Migración vertical del zooplancton en un lago de montaña tropical profundo

Elsa Ma. de Fátima Reyes Morales [1]/ fatimarys3@gmail.com, **Margaret A. Dix** [2] , **Jorge A. Ortiz** [3]

[1] Departamento de Investigación y Calidad Ambiental, Autoridad para el Manejo Sustentable de la Cuenca del Lago de Atitlán y su Entorno (AMSCLAE).
[2] Centro de Estudios Atitlán, Universidad del Valle de Guatemala (CEA-UVG).
[3] Centro de Estudios del Mar y Acuicultura (CEMA), Universidad San Carlos de Guatemala, Ciudad Guatemala, Guatemala.

RESUMEN: La distribución y migración vertical diaria (MVD) del plancton ha sido observada en muchas localidades y en muchas especies diferentes en el lago Atitlán. El objetivo de este estudio fue reconocer los patrones de migración vertical diaria de las comunidades de zooplancton y relacionarlas con algunos parámetros hidrológicos. La caracterización del agua y la migración vertical de zooplancton en el lago Atitlán fue medida entre abril y mayo del 2018 por un período de 20 h (5:00 - 22:00 h) y en múltiples profundidades (0 - 30 m). La comunidad de zooplancton del lago Atitlán fue dominada por *Ceriodaphnia*, *Keratella* y Cyclopoida. La densidad del zooplancton fue mayor en la bahía de Santiago entre los 10 y 15 m de profundidad y alrededor de las 16:00 y 22:00 horas. Los datos mostraron que la migración vertical ocurre en ambos sitios, la migración ascendente crepuscular fue observada en Cladócera y la migración inversa en rotíferos. La mayoría de las especies migran hacia arriba cuando la intensidad de la luz superficial decrece y hacia abajo cuando la intensidad de la luz incrementa. Sin embargo, la MVD es inducida principalmente por la fuente de alimento, el escape a la depredación y el estado trófico. Conocer las dinámicas fisicoquímicas y bióticas del plancton en el lago Atitlán es esencial para recomendar estrategias de manejo y así reducir los procesos de eutrofización.

PALABRAS CLAVE: Migración diaria horizontal; nauplios; migración nocturna; Panajachel; interacciones tróficas.

Diel vertical migration of zooplankton in a deep tropical mountain lake

ABSTRACT: The diel vertical migration (DVM) and distribution of plankton has been observed in many localities for many different species in Lake Atitlán. The present study was carried out to recognize the patterns of diel vertical migration of the zooplankton community and to relate them with some hydrological parameters. Water characteristics and vertical migrations of zooplankton in Lake Atitlán were measured between April to May 2018 over a 20-hr period (5:00 - 22:00 h) and at multiple depths (0 - 30 m). The zooplankton community in Lake Atitlán was dominated by *Ceriodaphnia*, *Keratella* and Cyclopoida. The zooplankton density was higher at Santiago bay at 10 to 15 meters depth and around 16:00 to 22:00 hours. Our data show that Diel Vertical Migration occurred in both sites, twilight upward migration was observed in Cladocera and inverse migration in the rotifers. Most species migrated upward as the surface light intensity decreases and downward with an increase in light intensity. Nevertheless, DVM was induced mainly by food source, predation avoidance and trophic state. The knowledge of the plankton behavior in Lake Atitlán is essential to understand the physicochemical and biotic lake dynamics and recommend management strategies to reduce the eutrophication process.

KEY WORDS: Diel horizontal migration; nauplii; nocturnal migration; Panajachel; trophic interaction.

Introduction

Diel vertical migration is defined as vertical displacement of an individual or a group of individuals that occurs with a daily periodicity (Torres y Estrada, 1997). Ohman (1990) describe that there are three types of diel vertical migration behavior for zooplankton populations: (1) reverse migration (nocturnal descent), (2) normal migration (nocturnal ascent), and (3) no detectable migration. Zooplankton diel vertical migration (DVM) is an ecologically important process, affecting nutrient transport and trophic interactions in lakes and oceans. Predation, light, food availability, and temperature are recognized as the main DVM drivers; however, there are others like moon illumination, ultraviolet radiation, competition, chemical and physical characteristics (Kumar et al., 2015; Last et al., 2016; Dumont, 2019; Simoncelli et al., 2019). The predominant migration behavior (reverse, normal, or no migration) varies depending on whether the primary mortality source is predation by nocturnally feeding zooplankton or visually hunting planktivorous fish (Ohman, 1990). However, it has been proposed that migratory behavior is not structured by the degree of predation in surface waters but by temperature gradients in the water column (Torres y Estrada, 1990; Werner y Buchholz, 2013). Changes in temperature and thus viscosity over time impact upward migration velocity and by extension escape velocities from predators: in warmer and less viscous waters zooplankton can escape faster and more efficiently thus reducing, their predation risk (Simoncelli et al., 2019).

The diel vertical migration and distribution of plankton has been observed in many localities for many different species, in the case of Lake Atitlán by Meek, 1908; Juday 1915; Weiss, 1971; and De Leon and Reyes, 2017. Weiss (1968) sampled series at 22 lake stations in an attempt to establish some order of magnitude to the vertical distribution patterns of the dominant phytoplankton species and the total zooplankton along a 20 m depth transect. The results were compared with those of Juday (1915) and some differences were found, especially in taxa diversity. Weiss (1971) also observed no regular zooplankton pattern distribution in Lake Atitlán during the whole survey period (Jul '68, Nov '68 and Jan '69) and noted that zooplankton populations were probably associated with diurnal vertical migration, a characteristic seasonal change in population structure and showed that the richest stations were in the two shallower bays of the lake. Nevertheless, he did not perform any analysis that linked migration patterns with physical parameters. For this reason, this study aims (1) to evaluate the diel vertical migration of zooplankton, explore and explain for the first-time diel migration in the field and (2) to understand its relationship with some environmental factors, which drive the rate of zooplankton migration under real field conditions.

Materials and methods

Study area: Lake Atitlán is of volcanic origin and is situated at 90°11' west longitude and 14°42' north latitude in the republic of Guatemala. It is 18.91 kilometers long, 13 kilometers wide, 327.56 meters maximum depth and located 1556 meters above sea level. The surface temperature of the lake throughout the period of this investigation remained uniform, less 2 °C during the day but dropping 3 or 4 degrees within a few hours after sunset. Lake Atitlán is in an eutrophication process changing from oligotrophic to mesotrophic associated with changes in phytoplankton assemblage dominated by *Limnoraphis* and *Microcystis* (Rejmánková et al., 2011; Dix et al., 2012).

Two stations were established in Lake Atitlán (Fig. 1): Santiago Bay (428009 W, 1629273 N), 50 m depth and Panajachel (420215 W, 1618127 N), 230 m depth. The water is clear, with an average Secchi disc depth of 6.52 ± 1 m (Santiago Bay) and 7.23 ± 2.5 m (Panajachel). Heavy winds generate high waves that occur from 11:00 onwards, mixing the upper water column (20 m), every day. The study was carried out in April and May 2018 at the first quarter moon phase. Santiago Bay is a very productive site with an annual average chlorophyll-*a* concentration of about 3.39 μg L^{-1} whereas Panajachel averages 2.44 μg L^{-1}. The ambient light in the water column decays near 10 m depth with a photosynthetically active radiation < 50 μE m^{-2} s^{-1} (AMSCLAE, 2017; Dix et al., 2012)

Field survey and data collection: Samples were taken from 5:00 to 22:00 hours (5:00, 8:00, 12:00. 16:00, 19:00 and 22:00) on April 26 (Panajachel) and May 22 (Santiago Bay) at 0, 5, 10, 15, 20, 25 and 30 m. The sampling device was a 3.2-liter Van Dorn bottle, which could be closed from the surface
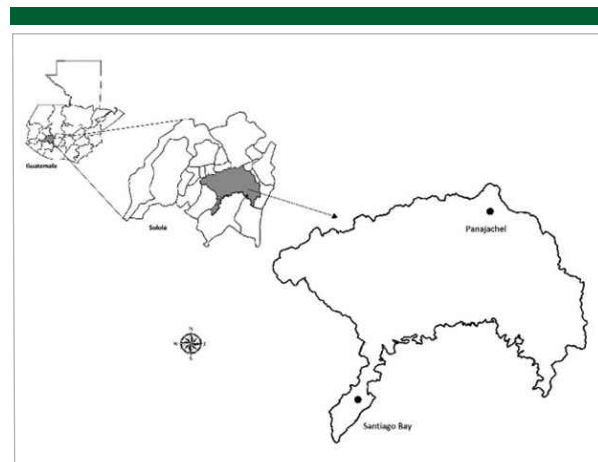

Figure 1. Study area and stations, Lake Atitlán.

by a messenger weight. Two samples were collected at each depth for a 6.4-liter total sample. The samples were filtered through a 20-μm plankton mesh net and were preserved in a 4 % formaldehyde solution.

In the laboratory, three quantitative counts were made using a Ward counting wheel (10 ml) under a phase contrast microscope at 100 x for a total of 30 ml per sample. The identification of the organisms was carried out to the lowest taxonomic level possible using taxonomic keys (Thorp and Covich, 2001; Witty, 2004).

The population density (expressed as Ind L^{-1}) of each taxon was calculated using the number of individuals per sample, initial volume, final volume and counted volume. For the kite charts, the density data was log-transformed (log +1) and plotted using R v3.4 base package (R Core Team, 2017).

Temperature, pH and dissolved oxygen concentration were recorded at each sampling point and at each depth and hour of sampling with a multiparametric probe (HACH HQ40). Transparency was recorded with a 2 cm diameter Secchi disc. Chlorophyll-a concentration profiles were acquired using a multiparametric probe (RBR Maestro) a week before zooplankton sampling and between 7:00 to 10:00 h.

Data analysis: To analyze diel vertical migration (DVM), taxon densities at each location were plotted according to depth and hour to produce a profile kite of zooplankton abundance per site per time of day. The mean density by hour (MDH) was used to evaluate the differences between the diurnal (mean of 8:00, 12:00 and 16:00) and nocturnal (mean of 19:00 and 22:00) vertical distribution of zooplankton in the two sampling sites. Samples from 5:00 hour were not included on the statistical analysis because samples were collected under dark conditions and the rest of samples under light conditions. A non-parametric Kruskal-Wallis test was applied to test the differences between day and night vertical distributions. A multifactorial ANOVA was used to determine if zooplankton density was significantly different at each depth and at each time of day. All statistical analyses were performed with R v3.4 base package (R Core Team, 2017).

Results and discussion

The zooplankton taxa found in Lake Atitlán were cladocerans (*Bosmina*, *Ceriodaphnia*, *Daphnia* and *Diaphanosoma*), copepods (calanoid and cyclopoid) and rotifers (*Asplanchna*, *Brachionus* and *Keratella*) (Table 1). The zooplankton population was composed mainly of cladocerans (*Ceriodaphnia* and *Daphnia*), rotifers (*Keratella*) and copepods (Table 1), the remaining genera had lower frequencies. Copepod nauplii represent 48% of the zooplankton population (Ind. L^{-1}) (Table 1) and their distribution was uniform along the water column. Diurnal zooplankton abundance at Santiago Bay and Panajachel was low but high nocturnal abundance was observed (Fig. 2). Zooplankton density was higher at Santiago Bay, around 10 to 15 meters depth and at night in comparison to Panajachel (Fig. 2).

Table 1. Panajachel and Santiago Bay relative frequency and total density of zooplankton taxa.

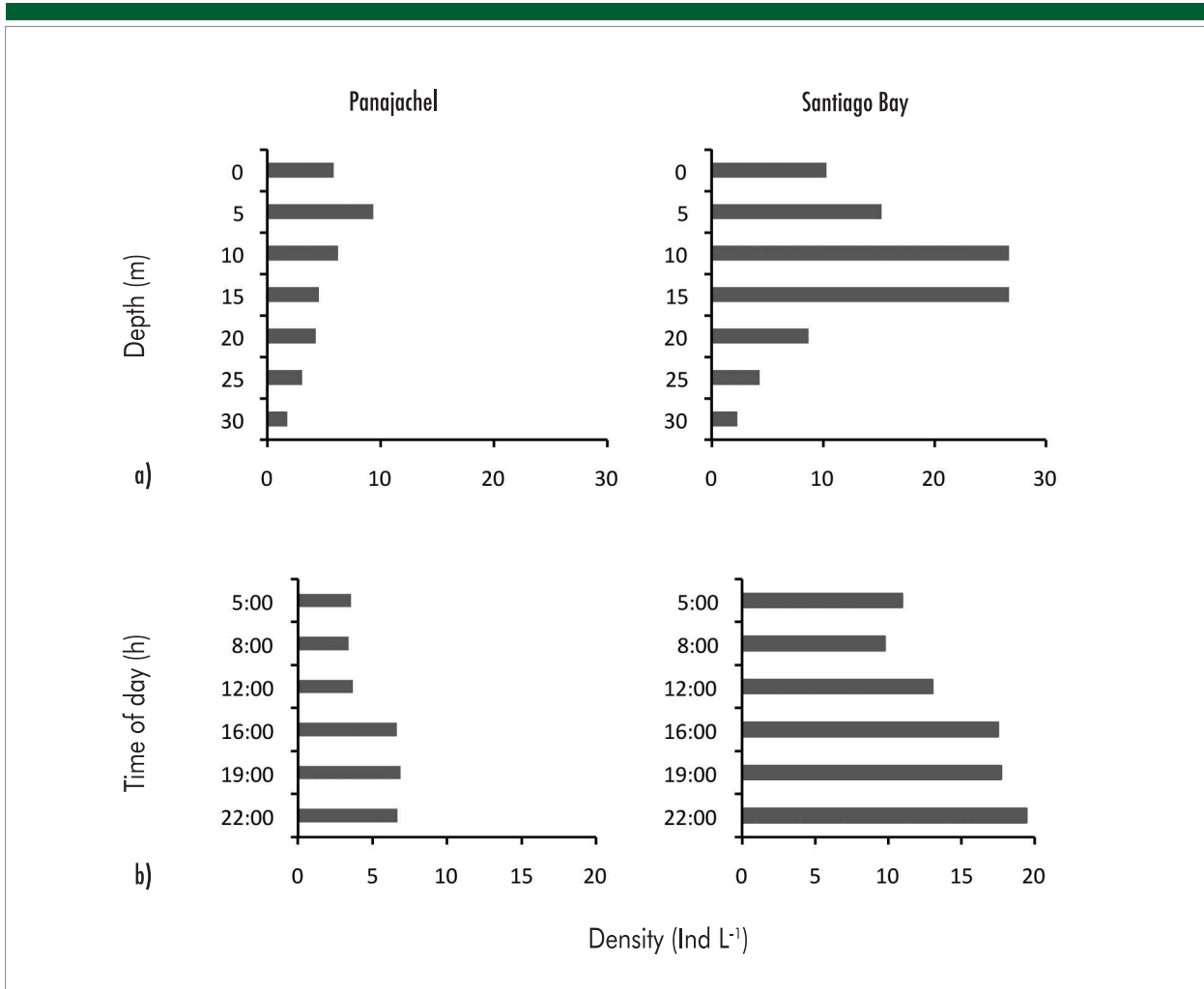| Taxa		Relative Frequency (%)	Total Density (Ind. L^{-1})	
			Panajachel	Santiago Bay
Cladocerans	*Bosmina*	6	23	10
	Ceriodaphnia	13	573	575
	Daphnia	11	23	154
	Diaphanosoma	9	27	83
Copepods	*Calanoidea*	12	56	295
	Cyclopoida	13	196	483
	Nauplii	13	482	2974
Rotifers	*Asplanchna*	6	1	238
	Brachionus	4	0.3	19
	Keratella	13	159	812

Figure 2. Average value of zooplankton density by depth (m) and time of day (h) in Panajachel (left) and Santiago Bay (right).

DVM was evident in most genera. There were two basic migration patterns: nocturnal, with a major density at surface, between sunset and dawn, and diurnal, with a zooplankton rise to the surface during daylight (Fig. 3). Most crustaceans showed nocturnal migration (*Daphnia, Ceriodaphnia, Diaphanosoma*), rotifers didn't show a clear migration pattern. Cladocerans and copepods migrated from both the epilimnion (downward) and the hypolimnion (upward) (Fig. 3) during the day. However, some genera appeared to have migrated from the epilimnion (downward) to deeper zones below 30 m and some genera remained at the surface (0 - 10 m) all day and night. The greatest densities of juvenile copepods (nauplii) (41 ± 63 Ind L^{-1}) were found at sunset between 0 to 15 m depth (Fig. 3), and in some cases, remained uniform along the water column. Rotifers in Santiago Bay were present all day and at all depths, especially *Keratella*. *Asplanchna* and *Brachionus* were scarce in Panajachel, and only appeared sporadically (Fig. 3), in Santiago Bay, they occupied different niches; *Asplanchna* remained at the surface (0-15 m) and *Brachionus* between 10 and 20 m.
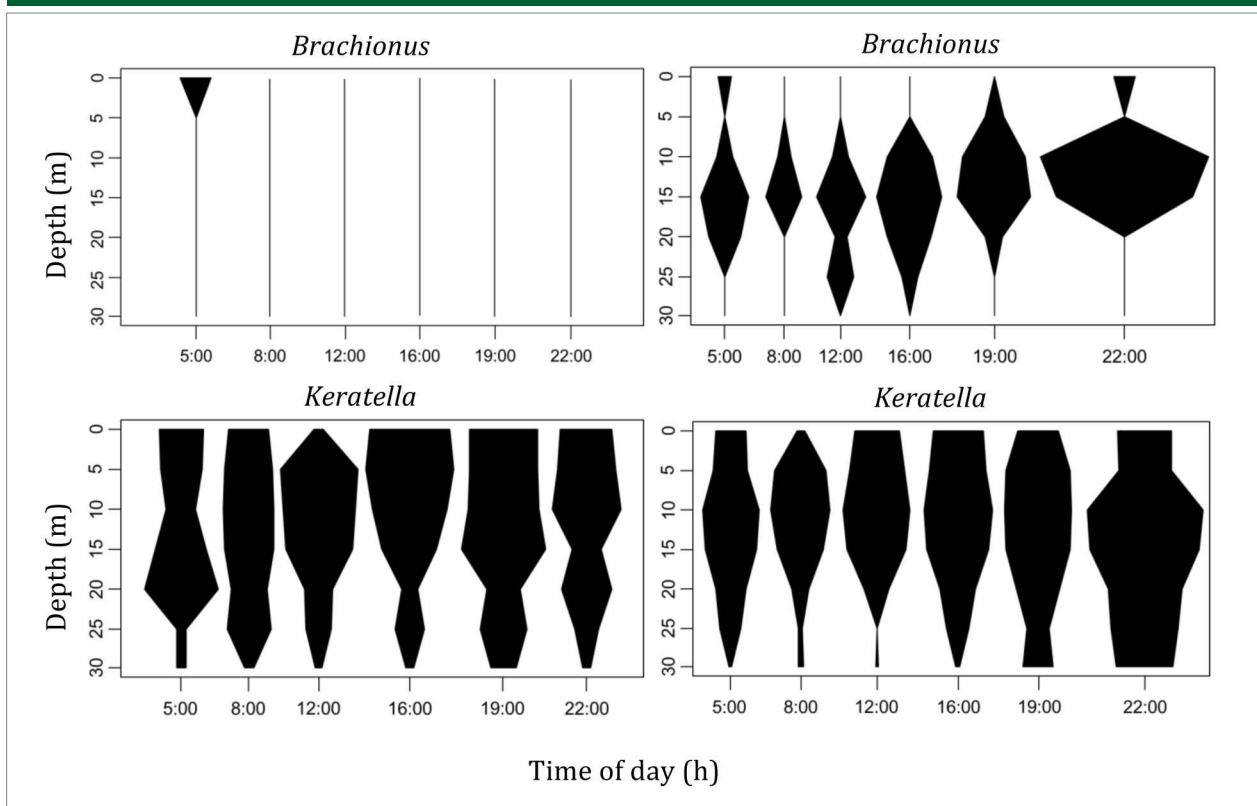
Calanoidea

Cyclopoida

Nauplii

Bosmina

Time of day (h)
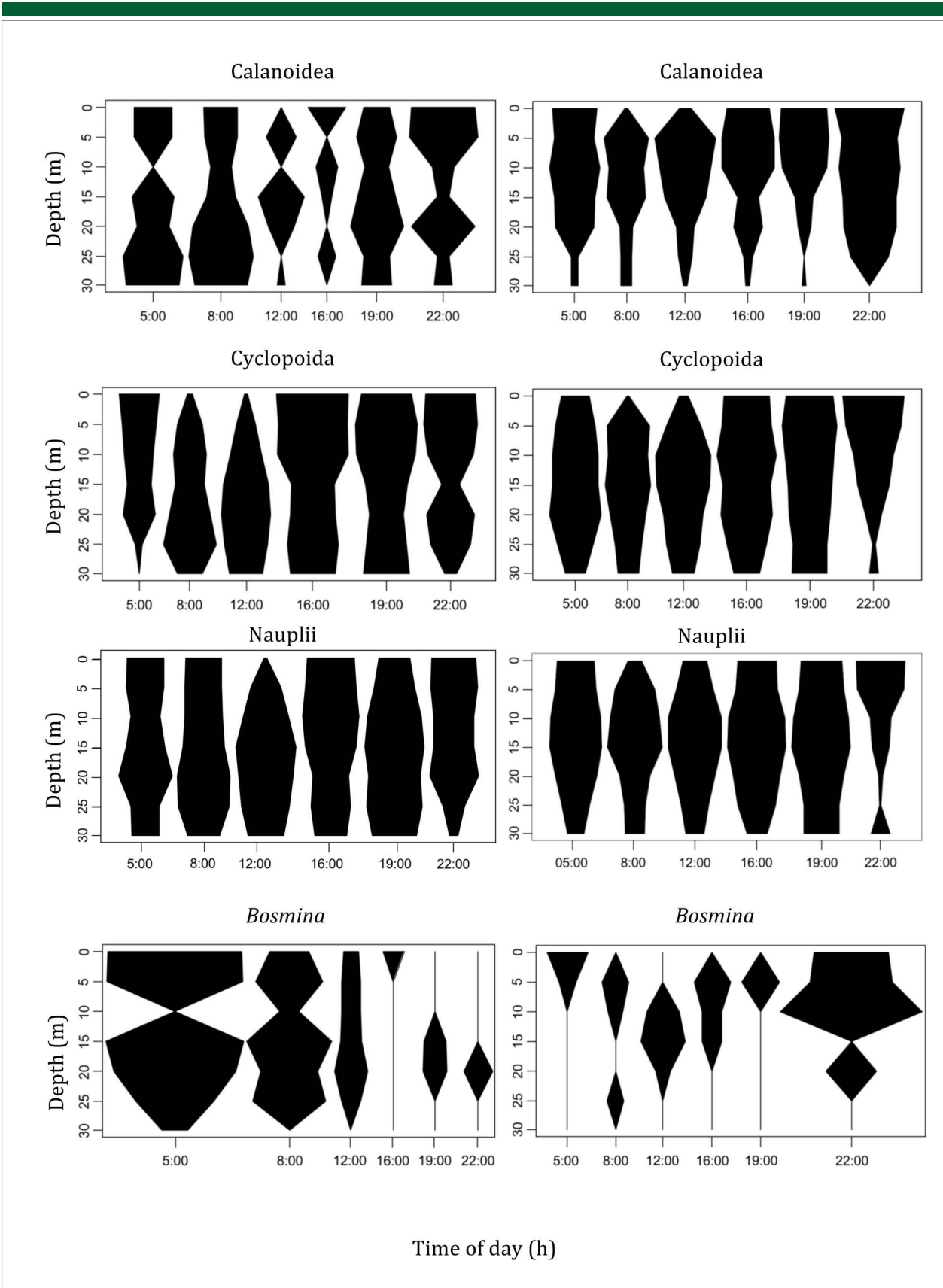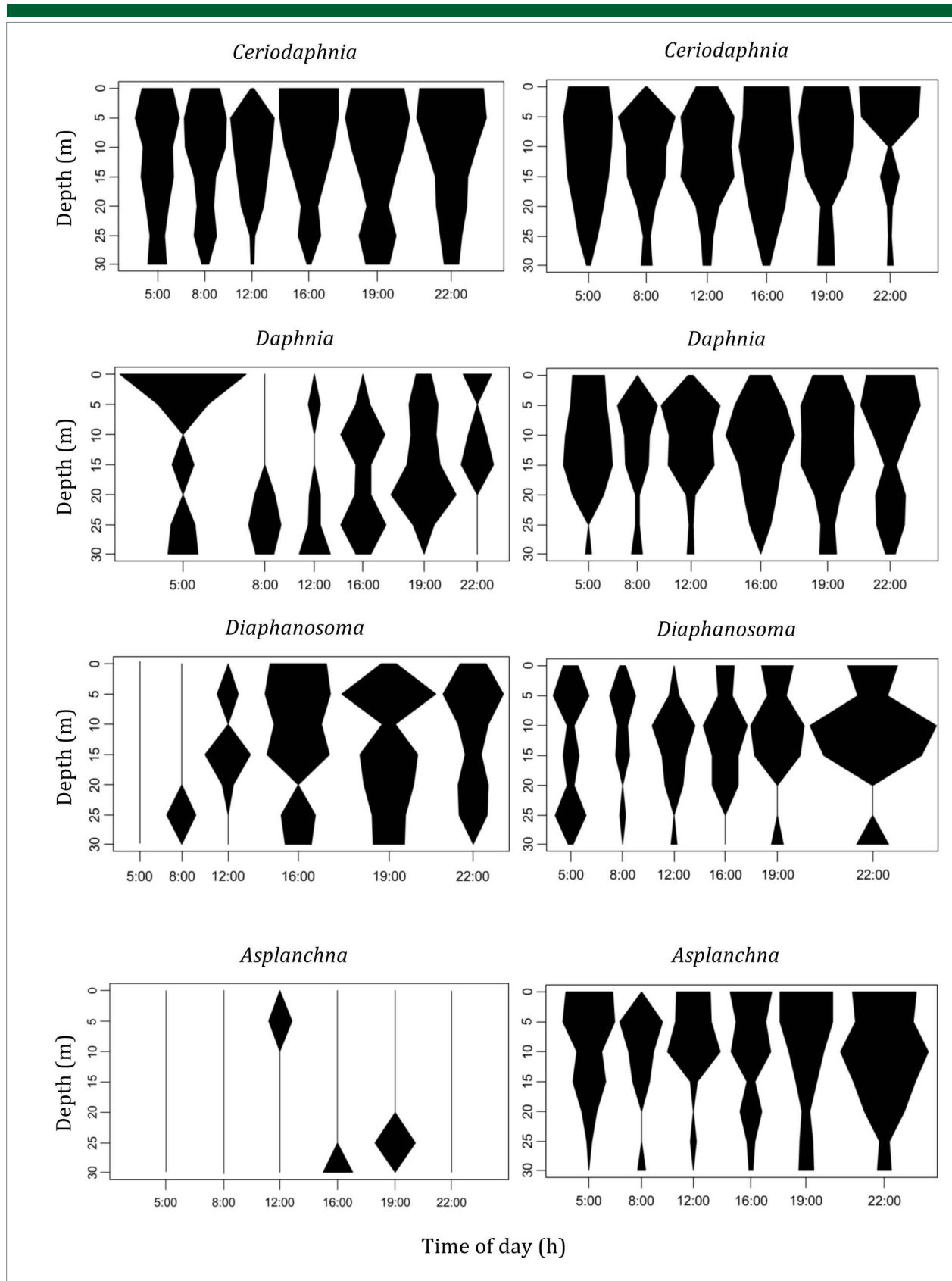
Figure 3. Kite diagrams of zooplankton (Ind L^{-1}) diel vertical migration patterns in Lake Atitlán. Panajachel (left) and Santiago Bay (right).

On the sampling dates, environmental parameters were relatively constant. The average surface dissolved oxygen was 7.5 mg L-1 and decreased to 4 mg L^{-1} at 30 m depth. The oxycline was between 15 to 20 m and, after 16:00 h, the surface concentration of dissolved oxygen decreased 1 mg L^{-1} (Fig. 4). The thermocline was at 35 m below the sampling depths (Fig. 4). Water temperature ranged from 21 to 24 degrees (°C), along the 30 m gradient and stayed constant throughout the day, except from 22:00 to 5:00 h when a one-degree decrease was observed (Fig. 4). pH was uniform along the water column (8.4 ± 0.3) with small variation below 20 m (8.2 ± 0.2) and the pH variations experienced by zooplankton during de DVM were small, 0.013 ± 0.07 units of difference. Water transparency was ranged from an average Secchi depth of 5.8 ± 1 (12:00 and 16:00 hr) to 9.4 ± 2 m (5:00 and 8:00 hr) and transparency decayed after noon due to wave action. The concentrations of chlorophyll-a in Panajachel and Santiago Bay were low (1.07 ± 0.71 µg L^{-1}) (Fig. 5), in both sites the maximum concentration, 2.9 and 2.2 µg L^{-1} respectively, was registered between 12 m and 17 m.

Zooplankton in Lake Atitlán exhibited, in some genera, diel vertical migration patterns. However, the Kruskall-Wallis test did not demonstrate any differences between the diurnal and nocturnal vertical distribution of zooplankton (Chi square = 3, df = 1, p = 0.08). Panajachel showed a statistically significant difference in zooplankton density distribution with hour and depth, F (6, 204) = 11.29, p < 0.001, but not Santiago Bay, F (8, 273) = 0.201, p = 0.99.

The two sites in Lake Atitlán differ in their patterns of migration, and these differences are not derived from any measured physicochemical characteristic. Zooplankton migrate to the hypolimnion during the day for multiple causes, among them fish predation, stratification, light intensity, food availability, feeding activities, interspecific competition, chemical cues (Kairomones) and return to the epilimnion at night to feed (Zaret, 1976; Matsumura-Tundisi et al.,1984; Forward, 1988; Haney, 1988; Murby, 2006, Baumgartner et al., 2011; Dumont, 2019; Simoncelli et al., 2019). Santiago Bay and Panajachel showed low diurnal zooplankton abundance, and high nocturnal abundances. This suggests that only under the cover of darkness can zooplankton take advantage of food resources (phytoplankton) (Matsumura-Tundisi et al.,1984; Fischer et al., 2015; Arcifa et al., 2016; de León y Reyes, 2017; Nowicki et al., 2017; Simoncelli et al., 2019). Zooplankton often migrate upward at night due to light cues, feeding on higher concentrations of phytoplankton in the

epilimnion when visibility and reaction distance by planktivorous fish is reduced (Confer and Blades 1975; Haney et al. 1990; De León y Reyes, 2017). Zooplankton upward migration at dusk could be related not only to food availability but also to the reduction of predation by fishes, in the daytime there is little refuge from visual predators near the surface. Because of the paucity of data on fish abundance, we could not directly include predation pressure in our analyses. However, we can speculate about its possible effect. Predation on zooplankton by planktivorous fish is generally determined by visibility, reaction distance, and overall ease of prey capture (Confer y Blades 1975). In the pelagic areas of Lake Atitlán plankton is only exposed to predation pressure by fishes since there are no other planktivorous species such as invertebrate *Chaoborus*. In the limnetic zone, predation is more intense by Chaoborus larvae and mites, which prey on small and large organisms (*Bosmina, Ceriodaphnia* and *Daphnia*) (Arcifa et al., 2016). Visual planktivores feed most efficiently at high light intensities, however small zooplankton species and immature organisms can remain in more highly illuminated waters because their small size reduces their visibility (Haney, 1988). This could explain the uniform diurnal distribution of nauplii along the water column, 5 to 25 m, both in Santiago Bay and Panajachel.

In addition to food web structures, watercolor and productivity may also affect diel migration patterns of zooplankton (Simoncelli et al., 2019). Santiago Bay is relatively shallow (58 m), with a mixed water column and high primary productivity (Weiss, 1971; Ochaeta, 2014) so that food is always available. This can explain the relatively unchanged zooplankton migration in Santiago Bay compared to the Panajachel site, which is located in a limnetic zone (200 m), where the primary productivity and planktivorous species are lower decreasing the risk of visual predation on zooplankton. In addition, diel horizontal migration (DHM) might be a more effective in Santiago Bay as an antipredator defense due to the lack of a hypolimnetic refuge (Arcifa et al., 2016). Burks et al. (2002) predicted that if DHM were occurring, zooplankton abundance would be highest in the shores or shallow zones during the day. They hypothesized that the zooplankton would use the macrophyte vegetation in the littoral zone as shelter from predators during the day and return to the pelagic epilimnion to feed at night. Thus, in Santiago Bay zooplankton could be migrating to the limnetic zone at night from the shore, where there is high density and refuge in mats off *Hydrilla verticillata* (Rejmánková et al., 2018).
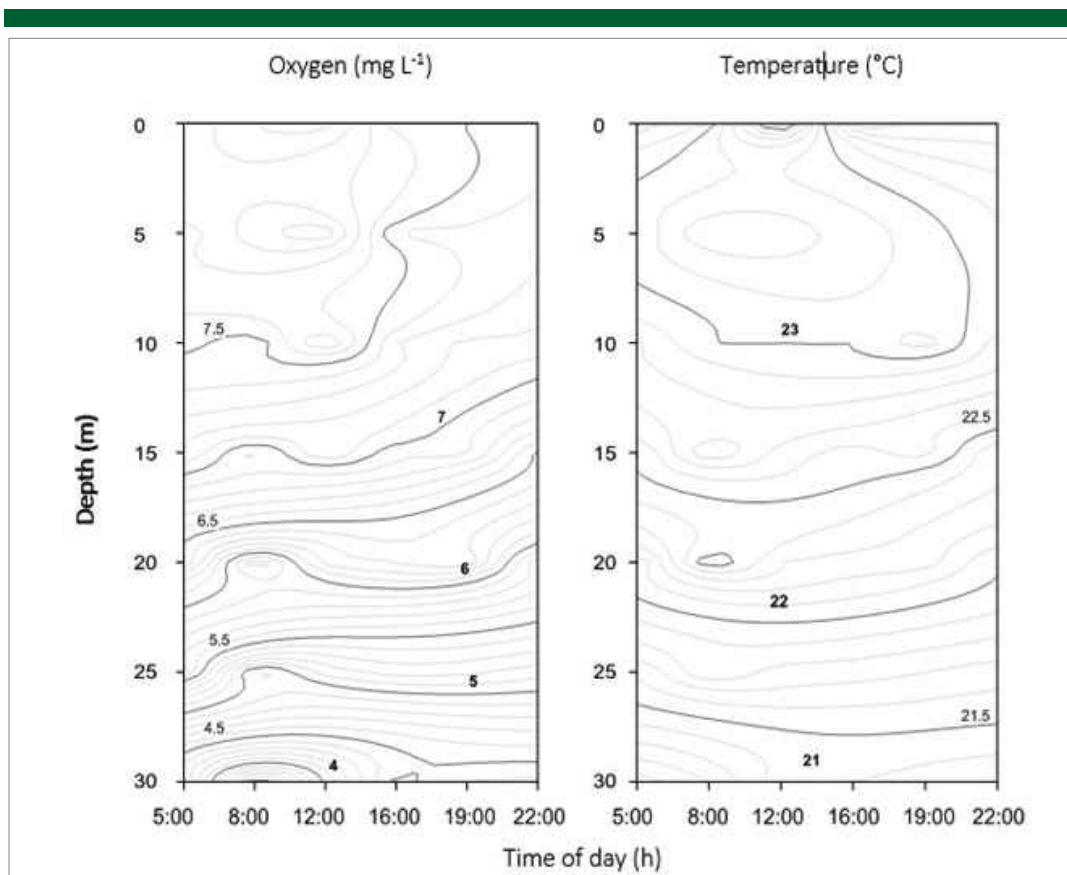

Figure 4. Contour plot of average values of diel variation of dissolved oxygen and temperature over depth in Lake Atitlán.
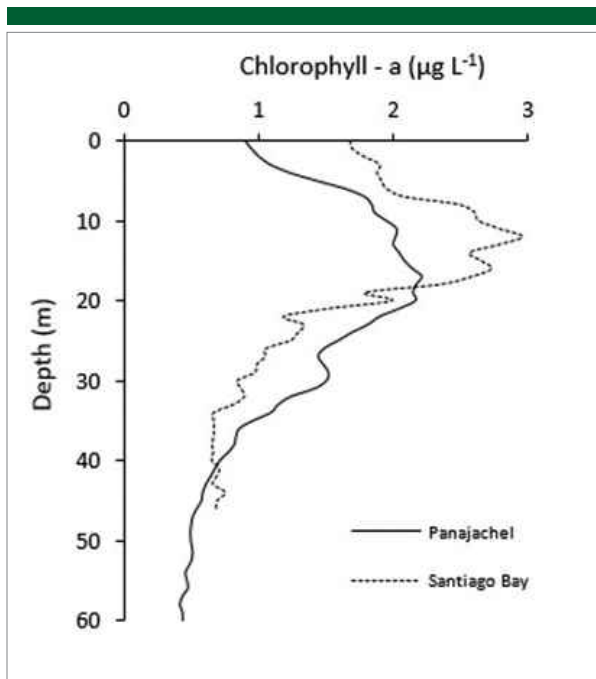
Figure 5. Chlorophyll-a concentration profiles collected in Santiago Bay and Panajachel.

Transparency could be an important driver of the observed trend in zooplankton migration in Panajachel. Water transparency has been shown to be a very important factor in the structuring of zooplankton in shallow waters (Cottenie and De Meester, 2003). According to Han and Straškraba (2001), predation pressure and light are necessary for organisms to undertake diel vertical migration. The degree of transparency modifies the vertical movement of the zooplankton, with faster migration in clear waters with a low attenuation coefficient (Haney, 1988; Ringelberg, 1995; Dodson et al., 1997; Weigand and Escalante, 2008; Dumont, 2019). *Bosmina, Daphnia* and *Diaphanosoma* in Panajachel had a high migration rate in the limnetic zone associated with higher clarity and less contact with pelagic planktivorous fish.

The presence of copepods throughout the water column and during the day might be related to the lack of other predators and the avoidance by fishes. In some lakes, copepods are the top invertebrate predator, as reported by Fisher et al. (2015). Arcifa et al. (2016) reported that the predation pressure on copepods is lower than on cladocerans because copepods were not preyed by invertebrates (*Chaoborus*) and were avoided by a planktivorous fish *Tilapia rendalli*. Arcifa et al. (2016) and Baumgartner et al. (2011) reported that copepods are opportunistic and able to change their behavior, copepods can switch their DVM when predation risk decreases or when thermal stratification is strong or weak.

Another factor that might explain the depth distribution of copepods is their higher tolerance for ultraviolet radiation (UVR) as reported by Fisher et al. (2006), who observed no significant effect of UVR on DVM behavior of copepods in large *in situ* mesocosms and in smaller columns. They suggested that the UV tolerance is due to the accumulation of carotenoids. We did not directly measure pigments, but the red color of copepods in our samples (before preservation) suggests that our copepods could be using both photoprotection and behavioral avoidance as part of their defenses and undrivers for migration.

The distribution of the rotifers, *Brachionus* and *Asplanchna,* in Santiago Bay could be a behavioral response of *Brachionus* to the predator *Asplanchna* or to competition with cladocerans that are the main predator of rotifers in the wild (Dumont, 1972; Matsumura-Tundisi et al., 1984). Gilbert (2014) reported a *Brachionus* effective defense response to *Asplanchna* predation; without *Asplanchna* most individuals were actively swimming, whereas locomotion was reduced in the presence of *Asplanchna.* Many planktonic rotifers develop morphological defenses (e.g., longer spines, larger lorica) to reduce their capture and ingestion and a kairomone from *Asplanchna* has been shown to induce spine development in *Brachionus* and *Keratella* species (Gilbert, 2014). Dippolito (1988) and Nurminen and Hoppila (2002) concluded that the vertical and temporal distribution of rotifers was associated with algal blooms, high temperatures and pH changes under a heavy phytoplankton bloom. The absence of *Asplanchna* and *Brachionus* in Panajachel might be related to its trophic state. Panajachel is less productive and slightly colder (22.1 ± 0.65) than Santiago Bay (22.6 ± 0.72) also has less algal bloom episodes than Santiago Bay, due its physical characteristics (depth, wind direction, pH and nutrient inputs) (Rejmánková et al., 2011; Reyes Morales et al., 2017).

Conclusions

Physical and chemical parameters of a lake can largely define the physical niche of an organism (Lampert & Sommer 1997; Roldán & Ramirez, 2008). That is why it is important to consider plankton interactions (direct or indirect) when studying plankton migration. Even though we did not directly evaluate the relation between physical parameters and zooplankton migration, some speculations were made of their possible effects and how these variables, temperature and light, can influence the upward and downward zooplankton migration. As was suggested with the zooplankton distribution and densities along the water column in this study, these influences can occur simultaneously, pressuring the organisms to a specific niche or depth.

This work is the first contribution to the knowledge of the vertical distribution of zooplankton in Lake Atitlán. However, future studies must include both vertical and horizontal distribution profiles aimed at analyzing and determining the factors that induce planktonic movements, such as reproductive condition or food availability. Finally, as global browning of freshwater ecosystems continues to rise, these migration patterns are subject to change. The more that is understood about diel migration of zooplankton the better we will understand the zooplankton migration in the future. To provide management recommendations, it is important to focus on obtaining a better understanding of plankton dynamics, nutrients recycling processes and physicochemical conditions in Lake Atitlán.

Acknowledgments

References

AMSCLAE. 2017. *Informe anual. Monitoreo limnológico.* Autoridad para el Manejo Sustentable de la Cuenca del Lago de Atitlán y su Entorno. Panajachel, Sololá, Guatemala.

Arcifa, M., Perticarrari, A., Bunioto, T., Domingos, A., Minto, W. (2016) *Microcrustaceans and predators: diel migration in a tropical lake and comparison with shallow warm lakes* Limnetica 35 (2): 281-296.

Baumgartner, M., Lysiak, N., Schuman, C., Urban-Rich, J., Wenzel. F. (2011) *Diel vertical migration behavior of Calanus finmarchicus and its influence on right and sei whale occurrence* Marine Ecology Progress Series 423: 167-184.

Burks, R. L., lodge, D. M., Jeppesen, E., Lauridsen, T. (2002) *Diel horizontal migration: costs and benefits of inhabiting the littoral* Freshwater Biology 47: 343-365.

Confer, J., Blades, P. (1975) *Omnivorous zooplankton and planktivorous fish* Limnology and Oceanography 20 (4): 571-579.

Cottenie, K., De Meester, L. (2003) *Connectivity and cladoceran species richness in a metacommunity of shallow lakes* Freshwater Biology 48 (5): 823-832.

De León, A. I., Reyes, F (2017) *Vertical migration of phytoplankton in Lake Atitlán* Revista Científica 27(1): 44-57.

Dippolito, A. (1988) *Distribución vertical y temporal de rotíferos del embalse Cassaffousth (Córdoba, Arg.)* Revista de la Asociación de Ciencias Naturales del Litoral 19 (2): 155-166.

Dix, M., M. Dix, M. Orozco, D. Cabrera, E. Bocel, A. Toledo & E. Symonds. (2012) *El Lago Atitlán, Guatemala. Su estado ecológico octubre 2009 - diciembre 2011* Revista de la Universidad del Valle de Guatemala 24: 35-50.

Dodson, S., Tollrian, R., Lampert, W. (1997) *Daphnia swimming behavior during vertical migration* Journal of Plankton Research 19 (8): 969-978.

Dumont, H. J. (1972) *A competition based approach of the reverse vertical migration in zooplankton and its implications, chiefly based on a study of the interactions of the rotifer Asplanchna priodonta (Gosse) with several crustacean entomostracan* Internationale Revue der Gesamten Hydrobiologie 57: 1-38.

Dumont, H. (2019) *Zooplankton vertical migration in two Sahara lakes with contrasting biotic environment* Limnetica 38 (1): 95-101.

Fischer, J., Olson, M., Theodore, N., Williamson, C., Rose, K., Hwang, J. (2015) *Diel vertical migration of copepods in mountain lakes: The changing role of ultraviolet radiation across a transparency gradient* Limnology & Oceanography 60: 252-262.

Fischer, J., Nicolai, J., Williamson, C., Persaud, A., Lockwood, R. (2006) *Effects of ultraviolet radiation on diel vertical migration of crustacean zooplankton: An in situ mesocosm experiment* Hydrobiologia 563: 217-224.

Forward, R. (1988) *Diel vertical migration: Zooplankton photobiology and behavior* Oceanography and Marine Biology, an Annual Review 26: 361-393.

Gilbert, J. (2014) *Morphological and behavioral responses of a rotifer to the predator Asplanchna* Journal of Plankton Research 36 (6): 1576-1584.

Han, B., Straškraba, M. (2001) *Control mechanisms of diel vertical migration: theoretical assumptions* Journal of Theoretical Biology 210 (3): 305-318.

Haney, J. (1988) *Diel patterns of zooplankton behavior* Bulletin of Marine Science 43 (3): 583-603.

Haney, J., Craggy, K., Kimball, K.,Weeks, F. (1990) *Light control of evening vertical migrations by Chaoborus punctipennis larvae* Limnology Oceanography 35 (5): 1068-1078.

Juday, C. (1915) *Limnological studies on some lakes in Central America* Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 18: 214-250.

Kumar, S., Nagar, S., Chowdhary N. (2015) *Effect of ultraviolet radiation and temperature change on zooplankton - Cladocera and copepoda* International Journal of Pharmacology and Biological Sciences 9 (3): 1-7.

Lampert, W., Sommer, U. (1997) *Limnoecology: the ecology of lakes and streams* Oxford University Press.

Last, K., Hobbs, L., Berge, J., Brierley, A., Cottier, F. (2016) *Moonlight drives ocean-scale mass vertical migration of zooplankton during the arctic winter* Current Biology 26 (2): 244-251.

Matsumura-Tundisi, T., Tundisi, J., Tavares, L. (1984) *Diel migration and vertical distribution of Cladocera in Lake D. Helvecio (Minas Gerais, Brazil)* Hydrobiologia 113: 299-306.

Meek, S. E. (1908) *The zoology of lakes Amatitlán and Atitlán, Guatemala, with special reference to ichthyology* Field Columbian Museum, Zoological Series 7 (6): 159-206.

Murby, A. (2006) *Migration of net phytoplankton and zooplankton in Mendum's Pond, New Hampshire* UNH Center of Freshwater Biology Research 8 (2): 18-30.

Nowicki, C., Bunnell, D., Armenio, P., Warner, D., Vanderploeg H., Cavaletto, J., Mayer C., Adams, J. (2017) *Biotic and abiotic factors influencing zooplankton vertical distribution in Lake Huron* Journal of Great Lakes Research 43 (6): 1044-1054.

Nurminen, L., Horppila, J. (2002) *A diurnal study on the distribution of filter feeding zooplankton: Effect of emergent macrophytes, pH and lake trophy* Aquatic Sciences 64 (2): 198-206.

Ochaeta, G. (2014) *Análisis temporal y espacial de la comunidad de fitoplancton en los puntos Panajachel, Centro Weiss G y Santiago en el Lago Atitlán, Sololá, Guatemala, durante el año 2013* Informe de tesis para optar al grado de licenciatura en biología. Facultad de Ciencias Químicas y Farmacia, Universidad de San Carlos de Guatemala. Pp 101.

Ohman, M. (1990) *The demographic benefits of diel vertical migration by zooplankton* Ecological Monographs 60 (3): 257-281.

R Core Team (2017) *R: A language and environment for statistical computing. R Foundation for Statistical Computing,* Vienna, Austria. URL. https://www.R-project.org/.

Rejmánková, E., Sullivan, B., Ortiz Aldana, J., Snyder, J., Castle, S., Reyes Morales, F. (2018) *Regime shift in the littoral ecosystem of volcanic Lake Atitlán in Central America: combined role of stochastic event and invasive plant species* Freshwater Biology 63: 1-19.

Rejmánková, E., Komárek, J., Dix, M., Rejmánková, J., Girón, N. (2011) *Cyanobacterial blooms in Lake Atitlán, Guatemala* Limnologica 41 (4): 296-302.

Reyes Morales, F., Ujpan, D., Valiente, S. (2017) *Bathymetry and morphometric análisis of Atitlán Lake* Revista Científica 27 (2): 48-58.

Ringelberg, J. 1995. *Changes in light intensity and diel vertical migration: A comparison of marine and freshwater environments* Journal of the Marine Biological Association of the UK 75: 15-25.

Roldán, G., Ramírez, J. (2008) *Fundamentos de Limnología Neotropical.* Editorial Universidad de Antioquia, Antioquia, Colombia.

Simoncelli, S., Thackeray, S., Wain, D. (2019) *Effect of temperature on zooplankton vertical migration velocity* Hydrobiologia 829: 143-166.

Thorp, J.P., Covich, A.P. (2001) *Ecology and Classification of North American Freshwater Invertebrates.* 2a. Edición. EEUU: Academic Press.

Torres, R., Estrada, M. (1997) *Patrones de migración vertical en el plancton de un lago tropical* Hidrobiológica 7 (1): 33-40.

Weigand, P., Escalante, A. (2008) *¿Existen migraciones verticales en el zooplancton de la laguna de Los Padres?* Biología Acuática 24: 165-172.

Weiss, C. (1971) *Water quality investigations in Guatemala, Lake Atitlan 1968-1970* University of North Carolina and ERIS. Pp. 164

Werner, T., Buchholz, F. (2013) *Diel vertical migration behaviour in Euphausiids of the northern Benguela current: seasonal adaptations to food availability and strong gradients of temperature and oxygen* Journal of Plankton Research 35 (4): 792-812.

Witty, L. (2004) *Practical Guide to Identifying Freshwater Crustacean Zooplankton* Cooperative Freshwater Ecology Unit, Department of Biology, Laurentian University, Sudbury, Ontario, Canada.

Zaret, T., Suffern, S. (1976) *Vertical migration in zooplankton as a predator avoidance mechanism* Limnology and Oceanography 21 (6): 804-813.

Aporte de autores

Elsa Ma. de Fátima Reyes Morales: Participó en la experimentación, recopilación de muestras, procesamiento y análisis de datos, redactor del artículo.

Margaret A. Dix: Participó en la revisión y redacción del artículo.

Jorge A. Ortiz: Participó en la experimentación, recopilación de muestras, identificación de organismos, tabulación de datos.