

The role of predation in the diel vertical migration of zooplankton in two tropical freshwater ecosystems

O papel da predação na migração vertical diária do zooplâncton em dois ecossistemas de água doce tropicais

Bezerra-Neto, JF.¹, Mello, NAST.², Maia-Barbosa, PM.³ and Pinto-Coelho, RM.¹

¹Laboratório de Gestão Ambiental de Reservatórios, Departamento de Biologia Geral – ICB, Universidade Federal de Minas Gerais – UFMG, CP 486, CEP 31270-901, Belo Horizonte, MG, Brazil
e-mail: josenet@icb.ufmg.br, rmpc@icb.ufmg.br

²Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre – ICB, Universidade Federal de Minas Gerais – UFMG, Belo Horizonte, MG, Brazil
e-mail: nelsonmellobio@yahoo.com.br

³Laboratório de Ecologia do Zooplâncton, Departamento de Biologia Geral – ICB, Universidade Federal de Minas Gerais – UFMG, CP 486, CEP 31270-901, Belo Horizonte, MG, Brazil
e-mail: maia@icb.ufmg.br

Abstract: Aim: This study aimed to examine and compare the different patterns of diel vertical migration (DVM) in two tropical freshwater ecosystems: Carioca Lake (PERD, MG), dominated by piscivorous fishes and Nado reservoir (Belo Horizonte, MG), dominated by planktivorous/omnivorous fishes. **Methods:** The vertical distribution of the zooplankton was examined at noon and midnight, in April 2003 in both systems, using a Schindler-Patalas trap. **Results:** In Nado reservoir, the larvae of the invertebrate predator *Chaoborus*, remained in the hypolimnion during the day and ascended into the surface waters at night. The same migratory behavior was observed for the population of the copepod *Thermocyclops inversus*, the dominant zooplankton, as well as for the rotifers. In Carioca Lake, the *Chaoborus* larvae did not migrate, and individuals were found occupying the entire water column in daytime as well as at night. The population of the copepod *T. minutus*, a potential prey of *Chaoborus* larvae, and most rotifers also did not migrate in Carioca Lake. **Conclusions:** In Nado reservoir, where planktivorous and omnivorous fishes dominate, the zooplankton was forced to adopt the diurnal vertical migration (DVM), a phenomenon that propagated through the different trophic levels. In Carioca Lake, in the virtual absence of vertebrate predators of zooplankton, no migration in the planktonic community was observed.

Keywords: diel vertical migration, rotifers, *Chaoborus*, cyclopoid copepods.

Resumo: Objetivo: O presente estudo visou examinar a distribuição vertical dia-noite das comunidades zooplanctônicas em dois ecossistemas de água doce tropicais: lagoa Carioca (PERD, MG), dominada por peixes piscívoros e no reservatório do Nado (Belo Horizonte, MG), dominada por peixes planctívoros/onívoros. **Métodos:** A distribuição vertical dos organismos zooplanctônicos foi examinada ao meio-dia e à meia-noite, nos períodos de abril de 2003 para os ambientes estudados, utilizando-se uma armadilha Schindler-Patalas. **Resultados:** No reservatório do Nado, a larva do predador invertebrado *Chaoborus* apresentou um comportamento migratório bem nítido, permanecendo no hipolímnio durante o período diurno e migrando para a superfície durante a noite. Mesmo comportamento migratório foi observado para os rotíferos e a população do copépodo *Thermocyclops inversus*, táxon dominante neste ambiente. Já na Lagoa Carioca, as larvas de *Chaoborus* foram encontradas em toda a coluna de água tanto durante o dia quanto durante a noite e não apresentaram comportamento migratório típico. O mesmo comportamento foi evidenciado para os rotíferos e a população do copépodo *T. minutus*, presas potenciais da larva de *Chaoborus* neste ambiente. **Conclusões:** O estudo mostrou que no reservatório do Nado, a migração vertical diurna (MVD) se propagou através dos diferentes níveis tróficos. Na lagoa Carioca, por sua vez, devido à quase ausência de predadores vertebrados de zooplâncton, não foi evidenciada a ocorrência da MVD.

Palavras-chave: migração vertical diária, rotíferos, *Chaoborus*, copépodos ciclopoídeos.

1. Introduction

Diurnal vertical migration (DVM) is a well-known behavior shared by many species of all major zooplankton groups, not only in marine but also in freshwater systems (Pearre, 2003). The typical DVM consists of an upwards displacement at sunset with the plankters spending the daylight hours in deeper, colder and darker waters. The most generally accepted hypothesis to explain the DVM behavior is the avoidance of predation (Zaret and Suffern 1976; Ringelberg, 1999).

Predation is one of the strongest selective forces shaping complex behavior in many groups of organisms, from rotifers to large mammals. Several field investigations as well as some well-conducted laboratory experiments have supported the supposition that most zooplankters would seek out darker and deeper waters only to avoid the risk of being captured by visually oriented predators (Ringelberg, 1999). Recently, some investigations have shown that some species are able to detect predators by means of chemical signals (kairomones), and they change their DVM amplitudes to increase their “fitness” (Loose and Dawidowicz, 1994; Nesbitt et al., 1996; Tollrian and Harvell, 1999).

The changes in behavior as well as other phenotypic constraints (Peacor and Werner, 1997) aimed to reduce the risk of predation can be viewed as an indirect (non-lethal) interaction between predators and their prey (Pangle et al., 2007). Romare and Hansson (2003) proposed the expression “behavioral cascade” to describe these indirect interactions, which affect not only the behavior of one prey species, but also the behavior of smaller fractions of prey. They suggested that this kind of general modification induced by a top predator on a series of behaviors of potential prey is parallel to the theory of “trophic cascade” (Carpenter et al., 1985). The “behavioral cascade” would act rapidly, since this mechanism does not require any demographic responses (changes in numbers or rates of increase) in order to cause major impacts on community structure. Good examples of “behavioral cascade” are seen in the DVM of zooplankton in aquatic communities (Trussell et al., 2006).

The purpose of the present study is to conduct a detailed analysis of the day-night vertical distribution of zooplankton in a tropical lake dominated by piscivorous fishes (Carioca Lake) and another dominated by planktivorous/omnivorous (Nado reservoir). Despite being of different natures (reservoir x lake), these systems have many similarities in their zooplankton communities. The taxonomic composition in both systems is made up of small rotifers dominating in the microzooplankton fraction. The mesozooplankton fraction includes few cladocerans, and is dominated by a single species of cyclopoid copepod: *Thermocyclops inversus* in Nado, and *T. minutus*

in Carioca Lake. The most striking feature of the zooplankton community of both systems is the high abundance of the invertebrate predator *Chaoborus* spp. (Diptera, Chaoboridae). The hypothesis being tested in this study assumes that, despite the structural similarity between the zooplankton communities, the DVM patterns developed by the zooplankton in these environments would be diverse, reflecting the different behavioral prey-predator interactions between these two systems. Specifically, we a) compared the migratory behavior of selected populations of zooplankton species (the most abundant) at different trophic levels; and b) investigated whether the DVM patterns were associated with the presence of top predator (vertebrate, invertebrate or both) in these systems.

2. Material and Methods

2.1. Study area

Nado reservoir (central point 19° 49' 56" S and 43° 57' 34" W) is a reservoir located in the Parque Municipal Lagoa do Nado, in the northern part of the city of Belo Horizonte, Minas Gerais (Figure 1). It is located in a small valley covered entirely with *Eucalyptus* spp. It has a conical catchment basin ($Z_{med} : Z_{max} = 0.35$) with a linear slope. The lake surface covers 1.5 ha, and the mean depth is 2.7 m. This is a meso-eutrophic system, with a stable thermal stratification from August through May. During the short “winter” period, the water column is isothermal. The epilimnion is usually well oxygenated, but an intense anoxia develops in the hypolimnion as soon as stratification begins in early September, and persists until the next circulation period (Bezerra-Neto and Pinto-Coelho, 2004).

The Rio Doce State Park is the largest preserved fragment of Atlantic Rain Forest in the state of Minas Gerais. The park has an area of 36,000 ha, and its surroundings are nearly completely covered by plantations of exotic *Eucalyptus* trees. The region contains one of the most important lake districts of Brazil (Barbosa et al., 1977). One of these lakes is Carioca Lake (central point 19° 45' S and 42° 37' W), located inside the reserve (Figure 2). The lake's shoreline is 1,718 m long, and its area is 14.1 ha. The deepest point is 11.8 m, and the mean depth is 4.8 m. The lake is mesotrophic, with a short turnover period during July and August (Henry and Barbosa, 1989).

The fish fauna of Nado reservoir is dominated by the exotic African *Tilapia rendalli* (tilapia) and three other small species, *Geophagus brasiliensis* (cará), *Astyanax* spp. (lambari), and *Poecilia* sp. (barrigudinho). The top predator is *Hoplias malabaricus* (traíra) (Bezerra-Neto, 2001). In Carioca Lake, the fish community includes only six species (Pinto-Coelho et al., 2008). Two exotic piscivorous fishes are the most abundant taxa: *Cichla* cf. *ocellaris* (tucunaré) and *Pygocentrus natterei* (piranha).

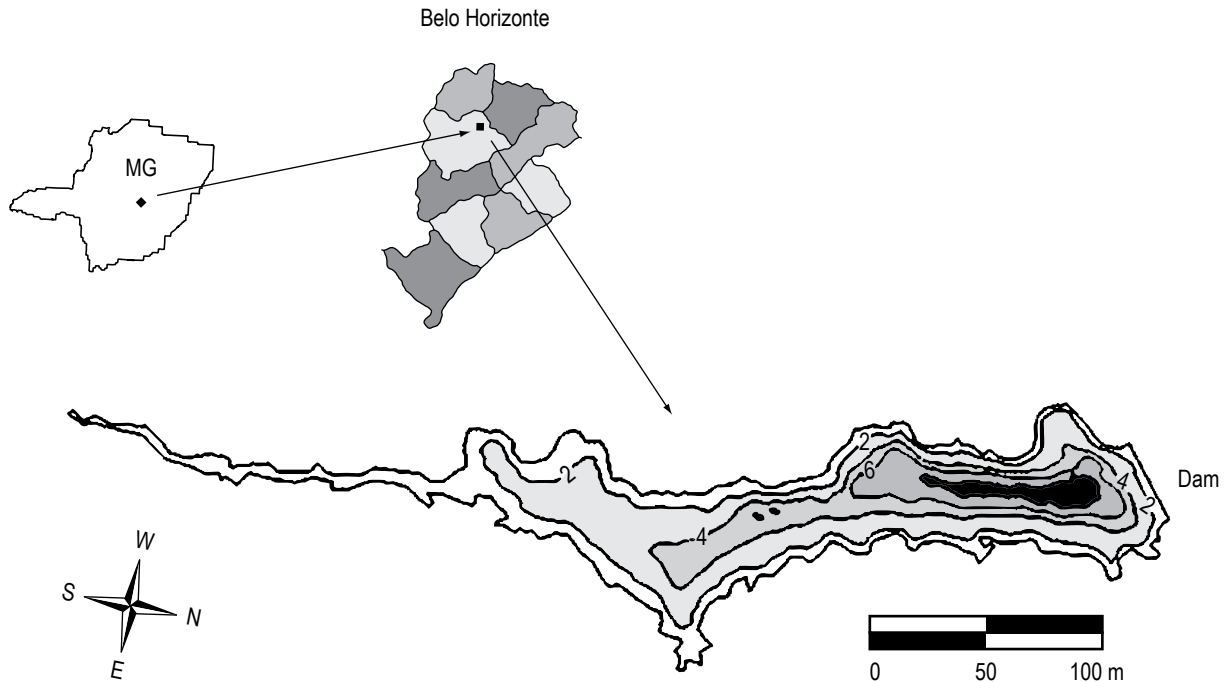


Figure 1. Location and bathymetric map of Nado reservoir.

2.2. Data collection

The study was conducted at noon (11:00 AM to 1:00 PM) and midnight (11:00 PM to 01:00 PM) on April 16, 2003 for Carioca Lake, and April 29, 2003 for Nado reservoir. Three permanent stations located within several meters of the deepest part ($Z_{\max} = 11.8$ m for Carioca Lake and $Z_{\max} = 7.6$ m for Nado reservoir), were marked with a floating device to which a boat could be attached. Profiles (measured every 0.5 m) of water temperature and dissolved oxygen were taken for the entire water column. A Yellow Springs Instruments Model YSI 55 meter was used for these measurements. The subaquatic radiation (PAR radiation, 400-700 nm) was also obtained using a Li-Cor radiometer equipped with a spherical sensor (model LI 193, Li-Cor Inc). At each station, samples for zooplankton were taken at each meter of the water column using a Schindler-Patalas trap of 17 L equipped with a 68 μm mesh net. Zooplankton organisms were quickly transferred to clean dry 300 mL polyethylene vials containing 5 mL of the vital stain Rose Bengal. After 5 minutes, 20 mL of a concentrated formalin-sucrose solution (250 g sucrose to 1 liter 37% formaldehyde, buffered to pH 7.0 with borax) was added, achieving a final concentration of 4-8% formalin (Haney and Hall, 1973).

The zooplanktonic organisms were counted in 1.0 mL Sedgwick-Rafter cell chambers by the use of a Leica DMLB binocular microscope. Subsampling was carried out using a 5 mL non-selective Stempel pipette when necessary. A minimum of 250 individuals were always counted in

each sample, in order to achieve a coefficient variation of 0.20 or less, according to McCauley (1984). Nauplii, copepodites and adult copepods (male and female) were counted separately.

All larvae of *Chaoborus* were counted and measured in all samples. 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. The measurements were done using the image-processing program *Scion Image* (Scion Corporation, Inc.) installed on a PC connected to the Sony CCD camera/Leica microscope. Further details of the measurement procedure of chaoborid larvae are given elsewhere in Bezerra-Neto (2001).

The vertical distribution of each zooplankton population was estimated using the mean depths for daylight and dark hours. A weighted mean depth was calculated as:

$$\text{WMD} = \frac{(\sum n_i d_i)}{(\sum n_i)} \quad (1)$$

Where n_i is the density (number of individuals per liter) of population i and d_i is the depth of sample i . This sample is considered to be the mean point of each depth. The data for total abundance in the water column were obtained by integrating each depth (ind.m^{-2}) using the Simpson technique.

We tested for the existence of DVM behavior by comparing the day and night WMD values using a two-tailed t -test for each population. The existence of a true DVM

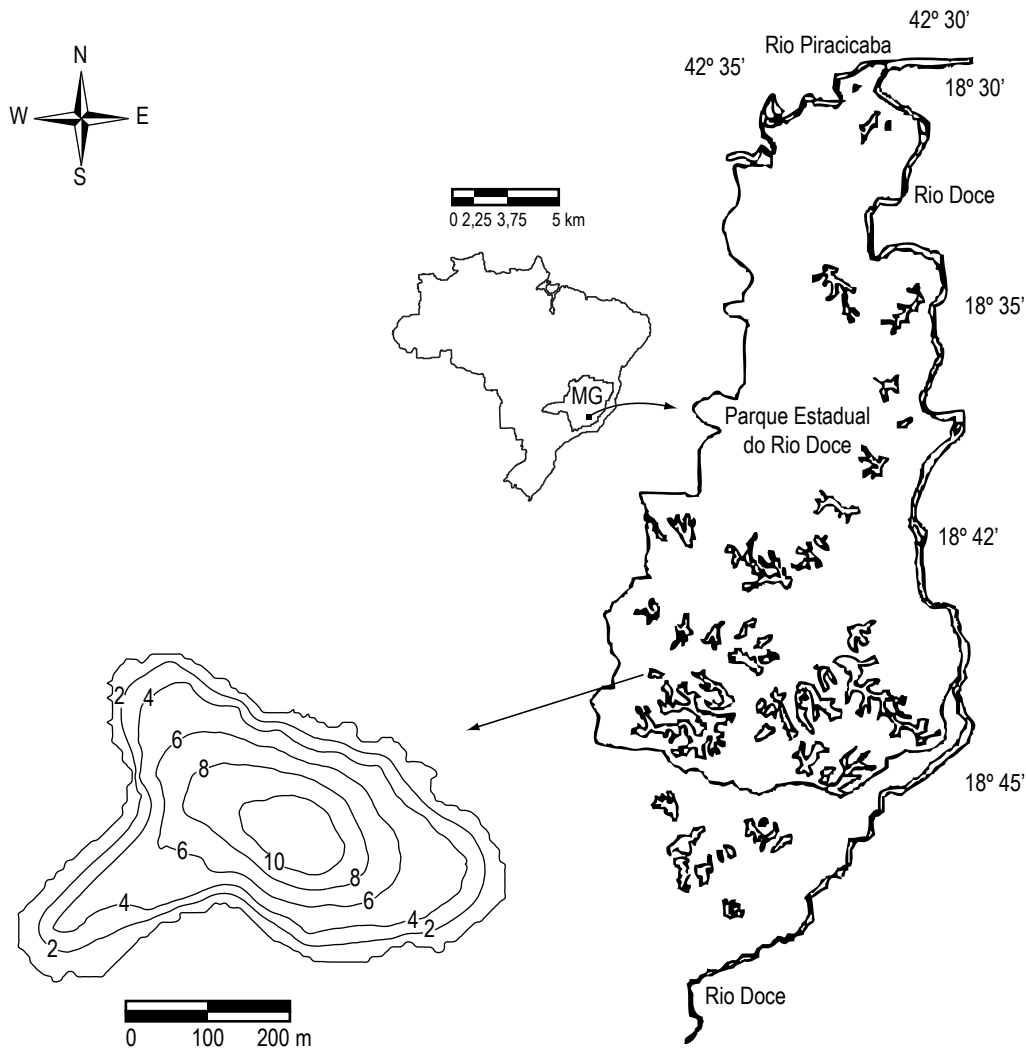


Figure 2. Map showing some of the lakes of the Rio Doce State Park in southeast Brazil. The arrow indicates Carioca Lake, and the detail map shows its bathymetry.

was granted if the test produced a WMD difference with a degree of significance of $p < 0.05$.

The amplitude of WMD (ΔZ) was estimated using the difference between day and night values of WMD. A typical DVM was considered each time to occur when this difference was positive, and a reversal DVM was considered when this difference was negative.

3. Results

3.1. Basic limnological features

Nado reservoir was stratified, with epilimnetic temperatures ranging between 24-25 °C. The epilimnion was about 1 meter thick. The temperature variation between day and night was always less than 2 °C, and the difference between surface and bottom waters was about 3 °C (Figure 3). The oxygen profile was typically clinograde, with values close

to zero near the bottom. The euphotic zone (>1% PAR) did not vary, remaining at about 2.5 m.

The water column of Carioca Lake was also stratified. The surface temperature ranged between 28-29 °C and the bottom temperature remained below 25 °C. The concentrations of dissolved oxygen also decreased strongly towards the hypolimnion, where they remained below 3.0 mg O₂·L⁻¹ (Figure 3). The euphotic zone (1% of PAR) reached the depth of 4.0 m.

3.2. Zooplankton density

The zooplankton community in Nado reservoir was represented by 13 rotifer species and only one species of copepod, the cyclopoid *Thermocyclops inversus*. The mean integrated density of zooplankton was 6.3×10^6 ind.m⁻² (means of day and night densities). As expected, the rotifers were the most abundant group, representing no less than 61.9% of the total mean zooplankton numbers, followed

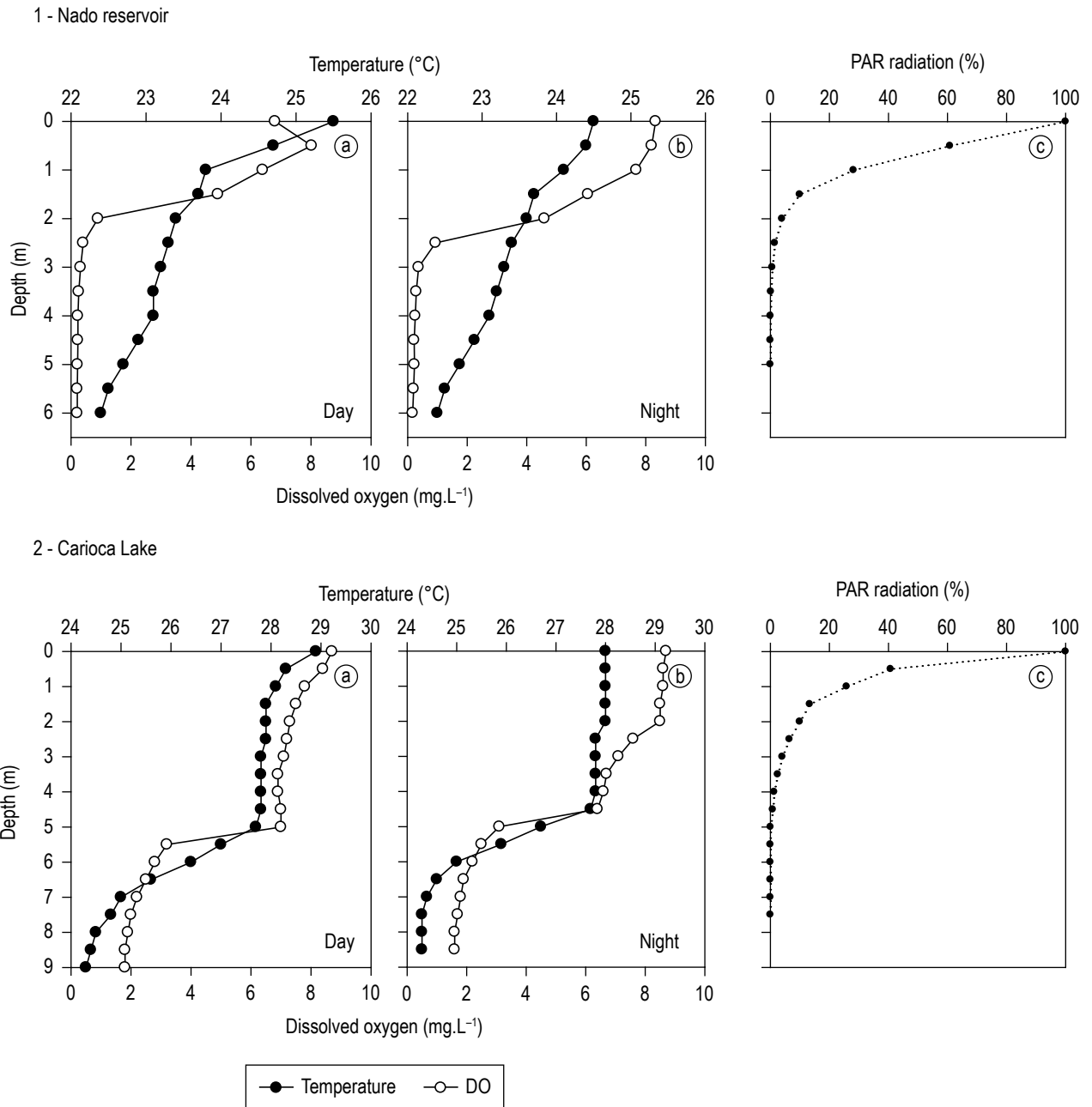


Figure 3. Vertical profiles of a) temperature ($^{\circ}\text{C}$), b) dissolved oxygen ($\text{mg O}_2\cdot\text{L}^{-1}$), and c) PAR radiation (%) in 1) Nado reservoir and 2) Carioca Lake.

by copepods with 38.1%. The population of *T. inversus* was dominated by naupliar instars that comprised 80.1% of the total density of copepods. Even considering the rich rotifer assemblage, only a few taxa dominated: *Brachionus falcatus*, *B. mirus*, *Keratella cochlearis* and *Kellicottia bostoniensis* (densities higher than 2% of total abundance for the sampling period). Therefore, only these species were included in the analysis of vertical migration of zooplankton (Figure 4).

A single species of chaoborid was found in Nado reservoir: *Chaoborus (Sayomia) brasiliensis* (Theobald, 1901).

This species has an average maximum length of about 8 mm and a cephalic capsule reaching 0.9 mm. The relative mean densities of the different instars were 1, 13, 30 and 56% for the 1st, 2nd, 3rd and 4th instars, respectively. Significant differences (*t*-test, $p < 0.05$) between day and night abundances of instars were found (data not shown).

The integrated densities of 2nd and 3rd instars were 2-3 folds higher at night (Figure 4). In the case of the 4th instar, this density increase at night was even higher and reaching a 22 fold difference (from 0.7×10^3 to $15.7 \times 10^3 \text{ ind}\cdot\text{m}^{-2}$) (Figure 4).

The zooplankton community of Carioca Lake was also represented by 13 species of rotifers and 2 cyclopoids (*Thermocyclops minutus* and *Microcyclops anceps*). *M. anceps* was quite rare, and contributed less than 1% of the samples.

In contrast to Nado reservoir, in Carioca Lake the cyclopoids were the most abundant zooplankters, contributing not less than 98.4% of all specimens counted. Again, the naupliar stages of cyclopoids were the most abundant ecophase, reaching 75.9% of the relative density of copepods (Figure 5).

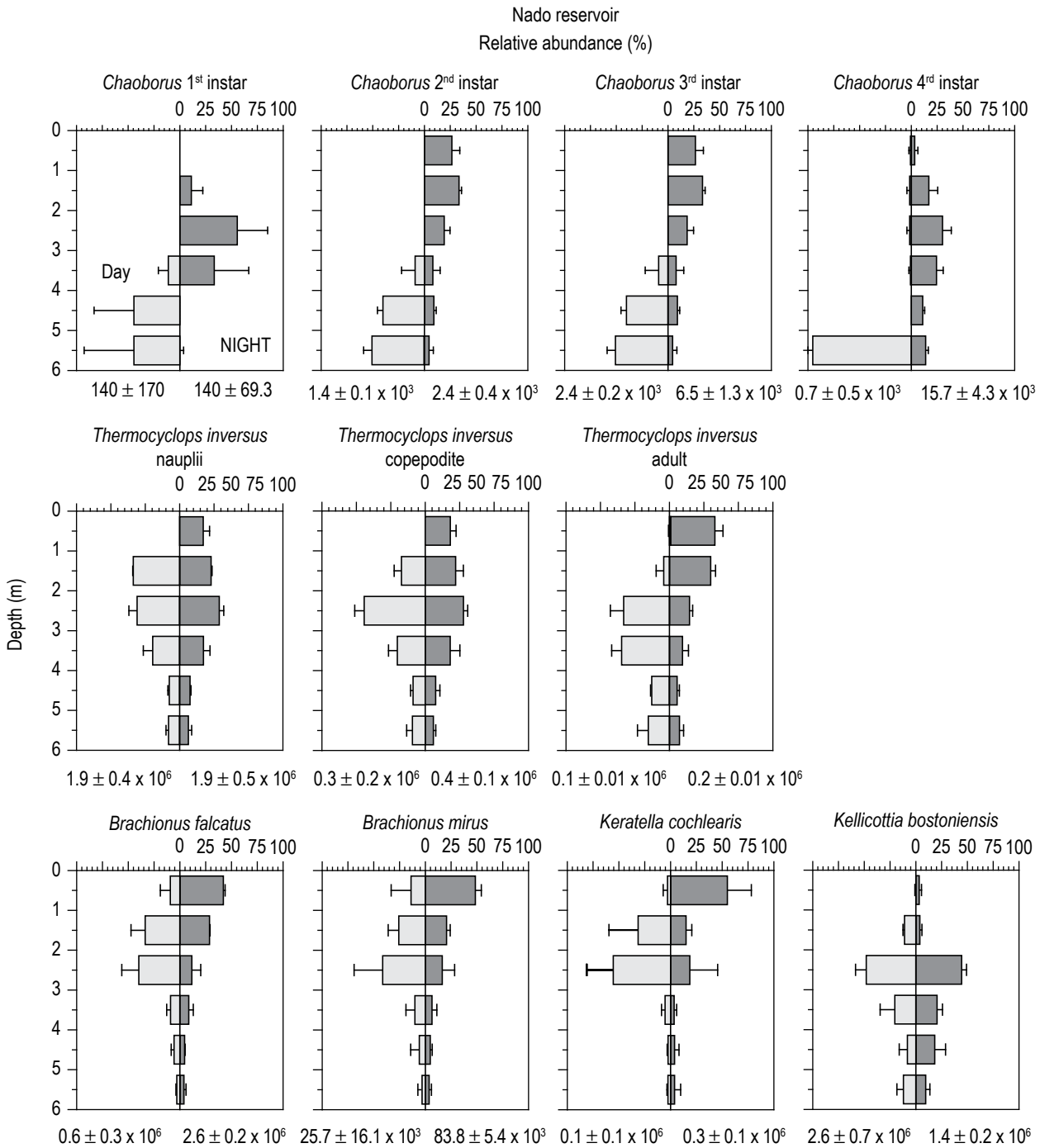


Figure 4. Vertical distribution of relative abundance (%) of the invertebrate predator *Chaoborus* and its zooplankton prey species during the day (shaded) and night (filled) in Nado reservoir on April 29-30, 2003. The data are expressed as the mean of three samples and a standard deviation. The figure below each graph indicates the mean density (ind.m⁻²) ± standard deviation for the entire water column.

Rotifers were present in much lower numbers in Carioca Lake (Figure 5). The mean integrated density was only $41.9 \times 10^3 \text{ ind.m}^{-2}$ (mean average for day and night samples considered together), and only *Hexarthra* sp., *Collotheca*

sp. and *Ptygura* sp., were abundant enough to be included in the DVM analyses (densities higher than 2% of overall zooplankton densities). A single genus, *Hexarthra* sp., contributed with 86% of the total relative density.

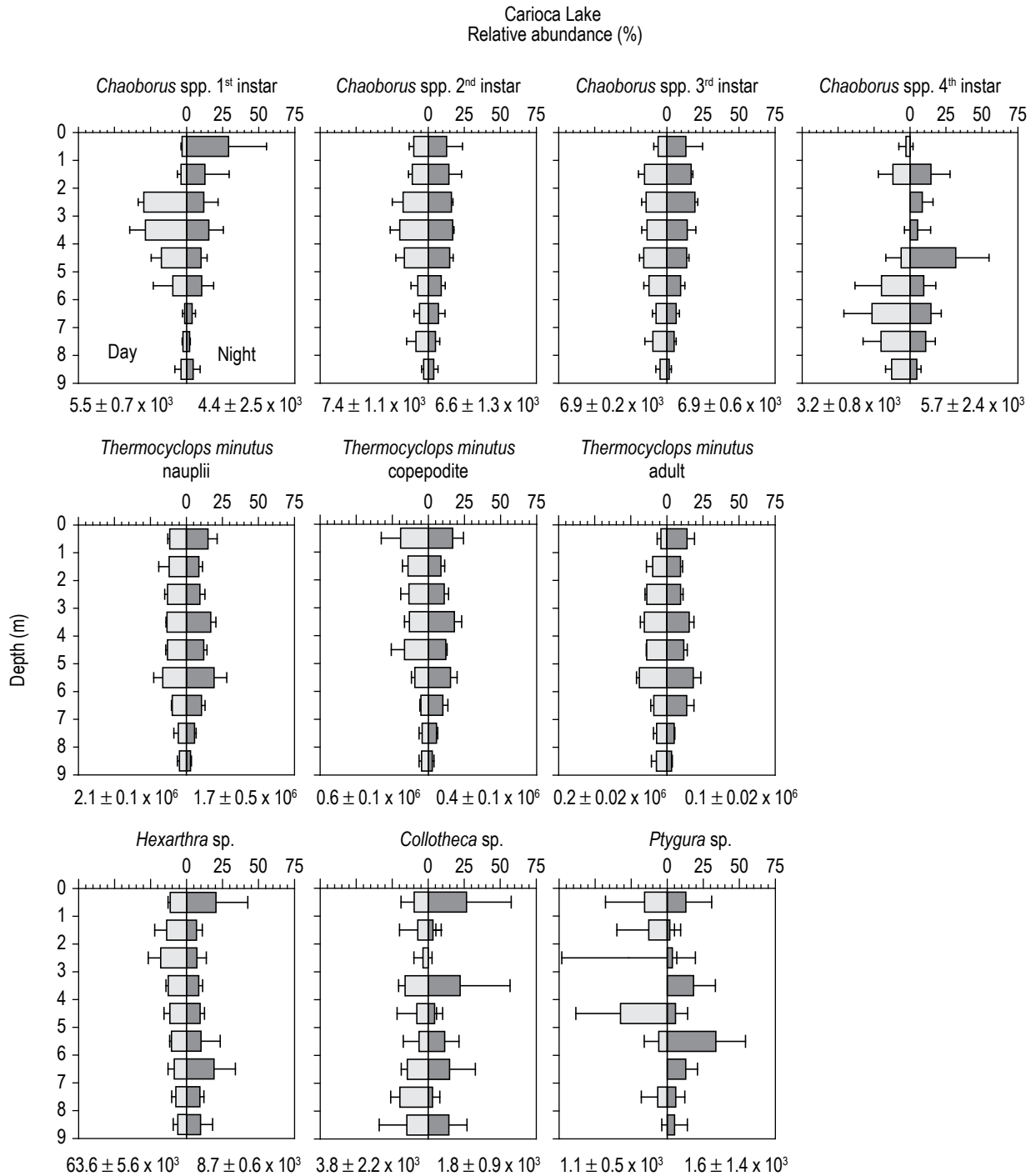


Figure 5. Vertical distribution of relative abundance (%) of invertebrate predator *Chaoborus* and its zooplankton prey species during the day (shaded) and night (filled) in Carioca Lake on April 16-17, 2003. The data are expressed as the mean of three samples and a standard deviation. The figure below each graph indicates the mean density (ind.m^{-2}) \pm standard deviation for the entire water column.

Two species of Chaoboridae were found in Carioca Lake. They have so far not been identified; however, differences in the length of the cephalic capsule allowed an accurate distinction of the instars of these two species. The maximum length of body length (12.4 mm) and the cephalic capsule (1.7 mm) found for both populations in Carioca Lake were clearly larger than the corresponding proportions for *C. brasiliensis* in Nado reservoir. The chaoborids of Carioca Lake also had a larger mouth opening (mean 0.67 mm for the 4th instar). The mouth opening for *C. brasiliensis* from Nado reservoir ranged between 0.47 and 0.54 mm.

The mean densities of *Chaoborus* were 21, 30, 30 and 19% for the 1st, 2nd, 3rd and 4th instars, respectively. There were no significant differences between day and night densities of chaoborids in Carioca Lake (*t*-test, *p* > 0.05) (Figure 5).

3.3. Vertical distribution of zooplankton

The significant differences (*t*-test, *p* < 0.05) found for the vertical distribution of *Chaoborus* (instars 1st through 4th) show that this species is clearly undergoing a daily vertical displacement behavior in Nado reservoir (Figure 6). The individuals spend the daylight hours in deeper layers and travel upwards after sunset. No difference was found for the vertical amplitude of this migration between the different instars. The ranges of vertical movement for the larvae of *Chaoborus* in Nado reservoir were: 2.1 m (± 0.19), 2.9 m (± 0.15), 2.9 m (± 0.19) and 2.2 m (± 0.19) for the 1st, 2nd, 3rd and 4th instars, respectively (Figure 6). All instars tended (>50% of mean relative density) to remain in the 2.5-3.5 m layer at night, where the dissolved oxygen concentrations usually remained below 2 mg O₂.L⁻¹ (Figures 3 and 4).

The nauplii, copepodites and adults of *T. inversus* in Nado reservoir also showed significant differences in their vertical distribution between day and night. This species also exhibited a nocturnal DVM (Figures 4 and 6). In contrast to *Chaoborus*, there was an increase in the ranges of vertical displacement according to the ontogenetic stage of *T. inversus*. The older stages made a longer vertical migration than the younger ones. The vertical ranges of vertical migration for the nauplii, copepodites and adults of *T. inversus* were 0.4 m ± 0.17 , 0.73 m ± 0.23 and 1.43 m ± 0.15 , respectively (Figure 6).

The DVM of *T. inversus* in Nado reservoir was associated with dissolved oxygen and light intensity. Copepods and adults were concentrated in layers with no light or with very low oxygen during the day (Figure 4).

Four rotifer species from Nado reservoir were considered in the analysis: *B. falcatus*, *B. mirus*, *K. cochlearis* and *K. bostoniensis*. They all exhibited a standard DVM, except the rotifer *K. bostoniensis*. There were significant differences between the day and night vertical positioning of these populations (Figures 4 and 6). However, the magnitude of the DVM was lower than 1.0 m in all cases:

0.6 m ± 0.3 (*B. falcatus*), 0.7 m ± 0.3 (*B. mirus*) and 0.8 m ± 0.6 (*K. cochlearis*).

There was almost no diel variation of vertical distributions of most zooplankton species in Carioca Lake (Figures 5 and 6). DVM was only detected for the 1st instar of *Chaoborus*. The different stages (nauplii, copepodites and adults) of *T. minutus* also did not migrate in Carioca Lake. In contrast to Nado reservoir, all individuals of this population were found homogeneously distributed in the water column (Figures 5 and 6). Finally, the rotifers in this lake also followed the non-migration trend, and there were no statistical differences between the mean depths for day and night hours (*t*-test, *p* > 0.05) (Figure 6).

4. Discussion

This study found differences in the vertical migration behavior of similar zooplankton species in two different tropical freshwater systems. Whereas practically no DVM was detected in Carioca Lake, this behavior was ubiquitous in Nado reservoir. The question at this point is why similar species adopt quite different DVM strategies under similar circumstances? The physical and chemical conditions of both systems were quite similar. Both systems are warm monomictic, with only one circulation period. They also share similar morphometric parameters. Both are small freshwater bodies, shallow, and with generally mesotrophic conditions. Therefore, it is possible that these general limnological features cannot explain the differences found in DVM of their zooplankton. As the features are similar in both lakes, one would not expect the DVM differences to be induced by the limnological features.

One possible reason for the different DVM strategies found in the two lakes may be linked to the differences in the composition of fish species. Between 1960 and 1970, there was a general introduction of several exotic fish species in most lakes of the Rio Doce Lake District. These introductions are well documented, mostly because they were carried out by government agencies for the general purpose of increasing fish production. Two piscivores fish species were particularly used by local fish fauna "managers": the tucunaré (*Cichla cf. ocellaris*) and the red piranha (*Pygocentrus nattereri*) (Godinho et al., 1994). Several detailed investigations have documented the spread of these two species to almost all of the lakes in the region (Latini, 2001; Latini et al., 2005; Vasconcellos et al., 2005). All the studies demonstrated that these introductions caused an acute erosion of native fish species in most of the Rio Doce lakes. Considering the specific case of Carioca Lake, Vasconcellos et al. (2005) reported the presence of a third exotic fish, the pimelodid *Clarias gariepinus* (in addition to the tucunaré and the red piranha), in a series of samplings conducted between October 2002 and July 2003. A comparison between these studies suggests that the fish fauna of Carioca Lake has lost at least seven native fish species

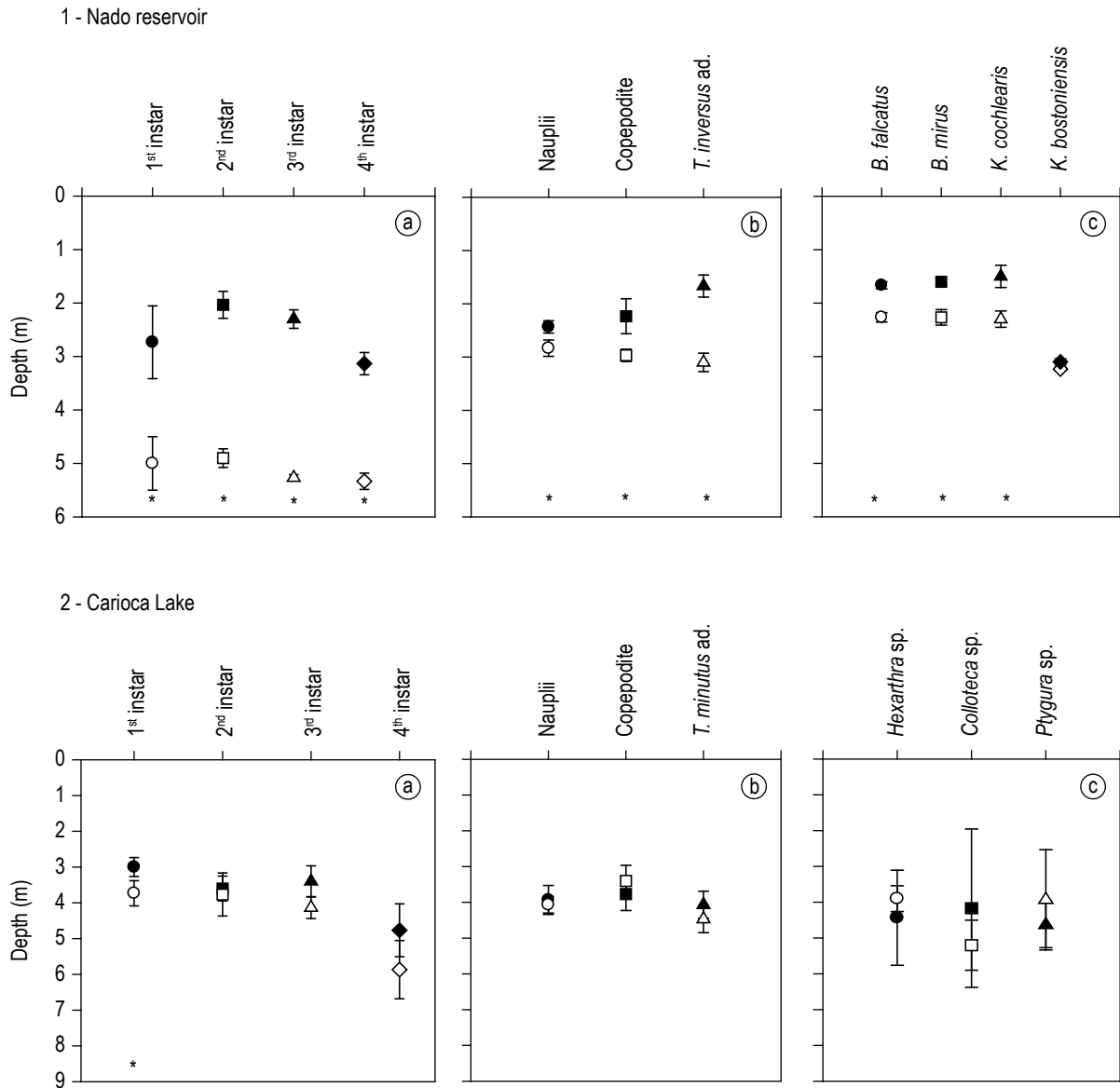


Figure 6. Weighted mean depth (WMD) of the a) invertebrate predator *Chaoborus* and b,c) its zooplankton prey species during the day (open symbols) and night (closed symbols) in 1) Nado reservoir and 2) Carioca Lake. The dispersion lines represent the standard deviation (SD), and the asterisks indicate significant differences ($p < 0.05$) between day and night.

in the last 20 years, a period coinciding with the stabilization of the populations of red piranha and tucunaré in this lake (Latini et al., 2005). More recently, a new investigation reported the worsening of the situation, since only three native species (*Hoplias malabaricus*, *Hoplerythrinus unitaenianus* and *Trachelyopterus striatulus*) were found in Carioca Lake (Pinto-Coelho et al., 2008).

There is good evidence indicating that *Chaoborus* larvae can develop uncontrolled large populations in lakes where piscivorous were accidentally or intentionally introduced (Wissel et al., 2000; Benndorf et al., 2000). The dominance of invertebrate predators in some lakes may also be associated with the existence of non-migrating larger

invertebrate predators. Some of these studies also support the hypothesis that predation pressure from chaoborids can be even greater than that due to planktivorous fish (Wissel and Benndorf, 1998). The buildup of large populations of this invertebrate predator can be seen as the result of the “ecological release” caused by the abrupt retreat of planktivores in the system.

The phenomenon of ecological release has probably occurred in Carioca Lake (Pinto-Coelho et al., 2008). In this lake, *Chaoborus* larvae can be found occupying large portions of the water column not only during the day but also at night. To avoid sharing the same space, and considering the absence of a refuge for its potential prey, most

zooplankton species in this lake have also adopted a non-migratory behavior. They are homogeneously distributed in the water column, independently of the diel cycle. The probability of being captured by a predator is practically the same at every depth, since all instars of *Chaoborus* can be found throughout the water column.

A completely different situation was observed in Nado reservoir. There were no exotic piscivorous species in the fish assemblage, and most fish species are small planktivores (Bezerra-Neto, 2001). DVM was a common behavior of the zooplankton community in this small reservoir. The clear migratory behavior of these invertebrate predators seems to be a determining factor shaping the migratory behavior of the entire community of zooplankton.

The difference between day and night densities of chaoborids observed in Nado reservoir suggests that the larval instars of these organisms remained in or near the upper layers of the sediment during the day (where they were not sampled by our Patalas trap), ascending to the upper strata of the water column at night. The mean depth of all larval instars was always close to the critical limit of dissolved oxygen of $1 \text{ mg O}_2 \cdot \text{L}^{-1}$ as proposed by Davis (1975). Even considering that Nado is a shallow reservoir ($Z_{\text{max}} = 6.5 \text{ m}$), there was a formation of a stable anoxic layer at around the depth of 2.0 m, for most parts of the year (Bezerra-Neto and Pinto-Coelho, 2001). This is an effective barrier for fish, and consequently this is a refuge for most planktonic organisms to avoid fish predation. But, even without the presence of the anoxic layer, the *Chaoborus* would have been protected from visual fish predation during the day because they remained in the dark. There is the possibility that the 1st and 4th instars remained below 2 m at night to avoid non-visual fish predation (Unger et al., 1984).

The DVM observed for chaoborids in Nado reservoir was observed in different zooplankters belonging to different trophic levels. The population of *T. inversus* showed a typical DVM and seemed to migrate into the surface waters to avoid principally the 4th *Chaoborus* instar, which also migrated upward at night but did not concentrate in the uppermost water layers. Another study in Nado reservoir (Bezerra-Neto and Pinto-Coelho, 2007) demonstrated that *T. inversus* is able to fine-tune the vertical distribution of its individuals, avoiding fish predation during the day and *Chaoborus* predation during the night. They found a relationship between DVM ranges and the ontogenetic stages of *T. inversus*, in accordance with other recent studies (Irigoien et al., 2004; Peticarrari et al., 2004). Older and larger copepodites as well as the adults of this copepod showed a greater range of vertical migration, possibly because: 1) they better tolerate the anoxic conditions in the hypolimnion (Makino et al., 2003); 2) they are stronger swimmers than the nauplii; and 3) the nauplii might not have been induced to swim deeper during the day as they

may be less vulnerable to fish predation than the older copepod stages.

DVM was also observed in different species of rotifers in Nado reservoir (e.g., *B. falcatus*, *B. mirus* and *K. cochlearis*), although this behavior was not as clear as observed for the copepods and dipteran larvae. These rotifer species remained below the thermocline during the day, and traveled upwards into the epilimnion at night, probable to avoid the *Chaoborus* (1st to 4th instars). This behavior is also explained by the fact that all instars of Chaoboridae are able to consume rotifers (Moore et al., 1994; Arcifa, 2000). The absence of the DVM to the rotifer *K. bostoniensis*, found during the study period in higher concentrations in the hypolimnion, can probably be explained to the protective nature of its very long spines, reducing its vulnerability to *Chaoborus* (Stemberger and Gilbert, 1987). Some field studies (Stich and Lampert, 1981; Ohman, 1983) have suggested that rotifers are able to undergo clear DVM with ranges of less than 1 meter. This vertical displacement is often correlated with the DVM of different predators, including the dipteran *Chaoborus* and the omnivorous cyclopoids. Gilbert and Hampton (2001), for example, demonstrated that *Polyarthra remata* undergoes reverse DVM, avoiding the predator *Tropocyclops extensus*.

5. Conclusions

In this paper, two tropical freshwater ecosystems for which the basic limnological features and fish faunas are well known, but with quite different patterns of DVM, were selected for a comparative study. Whereas no DVM was observed in Carioca Lake, in Nado reservoir DVM was ubiquitous in zooplankton. The data analysis indicates that this behavior is probably linked to the spatial interactions between the predators (vertebrate and invertebrate) and their potential prey species. From the results, it seems that the cyclopoid copepods and rotifers adjust their behavior to that of *Chaoborus*, and these in turn seem to perform DVM in response to the presence of fish. The data also illustrate the complex nature of the impact of the introduction of alien fish species in tropical freshwater systems, with their impacts extending far beyond the trophic levels of top predators. Finally, we stress the need for additional studies using simulation or new experimental or technological approaches aiming to test the amplitude of the “behavioral cascade” in shaping diurnal vertical migration through the different trophic levels of zooplankton.

Acknowledgements

The authors wish to thank Dr. J. W. Reid for revising the manuscript and for taxonomic assistance; to CNPq for a fellowship for the first author (No. 140486/2002-0). We also thank two anonymous referees for their many helpful suggestions that improved significantly the manuscript. This

studied was partially supported by the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (Proc. 5794- Fapemig/ Fundep/UFGM).

References

- ARCIFA, MS. Feeding habits of Chaoboridae larvae in a tropical Brazilian reservoir. *Bras. J. Biol.* 2000, vol. 60, no. 4, p. 591-597.
- BARBOSA, FAR., SOUZA, EMM., VIEIRA, F., RENAULT, GPCP, ROCHA, LA., BARBOSA, PMM., OBERDÁ, SM., and MINGOTI, SA. Impactos antrópicos e biodiversidade aquática. In Barbosa, FAR. and Souza, EMM. (Eds.). *Biodiversidade, população e economia*. Belo Horizonte: CEDEPLAR–ECMVS/UFGM, 1977. p. 345-454.
- BENNDORF, J., WISSEL, B., SELL, AF., HORNIG, U., RITTER, P. and BÖING, W. Food web manipulation by extreme enhancement of piscivory: an invertebrate predator compensates for the effects of planktivorous fish on a plankton community. *Limnologia*, 2000, vol. 30, no. 3, p. 235-245.
- BEZERRA-NETO, JF. *A influência da larva de Chaoborus (Insecta: Diptera) na distribuição espacial da comunidade zooplanctônica na Lagoa do Nado, Belo Horizonte – MG*. Belo Horizonte: Universidade Federal de Minas Gerais – UFGM, 2001. Dissertação de Mestrado.
- BEZERRA-NETO, JF. and PINTO-COELHO, RM. O déficit de oxigênio em um reservatório urbano: Lagoa do Nado, Belo Horizonte - Minas Gerais. *Acta Limnol. Brasil.*, 2001, vol. 13, no. 1, p. 107-116.
- BEZERRA NETO, JF. and PINTO-COELHO, RM. Estrutura térmica, o trabalho do vento e a estabilidade do reservatório tropical raso: Lagoa do Nado, BH, MG. *Bios*, 2004, vol. 10, no. 10, p. 89-95.
- BEZERRA-NETO, JF. and PINTO-COELHO, RM. Diel vertical migration of the copepod *Thermocyclops inversus* (Kiefer, 1936) in a tropical reservoir: the role of oxygen and the spatial overlap with *Chaoborus*. *Aquat. Ecol.* 2007, vol. 41, no. 4, p. 535-545.
- CARPENTER, SR., KITCHELL, JE. and HODGSON, JR. Cascading trophic interactions and lake productivity. *BioScience*, 1985, vol. 35, no. 10, p. 634-639.
- DAVIS, JC. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *J. Fish. Res. Board Can.*, 1975, vol. 32, no. 12, p. 2295-2332.
- GILBERT, JJ. and HAMPTON, SE. Diel vertical migrations of zooplankton in a shallow, fishless pond: a possible avoidance-response cascade induced by notonectids. *Freshwater Biol.*, 2001, vol. 46, no. 5, p. 611–621.
- GODINHO, AL., FONSECA, MT. and ARAÚJO, ML. The ecology of predator fish introductions: the case of Rio Doce valley lakes. In Pinto-Coelho, RM., Giani, A. and Von Sperling, E. (Eds.). *Ecology and human impact on lakes and reservoirs in Minas Gerais with special reference to future development and management strategies*. Belo Horizonte: SEGRAC, 1994. p. 77-83.
- HANEY, JF. and HALL, DJ. Sugar-coated *Daphnia*: a preservation technique for Cladocera. *Limnol. Oceanogr.*, 1973, vol. 18, no. 2, p. 331-333.
- HENRY, R. and BARBOSA, FAR. Thermal structure, heat content and stability of two lakes in the national Park of Rio Doce Valley (Minas Gerais, Brazil). *Hydrobiologia*, 1989, vol. 171, no. 3, p. 189-199.
- IRIGOIEN, X., CONWAY, DVP. and HARRIS RP. Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Mar. Ecol. Progr. Ser.* 2004, vol. 267, no. 1, p. 85-97.
- LATINI, AO. *O efeito da introdução de peixes exóticos nas populações nativas de lagoas do Parque Estadual do Rio Doce, MG*. Belo Horizonte: Universidade Federal de Minas Gerais – UFGM, 2001. Dissertação de Mestrado.
- LATINI, AO., PEREIRA, TL., LATINI, RO., GIACOMINI, HC., LIMA Jr., DP., OPORTO, LT. and ESPÍRITO-SANTO, HMV. Distribuição e efeitos de peixes exóticos sobre a ictiofauna nativa dos lagos do Médio Rio Doce, MG, Brasil. In Rocha, O., Espíndola, E., Verani, N., Verani, JR. and Rietzler, AC. (Eds.). *Espécies invasoras em águas doces: estudos de caso e propostas de manejo*. São Carlos: Gráfica Expressa, 2005. p. 99-118.
- LOOSE, CJ. and DAWIDOWICZ, P. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology*, 1994, vol. 75, no. 8, p. 2255-2263.
- MAKINO, W., YOSHIDA, T., SAKANO, H. and BAN, S. Stay cool: habitat selection of a cyclopoid copepod in a north temperate oligotrophic lake. *Freshwater Biol.*, 2003, vol. 48, no. 9, p. 1551-1562.
- McCAULEY, E. The estimation of the abundance and biomass of zooplankton in samples. In Downing, JA. and Rigler, AJ. (Eds.). *A manual on methods for the assessment of secondary productivity in fresh waters*. London: Blackwell Scientific Publishers, 1984. p. 228-265.
- MOORE, MV., YAN, ND. and PAWSON, T. Omnivory of the larval phantom midge (*Chaoborus* spp.) and its potential significance for freshwater planktonic food webs. *Can. J. Zool.*, 1994, vol. 72, no. 11, p. 2055-2065.
- NESBITT, LM., RIESSEN, HP. and RAMCHARAN, CW. Opposing predation pressures and induced vertical migration responses in *Daphnia*. *Limnol. Oceanogr.* 1996, vol. 41, no. 6, p. 1306-1311.
- OHMAN, MD. Reverse diel migration: an escape response from invertebrate predators. *Science*, 1983, vol. 220, no. 4604, p. 1404-1407.
- PANGLE, KL., PEACOR, SD. and JOHANNSSON, OE. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, 2007, vol. 88, no. 2, p. 402-412.
- PEACOR, SD. and WERNER, EE. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology*, 1997, vol. 78, no. 4, p. 1146- 1156.
- PEARRE, S. Eat and run?: the hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev.* 2003, vol. 78, no. 1, p. 1-79.

- PERTICARRARI, A., ARCIFA, MS. and RODRIGUES, RA. Diel vertical migration of copepods in a Brazilian lake: a mechanism for decreasing risk of *Chaoborus* predation?. *Braz. J. Biol.*, 2004, vol. 64, no. 2, p. 289-298.
- PINTO-COELHO, RM., BEZERRA-NETO, JF., MIRANDA, F., MOTA, TG., SANTOS, AM., MAIA-BARBOSA, PM., MELLO, NAST., MARQUES, MM., CAMPOS, MO. and BARBOSA, FAR. The inverted trophic cascade in tropical planktonic communities: impacts of exotic fish introduction in the Middle Rio Doce lake District, Minas Gerais, Brazil. *Braz. J. Biol.* 2008, vol. 68, no. 4 (Suppl.), p. 631-637.
- RINGELBERG, J. The photobehavior of *Daphnia* ssp. as a model to explain diel vertical migration in zooplankton. *Biol. Rev.* 1999, vol. 74, no. 4, p. 397-423.
- ROMARE, P. and HANSSON, LA. A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnol. Oceanogr.* 2003, vol. 48, no. 5, p. 1956-1964.
- STEMBERGER, RS. and GILBERT, JJ. 1987. Defenses of planktonic rotifers against predators. In Kerfoot, WC. and Sih, A. (Eds.). *Predation: direct and indirect impacts on aquatic communities*. Hannover: University Press of New England, 1987. p. 227-239.
- STICH, H. and LAMPERT, W. Predation evasion as an explanation of diurnal vertical migration by zooplankton. *Nature*, 1981, vol. 293, no. 5831, p. 396-398.
- TOLLRIAN, R. and HARVELL, CD. *The ecology and evolution of inducible defenses*. Princeton: Princeton University Press, 1999.
- TRUSSELL, GC., EWANCHUK, PJ. and MATASSA, CM. Habitat effects on the relative importance of trait and density-mediated indirect interactions. *Ecol. Lett.* 2006, vol. 9, no. 11, p. 1245-1252.
- UNGER, PA., LEWIS JR., WA. and McCLEARN, DH. Nonvisual feeding in a visual planktivore, *Xenomelaniris venezuelae*. *Oecologia*, 1984, vol. 64, no. 2, p. 280-283.
- VASCONCELLOS, MG., ASSUMPCÃO, AM., SOARES, AS., LUCCA, JV., VERANI, JR., FENERICH-VERANI, N. and ROCHA, O. Análise da diversidade de espécies de peixes de 4 lagoas do Sistema de Lagos do Vale do Médio Rio Doce – MG, em relação à ocorrência de espécies exóticas. In Rocha, O., Espíndola, E., Verani, N., Verani, JR. and Rietzler, AC. (Eds.). *Introdução e manejo de espécies exóticas*. São Carlos: Gráfica Expressa, 2005. p. 119-129.
- WISSEL, B. and BENNDORF, J. Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long term biomanipulation experiment. *Arch. Hydrobiol.* 1998, vol. 143, no. 2, p. 129-146.
- WISSEL, B., FREIER, K., MULLER, B., KOOP, J. and BENNDORF, J. Moderate planktivorous fish biomass stabilizes biomanipulation by suppressing large invertebrate predators of *Daphnia*. *Arch. Hydrobiol.* 2000, vol. 149, no. 2, p. 177-192.
- ZARET, TM. and SUFFERN, JS. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* 1976, vol. 21, no. 6, p. 804-813.

Received: 18 September 2008

Accepted: 03 February 2009