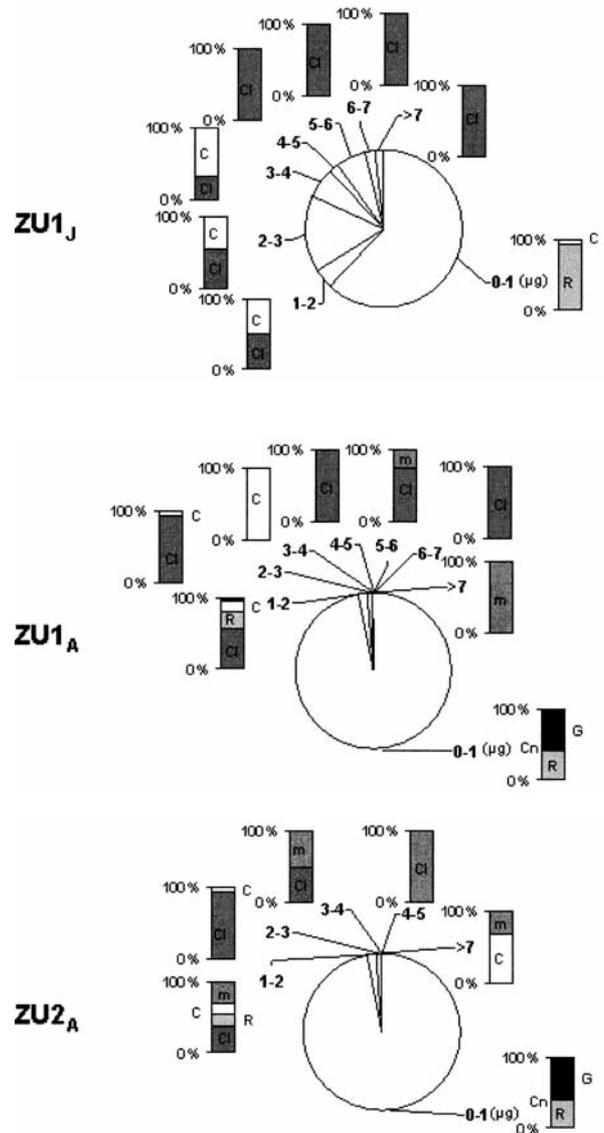

Fig. 4. Percentages of individual potential prey by biomass class (pie chart) and taxonomic composition of the various classes (histograms) sampled near U1 and U2 in June (ZU1$_J$) and August (ZU1$_A$ - ZU2$_A$). (Abbreviations: C, Copepoda; Cn, copepods nauplii; Cl, Cladocera; G, Gastrotricha; R, Rotifera; m, miscellaneous).

Water chemistry

While the waters in the pond were generally very weakly mineralized (conductivity <100 μS cm^{-1}), in August the end of the precipitation and evaporation led to a weak increase in conductivity relative to the level in June (Table 1). The concentrations of nutritive elements were always very low. In August, in connection with the increase in total incident irradiance, chlorophyll contents were present at nearly 10 times the level observed in June, with the bulk of it corresponding to active pigments. As a result, in the context of water that was strongly desaturated with oxygen (Table 2), significant circadian oxygen variations were observed in August (>3.5 mg l^{-1}). In contrast, in June, oxygen concentrations at the end of the day were equivalent or even inferior to those observed at the end of the night, indicating that the amount of photosynthetic production occurring during the day was lower than the level of respiration. Estimations of the respiration and

photosynthetic production based on *in situ* incubations of raw water were 2- and 30-fold lower, respectively, in June than in August. These experimental results thus confirmed the very low activity of the biological communities (plankton respiration) during the rainy season, particularly of the phytoplanktonic community (photosynthetic production).

Table 3. Density (N, ind l⁻¹) Biomasse (B, µg l⁻¹) and relative abundance of potential prey (Z) in terms of density (% N) and biomass (% B), near U1 and U2 in June (J) and August (A).

| | N | B | Gastrotricha | | Rotifera | | Cladocera | | | | Copepoda | | | | misc. | |
| | | | | | | | Macrothricidae | | Chidoridae | | Cyclopidae + Harpacticidae | | nauplii | | | |
			%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B
ZU1$_J$	4	9	-	-	53	25	2	2	30	60	12	13	4	0	-	-
ZU1$_A$	35	5	55	20	39	31	1	6	2	28	0	3	2	8	-	5
ZU2$_A$	36	6	55	16	39	33	0	1	2	24	0	9	2	6	1	10

Abundance of potential prey organisms

The total zooperiphytic and zooplanktonic communities (Z) are presented in Table 3. In August, the densities and biomasses of these communities (ZU1$_A$ and ZU2$_A$) were comparable. In June, however, their densities were seven-fold higher than in August, although they corresponded to a lower overall biomass. This apparent paradox reflects a significant change in the community structure that took place during the transition between the end of the rainy season and the beginning of the dry season. In June, these communities were dominated in terms of density by rotifers (1.9 ind l⁻¹) and in terms of biomass by cladocerans (6.4 µg l⁻¹, of which 5.2 µg l⁻¹ were Chidoridae). In August, however, the primary contributors to the zooplankton density were gastrotrichs (20 ind l⁻¹) and rotifers (14 ind l⁻¹). While these two groups made up 95% of the total density of the ZU1$_A$ and ZU2$_A$ samples, they only represented half of the total biomass. The rest of the biomass came from cladocerans and copepods (Table 3), whose densities were, however, less than two and more than ten times lower, respectively, than those observed in June.

Figure 4 shows the composition of the micro-fauna by size class (0.1 µg interval). Organisms having an individual biomass of between 0.0 µg and 1.0 µg represented 62% of the total number of individual organisms present in the ZU1$_J$ sample. This class was mainly made up of rotifers (6 families), particularly (and as a function of their abundances) the Lecanidae (4 species), Notommatidae (4 species), Trichocercidae (2 species), and Testudinellidae (2 species). In August, this size class comprised rotifers and gastrotrichs, and encompassed 97% of the total organisms. The rotifers were highly diversified, falling into 13 and 12 families (including the 6 observed in ZU1$_J$) for ZU1$_A$ and ZU2$_A$, respectively. The Trichocercidae (with 4 species, of which *Trichocerca sp.3* was highly abundant) dominated. The gastrotrichs, which were not observed in June, were represented by several species (D'Hondt *et al.*, 2005). In June, cladocerans (Chidoridae and Macrotricidae) represented most of the organisms in size classes greater than 1 µg. They were associated with

copepods (Cyclopidae) and with various other organisms (e.g., tardigrades, dipteran larvae). The taxonomic composition of the size classes above 1 µg was similar for ZU1$_A$ and ZU2$_A$, except for: 1) the absence of individuals in classes 5-7 µg for ZU2$_A$; and 2) changes in the distribution of copepods, which were only present in size classes 2-4 µg for ZU1$_A$ (Harpacticidae and Cyclopidae, including *Microcyclops sp.* and *Eucyclops sp.*) and mostly in the >7 µg class for ZU2$_A$ (Cyclopidae, including *Mesocyclops sp.*).

Plant organization and bladder morphology

The overall morphologies of the two species are different. In *U. gibba* (U1), the colonies form a very dense tangle of long, highly-ramified filiform branches, with each branch bearing one to two traps on short auxiliary branches (Fig. 1a). In *U. sp.2.* (U2), which were not fertile at the time of sampling, the leaves are organized into whorls of photosynthetic filaments. Each whorl includes three leaf lobes, each of which is subdivided into three secondary lobes (Fig. 2a). Each of these is then dichotomously divided into third order segments, which themselves bifurcate into superior order segments. Each leaf lobe contained an average of 10 bladders (range: 7-13), starting at the third whorl relative to the shoot tip. The maximal mean volume (1.82 mm³; standard deviation = 0.70, N=27) of the traps was generally observed on the eighth whorl.

Despite the differing overall organization of the two plant types (in U1, traps dispersed along the branches, and in U2, traps concentrated in whorls), their traps, which are vital organs in these carnivorous species, showed strong morphological analogies (Fig. 1b-1c; 2b-2c). Nevertheless, the external trigger hairs and antennae were significantly more developed in U1 than in U2. Also, unlike U1 in both June and August, the U2 traps were more or less covered with epiphytic autotrophs (diatoms and filamentous algae) and heterotrophs (bacteria, protozoa, and rotifers: *Floscularia ringens* and *Stephanoceros fimbriatus*). The extent of colonization by these epiphytes was linked to the size and/or the age of the bladders (Fig. 5). The progressive
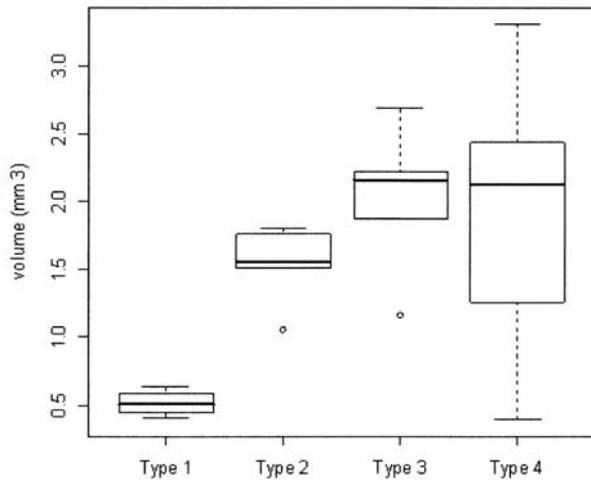
Fig. 5. Box plot representations of the volume (in mm³) of U2 bladders as a function of the degree of colonization by epibiont communities (for qualitative estimations of the degree of colonization, see Fig. 2b).

eutrophication of the pond during the dry season leads to a proliferation of epiphytic communities largely composed of filamentous algae. This chokes off the U2 colonies (Kemp et al., 1983), rapidly rendering their traps inoperative and ultimately causing them to disappear from the pond by the end of the dry season.

Morphological dimensions of the bladders

For the two species and the two sampling periods under study, the exterior bladder volumes categorized into different size classes did not follow a normal distribution (Fig. 6). Indeed, in June, the distribution of the U1 bladders showed two modes, with the principal mode centered on classes 0.30-0.45 mm³, and the second one on classes 1.20-1.35 mm³, with a maximum volume of 1.98 mm³. In August, only a single mode was observed, centered on class 0.15-0.30 mm³ and with a maximum volume of 1.75 mm³. The size-class distribution of the U2 bladders showed two modes, one centered on class 0.00-0.25 mm³ and the other on class 1.50-2.00 mm³, with maximum values reaching as high as 3.15 mm³. These two modes mainly corresponded to bladders from whorls situated at positions 3 and 7-8 relative to the shoot tip. In August, about a third (37%) of the U2 bladders had a volume that was greater than the maximum class observed for U1. In addition, the coexistence of these two species in August was accompanied for U1 by a downward shift in the principal mode and the disappearance of the second mode. As a result, the median external volume of the traps in August was only half the value observed in June (Table 4).
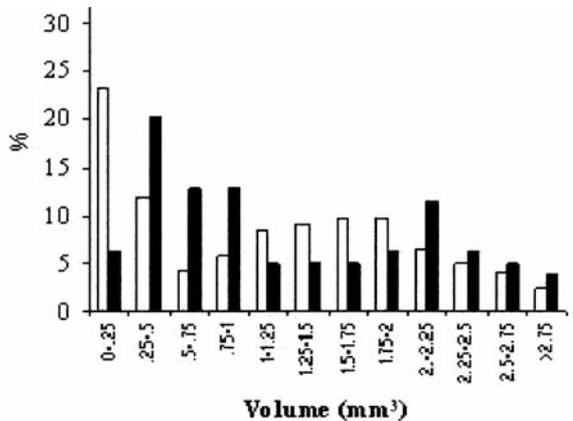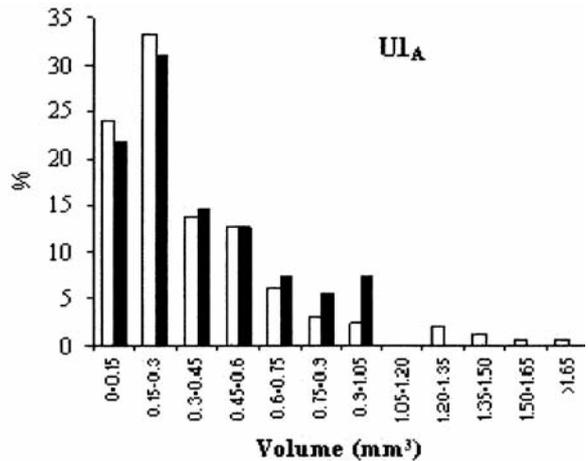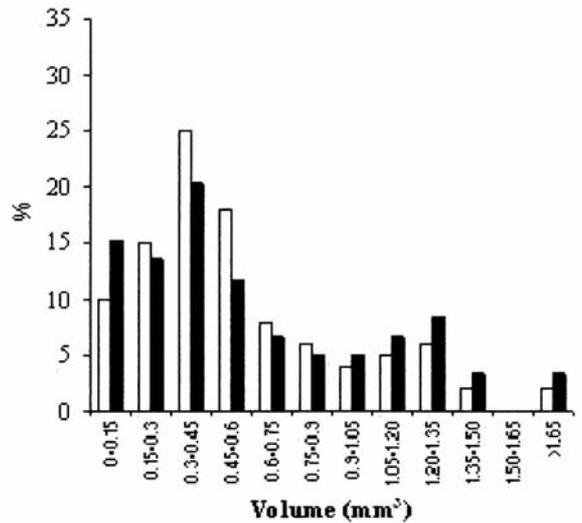

Fig. 6. Size-class distributions (volume in mm³) of all bladders (empty bar) and bladders selected to study their contents (full bar). U1 (0.0 to greater than 1.65 mm³); U2 (0.0 to greater than 2.75 mm³).

Table 4. Statistics and regression equations calculated using double-ln transformed data for U1 (June and August) and U2 (August): - bladder volume (V, mm³) and length (L, mm) - width (TDW, mm) and height (TDH, mm) of trap-door. Number of traps (Nb); Correlation (cor.) *** P <0.001, * P <0.05; n.s., not significantly different from P >0.05.

		Volume	Nb			Nb	r^2	t (cor.)	Exponent	t (exponent)
U1$_J$	Median	0.38		V	$0.304L^{2.65}$	101	0.979	22.67	<3.0***	9.03
	Mean	0.56	121	TDW	$0.248L^{1.34}$	88	0.706	14.38	>1.0***	4.34
	S.D.	0.39		TDH	$0.309L^{1.23}$	92	0.876	25.18	>1.0***	5.05
U1$_A$	Median	0.19		V	$0.304L^{2.81}$	50	0.957	32.53	<3.0*	2.26
	Mean	0.33	159	TDW	$0.233L^{1.33}$	50	0.843	16.04	>1.0***	4.34
	S.D.	0.30		TDH	$0.289L^{1.30}$	50	0.915	22.67	>1.0***	5.51
U2$_A$	Median	1.01		V	$0.264L^{3.07}$	132	0.976	73.15	n.s. 3.0	1.75
	Mean	1.12	346	TDW	$0.344L^{0.89}$	65	0.946	33.10	<1.0***	4.38
	S.D.	0.85		TDH	$0.256L^{1.30}$	197	0.953	63.07	>1.0***	14.75

Table 5. Comparison between slopes and intercepts of regression equations; length of bladder versus trap volume (V) and trap-door width (TDW) and height (TDH) for U1 and U2. (df, degree of freedom; n.s., not significantly different from P >0.05, and s, significantly different from P <0.05).

	Exponent			Intercept		
U1$_J$ vs U1$_A$	df	t		df	t	
V	147	7.02	s***	148	0.01	ns
TDW	134	1.78	ns	135	0.06	ns
TDH	138	1.32	ns	139	0.07	ns
U1$_A$ vs U2$_A$						
V	178	13.18	s***	179	0.04	ns
TDW	111	29.73	s***	112	0.28	ns
TDH	243	0.74	ns	244	0.07	ns

Independently of the trap size comparisons between the two species, allometric measurements were carried out in order to determine : 1) if the two species had different trap morphologies; and 2) if, for U1, its shape was modified over time and in the presence of U2. All of the relationships between large bladder diameter (Trap length, L), external volume (V), and the width (trapdoor width, TDW) and height (trapdoor height, TDH) of the trapdoor opening, were highly significant (Table 4). The exponents of the scaling relationships calculated from double-log regressions were tested for departure from 3.00 (for volumetric estimations) or from 1.00 (for linear dimensions). For U1, the slopes corresponding to the relationship between L and V were significantly below 3 (Table 4) and different between June and August (Table 5). In June, when there was a wide range of bladder sizes, the slopes for L vs. TDW and L vs. TDH were significantly greater than 1.00, with TDW increasing more rapidly than TDH (t = 5.56, df = 176, P(α=0.001) =3.29). In August, the slopes for L vs. TDW and L vs. TDH were above 1.00 and not significantly different between TDW and TDH

(t = 0.83, df = 95, P(α=0.2)=1.28). Thus, the width and height of the trapdoor grew faster than the diameter of the bladder (and, consequently, its volume as well), while the general shape of the trapdoor opening remained the same. For U2, the bladder morphology was spherical (the slope of L vs. V did not significantly differ from 3.00). Initially, the trapdoors of young bladders are wider than they are tall. However, as the bladders develop, the different growth rates (as evidenced by the L vs. TDW and L vs. TDH calculations) gradually result in the production of spherically shaped trapdoors.

Feeding ecology of carnivorous bladderworts

The contents were examined of 59 and 55 U1 traps from June and August, respectively, and of 79 U2 traps from August. Globally, the volume distribution of the examined traps was representative of the overall distribution of traps from the different samples (Fig. 6). More than 50% of the traps (56% for U1$_J$, 67% for U1$_A$, and 57% for U2$_A$) contained at least one prey item. In addition, the occurrence of prey rose with increasing trap size. For U1$_J$, the smallest functional traps measured 0.20 mm³ (corresponding to a trapdoor size of 0.05 mm²) and 0.07 mm³ in August (trapdoor of 0.02 mm²). For U2$_A$, the smallest functional traps were 0.32 mm³ (trapdoor of 0.10 mm²), and were present on whorls situated at positions 4-5 relative to the shoot tip.

The zooperiphyton and zooplankton present in the traps were often associated with phytoplankton (Desmidiaceae and Chlorophyceae) and with various species linked to the benthic domain (insect larvae). Taxonomic analyses of these prey gave similar results regardless of whether they were expressed in terms of frequency (F) or occurrence (O) (Table 6). The prey that was the most abundant in the traps was also the

Table 6. Frequency and occurrence of prey in the bladders of *U. gibba* (U1$_J$, U1$_A$) and *U. sp.*2 (U2$_A$). Number of traps and prey (Nb); miscellaneous (misc.).

		Nb	rotifers	Chidoridae	Macrotricidae	large cyclopids	small cyclopids	harpacticids	gastrotrichs	nauplii	misc.
U1$_J$	Prey	141	6	65	20	4	1	1	0	0	4
	Traps	32	16	84	50	16	6	3	0	0	13
U1$_A$	Prey	94	48	16	10	3	1	1	5	0	16
	Traps	36	58	36	22	8	3	3	14	0	39
U2$_A$	Prey	83	34	10	8	19	8	0	6	8	6
	Traps	43	40	16	16	37	16	0	12	14	9

most usually caught. In June, the principal U1 prey were cladocerans, primarily Chidoridae and Macrothricidae. Rotifers dominated in August, belonging to species falling into diverse families including (in decreasing order of prevalence): Notommatidae (including only one species, *Cephalodella sp.*, which was not observed in the water), Lecanidae, Bdelloida, and Trichocercidae. Associated with these rotifers were Chidoridae, Macrothricidae, gastrotrichs, and other prey from various taxonomic groups such as Ciliates, Rhizopoda, Tardigrades, Hydracarina, and insects.

Copepods and rotifers were the predominant prey of U2. The copepods were mainly cyclopoids, adults and copepodits (including *Eucyclops sp.*, *Mesocyclops sp.* and *Microcyclops sp.*), while the rotifers included Colurellidae (which were not found in the water), Lecanidae, and some Notommatidae, Trichocerchidae, and Bdelloida. Other observed prey included one Hemiptera as well as Dipteran larvae (Chironomidae).

The largest prey were not systematically present in the traps with the largest trapdoors. For example, in June and August, the largest U1 prey (the Chidoridae, with biomasses of 35 μg and 12 μg, respectively) were observed in traps that had trapdoors of 0.27 mm^2 in June and 0.08 mm^2 in August. Nevertheless, to address the possibility that trapdoor size (td) conferred some selectivity toward the choice of prey, prey occurrence was analyzed for three categories of trapdoor sizes. These classes, small (s), medium (m) and large (l), were defined as a function of the respective trapdoor sizes for the two species (Fig. 7). In June, the occurrence of copepods in traps with small trapdoors was zero, while that of the Chidoridae was 100% (Fig. 7a). For the largest trapdoor class, the occurrences of two cladoceran families, Chidoridae (cl1) and Macrotricidae (cl2), and of two copepod groups, large (c1, including *Mesocyclops sp.*) and small (c2, including *Microcyclops sp.* and *Eucyclops sp.*) were around 40%. Rotifers had equivalent occurrence levels in the three classes. For U1$_A$, there were few differences between the two size classes present (Fig. 7b). The occurrences of rotifers were higher

than in June, while the cladocerans were captured at a markedly lower level. For U2$_A$, there were marked differences between the three classes in the occurrence levels of large copepods (c1): 54% of the bladders with large trapdoors had at least one large copepod, compared to 7% for the traps with small trapdoors (Fig. 7c).
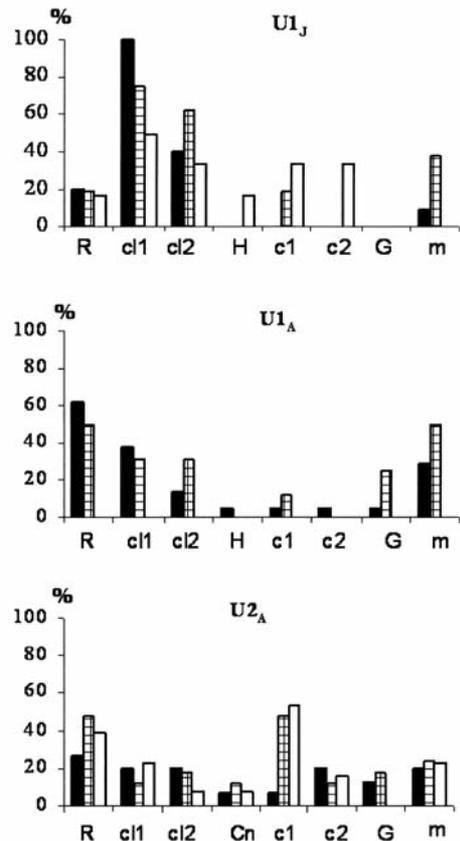

Fig. 7. Occurrence of prey according to the 3 categories of trapdoor sizes (td). These classes, small (s, full bar), medium (m, hatched bar) and large (l, empty bar), had the following size boundaries for U1: s, td <0.10 mm^2; m, 0.10mm^2< td <0.30 mm^2; l, td > 0.30mm^2. For U2, the size limits were: s, td<0.25 mm^2; m, 0.25 mm^2< td <0.40 mm^2; l, td >0.40 mm^2. (Abbreviations Cn, nauplii; c1, large cyclopids, c2, small cyclopids; H, Harpacticoida; cl1, Chidoridae; cl2, Macrothricidae, and see Fig. 2 for other abbreviations).
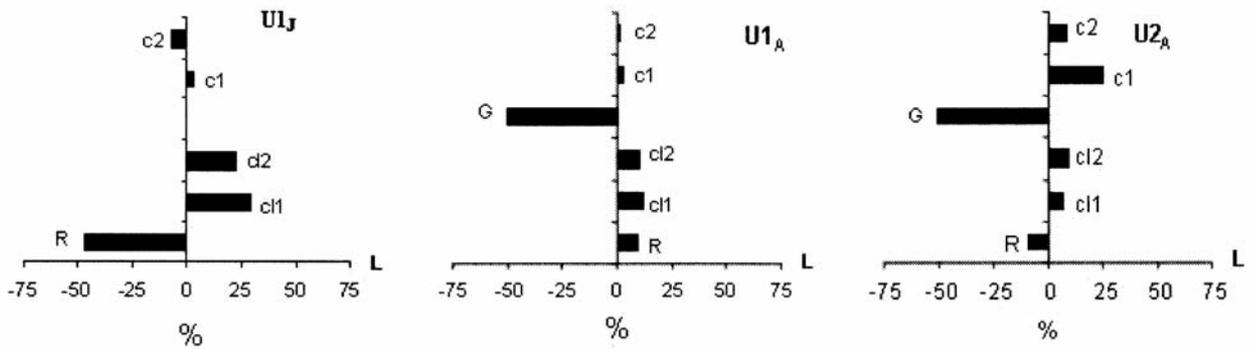
Fig. 8. Strauss Index (L) for zooplanktonic taxa (See Fig. 6 for abbreviations of taxa).

In June, an analysis of the $U1_J$ bladder contents revealed an overrepresentation of cladocerans among the identifiable prey relative to their levels among the micro-fauna in the water adjacent to the plants (Fig. 8a). Among the cladocerans, the chidorids (cl1, represented by various species) were captured much more often than the Macrothricidae (cl2, which were mostly represented by *Echinisca sp.*). In contrast to the cladocerans, rotifers were underrepresented in the bladders. Similarly, in August, gastrotrichs were only rarely observed in the U1 and U2 traps. For $U1_A$, the preferential choices according to the Strauss index were the Chidoridae, the Macrothricidae, and rotifers (Fig. 8b). For $U2_A$, the copepods and cladocerans were strongly targeted, at the expense of the capture of the two most abundant elements in the water community: gastrotrichs and rotifers. Finally, the largest copepod (*Mesocyclops*) individuals were preferentially captured (Fig. 8c), particularly by the traps falling into the largest size classes (Fig. 7c). At the other end of the scale, the smallest traps preferentially captured rotifers and cladocerans; the observed pattern was thus very similar to that described for $U1_A$.

Discussion

The humic acid water of the Kaw swamp is characterized by strong oligotrophy, which is favorable for the development of carnivorous aquatic plants such as the rootless and free-floating bladderwort (Adamec 1997). Bladder production in *Utricularia* is a strategy that offsets the ecological disadvantages associated with nutrient-poor environments (Guisande et al. 2004). Despite the apparent extreme poverty of the water in Annie pond, located in the heart of this swamp, the traps of the two most prominent bladderwort species (*U. gibba* and *U. sp.2*) contained relatively large numbers of micro-fauna. In the rainy season, in this water pond containing very low concentrations of dissolved oxygen, the absence of nycthemeral variations in oxygen concentrations, together with very low levels of estimated respiration, revealed a quasi-absence of photosynthetic activity. In this context of very limited autotrophic growth, the carnivory of *U. gibba* represents the sole alternative strategy. In August, when the precipitation is over, the presence of higher concentrations of dissolved elements due to evaporation, coupled with fertilizing inputs resulting from the reproduction of abundant communities of migrant herons, enrich the water and promote the growth of planktonic communities. Annie pond thus rapidly evolves from an oligotrophic state to a mesotrophic one. During this period, the micro-fauna becomes dominated by small organisms, particularly rotifers and gastrotrichs. When this happens, the two species *U. gibba* and *U. sp.2* greatly extend their coverage of the pond.

The consumed prey (based on the observation of identifiable remains) consisted mainly of cladocerans (Chidoridae and Macrothricidae) and rotifers for *U. gibba* in June. In August, it was rotifers associated with larger prey, cladocerans for *U. gibba* and copepods (Cyclopidae) for *U. sp.2*. Large individuals, which were very poorly represented among the zooperiphytic and zooplanktonic communities, thus appeared to be strongly predated. These prey are common to diverse bladderwort species (Skutch 1928, Botta 1976, Gordeev & Sibataev 1995, Pompêo & Bertuga 1996, Harms 1999, Guisande et al. 2000), although it is possible to overestimate their contributions because: 1) they are easier to observe due to their relatively large size compared to other zooplanktonic components; and 2) they persist longer because they take longer to digest than smaller prey (Jobson & Morris 2001). Nevertheless, the immediate fixation of the samples should have

minimized this bias linked to different digestion rates as a function of the size and type of prey. Our results show that cladocerans and cyclopoids were selectively captured over small prey, a preference that may be indicative of an optimization process at work in the functioning of the traps. According to this hypothesis, derived from the optimal foraging theory, the disturbances created by small organisms would be too weak to cause the bladder to fire. Although the trapdoor movements are completed in a few milliseconds, the trap is not ready to fire again for 20 (Ulanowicz 1995) to 40 minutes (Sydenham & Findlay 1975, Friday 1991), depending on the species. During that time, the trap is nonfunctional and is thus incapable of capturing new prey, regardless of the size of the prey. The gastrotrichs and rotifers observed in the traps would thus have been incidentally captured, similar to phytoplankton, in the firing triggered by an organism large enough to irritate the trigger hairs.

In addition to differences in the localization of the two species in the pond and in their organization (dense, partially attached colonies at the periphery of the floating vegetation and dispersed bladders in U1 vs. free-floating colonies in the pelagic subsurface and bladders concentrated in whorls in U2), we observed disparities in the allometric relationships between the diameter and volume of the traps in U1 and U2. For U1, despite a significant change in the size distribution of the traps between June and August, the shape of the traps did not change. The observed allometric relationships (trap volume and trapdoor size relative to the diameter) can thus be considered to be characteristic of the U1 species. For a given diameter, the spherical volume of the U2 traps was significantly greater than the volume of the U1 traps. Further, because the median and mean volumes of the U2 traps were markedly larger than those of the U1 traps, this modification and size structure necessarily leads to a greater ability to suct in water (and thus potentially to capture prey). These differences relative to U1 are all the more striking considering that in August, as compared to June, the U1 species displayed mostly small and/or young traps.

In June, *U. gibba* displayed a preference for cladocerans and, secondarily in the largest bladders, for copepods. This type of regime can be considered to reflect an ideal compromise in this species between its capturing potential (structure, sensitivity, and suction strength of the trap) and the available prey. In August, with the development of U2 with its larger traps, we observed a change in the size spectrum of the U1 traps (disappearance of the second mode, Fig. 5 U1$_J$ and

U1$_A$). The principal prey of U2 were copepods and, more particularly in its largest traps, large cyclopoids. In the context of competition with U2 at the level of the entire pond, U1 preferentially captured rotifers and cladocerans (although for the latter with lower occurrences and frequencies than in June). Therefore, in August, the divergence between the trap spectra of U1 and U2, and the resulting differences in capture ability, could correspond to strategies that were developed to limit their competition. The prey captured by U1 in August would thus correspond to a regime that was partially constrained by the predation carried out by U2, which primarily targeted large prey whose numbers were ten times lower than in June. The coexistence of U1 and U2 thus occurred in a period of strong decline of the zooplankton populations in the vicinity of the *Utricularia*.

The observed selectivity differences between *U. gibba* and *U. sp.2* could also reflect differences in the capturability of cladocerans and cyclopoids based on their distinct morphologies or swimming behaviors. In particular, because cyclopoids can alter their swimming speeds (Drenner et al. 1978), they may be better able than cladocerans to escape the suction force created by the opening of the relatively narrow trapdoor of *U. gibba*. In addition, for *U. sp.2*, we observed more and less colonization by epibionts. Mutualistic relationships between submerged aquatic plants and epibionts are thought to play an extremely important role in the structuring of freshwater communities, particularly in the vegetated littoral zone of lakes and reservoirs (Havens et al. 2001), and also to influence the interactions between predators and their prey (Jones et al. 1999). This type of relationship has been frequently described, and extensively documented, between bladderworts and epiphytic algae, bacteria, and sessile heterotrophic protozoa and rotifers, which benefit from the carbon and other nutrients lost to the water during the digestion of prey (Wallace 1978, Ulanowicz 1995, Guisande 2000, Englund & Harms 2003). Quantitatively, the development of periphyton favors the growth of Chydoridae, which are specialized feeders of epiphyton (Fryer 1968). This kind of the nutrition facilitates their capture (Harms 2002) by bladderwort species such as *U. gibba* that present bladders with extensively-developed antennae and triggers. Indeed, it has been shown that the structure of such filaments lure and guide prey towards the trapdoor that normally travel along algal filaments, eating epiphytes (Meyers & Strickler 1979). In contrast to the Chydoridae, cyclopoid species do not rely much on epiphyton as a food source, although many do use *Utricularia* as a resting

site (Harms & Johansson 2000). The observation that *U. sp.2.* preferentially preys upon cyclopoids rather than cladocerans (as also reported by Harms & Johansson (2000), for *U. vulgaris*) suggests that the facilitated capture of prey resulting from epiphytic colonization is more a strategy based on habitat complexity and providing a refuge zone for cyclopoids than it is a lure designed to trap cladocerans. Moreover, an active, indirect role for *U. sp.2* in attracting cyclopoids cannot be excluded through the production of mucilage as an attractant for zooplankton (Cheema et al. 1992) or by favoring the proliferation of epiphytic species (Wallace 1978 ; Fig. 2b type 4), thereby amplifying the refuge zones. There is evidence that the composition of algal periphyton can vary among aquatic plant hosts (Blindow 1987), raising the possibility that hosts might manipulate community compositions to their own advantage (Jones 1999). The specificity of the alimentary regimes and behaviors of the different prey types may thus underlie differences in their vulnerabilities to predation by bladderworts, which correspond to sit-and-wait predators. The exploitation of these prey specificities could thus constitute an operational way to enhance the individualization of the trophic niches of the U1 and U2 species. This analysis converges with that of Harms & Johansson (2000), who concluded that with sit-and-wait predators prey selection probably depends to a great extent on the characteristics of the prey and very little on predator behaviour. Thus, the differences observed with U1 between June and August could reflect more a shift in the amplitude of its trophic niche due to the presence and seasonal development of U2 than to alterations in the climatic, chemical, and ecological characteristics of its surroundings related to the shift from an oligotrophic to a mesotrophic environment.

In the context of the weak productivity of Annie pond, the growth of bladderwort species and their selective predation on certain elements of the microfauna are thought to have great functional significance. The period of strong biological activity (based on the use of nutritive elements resulting from the good climatic and lighting conditions) during the transition between the rainy and dry seasons was accompanied by a significant increase in microzooplankton densities (gastrotrichs and rotifers), as well as a paradoxical loss of mesozooplankton. The selective predation carried out by U1, and especially U2, of large prey could thus contribute to an almost exclusive exploitation of the high algal biomasses by the microzooplankton. This hypothesis is consistent with the work of Havens (1991), who attributes the seasonal decline in the cla-

doceran biomass in Triangle lake (a humic acid bog lake in Ohio, USA) to predation jointly carried out by a cyclopoid (*Tropocyclops prasinus*) and by bladderworts. Further, a fraction of the secondary production in the pond is used to support the development of bladderworts, which are thus probably competitors of larval- and juvenile-stage fish forms.

Conclusion

In the equatorial waters of Annie pond, situated within the immense Kaw swamp of French Guiana, bladderwort colonies show substantial seasonal evolution. The waters of this pond, which are acidic due to its richness in humic substances and desaturated with oxygen, are seasonally fertilized by waterbird droppings. Due to its function as a reproductive site, this pond corresponds to a highly unusual ecosystem characterized by an abrupt succession from an extreme oligotrophic state during the rainy season to a mesotrophic state during the dry season. The carnivorous plants exert a strong and selective predation on cladocerans and cyclopoids that likely contributes to their diminishing numbers among micro-fauna. The carnivorous plants therefore appear to play a major role in determining the community structure and size spectra of the zooplankton. This selective predation is the product of the specific features and behaviors of both the prey and the plants. Extreme sit-and-wait predators, the principal bladderwort species in the pond pursue diverse strategies (localization, types of morphological organization, size-class distribution of traps, differential attraction of prey) in order to limit their competition over the large prey. Moreover, this targeted predation has likely impacts at the ecosystem level: from the bottom up, affecting the abundance as well as the size and species structuring of phytoplankton and epiphyton; and from the top down, affecting the feeding of juvenile-stage fish. As this pond is also a major site for fish breeding at the end of the dry season (due to the constant presence of water), it would be interesting to evaluate, both quantitatively and qualitatively, the extent of competition between these active (larval fish) and passive (bladderworts) predators, and to examine the strategies that permit their co-occurrence.

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