

On the leaf litter community of the Amazonian blackwater stream Tarumazinho

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ABSTRACT. A study of the benthic leaf litter community of the Tarumazinho, a central Amazonian stream (03° S, 60° W) is presented. This small tributary of the Rio Negro is of the blackwater type with a very low nutrient content. The sampling stations were towards the mouth of the tributary where it flowed through annually inundated forest and the work was carried out during the low water season. Previous studies concluded that these acid waters were of very low productivity and held impoverished faunas. However, this study showed that leaf litter banks held a diverse aquatic community of unexpectedly high biomass. This was because the banks supplied food and shelter and were available during the low water period when other habitats had dried out. The macrofauna was dominated by fish and shrimps. From an examination of gut contents a food web was produced. Primary consumers were found to take mainly detritus and fungi and it was concluded that allochthonous inputs were the main source of energy and nutrients. No feeding specialists were found and all the predators took prey from more than one trophic level.

KEY WORDS: Amazonia, benthic community, blackwaters, freshwater ecology, food web, leaf litter, stream macrofauna.

INTRODUCTION

The ecology of Amazonian streams is still little understood. There is no significant *in situ* primary production and their fauna depends on allochthonous input such as fruits, blossoms, leaves and dead wood from the surrounding forest (Fittkau *et al.* 1975, Junk 1983, Sioli 1975). This fauna, although of considerable diversity, is nevertheless described as being low in biomass (Fittkau 1967, Irmiler 1975 and above cited authors). However, during recent studies on the food web of stream microfauna (Walker 1985) and on the population dynamics of shrimps (Walker & Ferreira 1985), it became increasingly clear that the stream fauna was aggregated in submerged litter and may reach considerable densities. This observation suggested that the animal community within the submerged leaf litter banks was of great importance to the ecology and productivity of these waters which had previously been underestimated. Hence, the aim of this study was to describe the structure and begin to quantify

this little known benthic community and so to obtain an appreciation of its importance within the forest ecosystem.

The study area was on the river Tarumazinho, a small tributary entering the Rio Negro approximately 03° 00' S, 60° 30' W. The water is of the blackwater type characteristic of central Amazonia (Leenheer 1980). Under the influence of the Rio Negro, the river depth can differ by about 4 m between the high and low water periods in the annual cycle. The surrounding low-lying *Igapó* forest is inundated annually. This study was carried out during the low water period (September to December), when the water was retreating into or confined within the permanent river banks. The main channel was about 10 m wide and the bed was a fine mobile, white sand. Leaf litter banks were formed on the inside of meanders and behind fallen trees.

METHODS

The sampling of the flora, fauna and water was undertaken over a number of years, but always during the low water season.

Quantitative sampling of the benthic macrofauna of the leaf litter was carried out between September and November 1981. Samples were obtained using hand nets of 0.1 m² mouth area which were plunged into the submerged litter and then rapidly lifted clear of the water. A summary of the sampling programme and a brief description of the litter banks sampled is given in Table 1. Because of the rapidly falling water level it was not possible to sample the same litter banks over the whole period of the study. Sampling effort was principally directed at the two large litter banks D and H. On the 16 September litter bank D was sampled using stations regularly spaced 3 m apart along the water edge (see Figure 1). On all other occasions sampling stations were chosen on our ability to sample adequately. However, care was taken to ensure that the set of samples obtained from a site came from a range of positions over the bank. The macrofauna was sorted in the field and immediately preserved in 70% alcohol. Subsequently the animals were allocated to species, given a name if known to science, and the number in each sample recorded. Micro-invertebrates and chironomids were not quantitatively sampled. The leaf litter from eight of these samples was retained to find the dry weight to quantify sample size.

To study feeding relationships, the gut contents of all the common species of vertebrate and invertebrate macrofauna and some species of microfauna were examined. The specimens came from the quantitative samples and from collections taken in previous years. For the shrimps data were available from Kensley & Walker (1982). The gut contents were, if possible, identified to the level of Order. Material in the gut was recorded as presence-absence data. For each species, the number of guts examined is given in Table 2. A target of 25 guts per species was often not achieved because of species rarity.

Physical measurements and water samples for chemical analysis were taken in the vicinity of litter banks D and H prior to sampling disturbance. The position of the sampling sites is shown in Figure 1. In 1981, water samples were

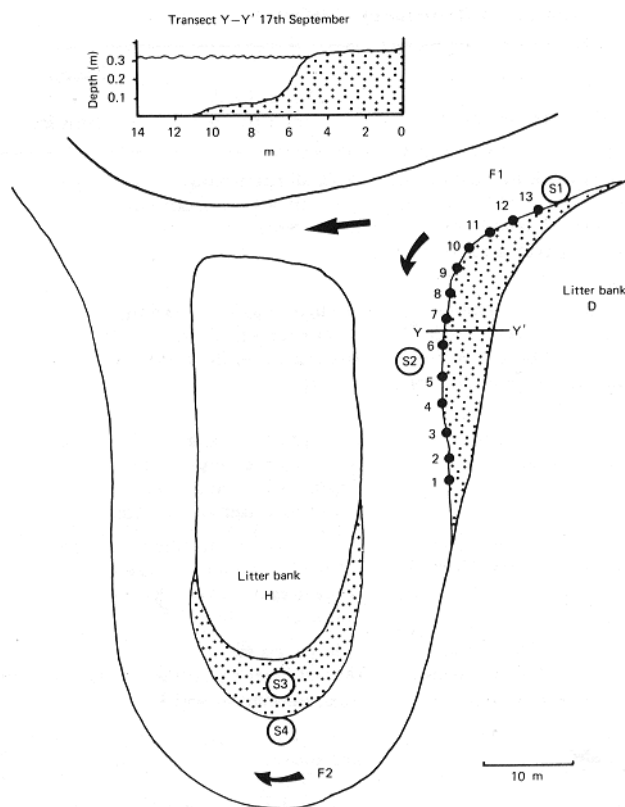


Figure 1. Sketch map of litter banks D and H showing their position on a recently cut meander and the position of the sampling stations. The numbers along D are the regularly spaced faunal sampling stations, S1 to S4 are the water sampling sites, and F1 and F2 are where the flow was measured.

collected for laboratory determination of pH, conductivity and dissolved oxygen. In November 1984 water samples were collected for inorganic chemical analysis. These samples were immediately filtered with a 25 µm millipore filter and stored in polypropylene bottles at 4 °C until analysed. *In situ* measurements of pH and temperature were undertaken using a portable glass electrode pH meter and a mercury glass thermometer respectively. Because of the unusually low pH values, readings were made on two independent instruments which were checked for accuracy in the laboratory. Dissolved oxygen was determined using the modified Winkler method (Mackenth 1963), the samples being fixed in the field. Surface flow rates were estimated by measuring the passage of orange peel over a set distance.

The concentrations of N^+ , K^+ , Ca^{2+} , Mg^{2+} , Al^{3+} , Fe^{3+} , Mn^{2+} and SO_4^{2-} were measured using a plasma spectrophotometer. An autoanalyser wet method was used for SO_4^{2-} and Cl^- . All concentrations were close to instrument detection limits. Aluminium was expressed as the concentration of the Al^{3+} form; given its complex chemistry in waters with a high organic content this would not be the only form present.

Table 1 Description of sample sites, Tarumazinho stream

Site code	Date 1981	Site description	Litter bank description	Number of samples	Physical measurements
A	15 Sept.	Litter bank formed on the inside curve of the stream on a small sand bank; stream width 8 m, maximum depth 2 m.	A small litter bank, area 3 X 2 m with a maximum litter depth of 20 cm.	3	Litter dry weight for 2 samples.
B	15 Sept.	Samples taken from a small side stream with low flow about 2 m from the Tarumazinho; heavy tree cover.	No litter bank formation; litter submerged on bed of stream; water depth 10 to 30 cm.	3	None.
C	15 Sept.	Litter bank formed on the inside of a 110° bend on a bank of sand.	A small litter bank 4 X 0.5 m with a maximum litter depth of 10 cm; 30 cm depth of water above litter.	3	Litter dry weight for 2 samples.
D	16 Sept.	Situated on the corner of a meander - see Figure 1.	A large well established litter bank which is known to have existed for 3 years and is probably older.	13	Litter dry weight for 2 samples.
E	16 Sept.	On bank of an island produced by the bifurcation of the stream.	A large, crescent shaped litter bank 9 m long, maximum width 2 m.	12 (1 lost)	Litter dry weight for 2 samples.
D	6 Oct.	See above.	See above.	5	(O ₂), temperature, pH.
F	6 Oct.	Litter bank in meander.	At least 1-2 years old, debris in diverse stages of decomposition.	12	None.
G	6 Oct.	Small litter bank.	Newly accumulated leaves.	4	None.
H	6 Oct.	Situated close to site D - see Figure 1.	The largest litter accumulation sampled. Established for a number of years.	13	None.
H	20 Oct.	See above.	See above.	19	(O ₂), temperature, pH, conductivity.
H	17 Nov.	See above.	See above.	24	None.
H	3 Dec.	See above.	See above.	10	Flow, velocity, pH, respiration of litter, fungal infection.

Dry weight and ash-free dry weights were obtained by drying samples at 100°C to constant weight and subsequently burning them at 600°C and weighing the residue. Respiratory activity of leaf litter heterotrophic micro-organisms was estimated by measuring oxygen uptake in a Warburg respirometer. Four standard nettings of leaf litter were returned to the laboratory on the day of collection in water-filled plastic bags. These bags were then left open overnight and the next day sorted to remove highly fragmented material and any macrofauna such as chiromomid larvae. Pieces with an area approximately 2.5 mm² were cut from the leaves to produce subsamples of 2 to 3 g wet weight, each

representative in leaf constitution to that of the original sample. The oxygen consumption of these four subsamples was measured over a 24 h period at a constant temperature of 26.6°C. Dry weight and ash-free dry weight of each subsample were then ascertained.

RESULTS

1. Physico-chemical description

Physical and chemical data for the stream in the vicinity of banks D and H are given in Tables 2 and 3 respectively. The flow rate controls the size of the litter fragments deposited, with the smaller, usually older, material, accumulating on the down-stream end of the banks. Similarly, smaller pieces of debris constituted a greater proportion of litter bank H than D. Continual accumulation results in the banks having a vertical gradient of decreasing particle size. Oxygen concentrations at S1 gives a measure of the level within the main stream, which is well mixed due to the turbulent flow. Lower concentrations were recorded at S2, S3 and S4 indicating a declining availability between banks D and H. This gradation was presumably due to respiration and reduced oxygen transport in the less turbulent conditions. Water temperature was very stable. Chemical analysis showed the water to have a very low ionic content

Table 2. Summary of physical data, Tarumazinho

	Date: 1981	Station (see Figure 1)	Measurements	
Oxygen concentration	6 October	S1	6.73 mg l ⁻¹	85% saturation
		S2	6.57 mg l ⁻¹	83% saturation
	20 October	S3	6.3 mg l ⁻¹	79% saturation
		S4	6.06 mg l ⁻¹	77% saturation
Water temperature	6 October	S1	26.5°C	
		S2	26.5°C	
	20 October	S3	26.6°C	
		S4	26.9°C	
Surface velocity	20 October	F1	0.42 m s ⁻¹	
		F2	0.2 m s ⁻¹	
pH	6 October	S1 and S2	3.5	
	20 October	S3 and S4	3.4	
	3 December	S3 and S4	2.8	
Conductivity	20 October	S3 and S4	13.8 µS cm ⁻¹ (25°C)	

Table 3. Inorganic chemical analysis of water from samples collected in November 1984. Tarumazinho

Inorganic ion	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Al ³⁺	Fe ³⁺	Mn ²⁺	SO ₄ ²⁻	*SO ₄ ²⁻	*Cl ⁻
Concentration (µEqu. l ⁻¹)	7.6	3.0	6.1	4.5	15.8	4.9	0.04	5.0	18.8	16.9

(Note. Plasma spectrophotometer used for all measurements except those marked with a * where an autoanalyser was used.)

which was reflected in the conductivity of only 13.5 p S cm⁻¹. Water pH was found to vary between 3.5 in the main channel and 2.8 within the litter banks. Given the low inorganic content of the water this acidity must be due to organic acids.

2. *Heterotrophic respiration within the litter*

The oxygen consumption of the four subsamples of leaf litter is given in Table 4. Mean O₂ consumption was 9.2 µl O₂ per gram of litter dry weight per hour. A microscopic examination of this litter found it to be heavily infested with fungal hyphae and no algae were found. The consumption therefore represents fungal and bacterial respiration. The ash content of the samples was about 5% by weight indicating that the litter was in the early stages of decomposition (Stark & Holley 1975).

A 1 m² area of the litter of 10 cm depth has a dry weight of about 1665 g. Using this weight and the measured respiration rate, the oxygen consumption by decomposers was calculated as 15.32 ml O₂ m⁻² h⁻¹. Assuming an RQ of 0.82 (Petrusewicz & Macfadyen 1970), this gives an energy release of 631 kcal m⁻² year⁻¹. The majority of the aerobic decomposition probably occurs in the upper 10 cm zone as lower material is more tightly packed, reducing O₂ diffusion, and is generally older and already well decomposed. This energy release should be taken as a conservative first estimate.

3. *Benthic macrofauna*

Appendix 1 lists the species of macrofauna found during the quantitative sampling, their mean population density and variance for each litter bank. As in other tropical systems, there were a great many species which occurred at low densities giving a high faunal diversity. Mean dry weight of litter per sample was 166.5 g (SD =612 g, range 92.5 to 269 g) and the mean macrofaunal density 18.24 individuals per sample. Nineteen species of fish and 11 species of insect were recorded. From the material collected over a number of years we know this is a small subset of the total species complement. For example, 44 species of insect were recognized in the material used for the gut analysis.

The shrimps were the dominant invertebrate group. Three species, *Euryrhynchus amazoniensis*, *Pseudopaelamon chryseus* and *P. amazonensis*, could always be identified, but two species of *Macrobrachium*, *M. natterri* and *M.*

Table 4. Respiration rate of blackwater litter, Tarumazinho

Sub-sample number	Wet weight (g)	Dry weight (g)	Ash-free dry weight (g)	µl O ₂ g ⁻¹ dry weight h ⁻¹
1	2.38	0.642	0.609	9.49
2	2.32	0.606	0.576	9.35
3	3.25	0.845	0.800	8.58
4	3.81	1.041	0.989	9.38

inpa, were lumped as they cannot be distinguished as juveniles (Kensley & Walker 1982). The *Macrobrachium* species were the dominant prawns both in mass and number with a mean density of 7.9 individuals per sample. They were calculated to have a biomass of 2.85 g dry weight per kg of litter dry weight.

The comprehensiveness of the fish sampling was assessed by plotting the cumulative number of species against the number of samples taken (Figure 2). The curve approaches an asymptote which indicates that the sampling intensity was sufficient to capture most of the species present. However, some species not recorded during the quantitative sampling are known to be occasionally common, e.g. a small catfish *Amblydorus* species. The commonest species was the goby *Microphlipnus* species, with a density of 2.76 per sample or 1 per 60.3 g of litter dry weight. This was an extremely small fish, the largest individual found being a mature female 10 mm standard length.

The spatial dispersion of the commonest species, the fish *Characidium* species and *Microphlipnus* species and the decapods *E. amazoniensis* and *Macrobrachium* species, were examined. For each species, the variance was greater than the mean indicating a contagious spatial distribution. This is illustrated in Figure 3 which shows the distribution along bank D of *E. amazoniensis*. The population was limited to 7 of the 13 stations with a peak density at station 9. The reason for this distribution was not found.

From September to November there was a continual decline in water depth resulting in a loss of litter bank habitat. This produced a corresponding increase in the faunal density in the remaining areas.

Patterns of association were examined for the more abundant species, the fish *Apistogramma* cf. *regani*, *Elachocharax* cf. *pulcher*, *Microphlipnus* species, *Characidium* species, *Chasmocranus* species and *Hypopygus* species and the crustaceans *E. amazoniensis*, *Macrobrachium* species and *P. amazonensis*. Table 5 gives the correlation coefficients for the number of species per sample for all species pairs. Significant levels of positive or negative correlation are boxed. *E. pulcher*, *Microphlipnus* species, *Characidium* species, *Macrobrachium* species

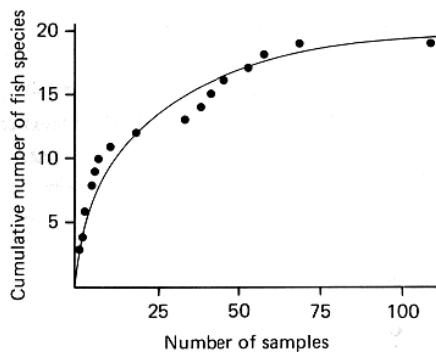


Figure 2. Species acquisition curve for litter bank fish.

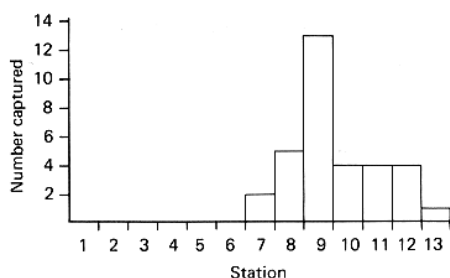


Figure 3. The distribution of the shrimp *Euryrhynchus amazoniensis* along litter bank D showing an aggregated distribution centred on station 9

Table 5. Correlation of occurrence between common species of animals, Tarumazinho

1	2	3	4	5	6	7	8	9
1	-0.01	0.17	-0.06	-0.07	-0.05	-0.07	-0.04	0.006
2		0.32	0.40	0.1	0.12	-0.17	0.38	-0.05
3			0.43	-0.04	0.08	-0.17	0.3	0.24
4				0.16	0.04	-0.27	0.36	0.11
5					-0.06	-0.18	0.07	-0.002
6						0	0.14	0
7							-0.2	-0.16
8								0.09

N = 109, $r > 0.19$ significant at 5% level.

Key to species: 1. *Apistogramma cf. regani*; 2. *Elachocharax cf. pulcher*; 3. *Microphilipnus* sp.; 4. *Characidium* sp.; 5. *Chasmocranus* sp.; 6. *Hypopygus* sp.; 7. *Euryrhynchus amazoniensis*; 8. *Macrobrachium* spp.; 9. *Pseudopalaemon amazonensis*.

and *P. amazonensis* formed a positively correlated group. The preferred habitat of these species was non-compressed areas made up of large fragments or whole leaves near the edge of the stream. The small crustacean *E. amazoniensis* was negatively correlated with all other species indicating the use of a different leaf litter habitat. This species was found to use areas made up of highly fragmented litter where there was little water movement and presumably low oxygen levels.

4. Trophic structure

The gut contents of the most numerous species of macrofauna within the litter banks is given in Appendix 2. A similarity analysis of the gut contents between species was undertaken using the program of Bamber (1982) for a bifurcating cluster analysis utilizing the Raabe (1952) similarity index. Figure 4 shows the resulting dendrogram. The program produced an ordering of the species based on trophic position; moving from left to right there is a progressive change from detrital-algal feeding to predation. Five principle clusters are discernible; algal-litter feeders, fungal-litter feeders, the shrimps, most fish and finally the Odonata and other predatory insects.

The food web (Figure 5) was constructed using the groups identified by the similarity analysis. In addition, a few rare observations were included which would have distorted the dendrogram. This refers particularly to the detritus-feeding Odonata larvae, Petaluridae and Gomphidae, about which little is known (Usinger 1963). The Hemiptera were a problem as only the Corixidae had identifiable particles in their guts. It must be stressed that this food web is constructed from limited observations and thus may be modified when more information is available.

From the recently constructed food web for the microfauna (Walker 1985), it appears that of the lower invertebrate phyla only the sponges, rotifers and

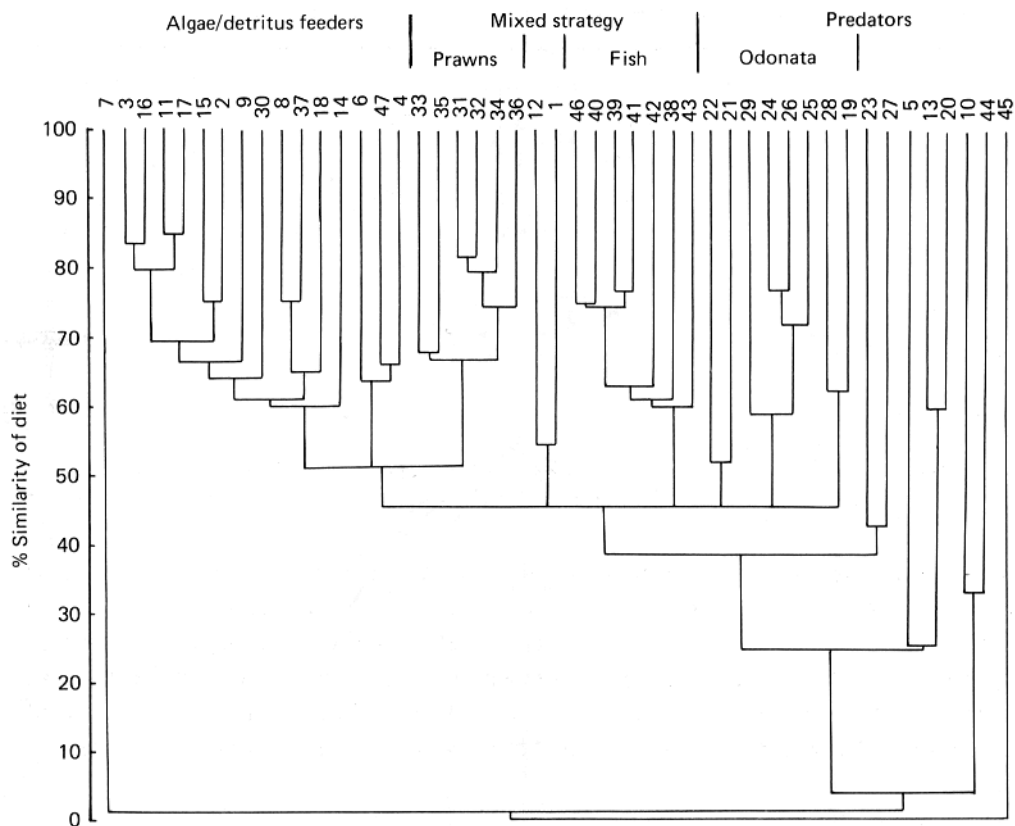


Figure 4. Dendrogram of gut contents similarity. The species are identified as numbers which correspond to the species list in Appendix 2.

thecamoebae enter the macrofauna food web in appreciable quantities. Most primary and higher level consumers accept them as prey. However, in terms of biomass this constitutes a minor input. The same is true of the algal input (Diatomacea and Conjugales), because algal densities are low. Algal feeding is more marked in the fish and in the shrimp genus *Pseudopalaemon*, whereas *Macrobrachium* shrimps feed more intensively on litter detritus and its fungi (Kensley & Walker 1982). Only the Plecoptera, Zygoptera and Odonata-Libellulidae abstain from primary input (algae, fungi and detritus).

There is no doubt that the food web depends primarily on the litter and its associated decomposing fungi. Note that the higher the trophic level of the consumer, the more varied the prey that each species takes. Not a single food specialist was found. The diversity of food intake makes it impossible to assign defined trophic levels to the consumer species. We therefore defined trophic stations on the basis of the longest food chains observed. The longest food chains are those of the fish, shrimps and Odonata; in addition, Odonata feed on Odonata and shrimps feed on shrimps.

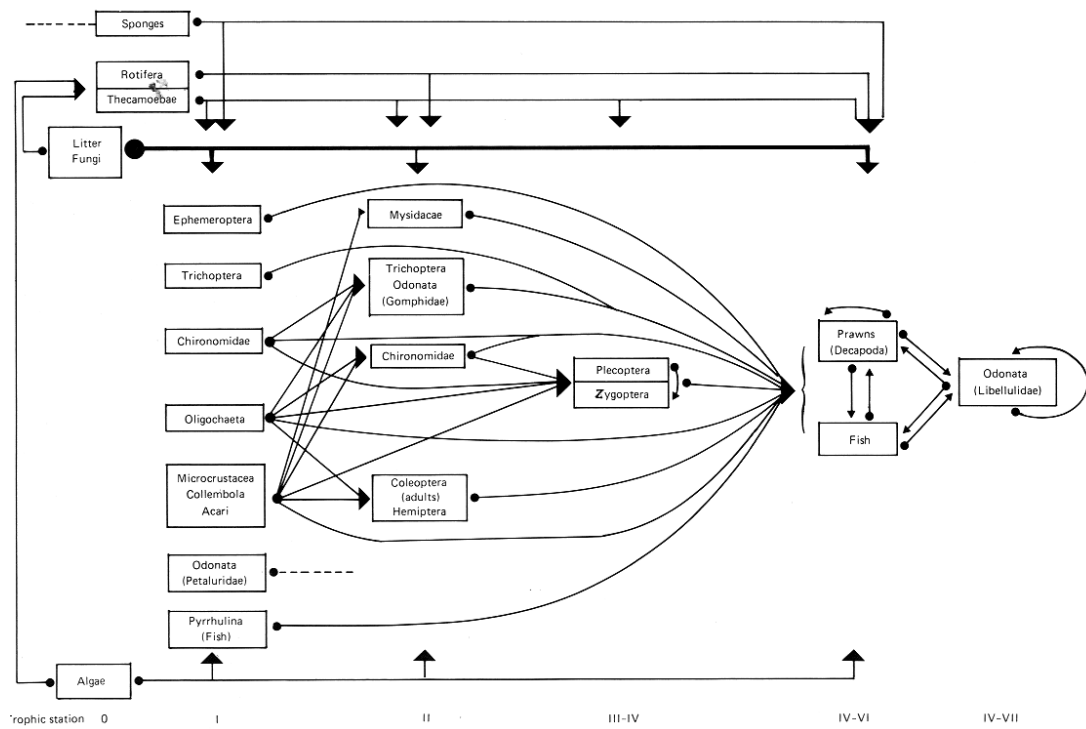


Figure 5. A generalized food web for the leaf litter community. The arrows point in the direction of energy flow and the flow line thickness gives a measure of the importance of the pathway.

DISCUSSION

Because of the great difference in the amount and type of habitat available between the high and low water seasons, the community we studied should be viewed as a seasonal assemblage. It is notable that some species such as tree-living sponges enter a resting stage during the low water season. However, this study has probably identified the common, permanent members of the black-water community.

The stream was of the typical blackwater type with a pH between 2.8 and 3.5, the lower figure being lower than any previously recorded for this water type. Leenheer (1980) attributes 85% of this acidity to organic acids and the rest to CO₂. Given the low level of inorganic ions in solution the acidity must certainly be due to organic compounds. However, humic acids which are frequently assumed to be the major constituent are not strong enough acids to produce such a low pH. A possibility is that fermentation within the litter banks is releasing strong organic acids such as acetic acid. In temperate regions acid waters are associated with reduced faunal diversity and fishlessness (e.g. Beamish & Harvey 1972), but we recorded over 20 species of fish, showing that naturally acidified systems can support diverse fish faunas. The exceptional acid tolerance of Amazonian fish has been discussed by Dunson *et al.* (1977).

Oxygen concentrations of the free flowing water were between 6 and 7 mg⁻¹ representing a percentage saturation of between 77 and 85%. 100% saturation could be expected given the rate of flow and turbulence of the stream. This reduction presumably reflects respiratory consumption and low photosynthetic generation. Oxygen availability undoubtedly influences the distribution of fauna within the litter banks. Most animals were found in the top 30 cm of the litter. Some fish show modifications for low oxygen levels, e.g. the modified gills of *S. marmoratus*.

In addition to being a source of food, the litter banks also give shelter and protection from predatory fish and birds. It is because they meet both these requirements that they have such a high faunal density. The only other hiding places are afforded by fallen trees and root mats. The allochthonous input, upon which the stream fauna depends, can be divided into two components: plant debris and small animals such as insects. The importance of the latter has not been assessed, but the presence of terrestrial insect remains in the gut contents of a number of species suggests that this material mainly enters the higher trophic levels. In comparison, the energy from plant debris is principally channeled via the decomposers. Given the pH of the water, it is likely that fungi and not bacteria are the dominant decomposers, as is known from temperate forest streams (Baerlocher & Kendrick 1981). Decomposition in the upper 10 cm of the litter bank was estimated to release 630 kcal m⁻² year⁻¹. This is based on the assumption that decomposition can occur during the high water season. In addition, there must be some decomposition at greater depths within

the banks. Teal (1957) estimated that micro-organisms in a small leaf-filled spring in Massachusetts, USA, respired $350 \text{ kcal m}^{-2} \text{ year}^{-1}$ of which 55 kcal was by algae, the rest being attributed to fungi. The estimate for the Tarumazinho indicates that energy flow is not as low as earlier authors had assumed to be the case in blackwaters. The stream biomass is also much higher than previously thought, because the leaf litter had not been sampled.

The benthic community was similar to that found in other streams; all the major insect groups listed by Hynes (1970) as typical of a stream community were present. However, there are some notable features. The dominant crustacean group was the shrimps, no isopods or amphipods were present and snails were very rare. The fish component is strikingly large and diverse.

Feeding niche overlap was often considerable, which raises the question of the role of competition in determining species packing. The patterns of dispersal of the common benthic macrofauna were all highly clumped indicating a subdivision of the habitat. The changing water level may well act to modulate competition by changing the area of habitat available. If this is the case then the habitat available during the low water period would determine population sizes.

In recent years widespread concern about the influence of man on the Amazonian ecosystem has been expressed, notably the rapid deforestation (Kerr 1977, Salati & Vose 1984, Schubert 1977, Sioli 1975, Walker & Franken 1983). Due to its dependence on allochthonous input from the forest, the aquatic community of blackwater streams can be expected to be highly vulnerable to deforestation. The loss of forest cover can initially be expected to release nutrients into the water and with decreased forest shading promote primary productivity. This would produce a major shift of energy flow away from fungal feeding species towards herbivores such as molluscs and microcrustacea. In addition, the loss of *Igapó* forest would remove niches available during the high water period.

The indications are that the leaf litter community is of great importance in assimilating energy from forest primary production into the blackwater aquatic system. Further, it acts to reduce the loss of nutrients to the forest which would inevitably occur if all the material which fell into the streams was washed downstream. This study demonstrates that the fauna of these acid streams is abundant and suggests that it may be an important component in the inundation forest ecosystem.

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Appendix 1. Mean density and variance of benthic macrofauna from sample sites A to B. The reference number corresponds to those used in Appendix 2

	15-16 September 1981										6 October								29 October		17 November		Total	
	A		B		C		D		E		D		F		G		H		H		H			
	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2		
Fish																								
39 <i>Elachocharax</i> cf. <i>pulcher</i>	3	4	0	—	0	—	0	—	0.82	3.4	0.8	0.7	1	4.5	1	0.67	0.92	0.91	1.6	9.7	0.08	0.08	83	
41 <i>Characidium</i> sp.	3	27	0	—	0.34	0.34	0	—	1.27	4.8	1.8	6.2	3.1	9.7	1.5	1.7	3.7	6.7	1.5	6.8	1.75	6.6	195	
47 <i>Pyrrhulina</i> sp.	0	—	0.34	0.34	0	—	0.85	1.97	0	—	0	—	0.17	0.15	0	—	0.08	0.08	0.05	0.05	0.04	0.04	17	
Characoides sp.	0	—	1	1	0	—	0	—	0	—	0	—	0	—	0	—	0.08	0.08	0	—	0	—	4	
Characoides sp.	0	—	1.67	2.3	0	—	0	—	0	—	0	—	0.17	0.15	0	—	0.08	0.08	0.05	0.05	0.04	0.04	10	
46 <i>Hypopygus</i> sp.	—	—	0	—	0	—	0	—	0	—	0	—	0.67	0.95	0.5	1	0.46	0.94	0.58	1.37	0	—	24	
<i>Hypopygus</i> sp.	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0.08	0.08	0	—	0	—	1	
<i>Hypopygus</i> sp.	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0.05	0.05	0.125	0.11	4	
<i>Acestridium</i> sp.	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0.25	0.25	0	—	0	—	0	—	1	
42 <i>Chasmoscranus</i> sp.	0.33	0.33	0	—	0	—	0	—	0.72	1.2	0.4	0.3	0.33	0.41	1.5	1.7	0.46	1.44	0.21	0.28	0	—	31	
38 <i>Apistogramma</i> cf. <i>regani</i>	1	1	1	3	0.67	0.34	0.077	0.077	0	—	1	0	0.5	1.5	0.25	0.25	0.38	0.76	0.11	0.21	0.08	0.08	30	
Cichlidae sp.	0.33	0.33	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	1	
43 Crenicichlid sp.	0	—	0	—	0	1.3	0	—	0.18	0.36	0	—	0.08	0.08	0	—	0.23	0.36	0.16	0.14	0	—	11	
Cichlidae sp.	0	—	0	—	0	—	0.077	0.077	0	—	0	—	0	—	0	—	0.15	0.14	0.05	0.05	0	—	4	
<i>Monocirrhus polyacanthus</i>	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0.08	0.08	0	—	0	—	1	
Cichlidae sp.	0	—	0	—	0	—	0	—	0	—	0.2	0.2	0	—	0	—	0.31	1.2	0	—	0	—	5	
44 <i>Synbranchus marmoratus</i>	0	—	0	—	0	—	0	—	0	—	0	—	0.08	0.08	0	—	0.15	0.14	0.1	0.1	0	—	5	
40 <i>Microphilipnus</i> sp.	11.3	10.3	2.3	10.3	6.7	16.3	1.46	8.6	1.2	4	1.4	2.3	2.9	10.3	0	—	9.5	60.9	1.42	7.7	0.83	1.6	306	
<i>Rivulus</i> sp.	0	—	0	—	0	—	0.15	0.14	0	—	0	—	0	—	0	—	0	—	0	—	0	—	2	
Insects																								
17 Heptageniidae sp.	0.33	0.33	0	—	0	—	0	—	0.09	0.09	0.06	0.3	0.08	0.08	0.75	2.25	1.07	9.1	1.42	13.8	0.17	0.69	54	
18 Heptageniidae sp.	0.67	1.3	0	—	0	—	0	—	0	—	0	—	0	—	0.5	1	0.23	0.30	0.05	0.05	0	—	8	
29 Odonata sp.	0	—	0	—	0	—	0	—	0	—	0	—	1.7	12.8	0	—	0.23	0.30	0.05	0.05	0	—	38	
30 Odonata sp.	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0.31	1.2	0.05	0.05	0	—	3	
24 Odonata sp.	0	—	0.34	0.34	0	—	0	—	0	—	0.2	0.2	0	—	0	—	0	—	0	—	0	—	2	
23 <i>Aeshna</i> sp.	0	—	0	—	0.34	0.34	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	1	
21 Zygoptera sp.	0	—	0	—	0	—	0	—	0	—	0	—	0.8	0.8	0	—	0	—	0	—	0	—	1	
5 Belastomatidae sp.	0	—	0.34	0.34	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	1	
6-7 Velidae sp.	0	—	0	—	0	—	0.15	0.14	0	—	0	—	0	—	0	—	0	—	0	—	0	—	4	
Velidae sp.	0.33	0.33	0.66	1.3	0	—	0	—	0.18	0.36	0.2	0.2	0.25	0.2	0.25	0.25	0.38	0.76	0.21	0.4	0.29	0.56	26	
13-16 Trichoptera sp.	0	—	0	—	0	—	0	—	0	—	0	—	0.08	0.08	0	—	0.23	0.36	0.1	0.1	0.04	0.04	7	
Crustacea																								
32-34 <i>Macrobrachium</i> spp.	1.48	16.95	0	—	7.7	58.3	0.54	2.1	5.8	38.4	4.8	17.2	5.4	21	20.25	56.9	11.5	64.4	7.47	89.4	12.08	88.3	879	
35 <i>Pseudopalaemon amazonensis</i>	0	—	0	—	0.34	0.34	0.077	0.077	0.18	0.36	0.2	0.2	0.33	1.33	1.25	3.58	0.54	0.6	0.16	0.47	0	—	24	
31 <i>Euryrynchus amazoniensis</i>	1	1	6	4	0	—	2.5	13.6	0.09	0.09	0	—	2.6	28.6	0	—	1.1	3.7	3.89	41.5	2.7	5.8	242	

Appendix 2. Summary of the gut contents of the common benthic fauna. The reference number beside each consumer species corresponds with those in Figure 4 and Appendix 1

	Material present in guts																												
	Number of guts examined																												
	1. Leaf litter	2. Algae	3. Fungi	4. Protozoa	5. Porifera	6. Nematoda	7. Rotifer	8. Annelida indet.	9. Naididae	10. Arthropoda indet.	11. Acari indet.	12. Hydracarina	13. Cladocera	14. Copepoda	15. Ostracoda	16. Mysidacea	17. Decapoda	18. Insecta indet.	19. Collembola	20. Ephemeroptera	21. Odonata	22. Zygoptera	23. Plecoptera	24. Trichoptera	25. Chironomidae	26. Coleoptera	27. Hemiptera	28. Teleostomi	
<i>Consumer species</i>																													
1 Platyhelminthes indet.	22	1					7			8	1		9	5				1		1						2			
2 Oligochaeta indet.	3	3		2		1																							
3 Naididae indet.	1	1	1	1	1																								
4 Collembola indet.	2	2	1							2																			
5 Hemiptera: Belastomatidae (2 spp.)	20	3	1							12																			1
6 Hemiptera	4	1	1	1				1		1																			
7 Hemiptera (3 spp.)	4		1	2																									
8 Coleoptera (3 spp.)	6	1		1			1						1																
9 Hydrophiloidea	2	2	2	2		2																							
10 Gyrinidae (3 spp.)	10																	8		1									
11 Chironomidae (4 spp.)	26	23	3		25	6	2																						
12 Chironomidae (2 spp.)	6			2	1			1		2	2			2	1														
13 Trichoptera	4							2																			3		
14 Trichoptera	12	3	7	3	5		7			2	5	1	2					3								4			
15 Trichoptera (2 spp.)	3	1	1	3	1																								
16 Trichoptera	5	5		5			1																						
17 Ephemeroptera	23	17	6		22	4	5		1																				
18 Ephemeroptera (2 spp.)	2	1	1	1			1																				1		
19 Plecoptera	12			2	2		4	1	4		1		5	1				1		1							11		
20 Zygoptera	2									1																	2		
21 Zygoptera	19		1				1				1	1	1					2		3	4			2	1		9		
22 Zygoptera	11			1													1			7	1					8			

Appendix 2 is continued on the next page

Appendix 2 - continued

Consumer species	Material present in guts																													
	Number of guts examined	1. Leaf litter	2. Algae	3. Fungi	4. Protozoa	5. Porifera	6. Nematoda	7. Rotifer	8. Annelida indet.	9. Naididae	10. Arthropoda indet.	11. Acari indet.	12. Hydracarina	13. Cladocera	14. Copepoda	15. Ostracoda	16. Mysidacea	17. Decapoda	18. Insecta indet.	19. Collembola	20. Ephemeroptera	21. Odonata	22. Zygoptera	23. Plecoptera	24. Trichoptera	25. Chironomidae	26. Coleoptera	27. Hemiptera	28. Telostomi	
23 Aeshnidae	11	1					1							1		1	1		3						1				1	
24 Odonata	10	1								3			1			2	1		3						1	4				2
25 Odonata	4									1								1	3		2				1	1		1		1
26 Odonata	4									3			1			1	3		2		2				1	2				1
27 Odonata (2 spp.)	3	1													1			1							1					1
28 Odonata	6			1	1			1																1	2	2				
29 Odonata	51	2	1		1		1			9	2		3			2	2		2	5	1	1	1	1	2	8		4		2
30 Odonata (2 spp.)	5	3	1	1		1												1							2					
31 <i>Euryrhynchus amazoniensis</i> Tiefenbacher	25	12	2	13	3	10	1	3		7	18	5		4	2										1	3	4			
32 <i>Macrobrachium nattereri</i> (Heller)	25	6	3	12	2	11		3	1	7	21	3	1	4						3	2			4	1	7	7			2
33 <i>Macrobrachium inpa</i> Kensley & Walker	25	6	1	15	1	3	1		1	14	13	1		2			6			2	3			7	3	9	13			
34 <i>Macrobrachium chyseus</i> Kensley & Walker	25	6	14	11	3	9		2		8	15	4	1	1						3				2	2	4	10			
35 <i>Pseudopalaemon amazonensis</i> Ramos-Porto	25	4	6	13	1	8	1	6	1	11	12	11	2	4	4	1	3			6				9		12	6			
36 <i>Palaemonetes carteri</i> Gordon	10	3	7	8		6		1		4	7			2													2			
37 <i>Parvimysis pisciscibus</i> Henderson & Bamber	1		1	1				1						1																
38 <i>Apistogramma</i> cf. <i>regani</i>	15	2	13	7	4	7		3	8		5	4	1	7	5			7		3				1		7				1
39 <i>Elachocharax</i> cf. <i>pulcher</i>	20		9	3	1				8		3	1		10	5			3		1	1			1		8				
40 <i>Microphlipnus</i> sp.	20		3	1				1	5		1	1		14	4			1		1				1		10				
41 <i>Characidium</i> sp.	21		9		3			1	6		4	3		7	2			3						1		14				
42 <i>Chasmocranus</i> sp.	8		2			1			2		1			4	2	1		2		3	1			1	1	4				
43 <i>Crenicichla</i> sp.	4		2	1			1		2					1	3		1	3		2			1			2				
44 <i>Synbranchus marmoratus</i> Bloch	2						1		1									1												
45 <i>Amblydorus</i> sp.	5								4		3																			
46 <i>Hypopygus</i> sp.	12		6	2	1	1	1		9					10	2			3		1						8				
47 <i>Pyrrhulina</i> sp.	4	4	3	1		1					2	1														1				