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Seasonal dynamics and production of *Campsurus violaceus* nymphs (Ephemeroptera, Polymitarcyidae) in the Baía River, upper Paraná River floodplain, Brazil

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Abstract

The production of *Campsurus violaceus* nymphs was investigated from October 1987 to September 1988 in the Baía River, a secondary channel of the Paraná River, Brazil. The annual production of this species during this period was 16.48 g dry wt m^{-2} y^{-1} and the P:B ratio was 4.9. This low ratio compared to other rivers occurred because the Baía River was strongly influenced by the hydrological regime of the Paraná River, where nymphs migrated to avoid adverse conditions in the river during the flood phase.

Introduction

Secondary production estimates formation of heterotrophic biomass through time (Benke, 1993) integrate survival, growth, and voltinism in a single figure, and indicate the success of a population and its functional importance in the ecosystem (Benke et al., 1988). Although studies of secondary production in running waters have greatly increased in recent years, little is known about secondary production in subtropical rivers (Benke, 1993). Our objective was to quantify abundance, biomass, and secondary production of *Campsurus violaceus* Needham & Murphy, 1924, in the subtropical Baía River. Nymphs of this species are relatively large and abundant organisms in the Baía River (Melo et al., 1993) and they are important members of the benthic community for cycling of organic matter, as well as, according to Hahn et al. (1991) and Fugi et al. (1996), a significant food supply for fishes.

The zoobenthos of the Baía River floodplain is influenced by the hydrological regime of the Paraná and Ivinheima Rivers (Takeda et al., 1991a,b,c). Some research on spatial and temporal variation has been undertaken in this region (Takeda et al., 1991a,b,c; Melo et al., 1993). The macroinvertebrate community of the floodplain plays an important role in the trophic structure of rivers with extensive floodplains (Ward, 1989; Gladden & Smock, 1990; Smock, 1994 and Agostinho & Zalewski, 1996).

Study area

The Baía River is an 86 km long secondary channel in the floodplain of the Paraná River, Brazil (22 ° 42′ 35″ S and 53 ° 15′ 02″ W). Two sites were selected at the sampling station: the middle and near the right bank of the channel (Figure 1). The hydrological regime at this station is influenced mainly by the Paraná River. Most of the time, the current is very slow and macrophytes, mainly *Eichhornia azurea* grow along the banks, while the riparian vegetation is composed mainly of *Polygonum* spp., *Paspalum* sp., and *Panicum* sp.

Materials and methods

Observations of life history and production were based upon samples taken from two sites of the Baía River between October 1987 and September 1988. Quantitative collections were made monthly with a modified

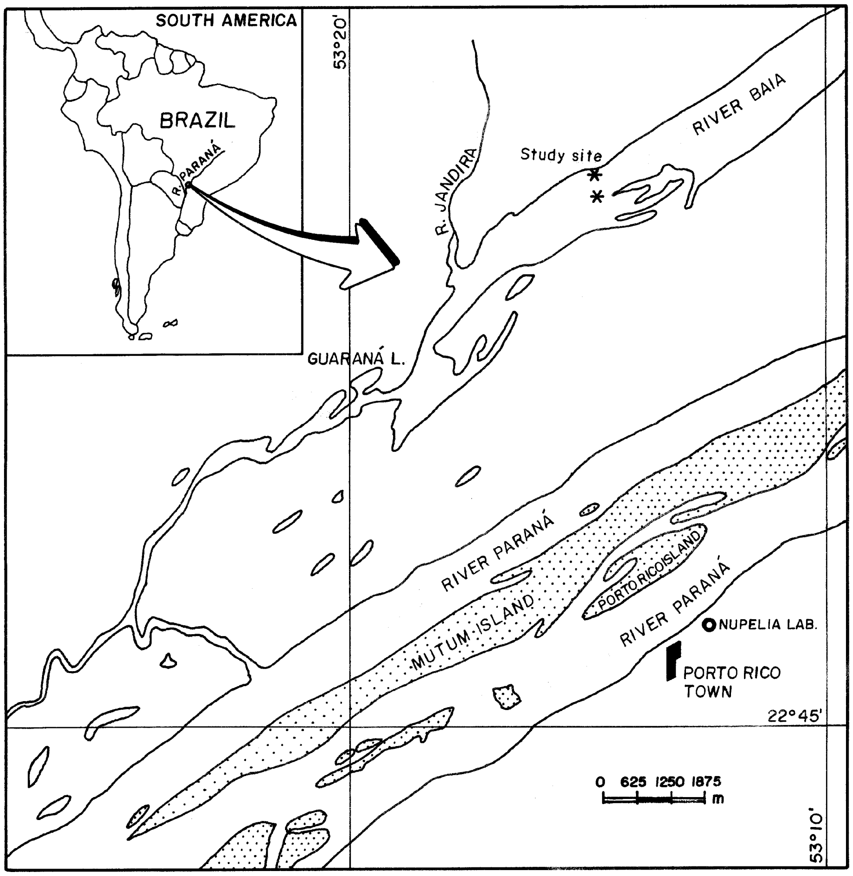

Figure 1. Map of the study area.

Petersen grab (0.0345 m^2) from two sampling locations, at the bank and in the main channel. On each sampling date, 10 samples were taken from each site and washed in sequential sieves: 2.0, 1.0 and 0.5 mm. The sediment retained in the last sieve was fixed in 4% neutral formalin and sorted using a stereomicroscope. All *C. violaceus* nymphs from these three fractions were preserved in 80% ethanol and were used to estimate secondary production. At each site, a sample of the sediment taken for analysis of granulometry and organic matter content was stored in a freezer and later oven-dried at 80 °C. Organic matter content was determined from a 10 g sediment subsample, by incineration at 560 °C for four hours in a muffle furnace.

The sample of bottom water was taken concomitantly with the sediment sample. We measured water transparency (by Secchi disc), depth, and temperature (by thermistor). Water samples were collected with a Van Dorn bottle, transferred to polyethylene flasks, and taken in insulated continers on ice to the laboratory. The following analyses were performed: pH; electrical conductivity; dissolved oxygen concentration by the Winkler method, as modified by Golterman et al. (1978); and total alkalinity by titration as described by Mackereth et al. (1978). An aliquot of each sample was filtered through Waterman GF/C filters, which were dried and frozen for later determination of the chlorophyll-a concentration (Golterman et al., 1978). A second aliquot was fixed with concentrated H_2SO_4, for determination of total phosphorus and Kjeldahl nitrogen (Mackereth et al., 1978). Daily water levels of Paraná River were furnished by the National Department of Waters and Electrical Energy (DNAEE).

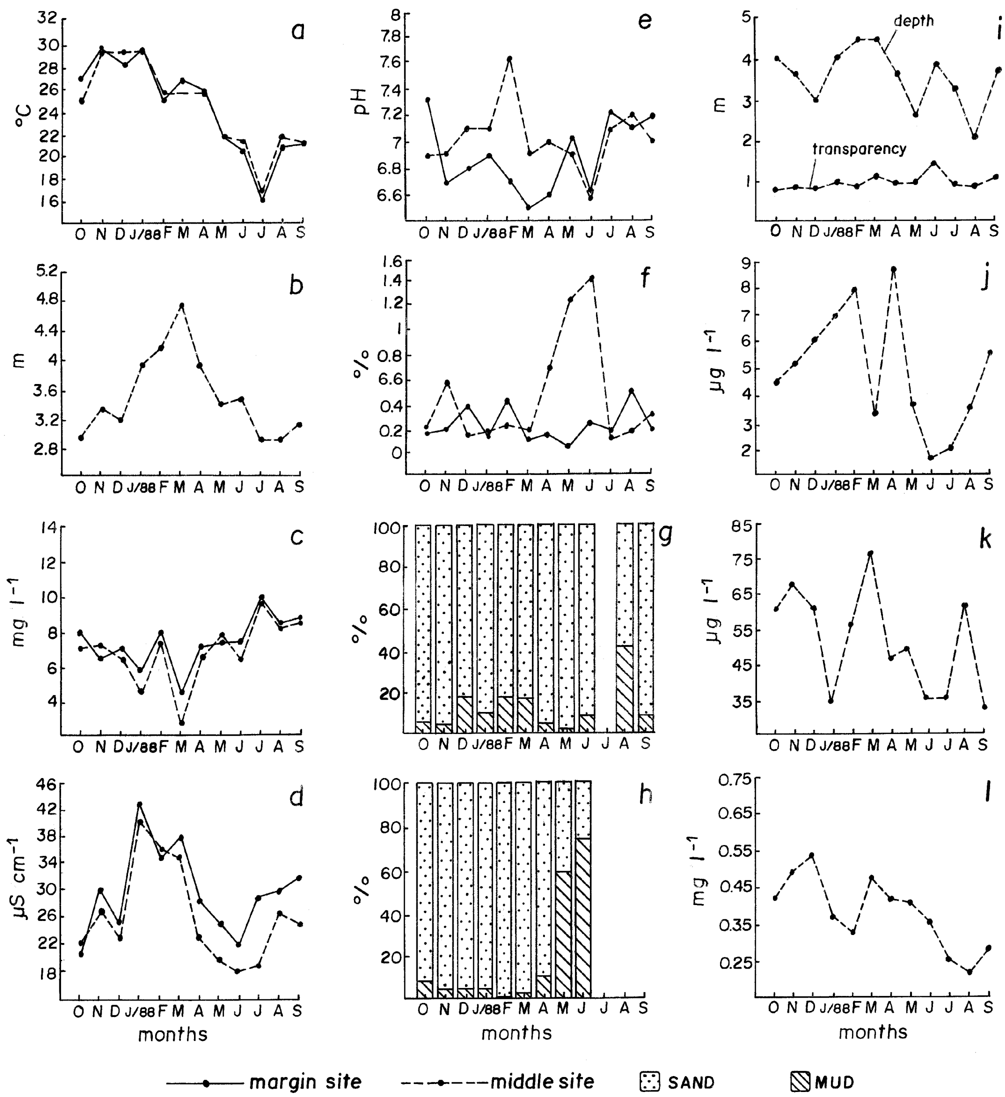

Figure 2. Selected physical and chemical parameters of the study site in the Baía River: a – temperature (°C), b – average changes in water levels of the Paraná River (m), c – dissolved oxygen (mg l^{-1}), d – conductivity (μS cm^{-1}), e – pH, f – bottom organic matter (%), g – % of the sand and mud at the bank location, h – % of the sand and mud at mid-channel, i – upper line, depth (m), bottom line, transparency (m), j – chlorophyll a (μg l^{-1}), k – total P concentration (μg l^{-1}), l – total N concentration (mg l^{-1}).

We used the size-frequency method (Hynes & Coleman, 1968), as modified by Hamilton (1969) and Benke (1979), to estimate annual production.

The mean theoretical body weighed for each size class was calculated using the formula:

$$W = a.H_{\mathrm{w}}^{b},$$

where W = wet weight, H_{w} = head capsule width, and a and b are coefficients, the values of which were determined empirically.

Mayflies were grouped into nine classes according to head capsule width (Cushman et al., 1978). In order to estimate dry weight, individuals of all size classes were weighed, dried at 60 °C for 24 hours and reweighed.

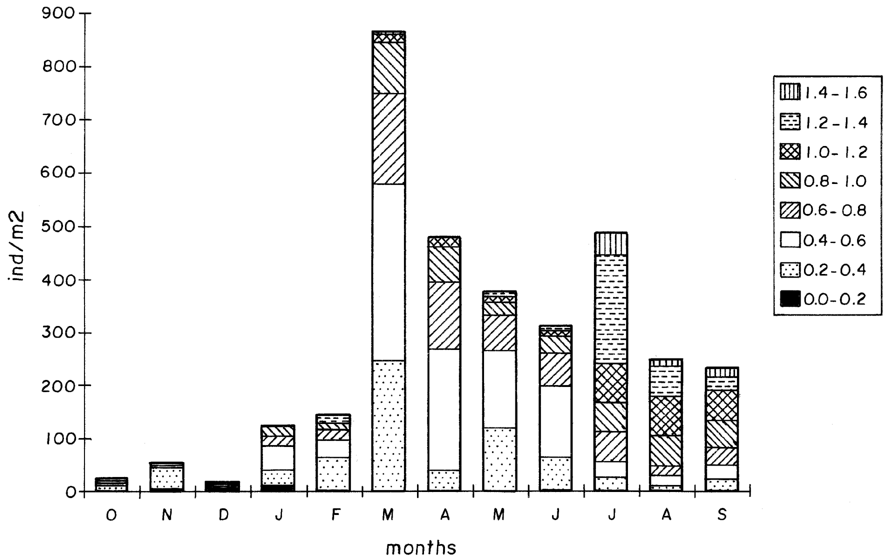

Figure 3. Monthly variation of total density (two sites) of *C. violaceus* nymphs according to head capsule size groups.

Results

Physical and chemical variables

Water temperature showed the normal seasonal variation of the subtropical region, with high temperatures during the summer. The mean annual water temperature was 23 °C. Water levels peaked in the Upper Paraná River during March, when the water overran the banks. During this time, submerged vegetation began to decompose, oxygen concentration decreased, electrical conductivity increased, and pH decreased. Chlorophyll-a concentration decreased sharply, probably because of the strong current of the Paraná River entering the Baía River. This tendency was verified by analysis mid-channel sediments of the Baía River, where the proportion of mud decreased during the flood period (Figure 2).

Production

Over the period investigated the mean annual density of macrobenthic organisms was 478 ind m^{-2} $\pm$ 250 ($\bar{x}\pm$ SD) and that for *C. violaceus* was 283$\pm$256 (about 59% of the total macrobenthic abundance). The largest mayfly nymphs were found in July, August and September (Figures 3 and 4).

The results of linear regression analysis for interocular length (head capsula width) vs body length were significant ($P < 1\%$), and the following regression equation was estimated:

$$W = 0.011.\mathrm{e}^{2.773}.$$

The linear form of this equation is:

$$\ln W = -4.510 + 2.773H_{\mathrm{w}}.$$

The content of dry weight in wet weight of the species was 17.6%.

From October 1987 to September 1988, the biomass (B) of *C. violaceus* was estimated at 3.350 g dry weight m^{-2} y^{-1} and the secondary production (P) was 16.48 g dry weight m^{-2} y^{-1}. Thus the calculated turnover ratio (P:B ratio) for this species was 4.9 (Table 1).

Discussion

Values of secondary production may depend to a certain degree on the method of calculation. The earliest attempts to estimate production involved single-species populations with simple life histories. In these instances, a series of standing crop estimates were made throughout the life of a single cohort or generation. A variety of methods can be used to estimate secondary production for the entire macrobenthic community. Waters & Crawford (1973) calculated the annual production of the mayfly *Ephemerella subvaria* by four methods: the removal-summation

Table 1. Calculation of production of *Campsurus violaceus* by the Hynes-Coleman method

Head capsula size group (mm)	Sum/12	Weight exp	Biomass (gm^{-2})	Loss number	Loss biomass	Production (gm^2) yr^{-1}
0.0 – 0.2″	2	0.00006	0.00002	–51	0.00022	–0.1015
0.2 – 0.4″	53	0.00246	0.02293	–32	0.00147	–0.4238
0.4 – 0.6″	85	0.01426	0.21336	37	0.00525	1.74866
0.6 – 0.8″	48	0.04541	0.38363	15	0.01349	1.82078
0.8 – 1.0″	33	0.10785	0.62641	10	0.02843	2.55844
1.0 – 1.2″	23	0.21518	0.87106	4	0.05259	–1.8932
1.2 – 1.4″	27	0.38241	1.81719	20	0.08872	15.97
1.4 – 1.6″	7	0.6258	0.77099	7	0.05507	3.46945
	278		4.70559			23.1489

P:B = 4.92

method, the instantaneous growth method, the Allen curve, and the Hynes-Coleman method. The most obvious generalization that emerged from comparison of the results is that production estimates from the removal-summation, instantaneous growth, and Allen curve methods generally agree, while estimates using the Hynes-Coleman method are 20% higher. In spite of this conclusion, the majority of workers have used the Hynes-Coleman method to calculate secondary production of many macrobenthic groups, including mayflies. This procedure has the advantage of allowing comparisons of results from lotic and lentic ecosystems.

Secondary production in the Baía River is among the highest ever reported from lotic habitats in north temperate and subtropical and tropical regions. But it should be emphasized that the Baía River is a semi-lotic environment. Secondary production estimated for the population of *C. violaceus* in a more typical lentic habitat in a tropical region reached 46.15 g dry w m^{-2} y^{-1} (Lake Valencia, Cressa, 1986), approximately 2 times higher than in the Baía River.

Melo et al. (1993) suggested in the Baía River, *C. violaceus* is bivoltine and may emerge during winter, early spring, and summer. But our data did not allow a conclusive answer because we did not record flight period of adult ephemerids, it concluded that the species is univoltine.

The Baía River is a lentic water body during most of the year, with low current speeds. During flood periods, it is invaded by the Paraná River, when it becomes a lotic environment. The majority of abiotic variables of the Baía River were influenced by the hydrological regime of the Paraná River.

The life cycle of *C. violaceus* in the Baía River is probably adapted to this periodic inundation by the River Paraná, because most of the nymphs are small and move from mid-channel to near the bank during flood months (Melo et al., 1993). These authors concluded that this migratory pattern enables, the nymphs to avoid adverse conditions in the river during the flood pulse.

It is important to note that both stagnant conditions and abrasive flooding act as stressors, depressing productivity. During regular moderate floods, riverine waters overspill the banks, inundating plant detritus accumulated on the floodplain during the dry season. The ensuing release of nutrients and consequent rapid development of plants and plankton provides a rich food resource for both benthos and fish (Ward, 1989; Agostinho & Zalewski, 1996).

Turnover ratio

The ratio of production to mean biomass (turnover ratio or P:B) over a period of time approximates the mean growth rate, and the annual P:B is often used for comparison within or between groups of organisms or ecosystems (Waters, 1969). Growth rates for many macroinvertebrate groups increase with increasing temperature, thus annual P:B ratios and production might be expected to increase from polar to tropical regions (Benke et al., 1984). For ephmeropterans and dipterans in rivers where mean annual water temperature reaches about 20 °C, turnover ratios are about 100 (southern USA, Benke & Jacobi, 1986). Waters (1977) listed many empirical values which generally indicated much lower annual P:B ratios from northern

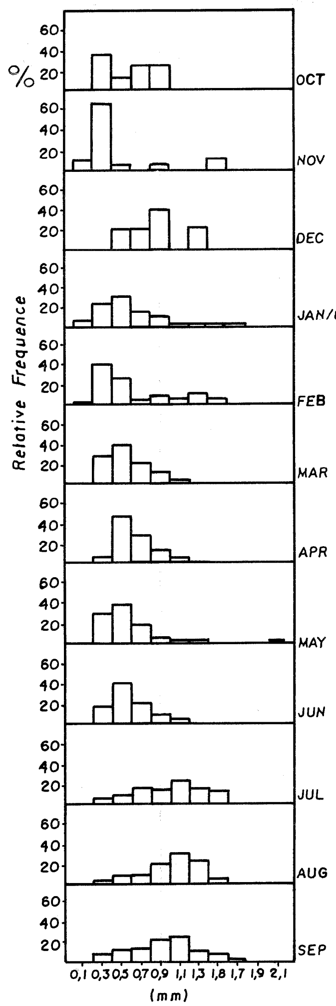

Figure 4. Frequency distribution of nymphs head capsule size (%) of *Campsurus violaceus* in the Baía River (Melo et al., 1993).

latitudes (lower than 10). Other investigations from the temperate zone confirmed this suggestion (MacFarlane & Waters, 1982; Krueger & Waters, 1983; Mortensen & Simonsen, 1983). However Gaines et al. (1992) estimated P:B ratio for mayflies in three cold streams of 31.5 (for 6 generations of *Baetis* sp.) and 45.0 (9 generations of *Tricorythodes* sp.) Grubaugh and Wallace (1993) estimated low P:B (5.0–12.3) ratios for some ephemeropteran species from a Piedmont rivers in spite of high mean annual water temperature (21–27 °C in summer and 4–14 °C in winter). Dudgeon (1996) reported low turnover ratios (above 7) for two species of Ephemeridae in a tropical forest stream in Hong Kong. Also, Benke et al. (1984) and Smock et al. (1985) observed the turnover ratio for some ephemeropteran species to be slightly above 10 in rivers with rather high mean annual water temperature. For *C. violaceus* in the Baía River, a low P:B ratio was calculated (4.9).

According to Benke & Jacobi (1994), secondary production analysis provides a means to assess resource overlap among closely related coexisting species and represents a linkage from population dynamics to ecosystem-level processes. The present investigation is the first on secondary production of invertebrates of the Paraná River floodplain and provides basic knowledge of invertebrate ecology in this region.

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