

# Diel Vertical Migration by Copepoda, Cladocera, and Rotifera in Lake Texoma (Oklahoma-Texas)

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# Abstract

The functional role of animals in marine and freshwater systems is as diverse as the many species occupying these unique habitats. Physical, chemical and biological parameters affect the behavior and distribution of aquatic organisms and influence the overall productivity of aquatic ecosystems. In planktonic communities, diel vertical migration (DVM) is a behavioral response to the physico-chemical and biological variables within oceans and lakes. There are several theories of DVM, which include predator avoidance, escape from harmful ultraviolet light, migrating to optimal temperature depths and migrating to food-rich zones. Three major taxonomic groups dominate zooplankton communities: phylum Rotifera, and two subclasses of crustaceans, the Cladocera and Copepoda. In this study, I tested DVM on these three groups of zooplankton in order to see if there is a relationship between DVM and the solar and lunar photoperiods. Copepods dominated the samples taken in all depths and sampling periods. Rotifers and cladocerans made up one fourth of the sampling effort. Cladocerans showed a significant migration towards the surface starting around sunset and had a maximum concentration right before midnight. Both copepods and rotifers exhibited significant migration to surface waters, beginning around local noon. Rotifer concentrations at the surface were greatest at midnight; however, copepod concentrations at the surface peaked at sunset. Relationships between surface migration and time of day was strong for all three groups. Correlation with vertical migration and apparent lunar position showed a strong association with copepods and rotifers.

Keywords: Diel vertical migration, zooplankton, predator avoidance theory, euphotic zone, photosynthetically available radiation, day-night photoperiod.

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# 1. Introduction

Zooplankton exhibit extraordinary migratory abilities, conducting massive migrations on a daily basis (Williamson, et. al. 1996). Both marine and freshwater planktonic communities are well documented to have shown some display of diel vertical migration (DVM), which varies among species, gender, reproductive status and even intrapopulational genetic variation (Hays et. al. 1995, King and Miracle 1995). General theories to the adaptive significance of DVM are predator avoidance (Hairston, 1979; 1981, Lueke and O'Brien 1981, Hays et. al. 1995, King and Miracle 1995, Nesbitt et. al. 1996), escape from photoinhibition by light attenuation through the absorption plant, alga, or cyanobacterium which lowers the efficiency of photosynthesis (Luecke and O'Brien 1981, Tyystjärvi and Aro 1996, Willamson, et. al. 1996), metabolic respiration and energy reserves ( Byron 1982, Hays et. al. 1995), and to increase fecundity by seeking lower temperature zones (Hays et. al. 1996).

 Numerous studies of DVM have been devoted to the predator avoidance theory, where zooplankton remain in the darker depths during daylight in order to avoid visually-oriented predators, migrating to surface waters at night to forage; an acumen in which visual predators are unable to see prey at night and the risk of predation is low (Turner 2004, Putri and Hadisusanto 2016, Govindarajan et al. 2023, Berger and Tarrant 2024, Hagemann and Venås 2024). In freshwater lakes, DVM is more prominent where there are abundant planktivorous fishes, and the opposite generally holds true in fishless lakes (Hays et. al. 1995, Berger and Tarrant 2024). Zooplankton DVM also contribute to nutrient cycling in lakes (Putri and Hadisusanto 2016).

 Zooplankton are generally observed to migrate to the surface during periods of darkness, where maximum concentrations are found between sunset and sunrise (Wetzel 1983). In some species, there are two maxima in surface waters, one at ending evening twilight, the other at beginning morning twilight (Wetzel 1983). Several physicochemical factors contribute to zooplankton DVM; the main abiotic factor being light penetration through the water column (Putri and Hadisusanto 2016). In an oligotrophic lake (relatively low in plant nutrients with more dissolved oxygen at deeper depths), zooplankton DVM is found at lower depths. On the other hand, a eutrophic lake such as Lake Texoma, is rich in nutrients which supports dense populations of phytoplankton. Dissolved oxygen and light through the water column are restricted to shallow depths of eutrophic lakes where zooplankton DVM is shown to occur more often at these depths (Putri and Hadisusanto 2016). In summa, there is evidence to suggest that there is a relationship between DVM and photoperiod.

 I tested the hypothesis that zooplankton exhibit DVM towards the surface during periods of darkness. My intent was to cover sampling periods from sunrise to midnight in order to observe any distinct migratory patterns towards surface waters. The study was done at Lake Texoma (Oklahoma-Texas) which is a meromictic, eutrophic freshwater lake and supports planktivores, to include planktivorous fish such as the American gizzard shad, Dorosoma cepedianum (Rolbiecki 1998).

#### 2. Materials and Methods

#### 2.1. Field site

I chose Intensive Station 3 (33º52'26"N, 96º50'01"W, depth 13m) at Lake Texoma (Oklahoma-Texas) as my study site because of its historical significance in water quality monitoring (Atkinson et.al. 1996; 1999). Lake Texoma is situated on the border between north central Texas and southeastern Oklahoma and is fed by the Red and Washita rivers. The watershed encompasses a  $102,870$ -km<sup>2</sup> area consisting of primarily agricultural land use that drains into the 36,000-hectare impoundment (Mathews et al. 1985).

 The lake has been documented to have four distinct zones based on historical water quality studies (Atkinson et al. 1996, Rolbiecki 1998) plus one recently identified zone. These four plus the additional are: 1) Red River Zone (where Station 3 is situated); 2) Red River Transition Zone; 3) Main Lake Zone; 4) Washita River Zone; and the addition of the Washita River Transition Zone (Fig. 1). The Red River and Washita River arms are reported (Mathews et al. 1985) to be shallow ( $\approx 18$  m); the Main Lake Zone being the deepest at the confluence of the two arms near the Denison Dam (22-26 m).

 Lake Texoma is separated into three distinct layers: 1) Epilimnion (the top layer of relatively shallow depth where the euphotic zone is limited to; 2) Metalimnion (the middle layer characterized by a steep change in water temperature known as the "Thermocline"; 3) Hypolimnion (the cold, dense layer of water exhibiting anoxic conditions and the substrate contains detritus material, and usually where a strong vertical "Chemocline" is detected containing higher concentrations of suspended solids and gasses; Rolbiecki 1998, Atkinson et al. 1999). Eutrophic lakes tend to be shallow; oftentimes being man-made reservoirs fed by rivers. Meromictic lakes tend to have little "mixing" of its three layers. During the summer and winter seasons, this generally holds true, and is the optimal time to measure the chemical, physical and biological properties of the lake at selected depth intervals. During the spring and fall seasons, where cyclonic storm systems bring about rain and high winds, mixing of the layers may occur (Rolbiecki 1998).

 Lake Texoma exhibits a steep longitudinal gradient of water quality from the shallow river zones to the deep body of the main lake near the Denison Dam. Water turbidity is greatest in the Red and Washita River Zones, and the Red and Washita River Transition Zones. It is gradually diluted as the river undercurrents flow into the Main Lake Zone (Rolbiecki 1998).





Fig. 1. Map of Lake Texoma (Oklahoma-Texas showing Intensive Study Site 3 along with the historic routine and intensive sites sampled from 1996-1997 during the University of Texas Water Quality Monitoring Program of Lake Texoma.

# 2.2. Sampling Protocol

The sampling took place from a boat on 15-16 March 1997 from 0630-0000h Central Standard Time (CST). A first-quarter moon was observable from 1400-2400h. Using a Wisconsin closing plankton net (12cm-diameter opening), I pulled 2-meter interval samples every 2h (day-night), from 12 m to the surface (Hays et.al. 1995). This procedure generally followed sampling methods by King and Miracle (1995) and Nesbitt and Ramcharan (1996). Each 2 m sample was washed into a 100 ml bottle and preserved with about 2 ml of Lugol's solution (Williamson et.al. 1996); labeled and stored for later lab analysis.

 Physicochemical factors of temperature, dissolved oxygen and light through the water column for each 2 m pull were measured using a YSI Model 10 temperature-dissolved oxygen meter, which was calibrated prior to each sampling hour. Downwelling solar light attenuation in the Epilimnion layer was measured for photosynthetically available radiation (PAR) every 2 m down to the euphotic zone with a Protomatic submarine photometer. The euphotic zone is the maximum depth  $(Z_{eu})$  in which light used for primary production in lakes and oceans by phytoplankton is at 1 percent of PAR (Rolbiecki 1998, Frouin and McPherson 2012, Wu, 2021).

#### 2.3. Laboratory Identification

Zooplankton specimens were sorted and identified by aliquot method (Lind 1983) using a Sedgwick-Rafter counting cell with coverslip under a compound microscope. A 1-ml-capacity Hensen-Stempel pipette was used to draw sample water from a stirred 100 ml beaker to place onto the counting cell. Specimens were counted and sorted into three major groupings: subclasses Copepoda and Cladocera, and phylum Rotifera, regardless of their life cycle or reproductive status.

# 2.4. Data Analysis

Number of zooplankton per 2 m pull was calculated by:

$$
V = \pi \times r^2 \times d \times 1000 \tag{1}
$$

where  $V =$  the volume of the 2m pull,  $r =$  the radius of the opening of the Wisconsin closing plankton net,  $d =$  the depth of the pull (in meters),  $1000 =$  the number of liters in a cubic meter

Using V, the number of zooplankton per liter from each 2m pull was calculated by:

No. of Zooplankton ⋅ L<sup>-1</sup> = No. of Zooplankton ⋅ ml<sup>-1</sup> × Volume of Sample (in ml) ÷ V (2)

 Percentages of the number of each major taxonomical group were obtained for the entire 18h sampling period. Differences in 12-, 6- and 2-meter sampling depths among the numbers of each taxonomical group per liter of lake water were analyzed using one-way ANOVA ( $p \le 0.05$ ) (Zar 1996) for sampling periods 1200-1800h and 1800-2400h. Linear regression was run to find if there was a relation between the number of zooplankton per liter by sample depth and time of day. Correlation analysis was used to determine the degree of association among the same samples and apparent lunar position.

# 3. Results

#### 3.1. Physical data

Apparent height (arc degrees above horizon) of the centers of the sun and moon, and dissolved oxygen and temperature taken every 2 m from a depth of 12 m to the surface were compared (Fig. 2 and 3). Sun and moon upper transits occurred around 1230h and 1830h, respectively. See Appendix I for physical data summary. Temperatures at 2 and 12 m remained fairly constant (within 1º C) whereas dissolved oxygen showed a distinct drop at both depths between 1800-2200h, indicating respiration taking place after photosynthesis shut-down following sunset (Fig. 2).



Fig. 2. Height of sun, moon and mean dissolved oxygen in the water column taken every 2m from a depth of 12m to the surface at Station 3, Lake Texoma from 15-16 March 1997.



Fig. 3. Height of sun, dissolved oxygen and temperature in the water column shown at 2m and 12m depths to the surface at Station 3, Lake Texoma from 15-16 March 1997.

Mean depth of the euphotic zone  $(Z_{eu})$  was 3.1 m by inverse prediction of the dependent variable (log natural % light transmission) and the independent variable (depth) from the regression model (Koenings and Edmundson 1991). Zeu is an important indicator of the vertical distribution of phytoplankton, where herbivorous zooplankton spend time foraging.

#### 3.2. Vertical distribution of zooplankton

Copepods dominated the three taxonomical groups in all sampling periods, followed by rotifers and cladocerans (Fig. 4). Although not recorded, nauplii of copepods and cladocerans were prevalent based on an eyeball assessment. Refer to Appendix II for a breakdown of samples by sampling period and depth. Distribution of cladocerans shows a downward migration from the surface down to12 m from 1130-1800h (Fig. 5). At 1800h a reverse trend occurred, reaching maximum numbers at 2230h at 2 m. Between 1600 and 2230h, a near linear relationship between the number of cladocera per liter and time of day was found ( $r^2 = 0.7651$ , n = 4, Fig. 6). Copepod distribution shows an increase in numbers per liter at 2 and 6 m beginning with the first sampling period to 1600h (Fig. 7). At 1600h, a sharp increase occurred at 2 m and peaks at 1800h. Copepod numbers at 12 m dropped significantly at 1600h and leveled out afterward. A strong, positive linear relationship between the number of copepods per liter and 1200-1800h sample periods, and a strong, negative relationship from 1800- 2400h ( $r^2$  = 0.892, n = 4;  $r^2$  = - 0.919, n = 4, respectively, Fig. 8).



Fig. 4. Percent zooplankton taken from vertical tow net pulls through the water column every 2m down to 12m every 2 hours at Station 3, Lake Texoma from 0630-2400h on 15-16 March 1997.



Fig. 5. Number of Cladocera per liter by depth taken with plankton vertical tow net pulls through the water column at 2m intervals down to 12m at Station 3, Lake Texoma from 0630-2400 hours 15-16 March 1997.



Fig. 6. Relationship between time of day and number of Cladocera per liter taken with plankton vertical tow net pulls through the water column at 2m intervals down to 12m at Station 3, Lake Texoma from 1600-2200h on 15 March 1997.



Fig. 7. Number of Copepoda per liter by depth taken with plankton vertical tow net pulls through the water column at 2m intervals down to 12m compared to the height of the sun at Station 3, Lake Texoma from 0630-2400 hours on 15-16 March 1997.



Fig. 8. Relationship between time of day and number of Copepoda per liter taken with plankton vertical tow net pulls at 2m intervals down to 12m from 1200-1800h and 1800-2400h on 15-16 March 1997.

 The distribution of rotifers showed an increase in numbers per liter at 2 and 6 m beginning at the first sampling period, all the way to 2400h, where they reached their maximum numbers (Fig. 9). Samples at 12 m showed a downward concentration throughout the entire sampling period. A strong, linear relationship is shown between the number of rotifers per liter and the entire sampling period ( $r^2$  = 0.842,



Fig. 9. Number of Rotifera per liter by depth taken with plankton vertical tow net pulls at 2m intervals down to 12m compared to the height of the sun at Station 3 Lake Texoma, from 0630-2400h on 15-16 March 1997.



Fig. 10. Relationship between time of day and number of Rotifera per liter taken with plankton vertical tow net pulls at 2m intervals down to 12m from 1200-2400h on 15 March 1997.

 The differences of 2, 6 and 12 m depths among each taxonomical group for 1200-1800h were not significant (one-way ANOVA, Table 1 (a)). However, from 1800-2400h the differences were significant among all three groups, with copepods and rotifers were highly significantly different (one-way ANOVA, Table 1 (b)).

# Table 1 (a) 1200-1800h



# Table 1 (b) 1800-2400h



Table 1. Vertical distribution (Number ∙ L -1) of zooplankton for sampling periods 1200-1800h (Table 1 (a) and 1800-2400h (Table 1 (b).  $S =$  significant,  $HS =$  highly significant,  $NS =$  nonsignificant (one-way ANOVA).

 Correlation between lunar height and zooplankton numbers was strong for only copepods and rotifers during upper lunar transit (Fig. 11). Copepods show a strong correlation during lower transit, whereas rotifers show a mild association.



Fig. 11a. (1200-1800h) Copepoda

Fig.  $11b. (1200-1800h)$ Rotifera



Fig. 11. Correlation between zooplankton and lunar height. Figures 11a and 11b represent sampling from 1200-1800h. Figures 11c and 11d represent sampling from 1800-2400h on 15 March 1997.

#### 4. Discussion

Temperature and dissolved oxygen, although important parameters affecting the distribution of living organisms (Wetzel 1983), did not directly affect the diel vertical distribution of zooplankton in my study. Temperature and dissolved oxygen were fairly constant throughout the study (Fig. 2 and 3) and did not exhibit any stratification that could influence vertical migration (Willamson, et. al. 1996). It would be interesting to see if temperature and dissolved oxygen plays a more significant role in diel vertical migration during periods of summer stratification, when the lake has a clear debarkation from epilimnetic to hypolimnetic values (Mathews, et. al. 1985, Atkinson, et. al. 1996). The day-night photoperiod was clearly the master abiotic factor affecting zooplankton distribution at Station 3.

 Cladocerans were more concentrated towards bottom during daylight hours and migrated upward in late afternoon and into the night (Fig. 6), which supports studies by King and Miracle (1995), and Williamson et. al. (1996). Cladocerans and rotifers both congregated near the surface in large numbers near the time of midnight (Fig. 5 and 9) which was similar to the results of the Hays et. al. (1996) study of Atlantic copepods. However, even though copepods and rotifers were similar in upward migration in my study, there was a distinct peak at 1800h for copepods (Fig. 8) that was not observed in the Hays study.

 Copepods constitute the largest zooplankton population in the world (approximately 70–90%; Turner 2004). Copepods at Station 3 showed a strong association with lunar transit and may time their upward vertical migrating using lunar illumination in order to detect prey with their photoreceptors; however, the primary method for prey capture is apparently by random encounters (Wetzel, 1983). In comparison to a shallow, temperate African estuary, my observations show the opposite effect on the influence of lunar activity, where Jerling and Wooldridge (1992) observed adult copepods migrating towards the bottom on full-moon nights. Their study takes into account instar stages, gender and reproductive status. There are not enough data in my study to support a hypothesis that increased lunar illumination causes copepods to migrate near the surface to find prey, and therefore it is purely speculative. A more concentrated effort on intra-species interactions to include reproductive behavior over an extended diel period of several days may see a trend in the behavior of zooplankton influenced by the lunar period.

 Although I did not conduct experiments on predator-prey interactions, these data may suggest zooplankton migrate towards to surface at night in order to exploit the resources at upper depths without the risk of predation by visual predators (Nesbitt et. al. 1996 and Williamson, et. al. 1996). Lake Texoma does have planktivores, to include other zooplankton, macroinvertebrates (Nesbitt et. al. 1996), and planktivorous fish, such as the gizzard shad, *Dorosoma cepidianum*. The adaptive significance in predator avoidance through vertical migration at night would be increased fitness of zooplankton that exhibit this behavior (Nesbitt et. al. 1996).

 In conclusion, I believe the zooplankton activity at Station 3 exhibits a strong tendency to migrate to surface waters in periods of darkness. My presumption is based only on the data collected from 15-16 March 1997 that diel vertical migration is contingent upon the photoperiod. Further data to include all four lunar phases over time is needed from all of the sampling sites on Lake Texoma to support this theory.

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# Appendices



Appendix I. Physical and chemical data taken at Station 3, 15-16 March 1997.





Appendix II. Volume of zooplankton per liter taken by vertical tow net at Station 3, Lake Texoma between 0630h 15 March and 0000h 16 March 1997 Central Standard Time (CST).



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