

Diel vertical migration of the copepod *Thermocyclops inversus* (Kiefer, 1936) in a tropical reservoir: the role of oxygen and the spatial overlap with *Chaoborus*

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Abstract The effect of water transparency, dissolved oxygen concentration and the invertebrate predator *Chaoborus brasiliensis* on the day–night vertical distribution of the copepod cyclopoid *Thermocyclops inversus* was investigated in a shallow tropical reservoir, Nado Reservoir, Belo Horizonte, Brazil. Diel cycles were carried out over a period of 12 consecutive months, between October 1999 and September 2000. The different developmental stages of *T. inversus* exhibited diel vertical migration (DVM) and displayed a clear ontogenetic trend, with the amplitude of DVM increasing with the age of the organism, and ranging from 0.4 m to 0.8 m for nauplii, 0.4 m to 1.2 m for copepodite, and 1.1 m to 2.1 m for adults. We observed that seasonal changes in dissolved oxygen and *C. brasiliensis* directly influenced the vertical distribution of the copepod population in this reservoir. Furthermore, it was showed that the diurnal vertical migration is an

important predator avoidance behavior since it diminished the spatial overlap between prey and its potential predator. This finding supports the hypothesis that the vertical migration is a defense mechanism against predation. Thus, *T. inversus* is able to remain in the anoxic layers during day light hours, and at night they move upwards avoiding hypolimnetic waters to escape from predation by *Chaoborus*.

Keywords DVM · Zooplankton · Water transparency · Copepods · Invertebrate predation · Anoxic hypolimnion

Introduction

Diel vertical migration (DVM), whereby aquatic organisms inhabit different layers of the water column at different times of the day, is a common behavior in zooplankton, and has been studied in marine as well as in freshwater habitats (see review in Pearre 2003). The light is considered the most important factor triggering this behavior (Ringelberg and Van Gool 2003). However, other environmental factors are also involved in vertical migration, such as temperature (Haney 1993), dissolved oxygen (Hanazato and Yasuno 1989; Horppila et al. 2000), and food availability (Leibold 1990). While several factors have been proposed to explain DVM, there is general agreement that the predator-avoidance hypothesis is the most recognized mechanism

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explaining the adaptive significance of vertical migration (Zaret and Suffern 1976; Neill 1990; Lampert 1993). Such migrants mostly ascend to epilimnion at night and migrate down into the colder, darker, and oxygen-poor waters in deeper layers at dawn to avoid predation by visually oriented planktivorous fish (normal DVM). Reversed diel migrations have also been detected in some studies, and have usually been connected to predation pressure by invertebrate predators (Lampert 1993).

In the pelagic zones of lakes, physical and chemical factors, e.g., temperature, light, and oxygen, can restrict foraging by fish and hence may work as refuge against predators (Horppila et al. 2000). Wright and Shapiro (1990) reported that the downward migrations by fish are restricted by concentration of oxygen of ca. 3 mg l^{-1} , and because most fish are not tolerant to low oxygen, zooplankton can escape predation by inhabiting and seeking refuge in these anoxic areas. Numerous other studies (Davis 1975; Hanazato et al. 1989; Tessier and Welser 1991; Horppila et al. 2000) support Wright and Shapiro's findings that imply reduction of predatory mortality of zooplankton in deep oxygen-poor layers. The existence of a deep-water refuge is generally accepted as the basis for vertical migration behavior of zooplankton (Tessier and Welser 1991; Lass et al. 2000). This probably happens because the predator-prey interactions depend on the spatial distribution of predator and prey, and DVM minimize predation risk by visual and tactile predators (González 1998).

Copepods are known to tolerate lower oxygen concentrations than fish and may exploit oxygen gradients as a refuge against predation (e.g., Taleb et al. 1992; Chang and Hanazato 2004). However, hypolimnetic low-oxygen layers may also favor the co-existence with invertebrate predators, especially the larvae of the midge *Chaoborus*, which are very tolerant to low-oxygen concentrations (Rine and Kesler 2001). *Chaoborus* larvae are known as voracious predators on zooplankton and can drastically alter the abundance and size structure and even the presence of their preys (Hanazato et al. 1989; Yan et al. 1991; Arcifa 2000). Since chaoborids themselves constitute a significant item in the diet of several fish species (Luecke 1986; Dawidowicz et al. 1990; McQueen et al. 1999), they also undergo a diurnal vertical migration (DVM) (Xie et al. 1998; Gliwicz et al. 2000). Then, in the presence of fish, the

Chaoborus larvae are forced out of the illuminated and oxygenated habitats during the day and share the same spatial refuge than the migrant zooplankton do to evade the common top predator, the fish.

The objective of this study was to investigate the occurrence of DVM in a copepod cyclopoid population (*Thermocyclops inversus*) in Nado Reservoir and to test the effects of water transparency, oxygen vertical gradients and presence of the invertebrate predator *Chaoborus* on the vertical positioning of the copepod population. Since this reservoir also contained several species of fish, we also aimed to investigate if the copepod population is able to manage its vertical position in such a way to minimize the risk of predation. The effect of the invertebrate predator *Chaoborus* on the vertical distribution of the *T. inversus* was assessed by analyzing the changes in the overlap between predator and prey during their observed diel vertical migrations.

Study site

Nado Reservoir is a shallow, meso-eutrophic reservoir with a surface area of 1.5 ha and a volume of $40 \times 10^3 \text{ m}^3$. The maximum depth (z_{max}) is 7.6 m and the mean depth (z_{mean}) is around 2.7 m. It is located in Belo Horizonte city, Minas Gerais State ($19^\circ 49' 56'' \text{ S}$; $43^\circ 57' 34'' \text{ W}$; altitude 790 m above sea level), in Southeastern Brazil. This is one of the largest cities in Brazil with more than 2.5 million inhabitants. 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 water level does not fluctuate since the outlet is superficial and the dam is not manipulated by man.

The climate of the region is classified as B-2 tropical, with a moderate hydric deficit (Ferreira 1992). The coolest period is usually restricted to the period from May to July. The rainy season occurs in the hottest months, from November to March. Annual precipitation during the period of study was 1,270 mm (data from Pampulha Airport Meteorological Station, Belo Horizonte).

In Nado Reservoir, the invertebrate predator *Chaoborus brasiliensis* (Theobald, 1901) co-existed with abundant fish mostly represented by the exotic African *Tilapia rendalli* and others such as,

Geophagus brasiliensis, *Astyanax* spp., *Poecilia* sp., and the predator *Hoplias malabaricus*. The zooplanktonic community is dominated by, among crustaceans, the cyclopoid copepod *Thermocyclops inversus* and the cladoceran *Moina micrura*. The most common rotifers are *Brachionus falcatus*, *B. angularis*, *B. caudatus*, *Keratella cochlearis*, *K. tropica*, and the exotic *Kellicottia bostoniensis* (Bezerra-Neto 2001).

Materials and methods

The data for this study were collected every month from October 1999 to September 2000 at its central region where it is 6.5 m deep. *Chaoborus* larvae and zooplankton were collected at each meter of the water column during 11:00–13:00 h as well as at night (23:00–01:00 h) with a 17 L Schindler-Patalas trap, equipped with a 60-µm mesh net. The samples were preserved in the field using a 4% sugared, buffered formaldehyde solution (Haney and Hall 1973).

In the laboratory, a known fraction of each sample was taken using a Hensel-Stempel subsampler for subsequent counting under a Leica DMLB dissecting stereomicroscope. *Chaoborus* larvae and low-density samples of copepods were counted in the whole sample, following McCauley (1984). *Chaoborus* instars were distinguished by differences in the head capsule length (Table 1). We used only the densities of third and fourth instar larvae (samples pooled) in the analyses, these instars being the main microcrustacean predators. *Thermocyclops inversus* were separated into three developmental stages: nauplii, copepodites, and adults.

To quantify the average depth of vertical distribution for copepod and *Chaoborus*, the weighted mean depth (WMD) was calculated according to equation given in Frost and Bollens (1992):

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

where n_i is density (number per liter) at depth d_i , which was taken to be the midpoint of each depth stratum. For determining the presence or absence of DVM behavior, we compared day and night vertical WMD by two-sample Kolmogorov–Smirnov non-parametric test statistic (K-S test) that tests the null hypothesis of equal depth distributions. We considered DVM to occur when the difference between day and night WMD was statistically significant, and then the migratory amplitude (ΔZ) was calculated as the difference between mean daytime and nighttime depths, with positive values indicating normal DVM, and negative values indicating reverse DVM.

On each sampling occasion, water temperature and dissolved oxygen profiles were measured at 1 m-intervals along the water column, using a YSI-54A oxygen meter. Water transparency was also recorded using a Secchi disk (25 cm diameter).

To understand the patchiness of predator and prey populations in the water column, we calculated the overlap index between *T. inversus* and *Chaoborus* late instars using the equation described by Williamson and Stoeckel (1990):

$$O_{ij} = \frac{\sum_{z=1}^m (N_{jz} n_{iz}) m}{\sum_{z=1}^m (N_{jz}) \cdot \sum_{z=1}^m (n_{iz})}$$

where z represents depth, m is number of depth points sampled, N_{jz} is the density of *Chaoborus* at a given depth, and n_{iz} is the density of copepod at a given depth. Overlap index <1 indicates spatial segregation between the copepod and *Chaoborus*. Overlap index = 1 indicates that copepod and/or *Chaoborus* are uniformly distributed in the water column.

Table 1 Intervals, mean, standard deviation, and coefficient of variation of head length of *Chaoborus brasiliensis* population from Nado Reservoir

Head length (µm)					
Instar	<i>n</i>	Intervals	Mean	Standard deviation	CV (%)
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

Overall index >1 indicates aggregation of the copepod and *Chaoborus* in certain strata of the water column.

The relative importance of biotic and abiotic factors in determining the vertical position of the *T. inversus* was evaluated through stepwise logistic regressions performed for day and night samples. The weighted mean depths of the three life-history stages of the *T. inversus* population were considered dependent variables. As independent variables, Secchi depth was chosen as a measure of water transparency, the depth of $<1 \text{ mg O}_2 \text{ l}^{-1}$ was used to assess the effects of oxygen depletion and the abundance, biomass and the weighted mean depth of *Chaoborus* late instars were used as biotic variables. To obtain normality, weighted mean depths of *T. inversus*, and independent variables underwent \log_{10} transformation.

Results

Seasonal variation of water temperature, transparency, and DO

During the study period, Secchi-depth transparency varied between 0.30 m and 1.40 m. Water transparency was lower in the warm-wet season (November–April) whereas the cool-dry season (May–August) exhibited the highest values of transparency, with averages of 0.40 m and 1.0 m Secchi depth for these seasons, respectively (Fig. 1a).

Surface water temperature ranged from 23°C to 27°C in the warmer season and from 18.9°C to 20.9°C in the cooler season. The differences in temperature and oxygen concentration between day and night were minimal. Thermal stratification was observed from September 1999 to May 2000; the thermocline gradually became deeper until the water column became thermally homogeneous in the winter (June and July, Fig. 1b). During the thermal stratification period, a clinograde pattern of distribution of oxygen was detected with the 1 mg $\text{O}_2 \text{ l}^{-1}$ boundary below the thermocline depth (Fig. 1c).

Densities of *Thermocyclops* and *Chaoborus* in the reservoir

The zooplanktonic community of Nado Reservoir was dominated by a simple array of species, most of them typical for eutrophic tropical freshwater.

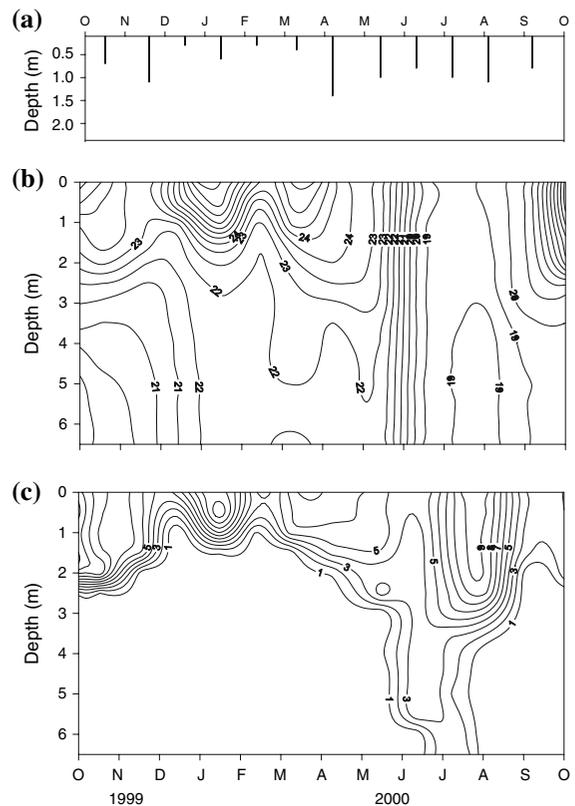


Fig. 1 Secchi depth in meters (a) and daytime isopleths plot of water temperature in °C (b) and dissolved oxygen in $\text{mg O}_2 \text{ l}^{-1}$ (c) in the Nado Reservoir during the study year (1999–2000)

Thermocyclops inversus, *Moina micrura*, and *Brachionus falcatus* were the most abundant organisms. The population of *T. inversus* exhibited their density minimum in January 2000 ($38.3 \times 10^3 \text{ ind m}^{-2}$) and the maximum in September 2000 ($5.2 \times 10^6 \text{ ind m}^{-2}$) (Fig. 2). Total larvae density of *Chaoborus* varied from 525 to 35,860 ind m^{-2} with an average density of $8,437 \pm 7,247$ (SD) ind m^{-2} (Fig. 2). The relative density of *C. brasiliensis* larvae from 1st, 2nd, 3rd instars larvae comprised on the average 7, 14, and 27% of the total population density of this dipteran, respectively, and the rest was contributed by 4th instar larvae.

DVM patterns and seasonal changes in the weighted mean depth of copepods

Changes in the vertical distribution patterns of developmental stages of *T. inversus* in Nado Reservoir were clearly discernible throughout the sampling

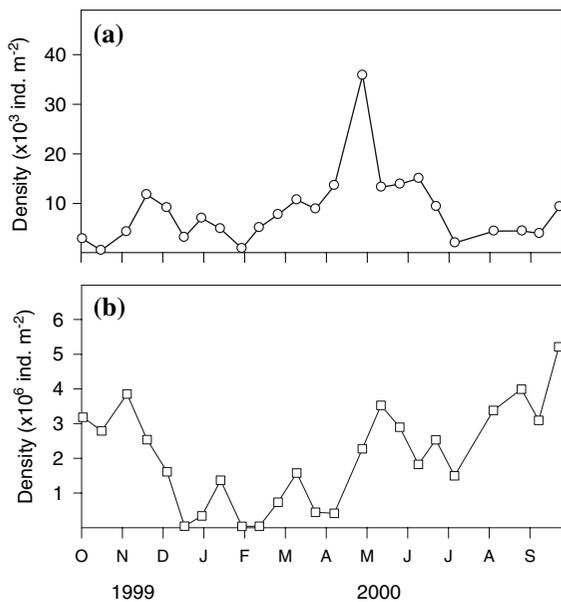


Fig. 2 Seasonal variation of *Chaoborus brasiliensis* (a), and total copepod population density (b), in Nado Reservoir throughout 1999 and 2000. Note the difference of scale between graphs

period (Fig. 3). During the summer stratification period, the relative abundance (percentage of total density in the water column) of the population was higher in the upper water layers (ca. 2 m). In May, with the downward sinking of the thermocline, copepodites, and adults also shifted to deeper layers. The animals avoided the surface layers during the daytime but moved back towards upper water layers at night, while peaks in abundance of nauplii were found in deeper waters both during day and at night.

There was a high, seasonal variability in daytime and nighttime weighted mean depths (DVM) among the different developmental stages of *T. inversus* (Fig. 4). Nauplii showed migration behavior only in November, February/99, and July/00 when day–night significant differences in vertical distribution were detected ($P < 0.05$, K-S test). In contrast, the mean depth of copepodites was significantly shallower at night than during the day ($P < 0.05$, K-S test) during all year, except in December 1999 and March 2000. The adult performed DVM more frequently and strongly than copepodites and nauplii, with day–night significant differences ($P < 0.05$, K-S test) throughout the study period, except in December 1999 when they were found in the same layer during both day and

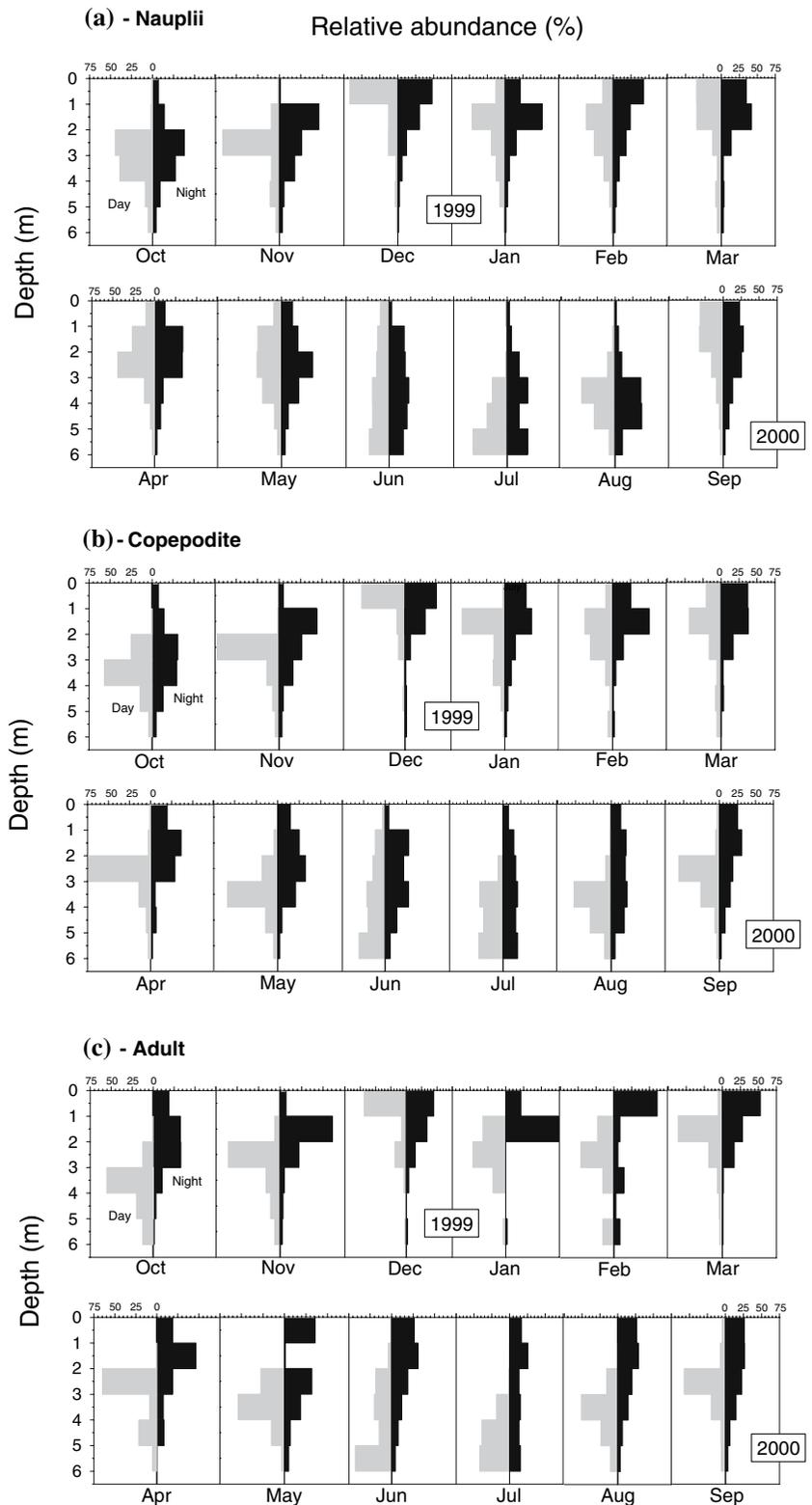
night. The DVM behavior of *T. inversus* displayed a clear ontogenetic trend, with the amplitude of DVM increasing with the age of the organism, and ranging from 0.4 m to 0.8 m for nauplii, 0.4 m to 1.2 m for copepodite, and 1.1 m to 2.1 m for adults.

The effect of oxygen gradient and invertebrates predators on copepod depth distribution

The behavioral strategy of *T. inversus* relative to depth and oxygen gradient became apparent when the WMDs and associated oxygen concentrations were considered together (Fig. 5). In the daytime, there was a progression of the WMD and oxygen levels inhabited by the different developmental stages. Nauplii were distributed at significantly shallower depths where oxygen was higher (paired *t*-test, $P < 0.05$) than the depth copepodites and adults. The mean WMDs for nauplii, copepodites, and adults were 2.66, 2.95, and 3.02 m, where mean oxygen values were 1.16, 0.74, and 0.81 $mg\ O_2\ l^{-1}$, respectively (Fig. 5). At night, the trend was reversed, with adults concentrated significantly in the upper and oxygenated waters (paired *t*-test, $P < 0.05$), while copepodites and nauplii were located at deeper and hypoxic layers. The mean WMDs were 2.39 for nauplii, 2.18 for copepodites, and 1.82 m for adults, with mean oxygen values at these depths of 1.44, 1.67, and 3.20 $mg\ O_2\ l^{-1}$, respectively (Fig. 5).

In order to test the environmental variables that influenced most significantly the distribution patterns of *T. inversus*, a series of stepwise logistic regressions were carried out. The analyses revealed that only the layers with low-oxygen levels ($<1\ mg\ O_2\ l^{-1}$ — ZO_2) and WMD of *Chaoborus*—as independent variables—significantly and differentially influenced the vertical position (WMD) of the population of *T. inversus* by day and at night (Table 2). Transparency (Secchi depth) never met the significance criteria to be included in the models. The depth of nauplii, copepodites, and adults during the day increased significantly with increasing depth of anoxic water, with R^2 values of 0.81, 0.79, and 0.73, respectively (Table 2). At night, the nauplii WMD was also predominantly influenced by oxygen depletion ($R^2 = 0.85$), while copepodites and adults were significantly and positively affected only by WMD of *Chaoborus*, with R^2 values of 0.78 and 0.77, respectively (Table 2).

Fig. 3 Vertical distribution of relative abundance (%) of *Thermocyclops inversus* in each developmental stage: (a) nauplii, (b) copepodite and (c) adult, during daytime (shaded) and nighttime (filled) in the Nado Reservoir, from October 1999 to September 2000



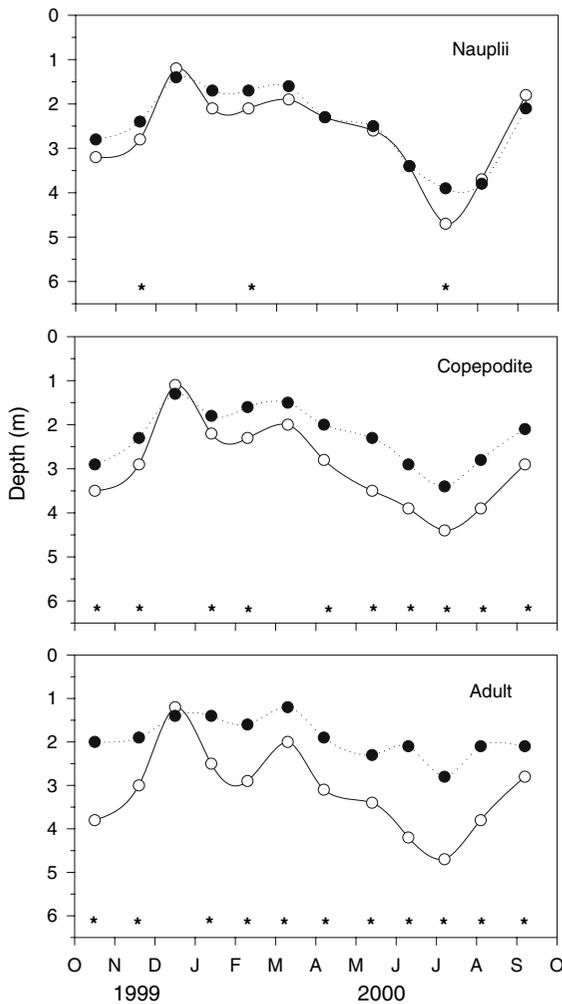


Fig. 4 Weighted mean depth (WMD) of *Thermocyclops inversus* (nauplii, copepodite, and adult) during the day (open circles) and night (closed circles) in the Nado Reservoir, from October 1999 to September 2000. Asterisks indicate significant differences between day and night

The weighted mean depths of the *Chaoborus* and life-history stages of *T. inversus* over time for both day and night distributions are shown in Fig. 5. *Chaoborus* exhibited normal vertical migration (up at night, down during the day). During the daytime, *Chaoborus* late instars were scarce or absent in the upper 4 m from September to April, and virtually disappeared from the water column during the dry season (May–August). The result was a minimal overlap between *Chaoborus* and *T. inversus* during the day and a variable one at night (Fig. 6). The mean daytime overlap values for the nauplii, copepodite,

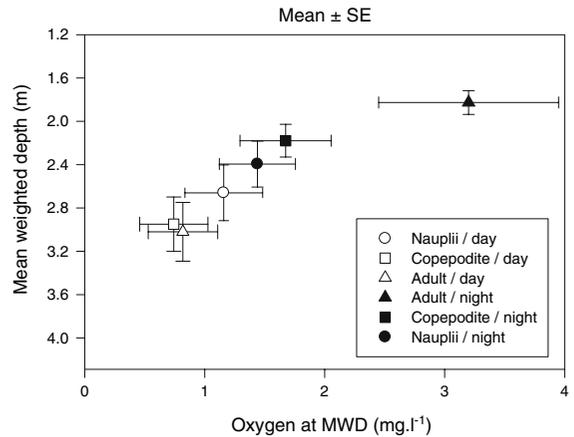


Fig. 5 Daytime (open) and nighttime (closed) weighted mean depth of each life stage (different symbols) of *Thermocyclops inversus* versus the oxygen at that WMD

and adult with *Chaoborus* were 0.34, 0.32, and 0.50, respectively. Thus, *T. inversus* population was segregated from *Chaoborus* during daytime in the study period. At night, the mean nighttime overlap values were 1.48, 1.34, and 1.15 for nauplii, copepodite, and adult, respectively, indicating that copepod and/or *Chaoborus* were almost uniformly distributed in the water column. If *T. inversus* did not perform DVM, except nauplii, the predator–prey overlap values would be significantly greater (paired *t*-test, $P < 0.05$) than the actual observed night distribution of predator and prey. The mean “without DVM” nighttime overlap values would be of 1.51, 1.77, and 1.71 for nauplii, copepodite, and adult, respectively.

Discussion

The data on the diurnal vertical distribution of *T. inversus* in Nado Reservoir provide evidence that this population performs diel vertical migration as a specific kind of depth-selection behavior. This statement is based on the significant differences detected between day and night vertical distributions. The migratory behavior of *T. inversus* can be characterized as normal vertical migration, with individuals ascending at dusk and a descending at dawn. The observed ontogenetic differences in the DVM behavior of *T. inversus*, confirm previous investigations concerning ontogenetic differences in migration of copepods (Taleb et al. 1992; Andersen et al. 2001;

Table 2 Multiple linear regressions summary for *Thermocyclops inversus* (nauplii, copepodite, and adult) weighted mean depth (WMD) using combined samplings daytime and nighttime dates

Stage	Model	R ²
<i>Day</i>		
Nauplii	LOG WMD = 0.218 + 0.518 LOG ZO ₂ day (<0.0001)	0.81
Copepodite	LOG WMD = 0.263 + 0.528 LOG ZO ₂ day (0.0001)	0.79
Adult	LOG WMD = 0.303 + 0.486 LOG ZO ₂ day (<0.0001)	0.73
<i>Night</i>		
Nauplii	LOG WMD = 0.235 + 0.447 LOG ZO ₂ night (<0.0001)	0.85
Copepodite	LOG WMD = -0.05 + 0.877 LOG WMD CHAO ₂ night (0.0012)	0.78
Adult	LOG WMD = -0.012 + 0.60 LOG WMD CHAO ₂ night (<0.0001)	0.77

Makino et al. 2003; Irigoien et al. 2004; Peticarrari et al. 2004). In Nado Reservoir, nauplii practically did not migrate, whereas copepodite and adults did show a distinct migration. Such differences have generally been attributed to large individuals, which being more conspicuous and, therefore more susceptible to visual predators, migrates to avoid being predated (Neill 1990).

Our work demonstrates that DVM occur during all year around in Nado Reservoir. The majority of the studies dealing with vertical migration of freshwater (e.g., Vuorinen et al. 1999; Gilbert and Hampton 2001; Winder et al. 2003; Chang and Hanazato 2004) and marine copepods (e.g., Andersen et al. 2001; Yoshida et al. 2004) does not shown the same pattern. However, seasonal variation was observed in the depth-selection behavior of *T. inversus* in the study period. The depth of vertical distribution is lesser during the period of marked stratification (October–April), but increases during the circulation period (June–September) (Fig. 4). The environmental changes in the water column during the winter season (circulation period from June to September) seems to be responsible for this trend. During this period, the upper layer is illuminated, the whole water column is oxygenated, and the copepods have only the darkness as a refuge zone. Consequently, day and night differences increase or, in other words, the amplitude of the vertical migration increases during the circulation period.

Our results indicate that the weighted mean depth (WMD) of different developmental stages of *T. inversus* correlate directly with depth of 1 mg O₂ l⁻¹ and with the WMD of *Chaoborus* larvae (Table 2). While Wissel and Ramcharan (2003)

suggest that the water transparency is the dominant factor affecting the daytime position for copepods our data show that, on a yearly basis, the oxygen concentration is the most important factor influencing the vertical position of the studied copepod population. However, as our study explores the seasonal variation in the depth distribution of copepods, the role of light on a diurnal basis in this environment is not completely understood. Apparently, a decreased oxygen concentration with depth has an overriding influence on the changes transparency with depth in our reservoir. Besides, considering the correlation between WMD of copepods and WMD of *Chaoborus* larvae, the results here presented are both intriguing and interesting because they suggest that DVM of *T. inversus* is triggered by the positioning of *Chaoborus* III and IV instars in the water column (Table 2). Irigoien et al. (2004), studying the DVM of the marine copepods *Calanus* spp. and *Pseudocalanus elongates* in the central and coastal Irish Sea, reported similar results. They stated that *Calanus* spp. and *P. elongates* appear to sense the position of the invertebrate predator chaetognaths in the water column, possibly using chemical cues, and adapt the amplitude and direction of their DVM accordingly.

Despite the absence of information on the abundance and the spatial distribution of fish populations, the migratory behaviors of both *Chaoborus* and the copepod *T. inversus* populations indicate that fish may play an important role in structuring the zooplanktonic community in the Nado Reservoir. The copepods seem to be continuously exposed to predation risks but can manage to escape through changes in habitat selection by DVM. *Thermocyclops*

inversus spends daytime hours well beneath the aerated surface layers of the reservoir while *Chaoborus* population is at or near the bottom. At night, these copepods ascend to superficial waters to escape from predation by *Chaoborus*. Our work provides evidence that the day–night vertical displacement of copepods in the water column is an important predator avoidance strategy since it reduces the

spatial overlap between prey (*T. inversus*) and its potential predator (*Chaoborus*) (Fig. 6).

Some studies have demonstrated that fish predation could cause the copepods to descend to deeper layers during the day, while the presence of *Chaoborus* could lead the copepods to ascend to upper layers at night (Taleb et al. 1992; Boeing et al. 2004). The depth-selection behavior of the copepod *Acanthodiaptomus denticornis* in Lake Aydat (France) observed by Taleb et al. (1992) is in accord with our field study. These authors concluded that the zooplankton growing in waters where both fish and *Chaoborus* are present simultaneously has to compromise between avoidance of: (a) the lighted and oxygenated surface water during the day to diminish predation by foraging fish predators, and (b) the hypolimnion at night when *Chaoborus* migrates out of the sediment.

The effect of the simultaneous presence multiple predators was also analyzed by Relyea (2003), who based on experimental field studies, the prey responds to the more risky of the two predator types. Thus, the optimal “decision rule” might be an intermediate strategy that balances the relative risk of the two predators. Otherwise, as Boeing et al. (2004) suggest, the zooplankton under the simultaneous, size selective pressures will be confined to a narrow water layer to minimize the risk of predation. In Nado Reservoir, the day and night vertical distribution of *T. inversus* is restricted by the two predators—fish and *Chaoborus*—and consequently its vertical position is concentrated in the metalimnetic layers (the narrow water layer as above described for Boeing et al. (2004)).

In conclusion, our results show that *T. inversus* exhibit normal DVM and can tolerate low levels of oxygen during daylight time during practically all year. These results emphasize the importance of anoxic layers as a refuge against vertebrate predators in eutrophic systems. This study also provided evidence of the major function of invertebrate predation for maintaining the vertical patterns of distribution of a dominant copepod population in a tropical and shallow reservoir.

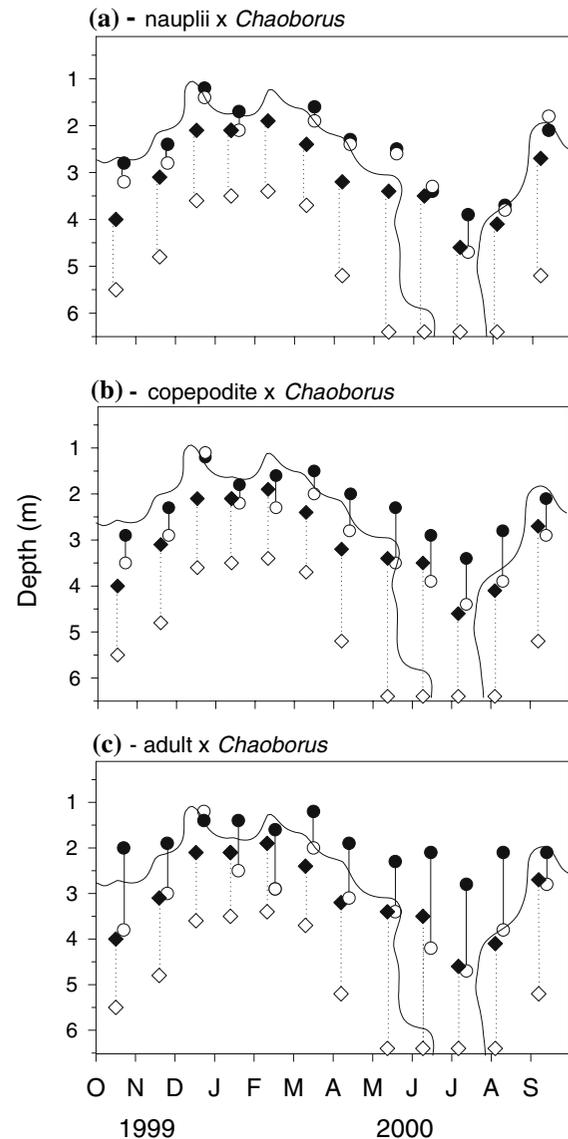


Fig. 6 Weighted mean depth (WMD) of predator *Chaoborus* (day, open diamonds; night, closed diamonds) and prey (*Thermocyclops inversus*—day, open circles; night, closed circles) in the Nado Reservoir during the study year (1999–2000). Isoleths indicates the depth of $<1 \text{ mg O}_2 \text{ l}^{-1}$

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