

Depth-selection patterns and diel vertical migration of *Daphnia ambigua* (Crustacea: Cladocera) in lake El Plateado

Patrones de selección de profundidad y migración vertical de *Daphnia ambigua*
(Crustacea: Cladocera) en el lago El Plateado

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ABSTRACT

Eutrophic temperate and sub-tropical lakes often exhibit a marked vertical structure during the warm season that involves important spatial differences of physical, chemical and biological variables. Therefore, zooplankton is exposed to a highly heterogeneous environment in the vertical dimension. In this work, we analyze the depth-distribution of the cladoceran *Daphnia ambigua* in the eutrophic, monomictic lake El Plateado at midday and midnight, along with its relationship with the vertical distribution of water temperature and dissolved oxygen concentration. We also attempt to define whether or not this population exhibits a diel vertical migration. The results show significant changes in the day/night vertical distribution of *D. ambigua* during its growing season, with the exception of the last date. Also, the data revealed that average depth selected by *D. ambigua* becomes shallower with time, and the amplitude of the vertical migration decreases throughout the season. During the period of lake stratification, temperature appears positively correlated, and oxygen negatively correlated to the frequency of *D. ambigua*. It is suggested that oxygen concentration plays a crucial role in modulating the vertical migration behavior of *D. ambigua* in lake El Plateado, which has important consequences for understanding the atypical pattern of population dynamics exhibited by this species.

Key words: Chile, *Daphnia*, depth-selection, diel vertical migration, zooplankton.

RESUMEN

Los lagos templados y sub-tropicales a menudo presentan una marcada estructura vertical durante la estación cálida que involucra importantes diferencias espaciales de variables físicas, químicas y biológicas. El zooplancton se encuentra por ello expuesto a un ambiente marcadamente heterogéneo en su dimensión vertical. En este trabajo analizamos la distribución vertical del cladóceros *D. ambigua* en el lago eutrófico y monomictico El Plateado, a mediodía y a medianoche, y su relación con la distribución vertical de la temperatura del agua y concentración de oxígeno disuelto. Intentamos también definir si esta población exhibe o no una conducta de migración vertical. Los resultados muestran cambios significativos en la distribución vertical día/noche de *D. ambigua* durante su periodo de crecimiento, con excepción de la última fecha. Los datos revelan también que la profundidad promedio seleccionada por *D. ambigua* disminuye en el tiempo, así como la amplitud de la migración vertical. Dentro del periodo de estratificación del lago, la temperatura aparece positivamente correlacionada y el oxígeno negativamente correlacionado con la frecuencia de *D. ambigua*. Se sugiere que la concentración de oxígeno juega un papel crucial en la modulación de la conducta de migración vertical de *D. ambigua* en el lago El Plateado, con importantes consecuencias para el entendimiento del patrón atípico de dinámica poblacional que presenta esta especie.

Palabras clave: Chile, *Daphnia*, migración vertical, selección de profundidad, zooplancton.

INTRODUCTION

In lakes, the vertical dimension of the system should not be disregarded, since both water conditions and resources of every freshwater population show a marked, though not necessarily overlapping, spatial structure. In temperate and subtropical lakes the water temperature is normally higher near the surface and,

consequently, the water-density is lower in the upper meters of the water column. During the warm season of monomictic temperate and subtropical lakes, with the exception of shallow ponds, the kinetic energy supplied by wind is able to mix only the upper part of the water column, while the lower part is resistant to mixing, which causes thermal stratification (Hutchinson 1957) and a well defined epilimnion (a superficial, less

dense and warmer water-layer) separated from a deeper, more dense and cooler layer or hypolimnion. This strong spatial heterogeneity of the environment of freshwater organisms can be enhanced by other physical, chemical and biological processes (Watanabe 1992). While photosynthesis is confined to the illuminated layers of water, accumulation of organic particles by settling is higher in deeper waters, where community respiration rate is enhanced and oxygen concentration decreases, specially in productive systems. In eutrophic systems, the oxygen depletion in the hypolimnion may cause the development of a deep hypoxic zone during the stratification phase.

On the other hand, most pelagic fish require a minimum of visible light to search for their prey, and therefore predation pressure on the zooplankton is generally restricted to the upper illuminated part (during daytime) of the water column (Zaret 1980, Gliwicz & Pijanowska 1989).

Since both phytoplankton growth and prey consumption by fish are restricted to the upper waters due to the light-dependence of these processes, the zooplankton may be able to exploit a larger spatial segment of the lake, in the vertical dimension.

Because the above-mentioned vertical heterogeneity in the physical and biological environment, the fitness of zooplankters and their potential for population growth are strongly dependent on the depth in which they are located at a given time.

In epilimnetic waters, relatively high temperatures enhance zooplankton fitness through increasing developmental rates, decreasing time to first reproduction and increasing intrinsic rate of population growth (McLaren 1963, Hall 1964, Bottrell 1975a, 1975b, Bottrell et al. 1976, Lei & Armitage 1980, Vidal 1980a, 1980b, Neill 1981, Meyers 1984). Moreover, food availability is often higher in superficial waters due to the photosynthetic activity and growth of microalgae, and the oxygen concentration is normally found at saturating levels therein. Nevertheless, survival probability is reduced in epilimnetic waters when zooplanktivorous fish are present. On the other hand, the hypolimnion is a convenient refuge against vertebrate predators (Wright & Shapiro 1990), but disadvantageous in terms of temperature and oxygen concentration during the stagnation period of eutrophic systems (Watanabe 1992, Hanazato 1992).

An optimal depth-selection behavior of zooplankters should give rise to a vertical distribution of the population where the animals find the best compromise between the several -physiological

and demographic- costs and benefits imposed by water conditions at each depth, in any given time.

This situation poses the question about depth-selection patterns in the field, namely: which is the vertical distribution of zooplankters in nature and how could it be related to the environmental conditions of the system? With the exception of some data collected in Rapel reservoir by Zúñiga & Araya (1982) and Andrew et al. (1989), no study has dealt with this topic in Chilean lake-ecosystems. The first study reported the vertical distribution of zooplankton only at two autumn close dates during one non-specified time of the day. The work of Andrew et al. (1989) dealt with zooplankton respiration, being the vertical distribution a subsidiary element. These authors provided data of a 24-h period in early spring, performed no statistical analysis to the distribution of zooplankton, and did not provide an ecological explanation to the observed vertical trend.

A particular case of depth-selection behavior is the diel vertical migration exhibited by many zooplankton species in marine and freshwater systems (Hutchinson 1967, Lampert 1989, De Meester et al. 1999). The normal pattern of diel vertical migration behavior is characterized by an ascending movement of the zooplankters at evening, followed by a descending movement at dawn. In this way, during stagnation the zooplankters exploit the epilimnion during the night (when there is not enough visible light for fish predators), and stay in the hypolimnion during the day hiding from visually-oriented predators. Theoretical studies show that this behavioral pattern could be both an optimal (Mangel & Clark, 1988, Fiksen & Giske 1995, Fiksen 1997), and an evolutionary-stable-strategy (Gabriel & Thomas 1988).

Since demographic components of the zooplankton population growth (reproduction, recruitment, mortality) are strongly determined by the particular set of conditions found at each depth, understanding the population dynamics of any zooplankton species requires information about its vertical distribution in the field, and their potential changes over time.

In Chilean lakes, the genus *Daphnia* is poorly represented in comparison with lakes of the northern hemisphere. The scarcity of *Daphnia* applies both to species richness and to population density. In fact, only two *Daphnia* species (*D. ambigua* and *D. pulex*) are found in most Chilean lakes (Villalobos 1994), and they rarely dominate numerically their zooplankton communities. Lake-ecosystem processes, such as the well reported clear water phase of northern lakes (Tilzer 1984, Lampert et al. 1986, Sommer et al. 1986) are

strongly influenced by the structure of the zooplankton community. The association between scarcity of *Daphnia* and the apparent absence of a clear water phase in Chilean lakes probably is not by chance. If so, existing models of biological dynamics of freshwaters (e.g., Sommer et al. 1986) need to be generalized or replaced.

Under the hypothesis that patterns of depth-selection behavior of a zooplankton population rest on some interacting process influenced by endogenous and exogenous stimuli, and, that depth-selection behavior can have a significant effect on the demographic process, which determines the dynamics of population abundance, this work is focused on the depth-selection patterns of a *Daphnia* population in a temperate lake of central Chile. Specifically, we evaluate the vertical distribution of *Daphnia ambigua* (Scourfield 1947) in lake El Plateado at midday and midnight over the growing season of this species. We also investigate relationships between the vertical distribution of *D. ambigua* and the distribution of water temperature and dissolved oxygen concentration in the lake. Furthermore, we attempt to detect whether or not this population exhibits a diel vertical migration behavior, and discuss the consequences of depth-selection behavior on the population dynamics of *D. ambigua* in lake El Plateado.

MATERIAL AND METHODS

The study site

El Plateado is a warm-monomictic and eutrophic small lake (Montecino & Cabrera 1984) located at 33° 04' 30'' S and 71° 39' 12'' W at 340 m altitude, between coastal hills at the southern end of Valparaíso, Chile. Its surface area is 0.019 km², with a maximum depth of 13 m and a mean depth of 4.8 m (Domínguez et al. 1976). Chemical and physical characterization of this lake can be found in Domínguez et al. (1976, 1981) and Ramos et al. (1997). A strong thermocline is present from September to May, with vertical temperature differences up to 6 °C m⁻¹, and the hypolimnion becomes anoxic (or severely hypoxic) during most of the stagnation period (Ramos et al. 1997). The zooplankton composition of El Plateado includes the cladocerans *Bosmina longirostris*, *Diaphanosoma chilense*, *Daphnia ambigua*, *Ceriodaphnia dubia* and *Moina micrura*, and the copepods *Tumeodiaptomus diabolicus*, *Tropocyclops prasinus* and *Mesocyclops longisetus* (Ramos et al. 1998, following nomenclature of Araya & Zúñiga 1985). Free-

swimming individuals of *D. ambigua* have been found from June to October of each year, with maximal population densities in August-September (Ramos et al. 1998).

Data collection and statistical analyses

Temperature and dissolved oxygen concentration were recorded weekly during the year, by using a WTW OXI 196 equipment with a calibrated WTW EOT 196 submersible probe. Readings were made every 0.5 m from surface to the lake bottom and back, and the mean value was used. Routine zooplankton sampling by means of biweekly single vertical hauls (125 mm mesh) was conducted in order to characterize the population trends. All measurements were made at midday, on the same area where the plankton samples were taken.

Sampling for the analyses of vertical distribution was made both at midday and midnight during the following dates: April 22, July 21, August 05, September 9, October 7, and December 16 of 1995. As expected from previous studies (Ramos et al. 1998), very few individuals of *D. ambigua* were found in the April and December samples, so these two dates were removed from further analyses. The samples were taken from the pelagic zone in lake El Plateado by using a 30 L Schindler sampler at depths of 0, 1, 2, 3, 4, 5, 7, and 8.5 m. For each depth, samples were collected from three different points, linearly arranged every 25 m along the major axis (North-South) of the lake. This procedure allowed to increase the number of organisms per sample as well as to broaden the sampling area. Zooplankton samples were fixed in the field with a sugar-formalin solution (Haney & Hall 1973). In the laboratory, a known fraction of each sample was taken using a Folsom-subsampler for subsequent counting under a WILD M5 stereomicroscope. Counting was made according to standard procedures (McCauley 1984).

In order to compare the vertical distribution of *D. ambigua* between day and night of each date, and between the different dates at a given time (day or night), a recently developed method was used (Solow et al. 2000), which is based on the Kolmogorov-Smirnov test and it is specially suited for comparing vertical plankton distributions. The significance level was estimated by running 10,000 randomizations on an electronic worksheet. This method will be referred here as KSS test. Weighted average depths were used as a measure of the center of the population vertical distribution (Wishner et al. 2000).

In looking for relationships between frequency of *D. ambigua* $F_i = N_i (\sum N_i)^{-1}$, in which F_i is the frequency and N_i is the density of *Daphnia* at each depth i , and physical conditions of the water, multiple regression analyses were run taking temperature and oxygen concentration as independent variables. In order to standardize the temperature and oxygen values over time, these variables were re-dimensioned to a zero-to-one scale, in which these two extremes are the minimal and maximal values of the variable observed in the field at each date, respectively. The conversion of variables was done by applying the following function:

$$Y' = \frac{Y - Y_{\min}}{Y_{\max} - Y_{\min}}$$

where Y' represents the re-dimensioned variable (temperature or oxygen concentration), Y_{\max} and Y_{\min} are maximal and minimal values of the observed variables, and Y is the root value. Normality of variables used in multiple regressions were corroborated by the Kolmogorov-Smirnov two-sample test, after square-root transformation of the independent variables (Sokal & Rohlf 1995).

RESULTS

Temperature and oxygen distribution of lake El Plateado during the year are shown in Fig. 1A and 1B. Of main interest it is the increase of epilimnetic temperature and the outstanding decrease of hypolimnetic oxygen occurring from July to October. The population trend of *D. ambigua* is shown in Fig. 1C, together with the sampling dates for the analysis of vertical distribution. The seasonal change in population size of *D. ambigua* shown here is similar in shape and temporal location to that reported for previous years in the same lake (Ramos et al. 1998).

The vertical spatial distribution of *D. ambigua* in lake El Plateado during the period of highest population density, both at midday and midnight, can be seen in Fig. 2, together with the vertical profiles of temperature and oxygen concentration at each day. It should be noted the vertical homogeneity of temperature and oxygen content during the two first sampling dates. In September and October, on the other hand, the water column was stratified and the hypolimnion turned severely hypoxic (Fig. 1 and 2). A visual inspection of the vertical distribution of *D. ambigua* reveals that differences between day and night frequencies are more evident in the uppermost layers, with a lower frequency of daphnids at midday (Fig. 2).

The midday distribution at each date was statistically compared with the midnight distribution to look for the occurrence of diel vertical migration in this population. Differences in vertical distribution during daytime and during nighttime were also tested in order to look for seasonal shifts. The results of the KSS test are shown in Table 1 and 2. Significant differences ($P < 0.05$) were found between day and night distributions in July, August and September, whereas no significant day/night differences were detected in October. Differences between the August and October distributions at midday were statistically significant, and those between July-September and July-October were marginally significant (Table 2). At night, differences among the four vertical distributions were not significant (Table 2).

To display the central tendency of the distribution of *D. ambigua* over time, the weighted-average depth (\pm one standard deviation) at each date and time is shown in Fig. 3. The graph also shows the difference between day and night mean depths as a measure of the amplitude of migration. Three aspects deserve attention: (1) the average depth of *Daphnia* is always shallower at midnight compared to midday, (2) the population concentrates closer to the surface as the season progress, and (3) the difference between mean day and night depth decreases with time.

Vertical distribution at midnight is more uniform than at midday. Because of this, the temporal shift in average nocturnal depth is not large enough to make distribution differences among the four dates statistically significant. The vertical distribution at midday is less homogeneous, and differences among them are more sensitive to shifts in their gravity point. Thus, KSS tests re-

TABLE 1

Kolmogorov-Smirnov-Solow (KSS) test for comparison of vertical distribution of *D. ambigua* between midday and midnight (see text and references therein)

Prueba de Kolmogorov-Smirnov-Solow (KSS) para la comparación de la distribución vertical de *D. ambigua* a mediodía y medianoche (ver texto y referencias incluidas)

Date	P-value
July	0.0072
August	0.0146
September	0.0241
October	0.2481

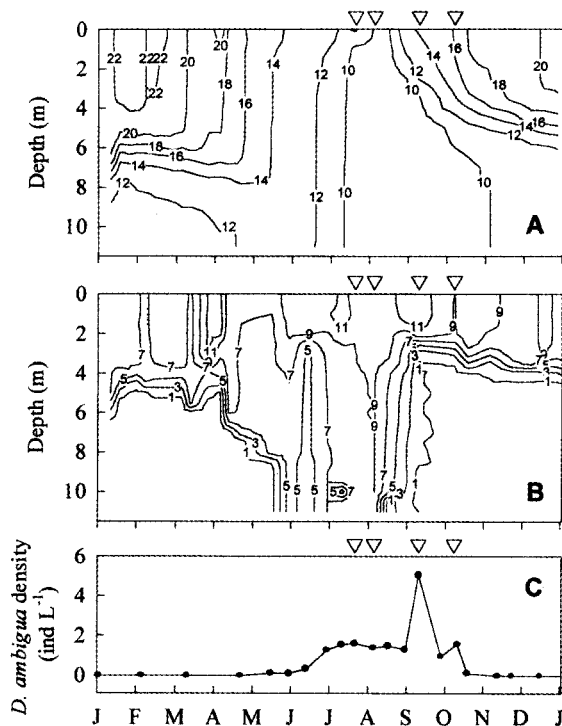


Fig. 1: Temperature isopleths in °C (A), dissolved oxygen isopleths in mg O₂ L⁻¹ (B) and population density of *Daphnia ambigua* (C) in lake El Plateado during the study year. Inverted triangles on the top of each plot indicate the sampling dates for zooplankton vertical distribution.

Isolíneas de temperatura en °C (A), isopletas de oxígeno disuelto en mg O₂ L⁻¹ (B) y densidad poblacional de *Daphnia ambigua* en el lago El Plateado en el año de estudio. Los triángulos invertidos sobre cada gráfico indican las fechas de muestreo para distribución vertical del zooplancton.

vealed levels of statistical significance close to 0.05 between every two non-adjacent dates (Table 2). On the other hand, the level of statistical significance of KSS tests during day/night comparisons is in agreement with the observed change in the depth-differences in each date (Fig. 3). So, the largest difference in average depth between day and night, detected in the July samples, is concomitant with the smallest P-value of the KSS test. The amplitude of the vertical migration, measured as a depth difference, diminishes monotonically with time, and no significant difference between the day and night vertical distributions was observed in October, when the amplitude was the smallest.

Possible relationships between temperature and oxygen concentration -as independent variables- and the frequency of *D. ambigua* -as the dependent variable-, were tested through multiple re-

gression analyses. If both midday and midnight are included (Table 3), the resulting model was highly significant ($P < 0.00001$), and the multiple correlation coefficient (R) gave an acceptable value of 0.56. Only the oxygen concentration explained variability in the frequency of *D. ambigua*, with a negative and highly significant regression coefficient. This result indicates that the frequency of *D. ambigua* is inversely related with the standardized values of oxygen present in the water column. On the other hand, the frequency of *D. ambigua* did not vary with temperature.

When only midday data were included in the analysis, the resulting regression model gave a high multiple correlation value ($R = 0.72$), and a high level of statistical significance ($P < 0.0001$, Table 4). As before, the frequency of *D. ambigua* was independent of temperature and was negatively correlated with oxygen concentration. The regression analysis run on the midnight data revealed no statistical significance of the model and suggested no influence of any independent variable (Table 4).

Before further regression analyses, the period of study was split into two phases on the base of the abrupt development of the lake's stratification: July-August, prior to stratification, and September-October, when dissolved oxygen and temperature exhibit large vertical differences in the water column. A regression analysis run on the July-August data showed no significant effects of temperature or oxygen at midday, but revealed a significant and negative effect of temperature on the frequency of daphnids at night (Table 5). It should be noted that the vertical profiles of temperature and oxygen during this phase were nearly homogeneous, with a slight increment in temperature very close to the surface. Thus, the observed negative effect of temperature was a consequence of the minimal density of *D. ambigua* in the uppermost layers at night.

The analysis of the second (stratification) phase revealed a significant relation between the frequency of *D. ambigua* and both temperature (positive effect) and oxygen concentration (negative effect). Such pattern was valid both for midday and midnight data (Table 5). These results entail that daphnids tend to concentrate at depths slightly above the thermocline plane, and somewhat below the oxycline plane when the lake is stratified.

DISCUSSION

This work addresses the depth-selection behavior of *D. ambigua* in lake El Plateado, and its main

results suggest that (1) this population performs diel vertical migration during most of its growing season, (2) that *D. ambigua* exhibits a seasonal change in its vertical migration pattern, and (3) that oxygen concentration seems to be the main modulator of this response. The consideration of these patterns could help to explain the population dynamics exhibited by *D. ambigua* in lake El Plateado.

The statement that *D. ambigua* performs diel vertical migration, as a specific kind of depth-selection behavior, is based on the significant differences detected between day and night verti-

cal distributions, with a deeper average location at midday. Nevertheless, these changes vanish at the end of the growing season of *D. ambigua*. Two basic modes of diel vertical migration are described in the literature (Lampert 1989). A first mode corresponds to the "normal" pattern, with an ascending movement of individuals at dusk and a descending movement at dawn, and a second mode of diel vertical migration is the opposite "reverse" vertical migration. It is now widely-accepted that the behavior of diel vertical migration is a predator-avoidance strategy (Zaret & Suffern 1976, Stich & Lampert 1981, 1984, but

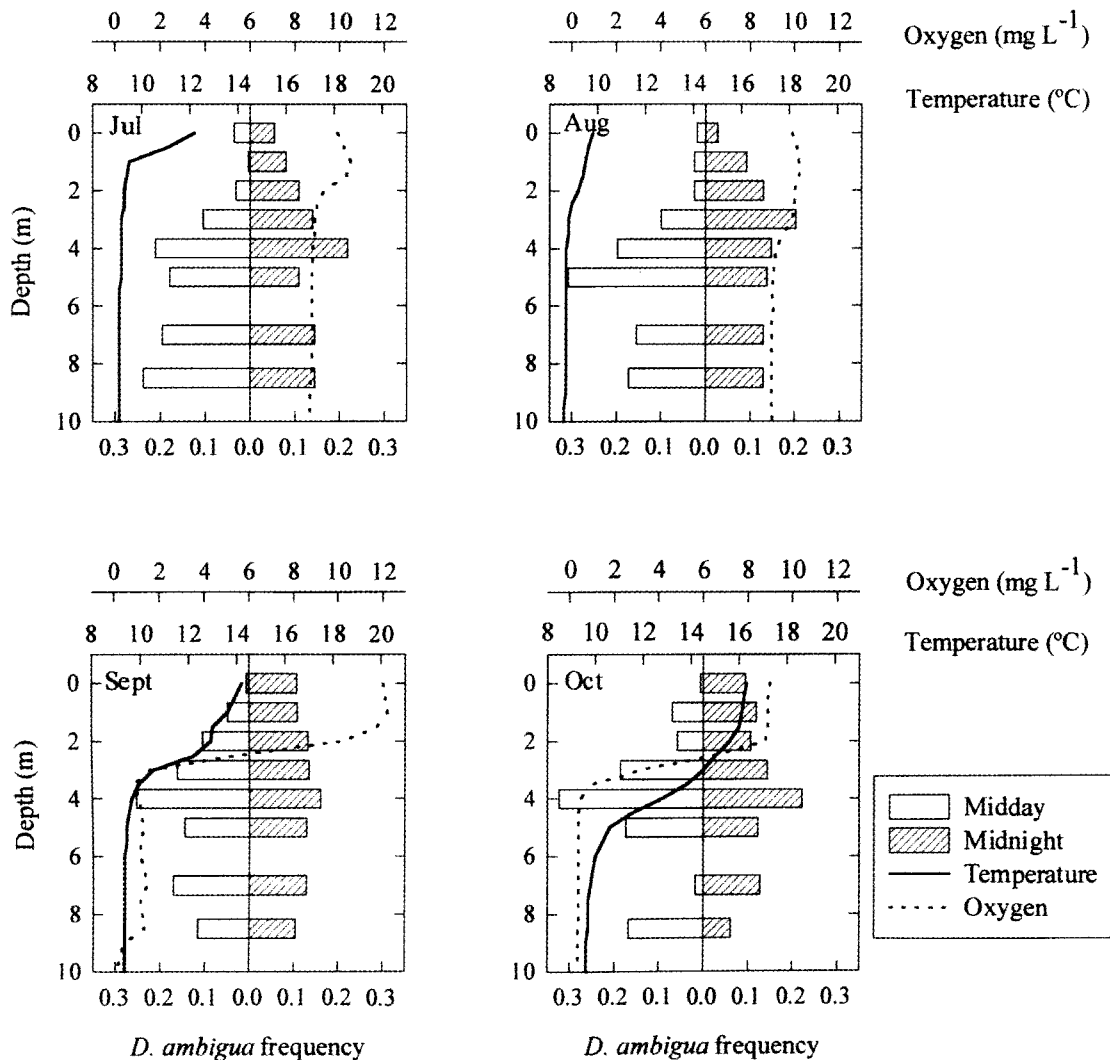


Fig. 2: Day (empty bars) and night (filled bars) vertical distribution of *Daphnia ambigua* in lake El Plateado during its higher-density period. For each date the temperature (continuous line) and dissolved oxygen concentration (dotted line) profiles are shown.

Distribución vertical de *Daphnia ambigua* en el día (barras claras) y la noche (barras oscuras) en el lago El Plateado, durante su periodo de mayor densidad. Para cada fecha se muestran los perfiles de temperatura (línea continua) y concentración de oxígeno disuelto (línea punteada).

TABLE 2

Significance levels of Kolmogorov-Smirnov-Solow (KSS) test probabilities for comparison between *D. ambigua* distributions between the dates at midday (upper right half) and at midnight (lower left half)

Niveles de significancia de la prueba Kolmogorov-Smirnov-Solow (KSS) para la comparación de distribuciones de *D. ambigua* entre las fechas a mediodía (mitad superior derecha) y a medianoche (mitad inferior izquierda)

Date	Jul	Aug	Sep	Oct
Jul		0.5092	0.0516	0.0556
Aug	0.5584		0.1124	0.0179
Sep	0.0929	0.2490		0.7610
Oct	0.1223	0.5183	0.6725	

see also Lampert et al. 1988, Lampert 1989, Guisande et al. 1991, Gabriel 1993, De Meester et al. 1999), and that this response is plastic and inducible, that is to say, the presence of a predator-released chemical cue is necessary to trigger the behavioral response (Frost & Bollens 1992, Loose & Dawidowicz 1994, Von Elert & Loose 1996, De Meester et al. 1999). While fish are responsible of the normal vertical migration response, invertebrate predators stimulate the reverse migration. The normal pattern of vertical migration applies to *D. ambigua* in El Plateado. This finding indicates that fish predation on *D. ambigua* could be important in this system, in agreement with frequent observations of silver-side fish *Odontesthes bonariensis* and *Basilichthys* sp. in El Plateado (R. Ramos-Jiliberto unpublished results), species that are known to be zooplanktivorous during their juvenile stage (Burbridge et al. 1973, Bahamondes et al. 1979, Escalante 1983).

Which kind of abiotic environment do daphnids experience as a result of their observed behavior?

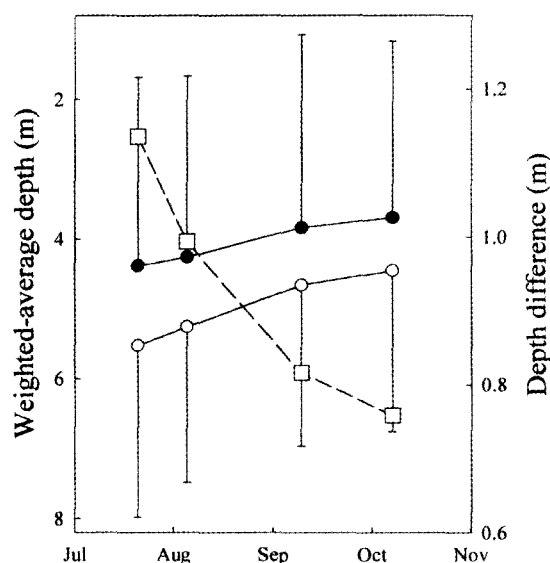


Fig. 3: Weighted-average depth of *Daphnia ambigua* in lake El Plateado during the sampling period. Closed circles: midnight samples, open circles: midday samples. Error lines show 1 standard deviation. The dashed line with squares shows the differences between midnight and midday average depth.

Promedio ponderado de profundidad de *Daphnia ambigua* en el lago El Plateado durante el periodo de muestreo. Círculos llenos: muestras de medianoche, círculos vacíos: muestras de mediodía. Líneas de error muestran 1 desviación estándar. La línea segmentada con cuadros muestra las diferencias entre la profundidad promedio a medianoche y a mediodía.

During the stratified phase, oxygen values range from nearly zero to 12 mg L⁻¹, and temperature lies between 9-16 °C, so the distribution of daphnids over these variables is meaningful at that time. Then, the density of daphnids correlates inversely with oxygen and directly with temperature, irrespective of time of the day. In other words, the depth-selection behavior of *D. ambigua* does not constrain the use of a favorable thermal environment, but the population experiences relatively

TABLE 3

Multiple regression summary for *D. ambigua* frequency as dependent variable. All data included

Resumen de resultados de un análisis de regresión múltiple para la frecuencia de *D. ambigua* como variable dependiente. Se incluyen todos los datos

	R = 0.561	F _{2, 61} = 14.008	P < 0.00001
Independent variable	Regression coefficient		P-value
Temperature	0.0231		0.8964
Oxygen	-0.5793		0.0017

TABLE 4

Multiple regression summary for *D. ambigua* frequency as dependent variable. (A) midday data; (B) midnight data

Resumen de resultados de un análisis de regresión múltiple para la frecuencia de *D. ambigua* como variable dependiente. (A) Datos de mediodía; (B) datos de medianoche

R = 0.717			
F _{2, 29} = 15.336			
P < 0.0001			
A	Independent variable	Regression coefficient	P-value
	Temperature	0.0838	0.7007
	Oxygen	-0.7822	0.0011
R = 0.349			
F _{2, 29} = 2.0153			
P > 0.1			
A	Independent variable	Regression coefficient	P-value
	Temperature	-0.1063	0.7167
	Oxygen	-0.2584	0.3805

low oxygen levels as a consequence of this behavior. This trend could indicate the use by *D. ambigua* of a thermally suitable oxygen-refuge against fish predators, or simply be a by-product of a trade-off between the surface-avoidance and unsuitability of deep hypolimnion for survival, growth and/or reproduction of zooplankters. This observation is in agreement with Hanazato (1992), who suggested a higher tolerance of *D. ambigua* to hypoxic conditions. It should be noted, however, that *D. ambigua* concentrates near the upper limit of the hypolimnion, and since we are recording differences in the population's vertical distribution instead of the behavior of each organism (Lampert 1989), it is conceivable that individuals could move up and down (on a short time-scale) within the hypolimnion-epilimnion boundary.

As quoted above, a seasonal differentiation was observed in the depth-selection behavior of *D. ambigua*. The central tendency indicator of the population distribution becomes shallower as the season progresses. While the average depth of daphnids during night did not change significantly with time, significant or marginally-significant seasonal differences were found during daytime. Although statistically weak, the results suggest that the average depth at night remains unchanged, while the average depth at day moves upwards on a monthly scale. As a consequence, day/night differences in the average depth decrease with time, till no significant differences in day/night vertical distribution are detected in October. In other words, the amplitude of the vertical migration diminishes with time.

Seasonal trends in *Daphnia* diel vertical migration in a northern mesotrophic lake were reported by Stich & Lampert (1981). They found, never-

theless, that the amplitude and depth of the vertical migration increases with time, whereas in this work the opposite pattern is displayed.

Although predation is widely accepted as the ultimate, evolutionary cause of zooplankton diel vertical migration, the specific pattern of response varies to a large extent among different populations due in part to genetic differences among *Daphnia* clones (King & Miracle 1995, De Meester & Weider 1999), and to exogenous stimuli acting as modulators of the zooplankton vertical migration behavior (Haney 1988, De Meester et al. 1999). Therefore, seasonal trends in vertical migration of a population have been thought to be caused by the same sort of processes (Stich & Lampert 1981, Young & Watt 1996).

Besides variation in predation cues, a number of environmental factors have been reported as modifiers of the zooplankton vertical migration behavior. They include seasonal changes of light penetration, food availability, temperature and oxygen limitations (Gliwicz 1985, Gliwicz & Pijanowska 1988, Haney 1988, De Meester et al. 1999, Lass et al. 2000). A decrease of predation risk through time is unlikely to occur in El Plateado within the period studied herein because young silverside fish are normally more abundant from September on. Additionally, both the water transparency and surface irradiance in El Plateado increase from July through the summer (Ramos et al. 1997), which should induce a deeper daytime distribution in order to avoid visually-oriented predators (Gliwicz 1985). Therefore, the reduction through time in both the average depth of *D. ambigua* distribution and the amplitude of the vertical migration seem to be determined by factors other than predation or visible light.

TABLE 5

Multiple regression summary for *D. ambigua* frequency as dependent variable. I: holomixis phase (July-August), II: stratification phase (September-October). (A) Midday data; (B) midnight data

Resumen de resultados de un análisis de regresión múltiple para la frecuencia de *D. ambigua* como variable dependiente. I: fase de holomixis (julio-agosto), II: fase de estratificación (septiembre-octubre). (A) Datos de mediodía; (B) datos de medianoche

		R = 0.838	$F_{2, 13} = 15.350$	P < 0.0005
I	A	Independent variable	Regression coefficient	P-value
		Temperature	-0.3462	0.1948
		Oxygen	-0.5346	0.0547
		R = 0.673	$F_{2, 13} = 5.376$	P < 0.05
II	B	Independent variable	Regression coefficient	P-value
		Temperature	-0.8698	0.0250
		Oxygen	0.2702	0.4457
		R = 0.769	$F_{2, 13} = 9.384$	P < 0.005
II	A	Independent variable	Regression coefficient	P-value
		Temperature	0.9294	0.0320
		Oxygen	-1.4659	0.0023
		R = 0.722	$F_{2, 13} = 7.074$	P < 0.01
II	B	Independent variable	Regression coefficient	P-value
		Temperature	1.4604	0.0040
		Oxygen	-1.5685	0.0024

Resource availability as a possible modulating factor of *D. ambigua* vertical migration is not analysed herein, but some available data of food concentration in El Plateado indicates that density of small algae increases from July through the winter, peaks in September, and subsequently drops somewhat in the epilimnion while it increases in the hypolimnion (Ramos-Jiliberto 1999). Furthermore, we have no evidence of inedible microalgae in the pelagic zone of this lake during the free-living season of *D. ambigua*. Under such conditions, vertical migration theory predicts an increase in average depth (see Gliwicz & Pijanowska 1988) and/or an increase in the amplitude of migration (see De Meester et al. 1999 and references therein), which is inconsistent with the observed trend. Therefore, food-based regulation of vertical migration by *D. ambigua* is unlikely to play a role in El Plateado.

Young & Watt (1993, 1996) demonstrate that temperature exert an important control on diel vertical migration of *Daphnia*. Their experimental results show that high temperatures promote reduced migration movements and a shallower

depth distribution of daphnids. On this basis, they interpreted the field observations of Stich & Lampert (1981) as a response to seasonal temperature changes (Young & Watt 1996). As mentioned above, the data of Stich & Lampert (1981) revealed the opposite tendency as compared with our data in chronological terms, but considering the seasonal changes of vertical migration over temperature evolution instead of time, we found a qualitative agreement with the results of this work. Migrating *Daphnia* in lake Constance increases the average depth and amplitude of migration from summer through fall (decreasing temperatures), whereas *Daphnia* in lake El Plateado decreases both traits from winter to spring (increasing temperatures), which is in agreement with predictions of Young & Watt (1993, 1996). Despite of this statistical association, the validity of an hypothesis based on temperature modulation of vertical migration may not be plausible from an ecological point of view.

Three lines of reasoning have been proposed in order to explain the origin of such temperature-driven seasonal changes in vertical migration

(Stich & Lampert 1981, Young & Watt 1993, 1996): (1) temperature could act as an environmental cue allowing daphnids to anticipate predictable changes in predation risk. In lake Constance (Stich & Lampert 1981) predation pressure increases from summer towards autumn, whereas temperature decreases. So, and under this hypothesis, information of decreasing temperature translates to daphnids into "a higher predation risk" and vertical migration is distended and deepened. In lake El Plateado, a diminishing response of vertical migration driven by increasing temperature as a cue of "less predators" is clearly not functional since predation risk is also increasing. On the other hand, if the temperature of El Plateado has the inverse meaning for *D. ambigua* (more temperature meaning "more risk"), the seasonal response should be more amplitude of migration and deeper positioning. Therefore, this argument is invalid as a general explanation. An argument of natural selection operating on a seasonal scale, and eliminating the organisms with non-optimal behavior (Stich & Lampert 1981) is rejected under the same logic. (2) The energetic cost of vertical migration could be minimized under coldness, so daphnids display the full behavior when temperatures are low enough (Young & Watt 1993, 1996). The benefit of energy saving by minimizing metabolism in general does not pay the cost of increased time of development at low temperature. Indeed, it is widely accepted that the highest cost of diel vertical migration come from cold exposition in the hypolimnion (Dawidowicz 1994, Loose & Dawidowicz 1994, De Meester et al. 1999), and no empirical support exists for this kind of metabolic advantage hypothesis (Lampert 1989). (3) Higher temperatures accelerate the bacterial degradation of fish kairomones, so daphnids perceive more risk at low temperatures (Loose et al. 1993). This effect may explain laboratory results in which predator kairomones are supplied by pulses to a tank containing zooplankters, but it seems unlikely to affect perceived risk by *Daphnia* in the field if fish density does not abruptly disappear.

Although it is not possible to discard temperature as the main factor responsible of the observed seasonal trend in *Daphnia* diel vertical migration, there is little logical and empirical support to it. Therefore, we could abandon this hypothesis if a better one is available.

Lampert (1989) stated that vertically migrating daphnids should exploit more shallow waters if they meet less favourable conditions in the hypolimnion. Although this hypothesis deals with changes in behavior across populations, it is also valid for seasonal shifts. In a recent paper, Lass et

al. (2000) showed experimentally that, by keeping predation risk constant, daphnids exhibit a shallower vertical positioning if hypolimnetic oxygen decreases. Furthermore, they recorded how *Daphnia* remains in the epilimnion when exposed simultaneously to high predation risk, low hypolimnetic temperature and low hypolimnetic oxygen. Such combination of variables are those we find in El Plateado when stratified, and the observation of Lass et al. (2000) on the depth-selection behavior of *Daphnia* is in close agreement with this field-work. Besides the theoretical (Lampert 1989) and empirical (Lass et al. 2000) evidence supporting the hypothesis of oxygen concentration as the main variable driving the seasonal changes of *Daphnia* diel vertical migration in El Plateado, its simplicity is also pleasing.

At the beginning of this article, it was acknowledged the accompanying interest in accounting for the population dynamics of *D. ambigua* in lakes of central Chile. Data of Ramos et al. (1998) (and of Fig. 1C in this study) reveal that *D. ambigua* exhibits a systematic seasonal pattern, closely repetitive from one year to the next. *Daphnia ambigua* start to grow in June, peaks in August-September and disappears in October. Typical seasonal patterns of *Daphnia* population fluctuations in northern-hemisphere lakes show that population density is low at winter, when the organisms usually persist as resting eggs. Afterwards, a population increase occurs from spring-time to early summer, and then it temporarily or definitively declines during midsummer (Sommer et al. 1986, Threlkeld 1987). The causes of this midsummer decline are attributed to food limitation and/or predation pressure (Hülsmann & Weiler 2000). The population pattern of *D. ambigua* in El Plateado is somewhat opposite with an increasing phase in winter, and a decreasing phase in early spring. Thus, *D. ambigua* is forced to grow under low temperature and poor food conditions, and to remain latent, apparently as resting eggs, from early spring to late fall. Our personal observations confirm that this population exhibit ephippia formation and sexual reproduction under laboratory conditions, as reported for many daphnids (Hebert 1987).

Does the knowledge about diel vertical migration tell us something in order to understand the population dynamics? Yes. Within the short period where free-living individuals of *D. ambigua* can be found in El Plateado, survival is enhanced by low water transparency, so visual predation is restricted to a thinner superficial layer, and by the predator avoidance strategy of diel vertical migration displayed by *D. ambigua* because the

hypolimnion is inhabitable. During October, the development of anoxia during lake stratification turns the refuge zone unsuitable for individual survival and reproduction. As a consequence, *D. ambigua* at daytime get closer to the surface, the zooplankters become more exposed to visual predators, mortality should increase by enhanced predation rate and the population declines (Wright & Shapiro 1990). This proposed mechanism may account for the abrupt decline of the population size of *D. ambigua* each year during October. Based on the indirect evidence of this work, it is suggested that the atypical seasonal population trend of *D. ambigua* in lake El Plateado is controlled mainly by the interaction of fish predation and oxygen concentration in the hypolimnion, through the influence of the last on the depth-selection behavior of *D. ambigua*.

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