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POPULATION DYNAMICS OF CHIRONOMIDAE (DIPTERA) IN THE CENTRAL AMAZONIAN BLACKWATER RIVER TARUMÃ-MIRIM (AMAZONAS, BRAZIL)

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Abstract:

Data on the emergence of adult chironomids and on the colonization of submerged litter by larvae collected between 1984 and 1992 in benthonic habitats of blackwater forest river Tarumã-Mirim, joining the Rio Negro ca 25 km North-West of Manaus, are presented. All species (as yet unidentified) breed continuously. However, the rates of colonization (larvae/leaf/24h) and emergence (adults/0.25m²/24h), as well as the density of potential predators of larvae, are functions of the annual inundation cycle. There is a drastic depression during high water levels (April to August), when the aquatic fauna disperses into the inundation forest, and a minor depression between November and January, when the water is confined to the river channel; this latter depression appears to be a function of predation. Standing stock reserves, however, remain high the year round (minimal estimates = 2300 - 11,264/m²), with peak values between October and December. The ratios of chironomid larval prey/predator vary between 30 (April) and 201 (Dec.); chironomids, however, are not the only prey of the benthic macrofauna, composed mostly of small fish, shrimps and Odonata larvae. The annual mean of litter colonization by larvae is 1.377 larvae/m²/day, 155 (= 11.3%) of which emerge as adults.

Key-words: Chironomidae, Population Dynamics, Inundation Forest, Rio Negro

Resumo:

“Dinâmica populacional de Chironomidae (Diptera, Insecta) no Rio Tarumã-Mirim, um rio de água preta da Amazônia Central (Amazonas, Brasil)”.

São Apresentados dados sobre a emergência de quironomídeos e colonização da serrapilheira (littera) submersa por larvas, coletados no Rio Tarumã-Mirim (Manaus, Amazonas) no período de 1984 a 1992, em áreas sob floresta primária alta. Todas as espécies (ainda não identificadas taxonomicamente) reproduzem continuamente. No entanto, as taxas de colonização (larvas/folha/24h) e de emergência (adultos/0.25m²/24h) variam em função do ciclo anual de inundação, com uma depressão prolongada no período de águas altas (abril - agosto) e uma mais curta entre Novembro e Janeiro, quando o rio está restrito ao seu canal. Esta última fase de redução é provavelmente o resultado de predação por pequenos peixes, camarões e insetos aquáticos principalmente. Ora, o estoque de larvas permanece alto durante o ano todo (2300 - 11.264/m²; média = 5.827/m²). A taxa média anual de colonização é de 1.377 larvas/m²/dia, dos quais 155 (= 11,3%) emergem como adultos. A razão presa/predador, considerando-se como presas as larvas de quironomídeos varia entre 30 e 201. Contudo, sabe-se que quironomídeos não são a única presa da macrofauna aquática no hábitat da littera submersa (Walker, 1987).

Palavras - chave: Chironomidae, Dinâmica de Populações, Florestas Inundadas, Rio Negro.

Introduction

The vast lowlands of Central Amazonia are drained by a dense net of streams and small rivers with generally acid nutrient-poor waters (SIOLI, 1984). In these running waters primary production is minimal, and FITTKAU *et al.* (1975) proposed that the aquatic foodchains started with allochthonous input from forest, such as fruits, flowers, leaf litter, decomposing woods etc. Numerous studies during the following twenty years, summarized in TUNDISI *et al.* (1995), fully confirmed this proposition. Apart from the biocenoses of the surface drift (FITTKAU, 1977), the fauna is essentially benthonic and aggregates preferably in submerged litter, which provides protecting niches as well as the materia prima for the aquatic food chains. These start with the decomposing tissues of the litter leaves, and most importantly, with the dense mycelia of the decomposer fungi, the hyphomycetes (BAERLOCHER & KENDRICK, 1981), beside a meagre crop of algae and bacteria (WALKER, 1985, 1987, 1995a). The litter leaves are colonized by a characteristic micro- and mesofauna, which reaches its maximum density within one week of submergence, with an average of 55 individuals of 11 species per leaf. Among the metazoa, the chironomids are the dominant colonizers, with 100% of leaves colonized by a mean of 14 larvae/leaf (WALKER, 1988). Of 100 species observed, 57, ranging from protozoa to insects and shrimps (Decapoda), ingested aquatic fungi, among them 5 species of chironomids.

The chironomids were found to be a key resource of the macrofauna of the litter habitat, principally of insects, shrimps and small fish (ENDERSON & WALKER, 1990), and this fauna, in turn, supports the larger predatory fish of the open waters, which constitute a major protein supply of the riverine, human population.

For these reasons, chironomid data, collected over the last 10 years, and as yet mostly unpublished, will be joined in this paper to provide a more or less coherent population study. Aside from the chironomids' special importance in Central Amazonian blackwater ecosystems, there has been a recent resurgence of interest in benthonic research in Chironomidae in particular. The periodical *Hydrobiologia* devoted the first two issues of 1996 to this topic, and, while I writing these lines, the mail delivered the announcement of the 2nd Brazilian Meeting on Chironomids at the Department of Hydrobiology of the University of São Carlos (São Paulo). There is still relatively little information on the chironomids' exact position in aquatic food webs (TAVARES-CROMAR *et al.*, 1996). The predator community will, therefore, receive special consideration in this study.

Study sites and sampling methods

Study sites

The Tarumã-Mirim is a ca 35 km long, meandering forest stream which enters the Rio Negro some 25 km north-west of Manaus. Including the meanders, its length increases 2-3 fold. Straight-line declivity is ca 10 - 20 cm/km and flow, during low-water

levels, varies from 10 - 25 m/min along the outer edge of meanders. Along the inner banks, flow is reduced or even inverted, this is where sand and/or litter banks build up. Older meanders eventually get short-cut by "atalhos" (short-cut in Portuguese), and thus may form closed or semi-closed oxbow lakes during lowest water levels. Channel width is about 6 - 12 m and depth 1 - 2 m. The water is "black", i.e. tinged orange-brown by humic substances in solution (12.7 mg/l), acid (pH = 4.5 ± 0.4) and nutrient-deficient (conductivity $10.2 \pm 1.4 \mu\text{S/cm}$). Temperature varies from 24° - 27°C in running water, but may reach 30°C in stagnating waters during the inundation phase. O₂ saturation is ca 80% (ca 6.5 mg/l), (ENDERSON & WALKER, 1986; WALKER, 1990). These and the following data refer to the middle stretch of the river, where the study sites are situated: the lower meander, called "Atalho Barão", and the upper meander, "Atalho de Cima", ca 18 Km and 20 Km respectively, from the river's mouth. The whole river stretch lies in undisturbed, primary forest, and both meanders are characterized by large, mostly submerged litterbanks. At the lower meander, the litterbank measures ca 50 m x 15 m; the litterbank of the At. de Cima is about half this size.

Both sites are subject to the annual inundations of the Amazonas / rio Negro river basins. The water rises from end of Dec./Jan. until June, and falls from mid-July to Nov./Dec. Water depth in June at the At. Barão is 4 m above the forest floor, but depth between years vary as much as 2 m. At the At. Barão, the water enters the forest in Feb./ March, and leaves in Aug./Sept. The delay at the At. de Cima is about 2 weeks. The water is virtually stagnating between May/June and July, with almost imperceptible flow in May and August. Owing to the inflow of cool and oxygen-rich water of side streams, deep water in the middle stretch of the Tarumã-Mirim during the inundation phase is not O₂-deficient. During high water levels, some collections were made in the inundation forest (= igapó) in the vicinity of the two meanders.

Sampling methods

Two different kinds of data were collected: firstly, number of adult chironomids emerging from the water surface and secondly, number of chironomid larvae found on single leaves of submerged litter. In addition, data on the macrofauna colonizing the submerged litter, and constituting the community of potential chironomid predators, are recorded from earlier studies (WALKER, 1994).

Emergence of adults

The adults were collected in 1 m long, funnel-shaped traps of black cloth mounted on a 50 cm x 50 cm wooden frame. The apex of the funnel consists of a white plastic bottle (1 litre), cut in two halves, the half with the bottle neck inserted into the lower part of the bottle. Animals entering the bottle are thus trapped. The bottle end of the traps was tied to an overhanging tree branch, while the wooden frame was set floating on the water surface, with the cloth funnel moderately stretched, but allowing for a few cm of water level variation during the $24 \text{ h} \pm 2 \text{ h}$ of exposure time. In this way,

adults emerging per 0.25 m² water surface and per day were recovered. The positively photo-tactic adults would move up along the black funnel, into the white bottle. On some occasions, traps with white cloth funnels were used to rest whether mature nymphs would react to luminosity. For retrieval of the adults the lower entrance of the trap was closed with a cover, the bottle untied and the cloth vigorously shaken, so that insects which had settled on the cloth would fall or fly into the bottle. They were then removed by , and stored in, 70% alcohol.

The traps were set over the litterbanks of the two meanders in series of 4 - 5, with a minimal distance of 5 m between traps. During the inundation phase, some series were mounted in the igapó. On occasions, strong flow and/or drastic changes of water levels, caused some losses.

Larvae colonizing litter leaves

Two measures of larval occupation of litter leaves were taken: firstly, colonization rate, and secondly, standing stock. The bulk of the litter leaves of the litterbanks and of the litter layers covering the ground of the inundation forest is of an average size of 40 - 80 cm² (WALKER, 1992). The size of randomly chosen leaves in the present study was: 76.7 ± 21.2 cm² (At. Barão) and 76.6 ± 28.1 cm² (At. de Cima). The number of loosely packed litter leaves, with more of 50% of their area intact, varied between 168 and 230/0.25 m², and they form a cover of 2-3 layers on the forest floor. This is the normal habitat of the benthonic fauna during the inundation period. In the meanders, litterbanks may reach more than one meter in depth, however, the bulk of the litter-dwelling fauna prefers the loosely packed top layers. As entire leaves only were assessed for colonization rate and for standing stock larvae, and, furthermore, as natural, submerged litter is partly covered by silt (WALKER, 1995b) the "colonizable" leaf area per 0.25 m² was arbitrarily set as being equivalent to 100 entire leaves, i.e. to half the number collected in the natural habitat. In this way, area on the ground occupied by larvae can be related to the area of the emergence traps (0.25 m²).

Colonization rate

Freshly shed litter leaves of average size were collected on the dry forest floor near the study site. Groups of 5 or 10 leaves were filled into rectangular baskets (1.8 litre volume) made of wire frames covered by 1 cm² mesh nylon netting. One basket was tied to the same branch or pole as the emergence trap, but sunk to the ground underneath or near the trap. Traps and baskets were exposed and retrieved simultaneously, that is, the leaves were at disposition during 24 h for larval colonization. After this period, the leaves of each basket were washed in alcohol (70%) with a soft paint brush. This leaf wash was then examined under the microscope (10 - 30 x magnification), the chironomid larvae were counted and, occasionally, measured. The colonization rate is given as number of larvae settling per leaf and per 24 h (or per 100 leaves). Statistical tests, however, were

based on the number of larvae counted in pool of 5 or 10 leaves exposed together in one basket. For comparison, data of an earlier study are given (Tab. 2; WALKER, 1988). In this case, single leaves were exposed at the At. Barão litterbank, the baskets were, accordingly, much smaller ($15 \times 15 \times 3.5 \text{ cm}^3$).

Standing stock

Single, submerged leaves were collected by hand along the shallow edge of the litterbanks and in shallow areas of the igapó. The leaves had to be clearly visible, hence, water depth did not exceed ca 50 cm. A first entire leaf was chosen at random, and collected with its 4 or 9 nearest neighbour leaves. These 5 or 10 leaves of a single sample spot were then washed in alcohol. Usually 2 - 4 such samples, at a distance of at least 5m, were taken at any one site and date. The leaf wash of the sample spots was processed as described for the colonization samples. Standing stock is given as number of larvae recovered per leaf or per 100 leaves (per $\cong 0.25 \text{ m}^2$).

As hand-collected leaves could be taken in shallow waters only, data of the earlier study (WALKER, 1988) are included. They refer to single leaves in small baskets exposed for one to two months at the At. Barão meander and hence, at the same water depth as the leaves exposed for 24 h colonization. It is supposed that the long exposure period makes them equivalent to "standing stock leaves".

Predator community

The community of potential predators consists of the macrofauna recovered between 1983 and 1988 at the meander of the At. Barão in monthly series of 10 baskets exposed for one month (WALKER, 1994). Each basket contained 20 leaves. The curve in Fig. 3 is adjusted to the number of animals found per 5 baskets, i.e. per 100 leaves (equivalent to 0.25 m^2 of habitat, see above; for species composition and frequencies see WALKER, 1994).

The gut contents of this fauna are examined continuously, hence, the list of chironomid predators given in the following section includes earlier (WALKER, 1987; HENDERSON & WALKER, 1986; KENSLEY & WALKER, 1982) and new results.

The new data published in this paper were collected between 1988 and 1992 and include the following samples: Emergence traps - 418 traps in 93 series, with regular, monthly collections trough 1989 and later additions. Leaf colonization / 24 h - 144 baskets in 35 series, 32 series accompanying the emergence traps trough 1989. Standing stock samples - 59 spots (of 5 or 10 leaves each) in 20 series (between 1984 and 1992).

Statistical analysis

As distribution proved to be largely non-normal, significance values given in the text refer to X^2 -tests if not otherwise indicated.

Results

The fauna collected and assessed

Adult Chironomidae

Although a variety of insects of other Orders and Diptera Families were recovered in the emergence traps, only the Chironomidae are assessed in this study. It is noteworthy, however, that Chaoboridae never appeared in the middle and upper course of the Tarumã-Mirim, while Irmiler (1975) collected their larvae in a muddy bottom substrate of the open, lake-like mouthbay area. The size of adult chironomids ranged from 0.5 - 4.0 mm, and most species were smaller than 3 mm. The most frequent species measured 0.7 - 0.8 mm (*Hydrobaenus* ?) and 1.5 - 1.7 mm (*Metriocnemus* ?); both types include at least two species, and they appeared the year round. Hence, they are breeding continuously, as is probably true for all other species.

In general, some 4 - 10 species were caught in each trap, but variability was considerable. To mention three examples: 7 individuals/3 species (At. Barão, Jan. 1989); 283 ind./15 spp. (At. de Cima, Jan. 1989); 15 ind./11 spp. (At. de Cima, Oct. 1988).

Chironomid larvae

As the adults, they were usually small, with a range of 0.4 - 4.0 mm for both categories of samples, standing stock and 24 h colonization, and smallest larvae were frequent during the whole year; this confirms continuous breeding. On the average, the larvae from 24 h colonizations were smaller than standing stock larvae (0.96 ± 0.14 mm versus 1.3 ± 0.63 mm; $P < 0.05$, t - test). Similar differences were established in a previous study (WALKER, 1988; 0.93 ± 0.52 mm for 24 h colonization versus means of 1.23 - 1.71 mm for colonization periods of 1 - 4 months). This indicates that firstly, newly hatched larvae measure about 0.4 mm, secondly, that leaves exposed for 24 h only are colonized mostly by very young larvae and thirdly, that there is larval movement between leaves, as larger larvae (up to 4 mm long) appear on leaves exposed for 24 h only. Thus, although colonization per day and per trap area (0.25 m^2 corresponding to about 100 leaves) is taken as measure of recruitment, this is not equivalent to the rate of reproduction. Eggs and larvae may get lost within 24 h, while older larvae move in.

The following Genera were explicitly noted among the larvae: *Corynoneura*, *Symbiocladius* attached to Ephemeroptera larvae, the large, predatory *Pentaneura*, and an ubiquitous litter-mining consumer of the decomposition fungi, probably *Stenochironomus* (?). Red *Chironomus* larvae, as they are common in eutrophic and O_2 - deficient waters, were never found.

The community of potential predators

The curve of the standing stock of potential predators (Fig. 3) summarizes data from 262 litter - filled baskets exposed for one month at the At. Barão meander. The

most frequent Trichoptera and Ephemeroptera species were shown to be continuous breeders (WALKER, 1994), while the shrimp (WALKER & FERREIRA, 1985) and the small litter - dwelling fish species (unpublished observations) have their annual reproduction period during rising and high - water levels and produce a single generation per year.

Eight of the 18 fish species found in the meander (WALKER & HENDERSON, 1996) had chironomids in their gut: *Rivulus* sp. (Rivulidae), *Characidium* sp., *Elachocharax pulcher* Myers (Characidae), *Grenicichla* sp., *Apistogramma* cf. *regani* Kullander (Cichlidae), *Microphylipnus* sp. (Gobiidae), *Hypopygus* sp. (Hypopomidae, Gymnotiformes) and *Chasmocranus* sp. (Siluriformes).

All of the five frequent shrimp species feed heavily on chironomids: *Macrobrachium nattereri* (Heller), *M. inpa* Kensley & Walker, *Euryrhynchus amazoniensis* Tiefenbacher, *Pseudopalaemon chryseus* Kensley & Walker and *P. amazonensis* Ramos-Porto.

Among insects, the following were found to be chironomid consumers: Pentaneura (Chironomidae) feeding on smaller larvae, Trichoptera (2 species), Ephemeroptera (1 species) Plecoptera (1 species), Zygoptera (3 species) and Anisoptera (8 species).

During the low water period, small fish and shrimps may reach peak densities of more than 100/m² each.

Annual pattern of chironomid emergence

Fig. 1 shows the annual pattern of adult chironomid emergence in the two meanders and in the nearby inundation forest (= igapó). The striking feature is the drastic reduction of emergence during the months of highest water levels. In both meanders, the Apr./May and Sept. values are higher than the Jun./Aug. values ($P < 0.05$), and so are, of course, the March and Oct. peak values for all three regions ($P < 0.01$). A second, significant depression occurs in December at both meanders.

The upper region (At. de Cima) and Igapó show higher chironomid production during the peak months (Jan./Mar.; Oct./Nov.) than the meander in the lower river stretch (At. Barão; Jan./Mar., $P < 0.01$; Oct./Nov., $P < 0.05$).

The series from the Cuieiras river - lake indicates that chironomid production in submerged litter of larger, open areas is comparable to the values in the lower meander of the Tatumã-Mirim (At. Barão)

Chironomid dynamics in relation to water depth (Fig. 2)

The overriding variable during the annual inundation cycle is, naturally, water depth. Low productivity from Jun. - Aug. is again obvious (Fig. 1), and includes a low rate of leaf colonization by larvae (Jun. - Aug. versus Sept. - May: $P < 0.01$, except for

deepest water in May). However, we find that deeper waters show relatively high productivity between Oct. and May. Thereby, peak emergence in Jan. - May is mainly due to emergence in Jan. - March, as productivity is low in April and May (Fig. 1).

Significantly more adults emerge in shallow areas during rising and high water levels (Jan. - Aug.) than in deeper water (Jan. - May, $P < 0.01$; Jun. - Aug., $P < 0.05$ for 0 - 50 cm versus 200 - 500 cm). The reverse is true for fast receding waters (Sept., $P < 0.05$) and possibly for lowest water levels (Oct. - Dec., $P \cong 0.20$). This reversal may be a function of oviposition in relation to the water edge.

The samples of shallow water from Jan. - Aug. were taken at the water edge in the igapó. During rising waters, the females evidently accompany the water edge for oviposition, and emergence of adults occurs within a few days, before water levels exceed 50 cm. At the meander sites, where most of the traps were set, production continues, albeit at a reduced rate. In September, the water is fast receding. Litter colonization by larvae in shallow water is still high, but the emergence rate is low. This means that either larvae are lost to more intense predation in shallower waters, or else, the larvae accompany the receding water and move into deeper areas nearer the river. From Oct. - Dec./Jan. the water is confined to the channel, where depth does not exceed 2 m, and shallow trap sites are mostly avoided because of the instability of the water edge in function of rain storms.

This still does not explain the low productivity during highest water levels (Jun. - Aug.). During this period, the area of the aquatic habitat is larger by several orders of magnitude as compared to Oct. - Dec./Jan. (hundreds of hectares versus fractions of ha of litter habitat in the channel). This may reduce chironomid population density. However, in contrast to larger animals, chironomid life cycles are short, thus, population density may remain high despite habitat expansion. With the data so far at hand, the drastic depression of chironomid production during the high - water period cannot be explained. Water depth per se is no argument, because deep waters show high rates of colonization and emergence during other periods.

The results from traps set on fruits floating on the surface of deep water indicate that females may prefer solid substrates near the surface to oviposit. In fact, green leaves of the submerged understory vegetation during high water levels, collected 15 - 60 cm below the water surface, were found to be occupied by 14 ± 7 larvae/leaf (7 sites, 5 or 10 leaves each). Now, this is standing stock, not colonization rate, still, these data show that solid surfaces nearer to the water surface aggregate chironomid larvae.

As from Sept./Oct. the water is again confined to the channel. This drastic reduction of the aquatic habitat undoubtedly increases chironomid density. The same is true for their predators. The question is, whether the reduction of chironomid production in Nov./Dec. in the At. Barão meander, and in Dec. in the At. de Cima meander (Fig. 1) may be due to predation.

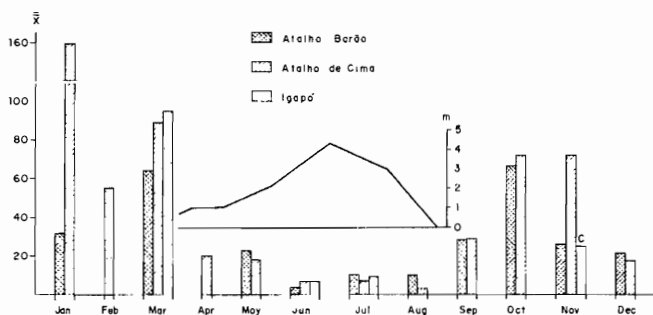


Fig. 1. Emergence of adult chironomids in the various localities. X = number of chironomids per trap (0.25 m^2) and 24 hours; mean of means within series of traps. Atalho Barão = meander of lower course of the river (total of 170 traps in 46 series). Atalho de Cima = meander in upper course (178 traps in 40 series). Igapó = inundation forest in the vicinity of the two localities (34 traps in 8 series). C = mean of 12 traps set along the Margin of a river - lake of the Rio Cuieiras ($\sim 60 \text{ Km}$ NW of Manaus). Inset curve: mean water levels (m) above the forest floor at the Atalho Barão meander (Walker 1994). Differences between years may reach 2 meters.

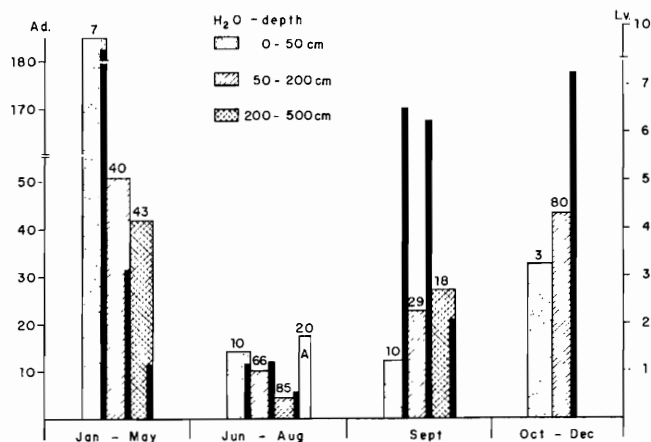


Fig. 2. Chironomid dynamics as a function of water depth and inundation period, irrespective of locality. Jan. - May: rising water levels and inundation of the forest (igapó). Jun. - Aug.: high water levels. Sept.: water receding from the forest. Oct. - Dec.: lowest water levels, water confined to river channel. Ad. = Adults emerging per trap and 24 h (means of series means). Lv. and narrow, black columns: number of larvae colonizing single leaves within 24 h, mean of series means. Number on columns: number of traps assessed. A: traps set on floating *Aldina latifolia* (Caesalpinaceae) fruits (water depth $\pm 200 \text{ cm}$).

The question of predation

Fig. 3 relates chironomid dynamics to predator density. For standing stock it should be considered that during the months of high water levels (May - Aug.) the leaves had to be collected in shallow water, that is at the edge of the inundated areas. It is more realistic, therefore, to use the data of the basket collections (crosses in Fig. 3) for comparisons, because the leaves in the baskets were exposed at the trap sites in deep water (for a period of 1 -2 months).

The rate of colonization (C) or input ranges from 35 larvae in June to 866 in December, while emergence (E) or output ranges from 5.9 in June to 96 in January. Expressing output in % of input ($100.E/C$) in relation to the inundation cycle, we find that during rising and high water levels (Jan. - Jul.) mean emergence is $24.4 \pm 10.5\%$, with a single value (April, 6%) falling below 10%. During falling and low-water levels (Aug. - Dec.), emergence ranges between 2% (Dec.) and 8% (Oct., Nov.), with a mean of $5.6 \pm 2.3\%$. This, despite the fact that the colonization rates have their peak values between September and December. Now, the 6% in April coincide with a seasonal predator peak of $24/0.25 \text{ m}^2$, and from July to November predator density rises from the annual minimum of 7.5 to its maximum of 31 as the result of aquatic habitat contraction and annual reproduction cycles during the previous inundation period (WALKER, 1994). It is reasonable, therefore, to assume that reduced ratios of emergence are a function of increased predator density and activity, and that the 75.6 - 94.4% of larvae not emerging enter the aquatic foodweb.

Does this mean resource limitation for the predator community and depletion of chironomid populations? This is obviously not the case. Standing stock is exceeding colonization numbers the year round, only in November 1989 did this ratio fall to close to one (1.04). The annual average of this ratio is 13.14. In other words, the low ratio of emerging adults during the period of highest predator densities is sufficient to maintain standing stock reserves and to guarantee recruitment. Moreover, chironomids are not the only resource available in this habitat. The community on higher trophic levels is therefore not resource limited. As shown by earlier investigations, space limitation is by far the more probable proposition (WALKER, 1994; HENDERSON & WALKER, 1990; WALKER *et al.* 1991).

The decline of predator density between November and January is probably due to predation from higher trophic levels. Large fish forage in the litterbanks of the meanders and in the litter deposits of stream inlets and recesses. This is where the local inhabitants are setting their fishing nets, and egrets and kingfishers occupy the riverbanks from September to December and move out in January (WALKER, 1990).

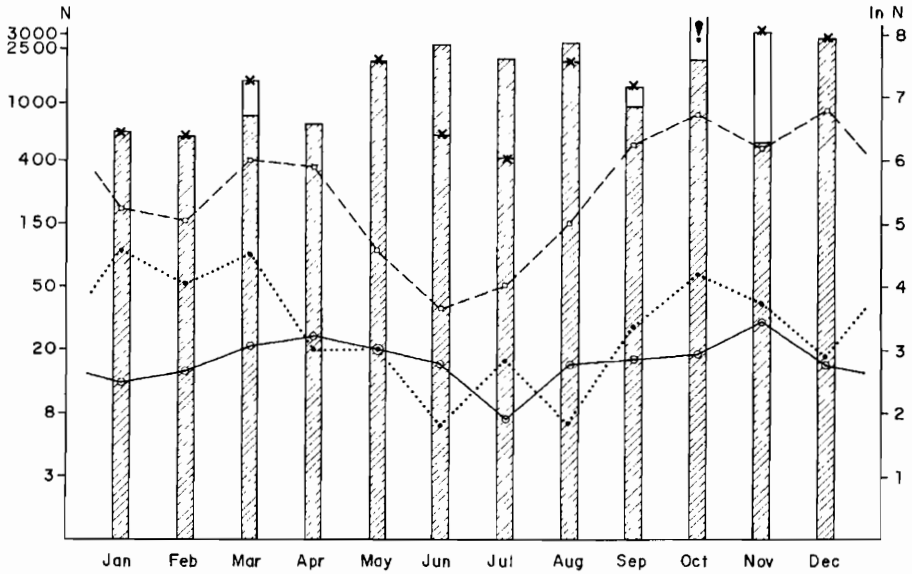


Fig. 3. Chironomid emergence (dotted line) including all localities, in relation to standing stock (columns, larvae per 100 leaves), to colonization rate (broken line, larvae settling per 100 leaves and 24 h) and to density of potential predators (solid line), assuming a mean number of 100 litter leaves per trap area (0.25 m²). Crosses and solid line: earlier data (Walker, 1988, 1994; field work, 1983-1986). !: highest mean number of chironomid larvae found per leaf = 72.2 ± 49.6; Oct. 1984, Atalho Barão meander. N = number of individuals, scale = log-normal (ln).

The non-randomness of colonization and emergence

In case of random distribution and settlement of larvae we would expect a normal distribution of larvae within submerged litter and of adults emerging. For given sample size, the equation $\bar{x} = SD^2$ must be valid. However, checking the values in Tab. I and II we find that the standard deviations (SD) are in most cases of the same order of magnitude as the means (\bar{x}), and hence, $SD^2 \gg \bar{x}$ (for values >1). This is true for the higher hierarchical level of means between series of traps or leaves ($\bar{\bar{x}}$). In other words, the patterns of distribution are highly irregular, i.e. "clumped". This observation has important biological implications, which will be discussed in the following section.

Table I. Emergence of adult chironomids: examples of non-random variation in relation to various variables. Note also the large variation within categories ($SD^2 \gg X$). $\bar{x} \pm SD$ = means and standard deviations of adults collected per trap and 24 h. T/n = total number traps per n different series. Where $n > 1$, the mean of the n series means is given. The differences between all categories are statistically significant (see text).

Variables Place, Date	Chironomidae		Chironomidae	
	N ^{traps} /Trap		N ^{traps} /Trap	
	$\bar{x} \pm SD$	T/n	$\bar{x} \pm SD$	T/n
Different years;	1988, 89, 91, 92		1990	
At. Barão, Sept.	14.0 \pm 17.4	27/9	94.7 \pm 16.3	8/2
At. Barão, Oct.	32.2 \pm 2.8	10/2	155.0 \pm 114.0	2/1
Successive days on same spots;	26.Oct.1989		27.Oct.1989	
At. Barão	52.0	1/1	3.0	1/1
At. de Cima	1.Mar.1989		2.Mar.1989	
	173.8 \pm 103.0	4/1	55 \pm 31.5	4/1
Same day on neighbour spots;	7. Dec.1988		19.Jan.1989	
	15.0	1/1	41.0 \pm 7.0	2/1
	284.0	1/1	34.8 \pm 31.7	4/1
Semi-closed oxbow meander,	Stagnating water, lower end		Inflow, upper end	
At. de Cima, 9. Jul. 1992	99.0 \pm 44.7	4/1	15.0 \pm 8.3	4/1
Surface substrate,	Floating <i>Aldina</i> fruits,		Clear water surface,	
Igapó > 1 m deep	Aug.1992		Aug.1988, 89	
	17.7 \pm 2.2	20/2	7.3 \pm 3.4	18/7
Trap colour	Black traps		White traps	
6.Jun.-12.Sept.1992	5.4 \pm 7.0	26/6	9.9 \pm 8.2	20/6

Table II. Litter colonization by chironomid larvae in the litter bank of Atalho Barão meander: comparison between months and years. $\bar{x} \pm SD$ = mean and standard deviation of larvae settling per leaf and 24 h. Lv = number of single leaves assessed. T/n = trap sites per number (n) of collection series; $\bar{\bar{x}}$ = mean of means as 5 or 10 leaves were pooled at each trap site. Where $n > 1$, the mean between series means is given.

Month	Chironomids per single leaf (\bar{x} or $\bar{\bar{x}}$)					
	1984 - 1986			1988 - 1990		
	$\bar{x} \pm SD$	Lv	Year	$\bar{\bar{x}} \pm SD$	T/n	Year
Jan.	2.15 ± 1.49	10	84			
	2.63 ± 1.80	8	86			
Feb.	0.80 ± 1.33	10	84			
	13.08 ± 8.59	12	85			
Mar.	1.67 ± 1.65	12	86	2.29 ± 3.08	12/4	89
	13.78 ± 9.99	12	85			
Apr.	5.70 ± 2.49	10	86			
	12.33 ± 12.48	12	85			
May	3.33 ± 2.17	12	86			
	0.40 ± 0.66	10	86	0.30 ± 0.29	10/1	89
Jun.	1.18 ± 0.83	11	85	0.30 ± 0.26	4/1	90
Jul.	2.30 ± 2.33	10	84	0.10 ± 0.06	5/1	89
	5.23 ± 4.30	7	84			
Aug.				2.17 ± 1.90	14/4	88/89
Sep.	16.90 ± 8.72	11	84	6.55 ± 3.08	9/3	89
Oct.	17.80 ± 12.31	10	84	6.70 ± 4.84	5/1	89
Nov.	9.00 ± 6.51	9	84	3.76 ± 1.15	5/1	89
Dec.	1.67 ± 1.80	12	85	12.20 ± 8.19	5/1	89
	10.67 ± 11.00	12	84			

Conclusions and discussion

Normal distribution versus organization

To take up the last point first: normal distribution means random distribution, while deviation from normality implies specific interactions between the units of a population and / or between the units and their environment. The statistics of normal distribution was derived in connection with the thermodynamic theory of gases. The basic assumption is that the molecules move randomly through space and collide randomly. This results in a mean temperature and pressure of a gas of a given density. Transferring these conditions to biological populations means that individuals move randomly through their habitat, and that encounters between mates, between competitors

and between predators and prey occur at random. These assumptions are, however, entirely unrealistic and disregard everything that is understood by "biological organization".

Living creatures are genetically coded, that is, programmed by specific information. Animals in particular, have a neuro-sensory system which enables them to choose particular paths and particular niches, to seek and avoid particular encounters with other organisms, and to assume more or less stereotyped habits. The deviation from the normality ($\bar{x} \geq SD^2$) may therefore be an important measure for the statistical effects of informational (genetic, neuro-sensory) causality on the patterns of biological populations (WALKER, 1993, 1994).

This does not, of course, exclude abiotic, environmental effects. Drastic differences of emergence between years (Tab. I) may be the result of annual variation of the inundation cycle, while different emergence rates under black and white traps probably imply animal reaction to luminosity.

An important aspect is the hierarchical structure of the system. The relation $SD^2 \gg \bar{x}$ holds for the means of the colonization rate between individual leaves, between baskets holding 10 leaves and between different series of baskets. Of course, environmental and / or physiological disturbance may randomize any hierarchical level; strong flow after heavy rains may mess up the litter habitat and disorientate the fauna for certain periods, for example. On the level of the analysed river stretch as a whole, there appear overriding long - term patterns: firstly, the order of magnitude of leaf colonization (\bar{x} varies from 0.4 to 17.8 larvae / leaf / 24 h from 1984-1986 and from 0.1 to 12.2 from 1988 to 1990); secondly, the general depression of colonization and emergence during highest water levels (May - Aug.) and thirdly, a period of depression somewhere between Nov. and Feb., depending on locality. Again, pooling large sample series over space and / or time may show normal distributions. However, it is fundamental for statistical (ANDRÉN, 1996) as well as for deterministic (WALKER, 1972; 1994) analysis of biological systems, that the characteristics of phase - spatial conditions on one hierarchical level cannot be extrapolated to higher or lower levels of the same system.

General features of chironomid productivity and diversity

The annual mean of litter colonization by chironomid larvae in the Tarumã-Mirim river system amounts to 1377 larvae / m² / 24 h and emergence of adults to 155 / m² / 24 h. Thus, 88.7% of larvae presumably enter the aquatic food chains and 11.3% develop into adults. Even minimal values between May and August, when the inundations extended over hundreds of hectares, result in an average of 48 adults / m² / 24 h. That is, about half a million chironomids disperse into the forest vegetation per hectare and day. Owing to their minute size, this is less than 500 g fresh - weight protein entering the

terrestrial food chains as resource for Odonata, frogs, birds and bats etc. However this emergence rate maintains a minimal standing stock of some 5000 larvae / m² in inundation forests (igapó). Thereby, standing stock and colonization rates, as determined in this study, are massive under - estimates, because the litter habitat only was sampled, while chironomid larvae settle on virtually any surface, on trunks, on the leaves of the understory vegetation, on floating roots in the river channel. Thus, a better estimate of chironomid density would be closer to ca 10.000/m². The exceptional value of 72 larvae / leaf in October 1984 in the At. Barão litterbank (Fig. 3) approaches the maximum chironomid density of 30,000 / m² recorded by FERRINGTON & PEHOFER (1996) for the bottom substrate of the Lago El Junco (Galapagos). As for emergence rates, the mean value of the Tarumã-Mirim (155 / m² / 24 h) is similar to adult emergence in a German lake (Mindelsee, Konstanz), which reached 163 / m² (SMUKALLA & MEYER, 1988). However, chironomid emergence is confined to the summer months in northern Europe. It thus appears that, despite the extreme poverty of Amazonian black waters, their chironomid productivity and density may be of the same order of magnitude as they are recorded for richer waters in other parts of the world.

In the litter habitat, the ratio of standing stock larvae to predator density varies from 30 in April to 201 in December with an annual mean of 92.3 ± 59.5 . Thus, while constant predator / prey ratios is a myth (WILSON, 1996), maintenance of standing stock reserves is reality. Predator density may be the cause for a reduced ratio of emerging adults, but standing stock reserves are not being depleted (Fig. 3).

At the present stage little can be said about chironomid diversity; it is hoped that taxonomic analysis of the Tarumã-Mirim populations will be done in the near future. What calls one's attention is the large number of species that emerge per single trap (0.25 m²); the maximum recorded was 16 species, while 5 - 10 was the norm. NESSIMIAN (1995) lists 15 species for a lake of some 30 ha in the region of Rio de Janeiro, and TRIVINHO-STRIXINO & STRIXINO (1991) collected 40 species in a hydroelectric reservoir of São Paulo State. I would not be surprized if the chironomid diversity of the Tarumã-Mirim river system exceeded these numbers.

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