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Diel vertical migration of zooplankton in a permanently stratified small tropical reservoir (Tierra Blanca, Venezuela)

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Introduction

According to Hutchinson (1967), the daily movement of zooplankton is a very widespread phenomenon. Daily (diel) vertical migration (DVM) is responsible for short-term changes in the vertical distribution of zooplankton (Zadereev & Tolomeyev 2007). Both marine and freshwater zooplankton exhibit a daily migration behavior (Lampert & Sommer 1997) that could confer some selective advantages (Infante 1988), such as more efficient utilization of resources or the avoidance of predation (Gliwicz 1986). The most common DVM pattern involves an upward migration from deeper waters at dusk, resulting in a population maximum in relatively shallow water at night, followed by sinking to deeper water at dawn. Deviations from this pattern include "reverse" DVM, with a single surface maximum during the day, and "twilight" DVM in which surface maxima occur both at dawn and dusk (Hutchinson 1967, Barbiero et al. 2003).

There are few studies of freshwater zooplankton vertical migration in the South American tropics, most of them in Brazilian (Arcifa 1978, Matsumura-Tundisi et al. 1984, Arcifa 1997, Perticarrari et al. 2004), Venezuelan (Infante 1978, Coraspe 1985, López & Zoppi de Roa 2005), and Bolivian (Rejas et al. 2007) lakes and/or reservoirs. We followed the daily vertical migration of the main zooplankton groups in a permanently stratified small reservoir (Tierra Blanca) in north-central Venezuela.

Key words: tropical reservoir, Venezuela, vertical migration, zooplankton.

Study area

Tierra Blanca is an oligo-mesotrophic reservoir, located in north-central Venezuela (9°58'N; 67°25'W; González 2006). It has a surface area of 4×10^5 m^2, a volume of 5×10^6 m^3, a mean depth of 12.5 m, a discharge of 0.40 m^3 sec^{-1}, and a residence time of 144 d.

González (2006), found the reservoir to be permanently stratified, with a well-defined and stable thermocline from 4–12 m of depth. Surface temperatures were always above 27 °C; temperature differences between the epilimnion and the hypolimnion ranged from 2.8 to 5.3 °C. High oxygen concentrations (>7 mg L^{-1}) were always found in the epilimnion, with a rapid decrease downward; hypoxic/anoxic conditions prevailed below 10-m of depth. Mean water transparency was 4.6 m, while specific conductance was around 270 µS cm^{-1}. Chlorophyll-*a* ranged between 2.8 and 37.3 µg L^{-1}. Phytoplankton abundance varied between 1.1 x 10^6 and 29.7 x 10^6 cells L^{-1}, and the community was dominated by green algae and diatoms throughout the year. Zooplankton abundance ranged between 92 and 226 individuals L^{-1}, with a mean value of 148 individuals L^{-1}.

Material and methods

Zooplankton DVM was followed in Tierra Blanca reservoir during a new moon phase on 8–9 December 2004. Samples were collected in the limnetic zone at selected depths (0, 2, 4, 6, 8, 10, 15, and 20 m) at 1000, 1200, 1500, 1800, 2100, 2400, 0300, and 0600 hrs with a Schindler-Patalas trap (30 L). Specimens were preserved in formaldehyde 4% (final concentration) and counted in a Sedgwick-Rafter chamber (1 mL), to determine abundance (Wetzel & Likens 2000). A Chi-square test was performed to search for significant differences between day and night distributions of the studied groups (Siegel 1988). In the case of *Chaoborus*, due to its low numbers, we performed the Spearman nonparametric correlation (r_s) (Siegel 1988) instead of the Chi-square test.

Results and discussion

The community was dominated by rotifers (49.2%), cyclopoid copepods (mainly *Thermocyclops decipiens*, 34.0%), cladocerans (mainly *Ceriodaphnia cornuta*, 9.2%), ostracods (6.8%), and other groups (*Chaoborus* and Hydracarina, 0.8%).

Vertical zooplankton distributions at noon and at midnight show that except for *Chaoborus*, most of the zoo-

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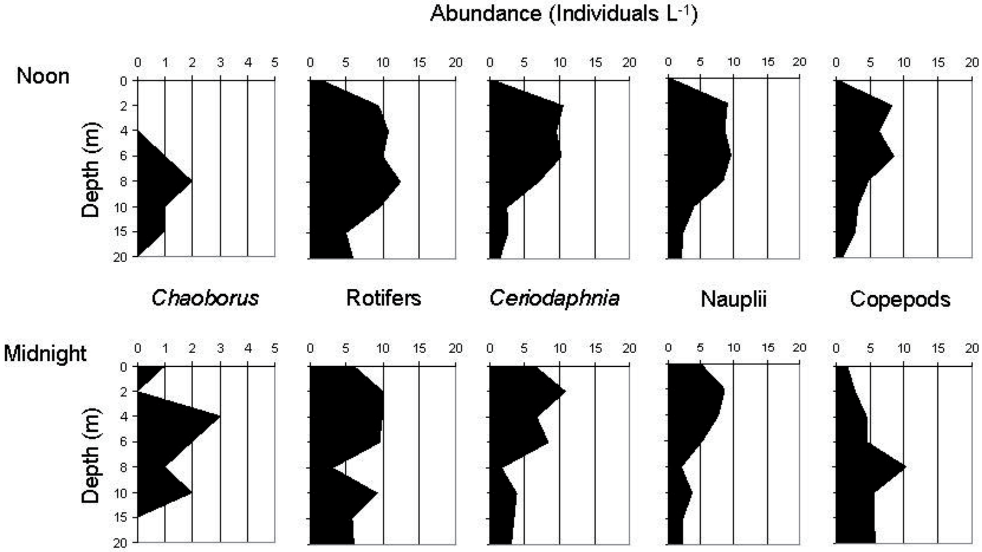

Fig. 1. Vertical distributions of *Chaoborus*, rotifers, *Ceriodaphnia cornuta*, nauplii and adult copepods at noon and midnight in Tierra Blanca reservoir.

plankton specimens were concentrated in the oxygenated layers (0–10 m of depth), above the hypoxic/anoxic hypolimnion; therefore, oxygen concentration seems to be an important regulator of the zooplankton spatial distribution in the reservoir (INFANTE 1988, WETZEL 2001). The same was noted by INFANTE (1978) in the eutrophic Lake Valencia (Venezuela) and by PERTICARRARI et al. (2004) in the eutrophic Monte Alegre reservoir (Brazil).

No significant ($p < 0.05$) vertical migration was detected for nauplii, rotifers or cladocerans (*Ceriodaphnia cornuta*). Nauplii and rotifers would be not affected by vertebrate or invertebrate predation due to their small size and negative predator electivity, as noted by LÓPEZ & ZOPPI DE ROA (2005) in Socuy Reservoir (Venezuela). Cladocerans were scarce in the reservoir, however, and this could have reduced the encounter probability with the predatory *Chaoborus*. Thus, the lack of an intense predation on this population could explain the absence of significant vertical movements of nauplii, rotifers, and cladocerans (PERTICARRARI et al. 2004).

No *Chaoborus* larvae were found in the upper layers during the daytime. This phantom midge was able to remain in the deeper and low oxygenated layers, even below 10 m, until sunset, when it began to migrate to the epilimnion, where its density reached up to 5 individuals L^{-1} at 2100 hrs, accounting for up to 75% of its population above 6 m of depth (Fig. 2). We found negative correlations between day and night distributions, although the only significant value was found between 1500 and 2100 hrs ($r_s = -0.77$; $p < 0.05$), indicating opposite distributions. Thus, *Chaoborus* larvae showed the typical vertical migration, with upward population displacement during the night and downward movement during the daytime, which was also observed in other tropical reservoirs by ARCIFA (1997) and LÓPEZ & ZOPPI DE ROA (2005). This pattern is common in *Chaoborus*, even in fishless lakes and ponds (LAMPERT 1993), although its amplitude is greater under fish predation.

Adult copepods apparently preferred the upper strata during the day and deeper layers during the night (maximal density of 48 individuals L^{-1} at 8 m of depth at 0300 hrs (not shown in the figures), which constitutes an example of reverse migration. A significant difference between day and night distributions was found ($\chi^2 = 14.28$; $p < 0.05$). These data seem to contradict the predation-avoidance hypothesis (LAMPERT 1993). However, this be-

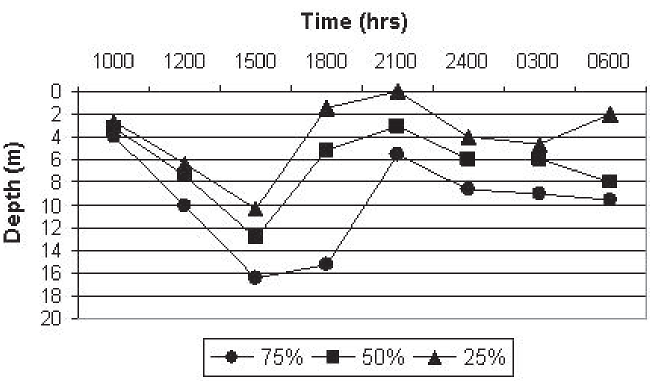

Fig. 2. Daily variation for the 25, 50, and 75% distributions of *Chaoborus* population in Tierra Blanca reservoir.

havior could be explained if zooplankton are not as affected by fish predation (visual predators) and migrate in a reversed pattern to escape predation by larger invertebrate predators that perform normal DVM, such as *Chaoborus* (Lampert 1993). The same pattern was detected in Lake Monte Alegre, when predation pressure of *Chaoborus* on copepods increased after the virtual disappearance of their main cladoceran prey (Perticarrari et al. 2004). This could also be the case in Tierra Blanca reservoir, where cladocerans are in lower abundance than copepods.

We can conclude that, in Tierra Blanca reservoir, only copepods and *Chaoborus* showed significant vertical displacements during the 24-h cycle. Copepod migration to deep layers during the night could be explained as an escape strategy from invertebrate predators such as *Chaoborus*, while *Chaoborus* remains in the hypolimnion during the daytime to evade vertebrate predators (fishes) and migrates to the upper layers at night to feed.

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