



Life cycle and production of *Campsurus notatus* (Ephemeroptera, Polymitarcyidae) in an Amazonian lake impacted by bauxite tailings (Pará, Brazil)

João José Fonseca Leal & Francisco de Assis Esteves

Lab. Limnologia, Universidade Federal do Rio de Janeiro, Dep. Ecologia, Inst. Biologia, CCS, Cidade Universitária, CP 68020, Rio de Janeiro, RJ 21940-590, Brazil
E-mail: joaoleal@biologia.ufrj.br

Received 18 October 1999; in revised form 11 July 2000; accepted 7 August 2000

Key words: life cycle, secondary production, Amazonian lake, Ephemeroptera, bauxite tailings

Abstract

Between 1979 and 1989, Lake Batata was subjected to $\pm 50\,000\text{ m}^3\text{ d}^{-1}$ of bauxite tailings effluent, which impacted about 30% of the lake's area. The present research had as its main goal to study the life cycle and secondary production of *Campsurus notatus* on the tailings-impacted region of Lake Batata. *Campsurus notatus* is the species most adapted to the conditions imposed by the bauxite tailings. A central site in the impacted region of Lake Batata was established and sampled at fortnightly intervals between July 1996 and June 1997. The nymphs of *C. notatus* in the impacted region had a 105-day lifespan, with individuals between 2 and 17 mm in length. Estimated secondary production for *C. notatus* was $2.5\text{ g DW m}^{-2}\text{ yr}^{-1}$ in the impacted region. This was high compared to production rates estimated for other species of ephemeropterans, indicating the degree of successful adaptation of *C. notatus* to the conditions imposed by the bauxite tailings.

Introduction

In some continental aquatic ecosystems, the benthic macroinvertebrates constitute the main community responsible for secondary production (Robertson, 1995; Grubaugh et al., 1997), assuring high values of biomass and representing the main pathway of energy transfer from lower to higher trophic levels. Macroinvertebrates feed on matter with a low energy content (detritus), converting it into matter of high energy value by secondary production. This matter then forms a food resource used by many species of fishes (Nystrom et al., 1996; Pierce & Hinrichs, 1997; Rosenfeld, 1997).

Among the many orders present in the benthic macroinvertebrate community, the order Ephemeroptera has been often used in biomonitoring of aquatic environments, because of the diversity of habitats in which they are found and, especially, to the sensitivity of some species to ecological disturbances (Merritt & Cummins, 1984; Da Silva, 1994). The

genus *Campsurus* Eaton, 1868 (Ephemeroptera: Polymitarcyidae) comprises some 50 described species. This genus is one of the largest and least defined of the order Ephemeroptera (Pereira & Da Silva, 1991). *Campsurus notatus* (Needham & Murphey, 1942) is only present in the southern hemisphere. The nymphs dig galleries in the soft silt or clay substrates where they live. This species is common in many Brazilian aquatic environments, including the Amazonian várzea (floodplain) lakes. It plays an important ecological role, as a food item in the diet of many species of fishes, and in bioturbation process (Fittkau et al., 1975; Nolte, 1987, 1988).

Edmondson & Winberg (1971) and Downing & Rigler (1984) stressed that secondary production studies offer information relevant to four areas: (a) explanation of energy or matter transfer among communities and ecosystems; (b) rational management of aquatic resources; (c) detection of pollution effects; and (d) formulation of general theories of biological production. Recent investigations have emphasised the effect

of anthropogenic disturbances on aquatic ecosystems, especially on production and alterations in the trophic relationships of communities. (Cressa, 1986).

Study of the communities of benthic macroinvertebrates of the Amazonian aquatic environments is of utmost importance for an understanding of its aquatic systems, especially regarding the maintenance of trophic chains through secondary production, nutrient cycling, processes of decomposition of organic matter and bioturbation, and as indicators of water quality (Nolte, 1987; Walker, 1995).

In Lake Batata, the macroinvertebrate community has been a principal bioindicator of the impact of the dumping of bauxite tailings (Callisto & Esteves, 1996; Fonseca et al., 1998). The population of *Campsurus notatus* has been shown to be extremely well adapted to the ecological conditions imposed by the presence of the tailings, exhibiting high densities and biomass in these areas, compared to the natural zone where the nymphs of *C. notatus* were found only in low densities and biomass during the low water and flood periods (Fonseca & Esteves, 1999). Therefore, research on the life cycle and secondary production of *C. notatus* is fundamental to understanding its adaptation to the bauxite-impacted area of Lake Batata.

The present research had as its main goal to contribute to understanding the life cycle of the population of *C. notatus* and to estimate the secondary production in the impacted area of Lake Batata.

Materials and methods

Study site

Lake Batata (Figure 1) is located between 1° 25' and 1° 35' S and 56° 15' and 56° 25' W, in the town of Porto Trombetas, Municipality of Oriximiná, State of Pará, Brazil. It is a typical floodplain lake, with pronounced variation of its water level during the year, in four distinct hydrological phases: high water, drawdown, low water and flooding.

From 1979 to 1989, approximately 50 000 m³ d⁻¹ of effluent originating in the bauxite washing process, rich in very fine clay solids and with high concentrations of iron and aluminum oxides and silicates (Lapa & Cardoso, 1988), were dumped directly into Lake Batata, impacting about 30% of its area (Roland & Esteves, 1998). According to Esteves et al. (1990), the sediment in Lake Batata was markedly influenced by the bauxite tailings, which formed layers of clay

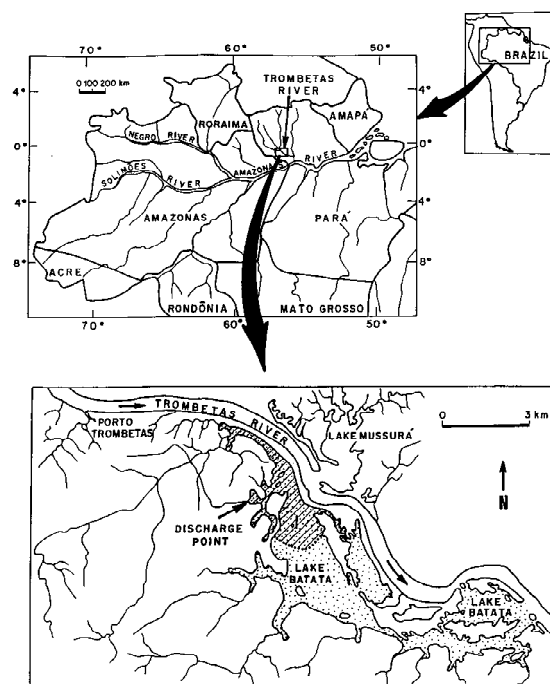


Figure 1. Map of the geographical location of Lake Batata (PA, Brazil) and the sampling station (I), located in the area impacted by bauxite tailings.

up to 7 m thick, resulting in low concentrations of phosphorus, nitrogen and organic matter (Fonseca & Esteves, 1999). Lake Batata has a slightly acid pH (5.4–6.9), as is usual in Amazonian clearwater environments (Sioli, 1984), and a mean conductivity of 11.5 $\mu\text{S cm}^{-1}$, with no evident differences between the impacted and natural areas (Bozelli, 1992; Esteves et al., 1994). These values are similar to those found in other lakes of the region.

Sampling

Sampling was undertaken at a station (I) located in the central region of the area impacted by bauxite tailings (Figure 1). Samples were collected fortnightly between July 1996 and June 1997. The sediment samples were collected with a corer (Ambühl & Bühner, 1975), 8 cm in diameter (area 50 cm²), with 10 samples taken at each visit, fixed with formaldehyde and then washed through a series of graded sieves (1.0, 0.5 and 0.21 mm mesh).

Secondary production and life cycle

The nymphs of *C. notatus* were measured with a Zeiss stereoscopic microscope fitted with an optical

millimetre reticle. The lengths of the nymphs were determined from the tip of the cephalic region to the last segment of the abdomen. Body length was used to determine the length–weight relationship, following the methodology proposed by Smock (1980) and Da Silva (1994), with the determination of a regression equation for the population of *C. notatus* in Lake Batata. Biomass was determined from the dry weight of the nymphs (oven-dried at 60 °C for 48 h) in a Mettler balance (model UMT2), precision 0.1 µg.

The secondary production of the nymphs of *C. notatus* was estimated by the size-frequency method (Hynes & Coleman, 1968; Downing & Rigler, 1984) as modified by Benke (1979) and Menzie (1980), described by the following equation:

$$P = [i \cdot \Sigma(n_j - n_{j+1}) \times (W_j W_{j+1})^{1/2}] \times 365 - 64 / \text{CPI}$$

with P = annual secondary production (mg DW m⁻² yr⁻¹); i = the number of size classes; n = the mean number of individuals in each size class; $(W_j W_{j+1})^{1/2}$ = the geometric mean of the weights of two size classes; CPI = the interval of production of the cohort; and 365–64 = the number of days in a year–number of the days without nymphs.

The life cycle of *C. notatus* was estimated through analysis of size-frequency distributions (in 10 size classes) of the fortnightly samples (Vieira, 1981). The size classes varied from 2 mm to 17 mm, with an interval of 1.5 mm for each size class. The variation in the frequency of individuals in each class in the course of 1 year (July 1996–June 1997) made possible the construction of a size-frequency histogram and the determination of the life cycle of this species in the impacted region of Lake Batata.

Results

Life cycle

Study of the life cycle of *C. notatus* in the impacted area of Lake Batata, using the 110 nymphs collected in the course of 1 year, indicated a life cycle varying from 90 to 120 days (Figure 2). It is a bivoltine population, with two generations per year (e.g. one generation from 23 May to 15 August, and another from 12 December to 11 April).

The body lengths of the nymphs ranged from 2 mm to 17 mm. Individuals with a body length of 17 mm were found only in November and December 1996; with the greatest lengths in the other samples being

from 12 to 14 mm. This indicates the possibility of separate growth in the sampling periods. No nymphs were found in the impacted sediment during one 49-day period and a second 15-day period.

Length–weight relationship

Figure 3 shows the relationship between the dry weight and the length of the nymphs of *C. notatus* in the impacted region of Lake Batata during the sampling period. One hundred and thirty nine individuals were measured, with lengths between 2.1 mm and 17.4 mm and dry weights from 0.02 mg to 12.02 mg. The correlation obtained was an exponential curve with $r = 0.8917$, best described by the equation:

$$Y = 0.036 * X^{0.406}$$

with Y = dry weight (mg) and X = body length (mm). From the graph, it can be inferred that the nymphs of *C. notatus* have two distinct phases in their growth. In the initial period, the nymphs gain in length but add little biomass. In the second phase (above 8 mm in length), there is more weight gain in relation to body length, shown by the area of the curve with a greater slope.

However, the linear regression curve derived from the log-transformed data (Figure 4) had a correlation coefficient of $r = 0.985$, with a confidence interval of 95%, thus showing a higher correlation between weight and length. From this regression the following equation was derived:

$$\ln Y = -5.758 + 2.8980 \cdot \ln X,$$

where Y = dry weight (mg) and X = body length (mm). This equation was used to determine the values of biomass of the nymphs of *C. notatus*, for the estimate of secondary production.

Secondary production

To determine the annual production of *C. notatus*, we used the CPI (Cohort Production Interval), estimated for the impacted region. The mean interval of 105 days for the CPI was established from the study of the life cycle of this species, and is related to the duration of the nymph phase.

Table 1 shows the estimate of secondary production of *C. notatus* in the impacted area during 1 year. A secondary production rate of 2.5 g DW m⁻² yr⁻¹, equivalent to an annual production of 25.0 kg DW ha⁻¹ was estimated.

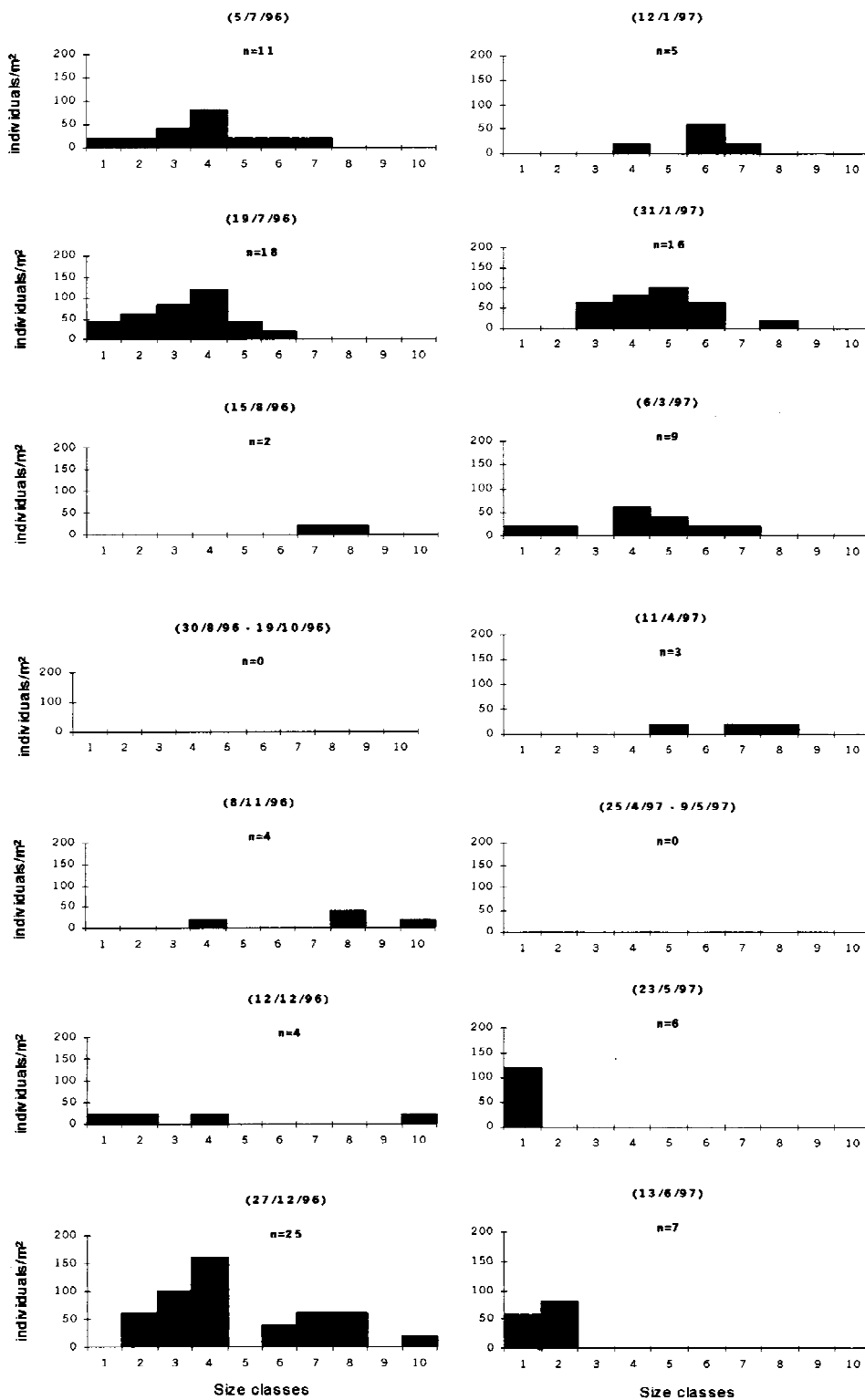


Figure 2. Histograms of the life cycle of *Campsurus notatus* in the tailings-impacted area of Lake Batata, with samples taken fortnightly between July 1996 and June 1997.

Table 1. Annual secondary production of *Campsurus notatus*, in the impacted region of Lake Batata between July/1996 and June/1997

| Size Class (<i>i</i>) (mm) | Density (N_i) (ind.m ⁻²) | Dry weight (W_i) (mg.ind ⁻¹) | $N_i \cdot W_i$ (mg.m ⁻²) | $N_i - N(i+1)$ (ind.m ⁻²) | $[W_i \cdot W(i+1)]^{0.5}$ (mg) | Biomass loss (mg.m ⁻²) |
|---------------------------------|---|--|--|--|------------------------------------|---------------------------------------|
| 2–3.5 | 15.50 | 0.07 | 1.04 | 0.00 | 0.12 | 0.00 |
| 3.5–5 | 15.50 | 0.22 | 3.42 | 1.10 | 0.34 | 0.37 |
| 5–6.5 | 14.40 | 0.52 | 7.46 | -16.60 | 0.72 | -11.95 |
| 6.5–8 | 31.00 | 1.00 | 31.06 | 18.80 | 1.31 | 24.67 |
| 8–9.5 | 12.20 | 1.72 | 20.96 | 0.00 | 2.16 | 0.00 |
| 9.5–11 | 12.20 | 2.71 | 33.04 | 3.20 | 3.30 | 10.55 |
| 11–12.5 | 9.00 | 4.01 | 36.12 | 0.00 | 4.77 | 0.00 |
| 12.5–14 | 9.00 | 5.68 | 51.08 | 9.00 | 6.63 | 59.63 |
| 14–15.5 | 0.00 | 7.74 | 0.00 | -3.30 | 8.90 | -29.36 |
| 15.5–17 | 3.30 | 10.23 | 33.77 | 3.30 | 10.23 | 33.77 |
| Total | 122.10 | 33.89 | | | 87.68 | |

CPI = 105 days.

$P = (i \times PB) \times 365 - 64 / CPI$.

$P = (10 \times 87.68) \times 301 / 105 = 2513.49 \text{ mg m}^{-2} \text{ yr}^{-1}$.

$P = 2.5 \text{ g DW m}^{-2} \text{ yr}^{-1}$.

Discussion

Ecological characteristics and life cycle of Campsurus notatus

The nymphs of *C. notatus* were found in high densities in the fine, unstable sediment of the impacted area of the lake, inhabiting it and digging extensive galleries. Similar behaviour was noted by Pereira & Da Silva (1991), who observed *Campsurus melanocephalus* (Pereira & Da Silva, 1991) in large swamp areas of the São João River (Rio de Janeiro, Brazil), where there was fine unstable sediment like that in Lake Batata. Pereira & Da Silva (1991) observed nymphs of *C. melanocephalus* digging galleries up to 0.6 m deep in the sediment. Nolte (1987) described the same kind of behaviour for *C. notatus* nymphs in an Amazonian várzea lake.

The body size of *C. notatus* (2–17 mm) found in this study agrees with the results of Irmiler (1975), who determined values between 1.6 mm and 17.0 mm for the same species. These results are similar to those of Cressa (1986) for nymphs of *Campsurus* sp. in a lake in Venezuela, with variations between 1.3 mm and 20.6 mm, and Melo et al. (1993), with *Campsurus violaceus* (Needham & Murphy, 1924), which varied from 1.6 mm to 12 mm in length. Pereira & Da Silva (1991) found a mean body size in subimagos of *C. melanocephalus* of 15–18 mm for females and 14–16 mm for males. There is, then, great similarity in the lengths of different species of this genus.

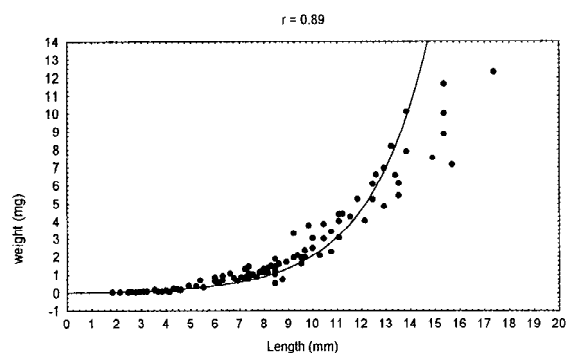


Figure 3. Relationship between the body length and dry weight of the nymphs of *Campsurus notatus*, sampled in the impacted area of Lake Batata from July 1996 through June 1997.

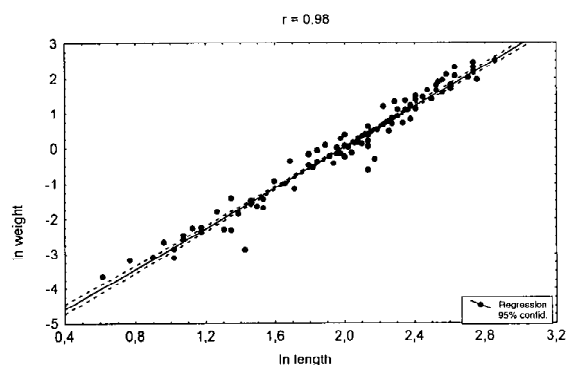


Figure 4. Linear regression of the log-transformed data (ln) of the length and dry weight of the nymphs of *Campsurus notatus*, sampled in the impacted area of Lake Batata from July 1996 through June 1997.

The results obtained for the life cycle of *Campsurus notatus* in the impacted area allowed us to identify the population as bivoltine. The nymphs develop over approximately 90–120 days (13–17 weeks), to the subimago stage, when the nymphs migrate from the sediment to the water surface and enter the aerial stage. An aquatic phase of 9–12 weeks is usual in most species of Ephemeroptera (Da Silva, 1994). The results of Irmiler (1975), who estimated an interval of 10–12 weeks between the development of the egg and the emergence of the subimagos of *C. notatus*, and of Nolte (1987), who determined a period of 3 months for the nymph stage of the same species, are similar to ours.

The intervals of 49 and 15 days during which no individuals of *C. notatus* were found in the sediment of the impacted area may be related to characteristics of the life cycle of this population, as well as to changes in environmental characteristics. This kind of population behaviour has been observed in other studies of ephemeropteran populations. Sweeney (1978), studying *Isonychia bicolor*, a bivoltine species, observed that the period between the laying and the hatching of the eggs of this species was from 4 to 5 weeks, resulting in an interval of 30–45 days between the generations, where no nymphs were found in the environment.

In respect to the influence of environmental factors, Melo et al. (1993) reported the effects of the fluctuation of the water level on the migration of the nymphs of *C. violaceus* from the central regions of the Baía River, to the near-bank zone, during the high water period. Nolte et al. (1997), studying the ephemeropteran community in a stream in the Pantanal (Mato Grosso), observed that the variation in the water flow resulted in a decrease in density and in the disappearance of some genera during the periods of lowest flow. We conclude that many factors may be related to the absence of nymphs of *C. notatus* in the impacted areas during these two periods. Further studies are necessary to better understand these questions regarding the complete life cycle of this species in the impacted areas of the lake.

Our observations and comparison with data from other studies indicate that the nymphs of *C. notatus* in the bauxite-impacted area showed no changes in life cycle, behavioural, physiological or ecological habits. The presence of the bauxite tailings created favourable ecological conditions for colonisation by this species.

Weight–length relationship of the nymphs of *Campsurus notatus*

The correlation between these two variables indicates the manner in which they fluctuated in relation to each other (Sokal & Rohlf, 1979), that is, it represents the coupled behaviour of the two variables (Vieira, 1981). The weight–length relationship in most aquatic insects can be represented by an exponential curve, in the equation

$$(Y = a.X^b),$$

by a quadratic regression, of the kind

$$Y = a + bX + cX^2$$

(Smock, 1980; Meyer, 1989) or by a log-linear regression log

$$Y = \log a + b \log X$$

(Meyer, 1989; Nolte, 1990).

These authors noted that studies have been successfully developed and obtained prognostic equations for the determination of biomass in relation to body length for many species of terrestrial and aquatic insects for temperate regions. This kind of information is rather sparse for the benthic macrofauna of tropical aquatic environments.

Comparison between the weight–length relationship curves for nymphs of *C. notatus* obtained in this study, shows that the linear regression with the log-transformed data showed a high correlation coefficient ($r = 0.98$) between these two morphological parameters. The use of the equation,

$$\ln Y = -5.758 + 2.8980.$$

$\ln X$, is therefore advised as a basis for determination of the biomass from the body length.

Secondary production of *Campsurus notatus*

The estimated CPI of 105 days for *C. notatus* is similar to that found by other authors (Irmiler, 1975; Nolte, 1987). However, Cressa (1986), studying the yearly production of *Campsurus* sp. in a lake in Venezuela, determined an interval of production of the cohort of 6 months. There is apparently a great variation in the values of CPI within this genus.

The result of $2.5 \text{ g DW m}^{-2} \text{ yr}^{-1}$, estimated for the secondary yearly production of *C. notatus* in Lake Batata, indicates a high production rate in the impacted area, compared to data obtained for yearly production of other ephemeropterans. Dudgeon (1996)

found a yearly production of 0.037 g m^{-2} , in two species of the family Ephemeridae in a brook in Japan. Da Silva (1994), using data from the literature, showed that secondary production in lotic environments fluctuates between $0.03 \text{ g m}^{-2} \text{ yr}^{-1}$ and $8.50 \text{ g m}^{-2} \text{ yr}^{-1}$. Da Silva (1994) found values of $0.17 \text{ g m}^{-2} \text{ yr}^{-1}$ for *Callibaetis guttatus* (Baetidae) in a temporary marsh in Rio de Janeiro.

According to Waters (1977), the expected production of nymphs of Ephemeroptera is from 0.12 to $4.45 \text{ g m}^{-2} \text{ yr}^{-1}$. However, there are few studies on ephemeropterans in lentic environments, and according to Da Silva (1994), the expected secondary production for the nymphs in this kind of environment is from $0.01 \text{ g m}^{-2} \text{ yr}^{-1}$ to $1.90 \text{ g m}^{-2} \text{ yr}^{-1}$. The value for the secondary production of *C. notatus* in Lake Batata is high compared to the values estimated by Waters (1977) and Da Silva (1994). Extremely high values of secondary production were also obtained for *Campsurus* sp. ($46.15 \text{ g m}^{-2} \text{ yr}^{-1}$) in a lake in Venezuela by Cressa (1986). However, those results were obtained in an artificially eutrophic environment, which may have favoured high production (Pereira & Da Silva, 1991). This indicates a high potential for colonisation by members of this genus in favourable environments.

The high productivity and abundance of ephemeropterans in Amazonian aquatic environments was mentioned by Junk (1973). Junk determined the secondary production in stands of floating aquatic macrophytes in three kinds of whitewater environments, underlining the importance of *Asthenopus* sp. (Polymitarcyidae) in the secondary production of this kind of environment. Irmiler (1975) drew attention to the highest secondary production of *Campsurus notatus*, of $2.6 \text{ g m}^{-2} \text{ yr}^{-1}$, and asserted that the high production of this species in flooding areas is directly related to the high sedimentation rates of fine particles, creating a loosely compacted sediment. Fittkau et al. (1975) and Nolte (1987) also noted the high productivity of *Campsurus* in Amazonian whitewater várzea lakes, mentioning that the nymphs of this genus were not found in any of the blackwater environments studied by those authors. Our results for secondary production of *C. notatus* are similar to the high values found for this species in the highly productive Amazonian whitewater environments (Sioli, 1984). However, the lack of data on secondary productivity in Amazonian clearwater environments prevents comparison of our results with environments of similar ecological characteristics.

The high value of the productivity of *C. notatus* in the impacted area, contrasting with the low frequency, density and biomass of this genus in the natural areas (Fonseca et al., 1998; Fonseca & Esteves, 1999), show how well this species is adapted to the environment there. Therefore, the habitat characteristics of the impacted area are one of the key factors involved in the maintenance of the high productivity of this species there, being probably related to two ecological factors: migration into the impacted area, and decrease in the predator-prey ratio.

The probable migration of *C. notatus* into the impacted areas, especially in the adult stage (in the periods of mating flights), may explain the low densities of *C. notatus* in the natural and transitional areas, and the high density, biomass and production in the impacted area. Ephemeropteran nymphs have previously been observed to migrate because of changes in environmental characteristics. Melo et al. (1993) emphasised the effect of the flood pulse in the migration of *C. violaceus* nymphs in the Baía River. These authors observed that in the flooding period, when fine sediment particles are carried to the central areas of the river, changing the granulometric characteristics, the nymphs migrate to near-bank areas where fine sediments dominate. Nolte et al. (1997) mentioned the effect of fluctuation of flow in a tropical stream on the presence and density of some genera of Ephemeroptera, showing their capacity to migrate to areas where conditions are more favourable.

According to Nolte (1988), *C. notatus* is able to colonise environments of fine sediment and muddy waters, with high concentrations of suspended particles (clays). Nolte (1988) also mentioned that in this kind of environment the nymphs of *Campsurus* were the primary colonisers, behaving as r-strategists, with high reproductive rates. In Lake Batata, migration of *C. notatus* to the impacted areas is related to the ecological changes imposed on this area by the presence of the bauxite tailings, creating favourable conditions to the colonisation of this area by the species.

The second factor influencing density is the possible decrease in the predator-prey ratio between the fish community and the population of *C. notatus* in the impacted areas, especially the effect of this ratio as a factor that regulates the populations (Begon et al., 1996). Many authors have shown the regulating, structural effect of this ratio on the benthic communities, due to the species of fish present, resulting, in some instances, in decreases in the abundance

and biomass as well as in the regulation of the productivity of the benthic macroinvertebrates (Nyström et al., 1996; Rosenfeld, 1997). According to Pierce & Hinrichs (1997), many factors are responsible for a larger or smaller regulating effect of predation by the fish community on the benthic community. Among the environmental factors, fluctuations in the composition and density of the fish, the composition of the macroinvertebrates and the abiotic variables, as well as the structural complexity of the sediment and turbidity, may be decisive factors affecting the way in which fish predation affects the invertebrate communities.

The importance of ephemeropteran nymphs as a dietary item for fish has been mentioned by several authors working in many kinds of aquatic environments, (Crowl et al., 1997; Rosenfeld, 1997), including in Amazonia (Santos, 1982; Almeida, 1984). Ferreira (1993), studying the fish community of the Trombetas River near the town of Cachoeira Porteira, observed that ephemeropteran nymphs are an important dietary item in most of the fish species. We note that fish predation on ephemeropteran nymphs in Amazonian aquatic environments is quite high, and probably results in the regulation of this population.

In Lake Batata, the nymphs of *C. notatus* are an important dietary item for some species of fish, such as *Geophagus altifrons* (Cichlidae), in the natural areas, but they are not important in the diets of individuals caught in the impacted area (Reis, 1997). According to Mannheimer (1998), nymphs of *C. notatus* were frequently found as items in the diet of some species of fish in Lake Batata, even in the impacted area, and were the main dietary item.

In Lake Batata, the bauxite tailings had a negative effect on the fish community, with a decrease in the density and diversity of fish in the impacted area (Halboth, 1995; Reis, 1997). This probably resulted in a decrease in the predation rate of the fish on the benthic organisms in the impacted area, and this phenomenon may be considered as one of the main factors responsible for the maintenance of the productivity of *C. notatus*. On the other hand, the nymphs of *C. notatus* constitute a potential food resource for benthic-feeding fish species that are able to persist and feed in the impacted areas. Nonetheless, more specific studies on the predator-prey relationship between the fish community and the population of *C. notatus* in Lake Batata are required, so that we can evaluate the role of the bauxite tailings in the reduction of the predator-prey ratio.

We may conclude that generally the nymphs of *C. notatus* colonising the areas impacted by the bauxite tailings have a life cycle of 90 – 120 days, with no differences from patterns recorded by other investigators. The ecological conditions imposed by the bauxite tailings favored high secondary production of *Campsurus notatus* in the impacted areas.

Acknowledgements

The authors gratefully acknowledge CNPq and Mineração Rio do Norte S.A for financial support, and Dr Jorge Luis Nessimian, Dr Marcos Callisto, Dr Robert Hart and Mr Maurício Mello Petrucio, for their invaluable criticism. We are especially grateful to the members of the Laboratory of Limnology and to Dr Reinaldo Luiz Bozelli, Mr Alex Prast, M.Sc. and Dr Fábio Roland for their help in the fieldwork, and to Paulo Brum and Dr Janet W. Reid for the English translation.

References

- Almeida, R. G., 1984. Biologia alimentar de três espécies de *Triportheus* (Pisces: Characoidei, Characidae) do lago do Castanho, Amazonas. Acta Amazônica 14: 48–76.
- Ambühl, H. & H. Bühler, 1975. Technik der Entnahme ungestörter Grossproben von Seesedimenten: ein verbessertes Bohrlot. Schweiz. Z. Hydrol. 37: 175–186.
- Begon, M., C. R. Harper & C. R. Townsend, 1996. Ecology. 3rd edn. Blackwell Scientific Publishers, Oxford: 1068 pp.
- Benke, A. C., 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24: 168–171.
- Bozelli, R. L., 1992. Composition of the zooplankton community of Batata and Mussurá Lakes and of the Trombetas River, State of Pará, Brazil. Amazoniana 12: 239–261.
- Callisto, M. & Esteves, F. A., 1996. Macroinvertebrados bentônicos em dois lagos Amazônicos: Lago Batata (um ecossistema impactado por rejeito de bauxita) e Lago Mussurá (Brasil). Acta limnol brasil 8: 137–147.
- Cressa, C., 1986. Variación estacional, distribución espacial y balance energético de *Campsurus notatus*. (Ephemeroptera, Polymitarcidae) en el lago de Valencia, Venezuela. Acta cient. Venez. 37: 572–579.
- Crowl, T. A., C. R. Townsend, N. Bouwes & H. Thomas, 1997. Scales and causes of patchiness in stream invertebrate assemblages: top-down predator effects? J. n. am. Benthol. Soc. 16: 277–285.
- Da Silva, E. R., 1994. Aspectos da biologia e ecologia de *Callibaetis guttatus* Navás, 1915 (Insecta: Ephemeroptera: Baetidae) em alagados temporários da Restinga de Maricá, Estado do Rio de Janeiro. Museu Nacional, UFRJ, Rio de Janeiro, RJ: 109 pp. (Master's Dissertation).
- Downing, J. A. & F. H. Rigler, 1984. A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters. 2nd edn. Blackwell Scientific Publications, Oxford: 500 pp.

- Dudgeon, D., 1996. The life history, secondary production and microdistribution of *Ephemera* spp. (Ephemeroptera: Ephemeridae) in a tropical forest stream. *Archiv Hydrob.* 135: 473–483.
- Edmondson, W. T. & G. G. Winberg, 1971. A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters. 1st edn. Blackwell Scientific Publications, Oxford: 358 pp.
- Esteves, F. A., R. L. Bozelli & F. Roland, 1990. Lago Batata: um laboratório de limnologia tropical. *Ciência Hoje* 11: 28–33.
- Esteves, F. A., S. M. Thomaz & F. Roland, 1994. Comparison of the metabolism of two floodplain lakes of the Trombetas River (Pará, Brazil) based on study of diel variation. *Amazoniana* 13: 33–46.
- Ferreira, E. J. G., 1993. Composição, distribuição e aspectos ecológicos da ictiofauna de um trecho do Rio Trombetas, na área de influência da futura UHE Cachoeira Porteira, Estado do Pará, Brasil. *Acta Amazônica* 23: 1–89.
- Fittkau, E. J., U. Irmeler, J. W. Junk, F. Reiss & G. W. Schmidt, 1975. Productivity, biomass and population dynamics in Amazonian water bodies. In Golley, F. B. & E. Medina (eds), *Tropical Ecological Systems*. Springer-Verlag, Berlin: 289–311.
- Fonseca, J. J. L., M. F. P. Callisto & J. F. Gonçalves, Jr., 1998. Benthic macroinvertebrate community structure in an Amazonian lake impacted by bauxite tailings (Pará, Brazil). *Verh. int. Ver. Limnol.* 26: 2053–2055.
- Fonseca, J. J. L. & F. A. Esteves, 1999. Influence of bauxite tailings on the structure of the benthic macroinvertebrate community in Amazonian lake (lago Batata, Pará - Brazil). *Rev. brasil. Biol.* 59: 1–19.
- Grubaugh, J. W., J. B. Wallace & E. S. Houston, 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. *Freshwat. Biol.* 37: 581–596.
- Halboth, D. A., 1995. Estrutura da comunidade de peixes do Lago Batata (Rio Trombetas, PA.), PPGE, UFRJ, Rio de Janeiro, RJ: 110 pp. (Dissertation.)
- Hynes, H. B. N. & M. J. Coleman, 1968. A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.* 13: 569–573.
- Irmeler, U., 1975. Ecological studies of aquatic soil invertebrates in three inundation forests of central Amazonia. *Amazoniana* 5: 337–409.
- Junk, W. J., 1973. Investigations on the ecology and production-biology of the 'floating meadows' (*Paspalo-Echinochloetum*) on the Middle Amazon. *Amazoniana* 4: 9–102.
- Lapa, R. P. & W. Cardoso, 1988. Tailings disposal at the Trombetas bauxite mine. *Proceedings 117th TMS Annual Meeting, Phoenix*. Ed. Larry: 65–76.
- Mannheimer, S., 1998. Distribuição, alimentação e aspectos da reprodução de *Auchenipterichthys longimanus* (Guenther, 1864) (Siluriformes, Auchenipteridae) em um lago amazônico impactado com rejeito de bauxita (lago Batata, PA, Brasil). Museu Nacional, UFRJ, Rio de Janeiro, RJ: 134 pp. (Dissertation.)
- Melo, S. M., A. M. Takeda & N. C. Büttow, 1993. Variação temporal de ninfas de *Campsurus violaceus* Needham & Murphy, 1924 (Ephemeroptera: Polymitarcyidae) do Rio Baía (MS - Brasil). *Unimar* 15: 95–107.
- Menzie, C. A., 1980. A note on the Hynes method of estimating secondary production. *Limnol. Oceanogr.* 25: 770–773.
- Merritt, R.W. & K. W. Cummins, 1984. An Introduction to the Aquatic Insects of North America. 2nd edn. Ed. Kendall/Hunt, Dubuque, Iowa: 711 pp.
- Meyer, E., 1989. The relationship between body length parameters and dry mass in running water invertebrates. *Arch. Hydrobiol.* 2: 191–203.
- Nolte, U., 1987. *Campsurus notatus* (Polymitarcyidae, Ephemeroptera) a bioturbator in Várzea lakes. *Amazoniana* 10: 219–222.
- Nolte, U., 1988. Small water colonization in pulse stable (várzea) and constant (terra firme) biotopes in the neotropics. *Archiv Hydrobiol.* 113: 541–550.
- Nolte, U., 1990. Chironomid biomass determination from larval shape. *Freshwat. Biol.* 24: 443–451.
- Nolte, U., M. J. Oliveira & E. Sturs, 1997. Seasonal, discharge-driven patterns of mayfly assemblages in an intermittent neotropical stream. *Freshwater Biology* 37: 333–343.
- Nystyrön, P., C. Brönmark & W. Granéli, 1996. Patterns in benthic food webs: a role for omnivorous crayfish?. *Freshwat. Biol.* 36: 631–646.
- Pereira, S. M. & E. R. Da Silva, 1991. Descrição de uma nova espécie de *Campsurus* Eaton, 1868 do sudeste do Brasil, com notas biológicas (Ephemeroptera: Polymitarcyidae: Campsurinae). *Rev. brasil. Biol.* 51: 321–326.
- Pierce, C. L. & B. D. Hinrichs, 1997. Response of littoral invertebrates to reduction of fish density: simultaneous experiments in ponds with different fish assemblages. *Freshwat. Biol.* 37: 397–408.
- Reis, R. A., 1997. Caracterização, distribuição espacial e temporal e alimentação de ciclídeos (Cichlidae, Perciformes) no lago Batata, Porto Trombetas, PA. PPGE, UFRJ, Rio de Janeiro, RJ: 201 pp. (Dissertation.)
- Robertson, A. L., 1995. Secondary production of a community of benthic Chydoridae (Cladocera: Crustacea) in a large river, U.K. *Arch. Hydrobiol.* 134: 425–440.
- Roland, F. & F. A. Esteves, 1998. Effects of bauxite tailings on PAR attenuation in an Amazonian crystalline water lake. *Hydrobiologia* 377: 1–7.
- Rosenfeld, J. S., 1997. The influence of upstream predation on the expression of fish effects in downstream patches. *Freshwat. Biol.* 37: 535–543.
- Santos, G. M., 1982. Caracterização, hábitos alimentares e reprodutivos de quatro espécies de 'Aracus' e considerações ecológicas sobre o grupo no Lago Januacá-AM. (Osteichthyes, Characoidei, Anostomidae). *Acta Amazônica* 12: 713–739.
- Sioli, H., 1984. The Amazon: Limnology and Landscape Ecology. Dr W. Junk Publishers, Dordrecht: 763 pp.
- Smock, L. A., 1980. Relationship between body size and biomass of aquatic insects. *Freshwat. Biol.* 10: 375–883.
- Sokal, R. R. & F. J. Rohlf, 1979. *Biometria*. Ed. H. Blume Ediciones, Madrid: 832 pp.
- Sweeney, B. W., 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnol. Oceanogr.* 23: 461–477.
- Vieira, S., 1981. Introdução à Bioestatística. Rio de Janeiro, Ed. Campus: 203 pp.
- Walker, I., 1995. Amazonian streams and small rivers. In Tundisi, J. G., C. E. M. Bicudo & T. M. Tundisi (eds), *Limnology in Brazil*. ABC/SBL, Rio de Janeiro: 167–193.
- Waters, T. F., 1977. Secondary production in inland waters. *Advanced Ecology Research*, London 10: 91–162.