Population dynamics and secondary production of *Chaoborus brasiliensis* (Diptera, Chaoboridae) in a small tropical reservoir: Lagoa do Nado, Belo Horizonte, Minas Gerais – Brazil.

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ABSTRACT: Population dynamics and secondary production of *Chaoborus brasiliensis* (Diptera, Chaoboridae) in a small tropical reservoir: Lagoa do Nado, Belo Horizonte, Minas Gerais – Brazil. The temporal dynamics and production of *Chaoborus brasiliensis* were investigated in a small tropical reservoir, Lagoa do Nado, located in Belo Horizonte, State of Minas Gerais, Brazil, during a seasonal cycle. The first and second instar larvae were found throughout the annual cycle possibly suggesting a continuous reproduction of this species in the reservoir. Total density amounted up to 35,860 individuals.m^{-2}, being the highest figures recorded during the dry season (April-May). The density of pupae ranged between 0 and 1,100 ind.m^{-2}. The complete larval cycle was estimated in 50 days. The total biomass of *C. brasiliensis* larvae oscillated between 2.6 and 2,460 mgDW.m^{-2} and the production ranged between 0.24 and 297.2 mgDW.m^{-2}.day^{-1}. The fourth instar larvae always made the bulk of larval biomass in the water column.
Key-words: *Chaoborus*, population dynamics, larval cycle, secondary production.

RESUMO: Dinâmica populacional e produção secundária de *Chaoborus brasiliensis* (Diptera, Chaoboridae) em um reservatório tropical raso: Lagoa do Nado, Belo Horizonte, MG – Brasil. A dinâmica populacional e produção secundária de *Chaoborus brasiliensis* foram estudados em um reservatório urbano raso, a Lagoa do Nado, Belo Horizonte, Estado de Minas Gerais, Brasil, durante um ciclo sazonal completo. Larvas de estádio I e II foram encontradas durante todo o ano, indicando a reprodução contínua da espécie no reservatório. A densidade total dos estádios na coluna d'água foi elevada, variando de 525 a 35860 ind.m^{-2}, com as maiores densidades concentradas durante o início da estação seca (abril – maio). A densidade da pupa variou de 0 a 1100 ind.m^{-2}. O ciclo larval completo no reservatório foi estimado em 50 dias. A biomassa total das larvas de *C. brasiliensis* na coluna d'água variou de 0,0026 a 2,46 gPSm^{-2}, e a produção secundária de 0,24 a 297,17 mgPS m^{-2}.dia^{-1}, com as larvas de estádio IV contribuindo com uma alta percentagem destes valores.
Palavras-chave: *Chaoborus*, dinâmica populacional, ciclo larval, produção secundária.

Introduction

The dipteran *Chaoborus* has a cosmopolitan distribution and is found both in tropical and high latitude temperate regions (Halat & Lehman, 1996). In its development shows four typical instars of the life cycle of a holometabolous insect: egg, larva, pupa and adult. The larval instar consists of four discrete instars with 1st and 2nd instar larvae entirely planktonic and 3rd and 4th instar larvae exhibiting a daily vertical migration between the water and sediment (Roth, 1968; Xie et al., 1998). The body of larvae is relatively transparent except for its hydrostatic organs, hence the common name "phantom midge"(Soranno et al., 1993).

Chaoborus larvae have been considered an important component in the planktonic trophic web. They feed from phyto and zooplankton and they can regulate the abundance and even the presence of their preys (Hanazato & Yasuno, 1989, Yan et al., 1991). In addition, they constitute a significant item in the diet of several fish species (Arcifa, 1997).

Several studies performed in tropical lakes and reservoirs have stressed the importance of *Chaoborus* for the zooplanktonic community. This importance is due, mainly, to the continuous reproduction exhibited by this dipteran in such environments (McGowan, 1974, Lewis, 1979, Cressa & Lewis, 1986), and also the relative absence of invertebrate pelagic predators in the tropics, such as cladocerans belonging to the Polyphemidae and Leptodoridae families (Fernando et al., 1990).

In Brazil, some studies on *Chaoborus* have evaluated the larval density in the sediment (Strixino & Strixino, 1980, Fukuhara et al., 1985) and temporal variation of this species in the water (Arcifa, 1997) and in sediment (Reiss, 1977); the migratory behavior (Fukuhara et al., 1993, Arcifa, 1997); determination of feeding habits of larval instars (Arcifa, 2000) and the emergence pattern of adults (Fukuhara, 1989, Fukuhara et al., 1992).

The present work has the main objective to contribute for the knowledge of the biology of the dipteran *Chaoborus* in Brazilian water bodies, addressing aspects not described in detail hitherto, such as biometric characteristics, aspects of larval cycle, population dynamics and larva secondary production in a small artificial reservoir of Minas Gerais State, the Lagoa do Nado.

Study area

The Lagoa do Nado (19° 49'56"S; 43° 57'34"W) is a meso-eutrophic urban reservoir located in Belo Horizonte, Minas Gerais, in Southeastern Brazil (Fig. 1). The superficial area of the lake is 1.5 ha; mean and maximum depths are 2.7 and 7.6 meters,

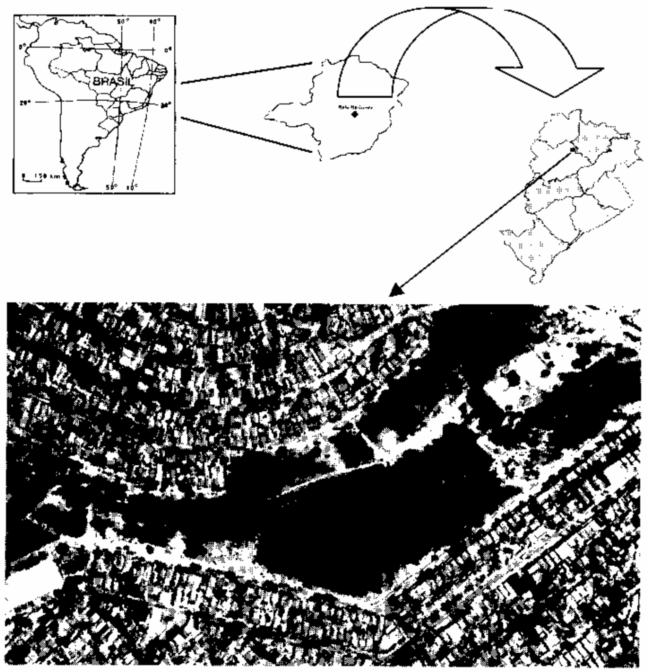

Figure 1: Location and aerial photograph showing to the center the Lagoa do Nado (Source: PRODABEL S/A).

respectively. The reservoir, situated in the center of a small valley surrounded by tall trees, develops a stable thermal stratification from August to May, showing only a period of circulation during the year (June-July). The epilimnion is well oxygenated, with development of intense anoxia in the hypolimnion during the stratification period (Bezerra-Neto & Pinto-Coelho, 2001).

The zooplanktonic community is dominated by, among crustaceans, the cyclopoid copepod *Thermocyclops minutus*, the cladoceran *Moina micrura* and, among other rotifers, *Brachionus falcatus*, *B. angularis*, *B. caudatus*, *Keratella cochlearis*, *K. tropica* and *Kellicottia bostoniensis* (Bezerra-Neto, 2001).

The climate of the region is classified as tropical B-2, with a moderate hydric deficit (Ferreira, 1992). The lowest temperatures are recorded between May and July. The rainy season occurs in the hottest months, i.e. November to March. Annual precipitation during the period of study was 1,270 mm (Pampulha Airport Meteorological Station).

Material and Methods

Chaoborus larvae and pupae were collected biweekly, from October 1999 to September 2000, in the central region of the reservoir (depth=6.5 m). Preliminary sampling has shown that *Chaoborus* larvae were present in the sediment during the day and absent at night. Thus, the sampling effort was restricted to during the night period. Samples were taken at each meter of the water column between 10 and 11 p.m. using a Schindler-Patalas trap of 17 L equipped with a 60 µm mesh net. Organisms were preserved in the field using a 4% sucrose/formalin solution.

Chaoborus larvae were identified according to Lane (1942) and Saether (1976). All larvae and pupae collected were counted. In order to determine the intervals of each size-class, the head length (from the antenna insertion point to the opposite end of the head) and total length (including the anal papilla) were measured. For pupae, only total length measures were taken. Measurements were done using a stereomicroscope equipped with a Sony- CCD video camera, connected to image analysis software (*Scion Image* – Scion Corporation).

Larvae dry weight was estimated through the equations obtained for *Chaoborus brasiliensis* (Cressa & Lewis, 1984), which relate head length to biomass of each instar:

$W = 2,6302\ .10^{-3}\ L^{1.28}$ (1st instar)

$W = 3,3884\ .\ 10^{-5}\ L^{2.07}$ (2nd instar)

$W = 0,3802\ L^{0.64}$ (3rd instar)

$W = 5,1286\ .\ 10^{-11}\ L^{4.29}$ (4th instar)

Where W is dry weight (µg) and L is head length (µm).

The secondary production of each developmental stage was computed separately according to the method of mass increment described by Edmondson & Winberg (1971):

$$P_i = \frac{N_i \cdot \Delta W_i}{D_i}$$

Where, P_i is production of stage i, N_i is density of stage i, ΔW_i is the change in weight over stage i and D_i is development time for stage i. D_i values were obtained from the cohort analysis (Lewis, 1979). For that, average development time values for each instar were considered. To obtain population production (P), P_i values were summed. The ratio P/B ("turnover rate") was also calculated for *Chaoborus* population from Lagoa do Nado.

Data about oxygen concentration in the epilimnion and hypolimnion were taken from Bezerra-Neto & Pinto-Coelho (2001) and were determined through vertical profiles with 50 cm intervals, in the central region of the reservoir, utilizing a YSI model 55 oxymeter/ thermistor. Data on zooplankton density were from Bezerra-Neto (2001) and were determined from samples fixed with formaldehyde/sucrose solution, collected from the same depths and sampling periods (1999 – 2000).

Results and Discussion

Taxonomy and biometrical characteristics

During the study period, only one Chaoboridae species was found: *Chaoborus (Sayomia) brasiliensis* (Theobald, 1901). This is a small species (maximum size found at Lagoa do Nado, 0.86 mm) when compared to the majority of the species of this genus from temperate regions (Cressa & Lewis, 1984). The geographic distribution of *C. brasiliensis* extends throughout the whole South and Central America, from Panama to Argentina (Lane, 1942).

The relationship between body size and head length of the larval instars of *C. brasiliensis* is shown in Figure 2. While body length distribution shows a certain degree of overlapping between the successive larval instars, head length allowed an accurate determination of larval instar, in accordance with several studies about *Chaoborus* morphology (Fedorenko & Swift, 1972; Hare & Carter, 1986; López & Cressa, 1996; Voss & Mumm, 1999).

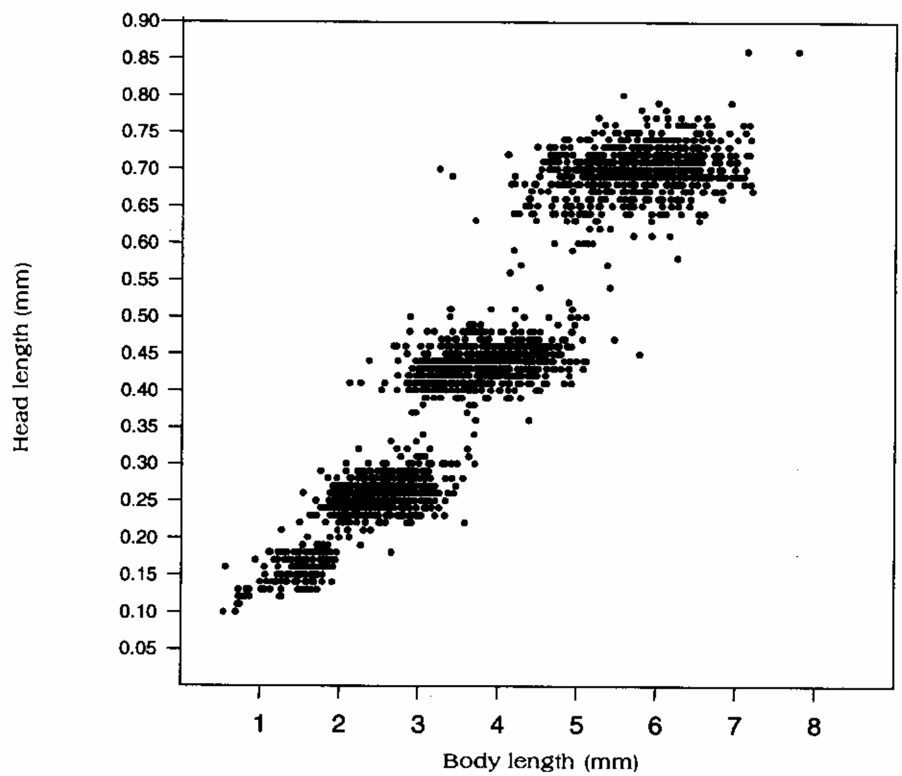

Figure 2: Interrelationship between body length and head length in *Chaoborus brasiliensis* larvae population of Lagoa do Nado (n=2121).

Mean, standard deviation (SD) and coefficient of variation (CV) of total body length and head length of *C. brasiliensis* population are summarized in Tab.I.

Table I: Intervals, mean, standard deviation and coefficient of variation of body length and head length of *Chaoborus brasiliensis* population, Lagoa do Nado.

Body length (µm)

Instar	n	Intervals	Mean	Standard deviation	C V (%)
1st	186	540 – 2,660	1,500	345	23
2nd	563	1,500 – 3,710	2,527	411	16
3rd	647	2,120 – 5,780	3,830	554	14
4th	724	3,250 – 7,780	5,730	686	12
Pupa female	32	3,840 – 4,340	4,040	15	3,7
Pupa male	28	3,430 – 3,790	3,640	12	3,2

Head length (µm)

Instar	n	Intervals	Mean	Standard deviation	C V (%)
1st	186	100 – 210	159	23	12
2nd	563	220 – 360	259	22	8
3rd	647	370 – 540	437	25	7
4th	724	560 – 860	697	35	4

Coefficient of variation values (SD/average x 100%) of head length between instars are low when compared to CV values for total body length. Mean body and head length values are similar to the ones registered for the same species in Lake Valencia, Venezuela (Cressa & Lewis, 1984). However, the coefficients of variation of head length were exceptionally low in the populations of *C. brasiliensis* in Lagoa do Nado. As reported by Cressa & Lewis (1984), a sexual dimorphism between pupae was detected, with females showing a larger body size than that of males.

Population Dynamics

Total larvae density of *Chaoborus* varied from 525 to 35,860 ind.m^{-2} with an average density of 8,436 ind. m^{-2}. Seasonal changes in density of the instars of *C. brasiliensis* are shown in Figure 3. In the average, the relative density of *C. brasiliensis* population larvae from 1st, 2nd and 3rd instars comprised 7, 14 and 27% of total density of this diptera, respectively, and the 4th instar larvae accomplished for 50% of the population. Voss & Mumm (1999), studying the composition of *Chaoborus flavicans* population in Lake Plußsee, Northern Germany, found the same pattern, i. e., the initial instars always exhibited lower densities than the final instars, during practically the whole period of study. Those authors related a series of factors that could account for this pattern: *(1)* abundance could decrease from one instar to another due to mortality; *(2)* existence of a populational "bottleneck" in the initial instars, due to the high energetic demand, as reported by Neill & Peacok (1980) and *(3)* the rapid larval development time in the initial instars.

The pupae density varied from 0 to 1,100 ind.m^{-2} and their appearance during the studied period was irregular, with a low representation in the sampled population (2%), similar to others tropical water bodies (Lewis, 1979; López & Cressa, 1996).

A comparison of the maximum density of *Chaoborus* in other lakes and reservoirs varying trophy degrees is shown in Tab.II. The density of *Chaoborus* population in Lagoa do Nado was high even when compared to eutrophic environments. The higher density of *Chaoborus* in eutrophic water bodies is due to the fact that eutrophication is usually associated to increases in zooplankton biomass, which guarantees abundant food source for *Chaoborus* (Xie et al., 1998). Another important factor is the development of oxygen deficit in the hypolimnion, which is common in eutrophic environments, favoring colonization of dense *Chaoborus* populations (Brylinsk, 1980). *Chaoborus* larvae can resist to anaerobic conditions for longer periods and can utilize the anoxic hypolimnion as a refuge against predators (LaRow, 1970; Rahel & Nutzman, 1994).

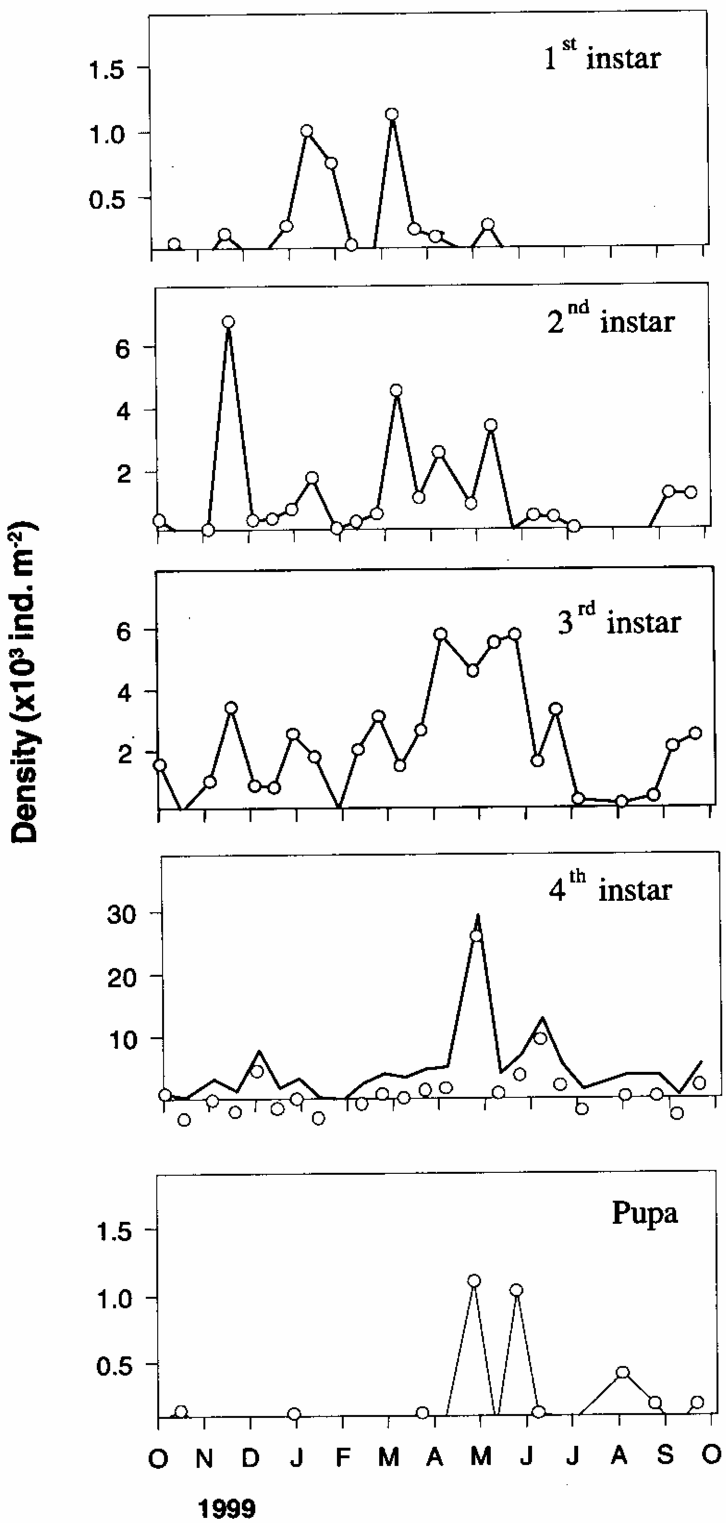

Figure 3: Temporal changes of the population density of *Chaoborus brasiliensis* in Lagoa do Nado throughout 1999 and 2000. Note the difference of scale between graphs.

Table II: Maximum density of *Chaoborus brasiliensis* larvae in the water column in lakes and reservoirs of different trophic levels.

Lake / Reservoir	Trophic state	Maximum density (ind m⁻²)	Author
Eunice (Canada)	Oligotrophic	1,100	Fedorenko, 1975
McCauley (Canada)	Oligotrophic	4,750	Wood, 1956
Dom Helvécio (Brazil)	Oligotrophic	2,130	Fukuhara et al., 1985
Jacaré (Brazil)	Oligotrophic	1,460	Fukuhara et al., 1985
Socuy (Venezuela)	mesotrophic	24,220	López & Cressa, 1996
L. do Nado (Brazil)	Meso-eutrophic	35,860	This study
Mikolajskie (Poland)	Eutrophic	14,700	Kajak & Rybak, 1979
Wintergreen (U.S.A.)	Eutrophic	33,500	Threlkeld, 1979
NIES (Japan)	Eutrophic	23,680	Xie et al., 1998
Frans (U.S.A.)	Eutrophic	8,000	Roth, 1968

Food source and refuge against predators seem to be important factors in the control of seasonal fluctuation of *C. brasiliensis* in Lagoa do Nado. During periods of high density of zooplankton, there was a high oxygen deficit in the hypolimnion, close to complete anoxia. At that time, *Chaoborus* population also exhibited high densities, especially during the Spring, 1999 and Fall, 2000 (Fig. 4). Nonetheless,

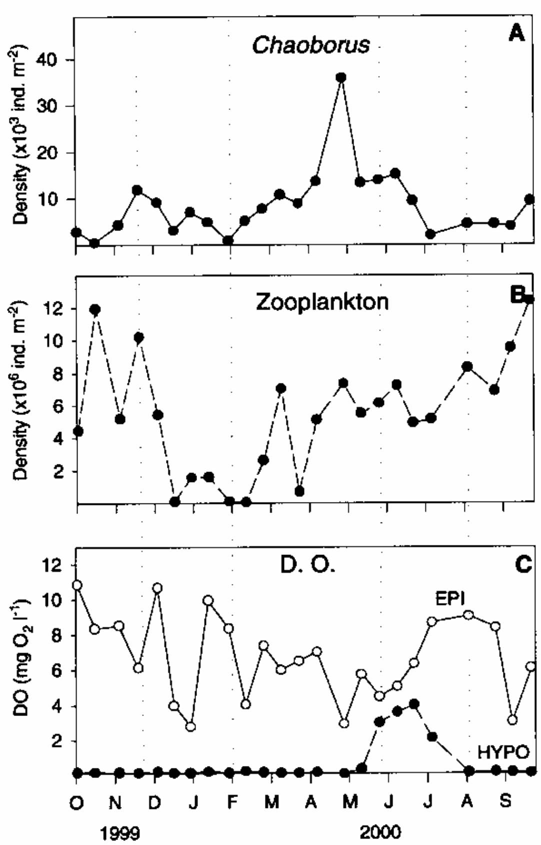

Figure 4: Seasonal variation of *Chaoborus brasiliensis* density (A); total zooplankton density (B), and dissolved oxygen concentration in the epilimnion (EPI) and hypolimnion (HYPO) (C), in Lagoa do Nado throughout 1999 and 2000. Dotted lines stress periods of abundance decrease of *C. brasiliensis*.

population density started to decline in two periods: *(1)* during the rainy season (Summer, from December, 1999 to February, 2000) and *(2)* during the reservoir circulation period, in the middle of the dry Winter (June and July, 2000), when there was an increase in the oxygen concentration in the hypolimnion. In these episodes of decline of the *Chaoborus* total population, it could be observed that the larval instars were differentially affected in each particular period.

The zooplankton exhibited high densities during the months of October and November 1999 (end of the dry season) and again, between the months of August to September 2000 (dry season). During these periods, the *Chaoborus* larvae densities were, in general, under 10×10^3 ind.m^{-2}. In the rainy season, the drastic decrease in the density of zooplanktonic populations, probably caused by wash out (Bezerra-Neto, 2001), coincided with decrease of larval densities of 3rd and 4th instars, whose diet consisted basically of zooplankton (Moore *et al.*, 1994). In contrast, 1st and 2nd instar larvae, especially the former, whose diet are constituted basically of phytoplankton (Arcifa, 2000), exhibited peaks of density in that period (Fig. 3).

During the reservoir circulation in winter period, the 1st and 2nd instar larvae were the most affected by the reduction of anoxic refuge and virtually disappeared from the water column, while the 3rd and 4th instar larvae (although also present in low densities) could still be observed (Fig. 3). We suggest the hypothesis that during this period *Chaoborus* larvae would be more exposed to predation by fish in practically the whole water column, and were thus obliged to protect themselves in the sediment or close to it during the day.

Since initial instars larvae are completely planktonic they would not be able to explore sediments or the water-sediment interface. This inability to be inert in the sediments is associated to the high energetic demand in the initial instars (Cressa & Lewis, 1984). On the other hand, 3rd and 4th instars larvae have the ability to bury themselves in the sediments during the day, hiding from predators. They also have lower energetic demand when compared to 1st and 2nd instar larvae (Cressa & Lewis, opt. cit.). They need to ingest only 2.8 to 6.6% of their own weight daily (Lewis, 1977) and can stand over 35 days without food (Moore, 1986).

The connection between physical and chemical characteristics of the environment and *Chaoborus* abundance can also be illustrated in the studies performed at Lake Valencia, Venezuela. In this lake, the *Chaoborus brasiliensis* population (the only species present) exerted an intense predation pressure over herbivores during the stratification period, showing low densities during the dry season, which coincided with the circulation period. During the stratification period, anoxia in the hypolimnion warranted *Chaoborus* population a refuge against predation by fish, which, on the other hand, allowed the larvae become very abundant and suppress the herbivorous production (Saunders & Lewis, 1988).

Larval cycle

C. brasiliensis reproduction in Lagoa do Nado is continuous with all instars found throughout the year. In other tropical water bodies such as Lake Lanao (Lewis, 1979), Lake Valencia (Cressa & Lewis, 1984) and Lake Monte Alegre (Arcifa, 1997), among others, an identical pattern has been observed. First to 4th instar larvae have shown 5-6 density peaks (Fig. 3), suggesting the occurrence of 5-6 generations during the year. From the cohort analysis, the average development time of 1st instar was estimated in 7.3 days and for the 2nd instar, 9.3 days. In the case of 3rd and 4th instars the average development time was estimated in 12.9 and 16.6 days, respectively. From the studies of Cressa & Lewis (1984), which suggested 2 days for pupa development, and 2 days for the time between egg laying and hatching, the *C. brasiliensis* larval cycle in the reservoir from egg to adult emergence can be estimated to be approximately 50 days. These values are very close to those that have been estimated for the larval cycle of a *C. brasiliensis* population in Lake Valencia, 43 days (Cressa & Lewis, 1986) and for *Chaoborus sp.* in the Socuy reservoir, 48 days (López & Cressa, 1996), both in Venezuela. However, Hare & Carter (1986) have estimated in 30 to 60 days the generation period for *C. edulis*, *C. anomalus* and *C. ceratopogones* at Lake Opi, in Nigeria.

Biomass and Secondary Production

The seasonal variation of the biomass of the *C. brasiliensis* instars obtained for Lagoa do Nado are shown in Figure 5. The larval biomass of 1st, 2nd, 3rd and 4th instars in the water column varied from 0 to 1.72 mgPS.m^{-2}, 0 - 23.47 mgPS.m^{-2}, 0 - 109.55 mgPS.m^{-2} and 0 - 2,369 mgPS.m^{-2}, respectively. The total larval biomass in the water column was higher during the Fall, April to June, 2000 (956 mgPS.m^{-2}) than in the Summer, December to March, 2000 (216.4 mgPS.m^{-2}) and in the Winter, 2000, July to September, 2000 (288.49 mgPS.m^{-2}). During the whole study period, 4th instar larvae contributed, on average, with about 89% of the total sampled biomass.

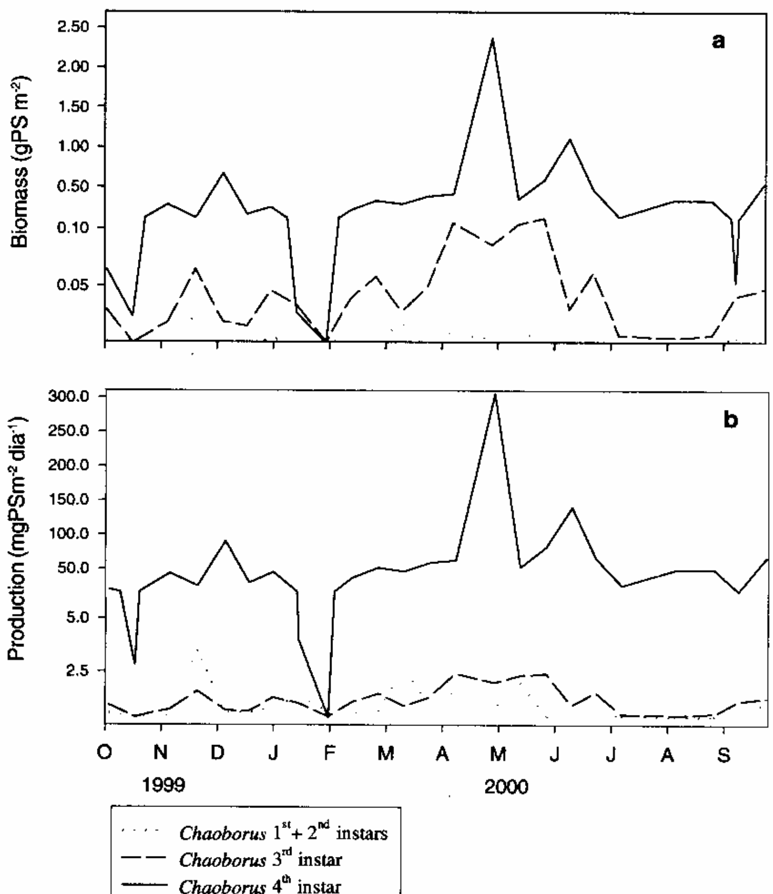

Figure 5: Seasonal variation of: (a) Biomass (gPS. m^{-2}) and (b) Production (mgPS m^{-2}.dia^{-1}) of different instar larvae of *Chaoborus brasiliensis*, Lagoa do Nado, throughout 1999 and 2000.

The annual production of *C. brasiliensis* was highly differentiated according to the development stage (Tab. III). The values for each instar are: 0.04 mgPS.m^{-2}.day^{-1} (1st instar), 0.53 mg.PS.m^{-2}.day^{-1} (2nd instar), 0.79 mg.PS.m^{-2}.day^{-1} (3rd instar) and 47.48 mg.PS.m^{-2}.day^{-1} (4th instar). Thus, the oldest larvae contributed to the highest percentage of the total production (97%). The average production and biomass values found in the present study are within the variation interval observed in other tropical environments (Lewis, 1979; López & Cressa, 1996).

Table III: Mean of biomass, annual production and P/B rate of *Chaoborus brasiliensis* in the Lagoa do Nado, for the period October, 1999 through September, 2000.

Instar	Biomass (mgPS m⁻²)	Secondary Production (mgPS m⁻² dia⁻¹)	P/B
1st	0,32	0,04	0,13
2nd	3,91	0,53	0,14
3rd	41,78	0,79	0,02
4th	395,35	47,48	0,12
Total	441,36	48,84	0,11

Table III also brings P/B ratio of the *C. brasiliensis* population from Lagoa do Nado. This P/B ratio represents the production rate per biomass unit and can be utilized as an index for the flow rate, relative to biomass (Brylinsk, 1980). The P/B ratio is an index widely utilized and it is reciprocal to the renovation time of a species. The average renovation time found for the *Chaoborus* population of Lagoa do Nado (9 days or 0.11.day^{-1}) was similar to the values shown by Lewis (1979) for a *Chaoborus* population at Lake Lanao. However, López & Cressa (1996) found a daily average P/B ratio of 0.06 for *Chaoborus sp.* in the Socuy reservoir, representing an average renovation of 15.92 days.

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