

**The benthic insect fauna of the blackwater forest stream
Rio Tarumã-Mirim (Manaus, Amazonas): patterns of population
dynamics and their implications for ecosystem stability***

by

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Abstract

The annual pattern of emergence of aquatic insects with benthic larval stages of a small, Central Amazonian blackwater river is presented. This pattern is primarily a function of the annual inundation cycle (= "flood pulse"; JUNK et al. 1989), but non-random variations within sampling-sites and -periods suggest that the organisms are choosing favourable micro-habitats. Comparison between the rates of benthic litter colonization (as reported previously; WALKER 1994, 1998) and emergence of adults shows, that grosso modo 90 % of the litter-colonizing juveniles enter the aquatic foodweb, while the few percent of emerging adults maintain standing stock and biomass flow of this insect fauna. The data are discussed within the context of ecosystem stability.

Keywords: **Aquatic insects, emergence, foodwebs, flood pulse, Amazon, Neotropics.**

Resumo

Apresentam-se dados sobre a taxa de emergência de insetos aquáticos adultos, cujas larvas estão colonizando a liteira submersa no Rio Tarumã-Mirim de água preta e pobre, na região de Manaus (Amazonas). O padrão de emergência é primariamente uma função das enchentes anuais (= "pulso de inundação"; JUNK et al. 1989), a taxa de eclosão diminui durante o período de inundação. Porém, a distribuição agrupada entre amostras indica, que os organismos reagem às diferenças dos micro-habitats, escolhendo condições favoráveis para a sobrevivência. Comparação entre taxas de emergência dos adultos e taxas de colonização da liteira por larvas (publicadas anteriormente; WALKER 1994, 1998) mostra, que cerca de 90 % das larvas desaparecem antes da eclosão, provavelmente na rede alimentar aquática. Estes resultados são discutidos no contexto dos problemas de estabilidade de populações.

Introduction

The fauna of the mineral-poor blackwater rivers in Central Amazonia has been under investigation for a long time (FITTKAU et al. 1975; SIOLI 1984). The notorious mineral poverty of these waters, and low light intensity under the closed canopy, inhibit the growth of phytoplankton in these rivers and in their "igapós", i.e. in the seasonally

*Dedicated to Prof. Dr. Wolfgang J. Junk on the occasion of his 60th anniversary.

flooded forests along the stream valleys. Thus, the aquatic food chains start essentially with the decomposition of submerged litter by aquatic fungi, and with the ingestion of these fungi by the benthic mesofauna that colonizes this habitat (WALKER 1987). A key factor of this foodweb is the dense and ubiquitous colonization of submerged litter by chironomid larvae, scrapers that ingest the fungi together with micro-organisms and detritus particles, and which are - in turn - a major resource for small predators, mostly aquatic insects, shrimps and small fish. To get some information on the population dynamics of chironomids (Diptera, Chironomidae), the rates of litter colonization by larvae and of emergence of adults were investigated in the natural habitat between 1984 and 1992. Sampling for adult emergence began in August 1988 by setting emergence traps on the water surface over the litter habitat (results see WALKER 1998). Naturally, these traps also caught any other aquatic insects that emerged on the spot, the main objective of this communication is therefore, to present these more general data including all insects. Emergence rates, in addition, allow to establish the relation between colonization of litter by larvae and survival of adults, and as data on the colonization of the litter habitat by the aquatic fauna were available from previous studies (WALKER 1994), some of these results, referring to aquatic insects, are presented again within the context of population dynamics. The resulting patterns are of special interest with regard to problems of species maintenance and ecosystem stability.

Study area and methods

Study area

The Rio Tarumã-Mirim is a ca. 35 km long northern blackwater tributary of the Rio Negro, which joins the Rio Negro some 25 km up-river from the Manaus harbour; including its wide meanders, its channel is two to three times longer. Sample collections were taken on the large litterbanks of two meanders and, during high water levels, in the closed-canopy "igapó" forest flanking the meanders, and subject to annual inundations between February/March and August/September. The lower meander is ca. 18 km from the river's mouth, and the distance between the lower (= Atalho Barão) and the upper meander (= Atalho de Cima) is ca. 2 km. The litterbanks cover areas of several hundred square meters, and include submerged parts even during lowest water levels (October-December). Between May and July, water depth reaches 3-4 m above the forest floor in the area of the lower meander, and 1-2 m along the upper meander. During these months of peak inundation, the water is virtually stagnating.

One additional collection refers to the same type of habitat from the blackwater river Rio Cuiciras, which enters the Rio Negro ca. 60 km further up-river.

Methods

Detailed descriptions of the methods of collection were given in WALKER (1994, 1998) in this place, therefore, information on methodology is confined to what is necessary to understand the results.

Colonization rates: For the estimation of colonization rates, the fauna was collected in wide-mesh (1 cm²) baskets of 1.8 liter volume, containing 10 or 20 freshly shed litter leaves with intact surface, chosen from the litter of the local forest floor. These baskets were exposed on the surface of the litter banks and/or the forest floor, and each basket was tied to a branch overhanging the sample spot. After 24 hours, the baskets were retrieved, and the content of each basket was examined in the field in a large white tray,

the animals were collected by hand and conserved in alcohol. This method allows to collect the "macrofauna", that is, organisms \geq ca.4 mm. These samples are referred to as *basket samples*. Animals $<$ ca. 4 mm body length were collected by washing single leaves of the basket samples in alcohol, these are *leaf-wash samples* which represent the "mesofauna". This includes all species of chironomid larvae, because practically all chironomids of this habitat are small; *Chironomus*, with its large red larvae, is not found in these poor waters. Single leaf-wash samples include the mesofauna of 5 or 10 leaves.

Standing stock: This term refers to the actual number of animals that may be found at a given time in the habitat under investigation. As such, it means *density* of individuals of single or of diverse species. As litter baskets are colonized to capacity within 24-48 hours (WALKER 1994), litter baskets exposed for periods of 1 week to 2 months are representative for the normal density of organisms in the habitat of submerged litter.

Standing-stock mesofauna, including chironomid larvae, was sampled by washing 5 or 10 leaves per sample in alcohol; these leaves were collected by hand from the natural litter habitat, or else, they were chosen from baskets exposed for 1 week to 2 months.

Emergence rates: Adult insects emerging from the water surface (Fig. 1) were caught in emergence traps, exposed for 24 hours. Their wooden frame (50 cm x 50 cm) was set on the water surface over the litter habitat, with the funnel-shaped areal trap tied to overhanging branches.

Sampling and evaluation: Usually, *series* of 12 litter baskets were exposed simultaneously in a given area, at 2-10 m distance, depending on obstacles, such as fallen trees or undergrowth. Series of leaf-wash samples, taken in shallow waters by hand, were equally spaced. As regards emergence traps, series of 4-5 traps were set on the water surface and tied to overhanging branches at ± 5 m distance between them. The emergence traps were accompanied by a litter basket sample; thus, in a minimum of 4-5 samples, colonization of litter leaves on a given spot was simultaneous with adult emergence.

Depending on weather conditions, of flow speed and of accessibility by canoe, 2-3 sample series were taken in a given area on the same, and/or on subsequent days within a given month. Difficult conditions also led to a certain loss of samples on many occasions, particularly in series that were exposed for periods of weeks and months.

Data of the rates of litter fall in the inundation forests of the Manaus region (ADIS et al. 1979; FRANKEN et al. 1979), together with analysis of litter conditions in relation to the inundation cycle (WALKER 1998), allowed to postulate a minimal long-term average quantity of one hundred "colonizable" litter leaves per area of the emergence traps (0.25 m²). This is, if anything, an under-estimate, but it allows to consistently relate the rates of colonization with the rates of emergence. An under-estimate of the the number of leaves per trap area would result in too high *relative* rates of adult emergence (E/C; see Table 3). The data presented in Figure 1 and in Tables 2 and 3 are given in means of monthly series means.

Results

Emergence of adults

Figure 1 shows the rate of emergence of all adult aquatic insects caught in a total of 351 trap samples.

Notable is the prevalence of Chironomidae and Collembola, and the relative rarity of all other Orders: in fact, only 16 of the 351 traps contained two or more individuals

being neither Collembola nor chironomids. The insects not itemized in Figure 1 (black columns) are: Hemiptera (Corixidae, Veliidae, Naucoridae, Gerridae, Hebridae, Belostomatidae); Ephemeroptera (Baetidae); Plecoptera (3 individuals); Trichoptera, Homoptera (1 individual); Odonata (Zygoptera, 6 individuals of two species); Coleoptera (Staphilinidae, Dryopidae, Elmidae, Curculionidae, Ptiliidae (?)); Diptera (Ceratopogonidae, Tipulidae, Tabanidae, Dolichopodidae, Psychodidae, Simuliidae, Culicidae). The notorious rarity of mosquitoes in these mineral-poor blackwaters was again evident (SIOLI 1984; HUMBOLDT 1959), only a total of 7 culicids were caught. Table 1 shows the average number of individuals collected per trap and per 24 hours for the various insects that were caught with notable frequency.

As regards the apparent rarity of the macro-insects (i.e. of all insects except Collembola and chironomids) caught in the traps, it must be taken into account, that only the litter habitat was sampled, and even as regards this particular habitat, the mean, permanent standing stock of larvae is some 50-100 individuals per square meter (WALKER 1994), a density which is similar to the one found by REISS (1977) for the larger benthic insects of Lago Tupé, a blackwater mouthbay lake that joins the Rio Negro some 10 km west of the Tarumã-Mirim mouthbay. Furthermore, an emergence rate of 1-2 individuals per trap (0.25 m² amounts to 40,000-80,000 insects per hectare per day; this includes the areas of the inundated forest between March and August/September (Fig. 1, and data given below). Still, the area covered by the 351 traps set for 24 hours is less than 90 square meters, large insects with extended life cycles are therefore poorly represented. For instance, only two species of Odonata (Zygoptera) were recovered, while a special study on the Odonata of the Tarumã-Mirim river lists 31 adult species (OLIVEIRA 1992), the main reason being, that dragon flies climb out of the water along the stems of trees and shrubs before emerging, and hence, would not be caught in traps set on the surface of open water. Problems of data interpretation also refer to Hemiptera and Collembola, because individuals found in the emergence traps are not necessarily newly hatched adults.

Apart from insects, water mites (Acari) were occasionally caught, particularly Oribatida.

Seasonal variation of emergence as a function of the annual inundation or "flood pulse" (JUNK et al. 1989) is concordant in both litterbanks, the minimal rates coincide with high water levels (2-4 m depth above litterbank, May to July). In late July/August the water runs out of the igapó in the area of the two meanders, and in September the fauna is again restricted to the litterbanks of the river channel, resulting in increasing population densities. The collection in the Cuieiras habitat (Nov. 1988) is similar to the one in the Atalho Barão. The decline of the chironomids and Collembola in November and December is significant (for Collembola: $P < 0.025$ and < 0.01 for the Atalho Barão and Atalho de Cima, respectively; X^2 -test), and might be due to predation, which intensifies during low water levels, when the predator fauna, confined to the river channel, is also relatively dense. During high water levels (May to July), chironomids may prefer shallow waters in the inundated forest for oviposition, in fact, it could be shown that chironomid emergence declines with increasing water depth (WALKER 1998). Prevalence of chironomid reproduction in more shallow waters was also shown by REISS (1977) for the Lago Tupé, while chaoborids dominated in deep waters. Chaoboridae, however, never appeared in the closed-canopy igapó of the Tarumã-Mirim (WALKER 1998).

Non-random distribution: Despite the numerical consistency of the overall seasonal pattern of emergence, as particularly evident for the most frequent types (chironomids and Collembola), distribution between traps of single localities, and between days and years in same localities, is highly clumped, suggesting an immediate reaction of the organisms to incidental conditions of the respective micro-habitats: The standard deviations (SD) are invariably of the same order of magnitude as the means (\bar{x}), i.e. $(SD)^2 \gg \bar{x}$. Examples for the Chironomidae were given in WALKER (1998); examples for the Collembola are shown in Table 2. Diverse Collembola species are notorious for the tendency to aggregate, and during the fieldwork, swarms of Collembola hopping over the water surface were frequently observed. However, upon setting the traps, the animals usually dispersed, and in single trap samples, 2-3 different species were recorded on several occasions. Their clumped distribution in trap-sample-series may therefore not simply stand for gregarious behaviour. Non-random patterns of emergence can also be shown for less frequent macro-insects, for instance for the Trichoptera. Of a total of 45 adults collected in the 158 traps of the Atalho de Cima, 39 individuals were caught either as singles in neighbour traps, or by 2, 3 and 5 within a same trap. According to random expectation, less than 4 such events should occur.

Standing stock, rates of colonization and of emergence

Material presented: Table 3 shows the relation between standing stock densities in the submerged litter, rates of litter colonization and of emergence per 24 hours. Three different categories are itemized:

Firstly, macro-insects: Shown are standing stock and colonization rates as determined via basket samples, the data are extracted from WALKER (1994) and exclude chironomids and Collembola; furthermore, their rate of emergence as presented in Figure 1 and Table 1.

Secondly, Ephemeroptera: Their larvae were by far the most frequent colonizers of the basket samples (41.3 % of the aquatic macro-fauna, including shrimps and fish, were Ephemeroptera larvae; WALKER 1994). Furthermore, adults appeared with reasonable frequency in the emergence traps.

Thirdly, Chironomidae: For comparison's sake, these data are extracted from WALKER (1998).

Relations between the rates of colonization and emergence: The fractions of adults emerging in % of recruitment, i.e. of colonization, for macro-insects in general, and for the chironomids, are remarkably similar, and show that grosso modo 90 % of larvae are lost in the aquatic habitat, while ca. 10 % of emerging adults are sufficient to maintain the long-term average of standing stocks, both, of larvae in the submerged litter, and - by implication - of adults in the terrestrial habitats, which reproduce the following generation of aquatic larvae.

Of the Ephemeroptera, only about 1 % of the larvae that colonize the baskets within 24 hours emerge as adults.

As regards the trophic structure of the benthic litter habitat of the river and of its inundation forest, the data in Table 3 suggest that 90-99 % of the juvenile insects enter the aquatic foodweb before reaching maturity, and that the few percent of emerging adults maintain recruitment and standing stock of their populations in the ecosystem of the litter habitat.

Discussion and conclusions

From a strictly mathematical point of view, a stable population of single and/or mixed species is easily defined: For maintaining a given standing-stock density of individuals within a given area, each parent must leave behind a single reproducing offspring (referred-to as "1:1 condition" in the following). As every ecosystem is finite, populations cannot grow continuously, and continuous decline leads of necessity to extinction. This simplistic basic condition of zero growth nevertheless hides the notorious complexity of population dynamics of species within their ecosystems, including abiotic factors as climate with seasonal and irregular variations etc. The first conclusion to be drawn is, that this 1:1 condition applies to the long-term average within areas that are large in relation to the short-term mobility of the constituent organisms, and this calls for explicit hierarchisation of any analytical approach as regards population stability.

Now, the basic objective of the Tarumã-Mirim research was getting to know the ecosystem as such, principally its trophic structure. In retrospect, though, the quantitative data allow for some realistic interpretations in terms of population- and ecosystem stability.

As far as hierarchisation of the data is concerned, there are individual samples, simultaneous sample series in sub-areas of two large meanders, there are monthly sample series, in most cases over periods of several years.

Not surprisingly for an ecosystem subject to annual inundation cycles, *variation* imposed by the "flood pulse" (JUNK et al. 1998) is the dominant feature for the emergence rates in both meanders (Fig. 1). A characteristic seasonal pattern could also be shown for basket occupation (WALKER 1994): Both, colonization rates and standing stock have reduced values between June and August during highest water levels; colonization rates increase between January and April during rising waters, and standing stock peaks in October/November, when the fauna is again confined to the river channel.

A consistent pattern of emergence rates between the two litterbanks (Atalho Barão, Atalho de Cima) appears also in Table 1, which presents *the frequencies of the different insect Orders*. There seems to be a characteristic quantitative composition of the aquatic insect fauna in the litter habitat, in that the *relative* frequencies between the different Orders are very similar in the two litterbanks. The large standard deviations are due to the seasonal differences between the monthly means.

A noteworthy feature is the clumped, i.e. *non-random distribution* of this insect fauna on the lower hierarchical levels, between samples of single series, and between series collected simultaneously in adjacent areas and/or on two subsequent days, as shown in Table 2 for Collembola ($SD = \pm \bar{x}$). The same could be shown for Chironomidae (WALKER 1998). Now, animals have a neural system, it is therefore reasonable to assume, that clumped distribution is a function of perception of micro-habitat quality, such as resource density and/or niches for hiding from predators, of adequate reaction to water flow etc. In this case, non-random distribution stands for mechanisms of fitness optimization via selection, which would increase the chances of long-term species persistence.

The *model of standing stock with colonization input and emergence output* (Table 3) suggests, that the system may not be too far from a 1:1 relation between parent generation and reproductive offspring, i.e. from a long-term, average growthrate = 0, considering that the 1-10 % surviving adults are in turn the victims of terrestrial predation by

birds, bats and spiders etc., which may attack before reproduction can take place, beside any other environmental accidents.

The only way to stabilize zero growth is, to maintain standing stock, and any given standing stock density can be maintained by very different input and output flows, provided only that the reproduction rate of emerging adults can balance the death rate. The Ephemeroptera are a case in point: as mentioned above, they have the highest larval densities of macro-insects in the basket series (ca. 50 ind./m², emergence = 1 individual, including both sexes; Table 3), and they are a major resource for the predators in the litter habitat, principally odonata larvae, small fish and shrimps (WALKER 1987). According to IMMS (1970), Ephemeroptera have exceptionally high rates of oviposition, depending on species, females lay several hundred and up to 4,000 eggs. Single surviving females per ca. 2 m², therefore, balance the massive loss due to predation in the litter habitat.

From a theoretical point of view, standing-stock densities can only be maintained under conditions of "resilience" (PIMM 1991), that is if *firstly*, resource is not limiting, and *secondly*, if there is redundancy of potential colonizers that will continuously fill empty niches, that is, if *space* is limiting.

According to the data in Table 3, *resource limitation* is an improbable condition. The chironomids alone maintain an average standing-stock of $4 \times 1477 = 5908$ larvae per m² while predation is in full operation, not to mention the remaining mesofauna of ca. 150 species (Protozoa, micro-Crustacea, Rotifera, Oligochaeta, etc.) that is recovered from leafwash samples (WALKER 1987).

In the case of *space limitation*, one would expect a community of potential colonizers in the free water, which cannot find niches in the litter habitat to settle down. In this case, litter baskets exposed in the water column of the stream, or on litter-free sandy bottoms, should immediately get colonized by the characteristic litter fauna. This was found to be the case: Such isolated baskets get colonized within 24 hours at the same rate as baskets exposed on the litter habitat, and during the following 2-8 weeks they contain significantly more species and individuals than the baskets in the litter habitat (WALKER 1994).

The available data so far at disposition thus lead to the conclusion, that the ecosystem of the benthic litter habitat of the Tarumã-Mirim with its colonizing insect species is relatively stable. Its phase-spatial dynamics is in tune with HUBBELL's (2001) "Neutral theory of biodiversity", which refers to "species-area relationships". The mechanics of this stability may be summarized by the apparently absurd statement, that stability, i.e. zero-growth, is maintained by resource redundancy and by excess reproduction.

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Table 1: Number of different insects recovered per emergence trap and per day in the two meander sites. \bar{x} = means of mensal series means. The large standard deviations (SD) are due to the seasonal inundation periods (see Fig. 1).

Place Insects	Atalho Barão		Atalho de Cima	
	\bar{x}	± SD	\bar{x}	± SD
Chironomidae	34.46	± 27.72	49.30	± 51.06
other Diptera	0.19	± 0.29	0.18	± 0.29
Coleoptera	0.07	± 0.08	0.04	± 0.04
Trichoptera	0.21	± 0.37	0.22	± 0.24
Ephemeroptera	0.10	± 0.29	0.13	± 0.16
Hemiptera	0.50	± 0.84	0.24	± 0.34
Collembola	5.74	± 4.97	5.29	± 6.68

Table 2: Special examples of clumped distribution (relatively large standard deviations SD) for Collembola caught in emergence traps within 24 hours ($= \bar{x}$). n = number of traps within series and number of replicated series respectively.

Date	Place	\bar{x}	\pm	SD	n
26. Oct.	Atalho Barão	11.2	\pm	7.04	5 between traps
27. Oct.	Atalho de Cima	20.6	\pm	19.60	5 between traps
March	Atalho Barão	12.13	\pm	12.67	3 between series
Oct.	Atalho Barão	14.27	\pm	5.48	3 between series
Oct.	Atalho de Cima	21.40	\pm	33.0	3 between series

Table 3: Standing stock, colonization and emergence of the litter-colonizing insects.

$\bar{x} \pm SD$ = means of mensal series means with standard deviations; n = number of mensal series.

ΣS = total number of samples assessed. Macro-Insects: all insects except Chironomidae and

Collembola. * = Baskets submerged for 1week to 2 months. A, B: from WALKER (1994); (n):

= number of mensal series, but mensal means were not assessed, as the respective data refer to the taxonomic composition of the collections. Chironomidae: from WALKER (1998).

Insect-categories	Standing stock Indiv./0.25 m ²				Colonization (C) Indiv./0.25 m ² x 24h				Emergence (E) Indiv./0.25 m ² x 24h				E/C %
	\bar{x}	\pm	SD	n	\bar{x}	\pm	SD	n	\bar{x}	\pm	SD	n	
Macro-Insects	A*				A								
ΣS	20.1	\pm	13.0	14	13.7	\pm	8.7	8	1.06	\pm	1.37	23	
Years	132 Baskets 1984-1988				95 Baskets 1984				351 Traps 1988-1992				7,7
Ephemeroptera	B*				B								
ΣS	12.9		(52)		12.7		(30)		0.12	\pm	0.24	18	
Years	488 Baskets 1983-1988				329 Baskets 1983-1988				377 Traps 1988-1992				0,95
Chironomidae	1477	\pm	923	12	344.2	\pm	266.8	30	38.7	\pm	30.5	31	
ΣS	59, Leaf-wash				142, Leaf-wash				382 Traps				11,3
Years	1983-1992				1984-1990				1988-1992				

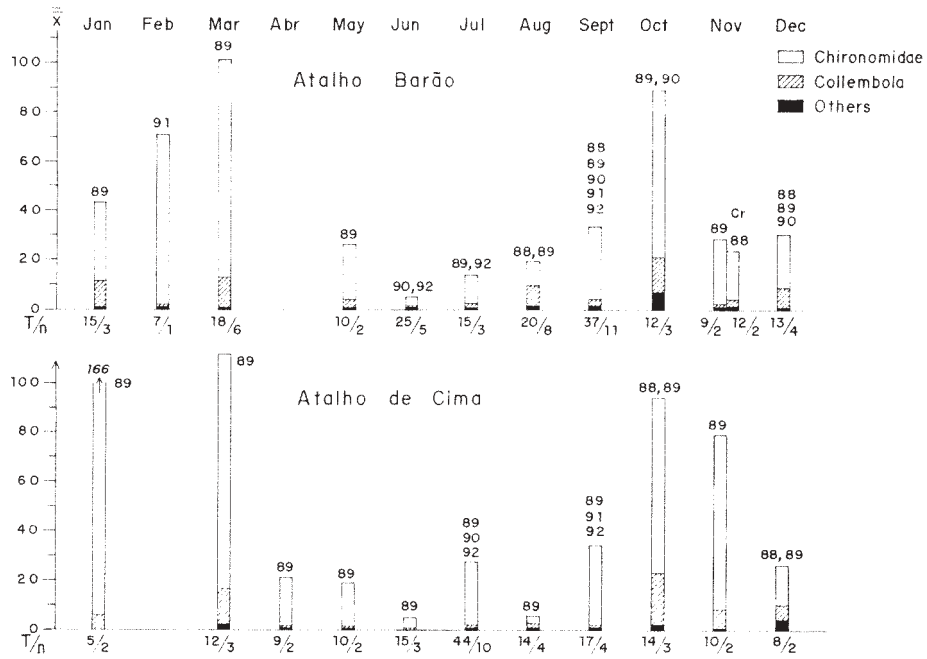


Fig. 1:
Emergence of adult insects in the two collection sites of the Taramã-Mirim River. Lower meander = Atalho Barão, upper meander = Atalho de Cima. Cr: single collection in the Cuieiras River site "Lago do Peixe-Boi". \bar{x} = monthly means of series means. T/n = total number of traps (T) in n series. Numbers on columns: years of collection (1988-1992).