CALANOID COPEPODS IN CENTRAL CHILEAN AND CHILEAN PATAGONIAN LAKES (33-55°S, CHILE), PROBABLE ECOLOGICAL KEY ROLE IN PELAGIC ENVIRONMENTS

BY

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ABSTRACT

The Patagonian lakes (38-55°S) are characterized by their marked oligotrophy, low number of species of crustacean zooplankton, and a marked predominance of calanoid copepods. Within this context, we considered that a review about the ecology of the zooplankton in central and southern Chilean lakes would be useful, aiming to understand the ecological importance of this group. Data obtained from the literature for freshwater bodies in central and southern Chilean lakes were analysed. In addition, data from various bays with widely differing trophic status in Llanquihue Lake were examined. The results revealed the existence of originally pristine and oligotrophic sites, all with a low number of species and marked calanoid dominance. However, in northern Patagonia there are many lakes in which human intervention has caused an increase in phytoplankton activity, with a consequent replacement of calanoid copepods by daphniid cladocerans. Other important factors that could affect the zooplankton community would be fish predation, which is due to generate a decrease in large-bodied groups of zooplankton; and stress due to exposure to natural ultraviolet radiation. Ecological, biogeographical, and evolutionary topics are discussed within the framework described.

RÉSUMÉ

Les lacs de Patagonie (38-55°S) sont caractérisés par leur oligotrophie marquée, le faible nombre d'espèces de crustacés du zooplancton, et une prédominance marquée des copépodes calanoïdes. Dans ce contexte, nous avons estimé qu'une analyse de l'écologie du zooplancton dans les lacs du centre et du sud du Chili serait utile, afin de comprendre l'importance écologique de ce groupe.

Les données de la littérature sur les lacs du Chili central et du sud ont été analysées. De plus, les données concernant différentes baies à état trophique différant très largement, du lac Llanquihue ont été examinées. Les résultats ont révélé l'existence de sites à l'origine intacts et oligotrophes,

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tous avec un faible nombre d'espèces et une dominance marquée des calanoïdes. Cependant, dans le nord de la Patagonie, il existe de nombreux lacs dans lesquels l'intervention humaine a provoqué une augmentation de l'activité du phytoplancton, avec le remplacement subséquent des copépodes calanoïdes par des cladocères Daphniidae. D'autres facteurs importants qui affecteraient la communauté du zooplancton seraient la prédation des poissons, qui engendrerait une diminution des groupes de zooplancton de grande taille et le stress dû à l'exposition aux rayonnements ultraviolets naturels. Les sujets écologiques, biogéographiques et évolutifs sont discutés dans le cadre décrit ici.

INTRODUCTION

The crustacean zooplankton communities in Chilean lakes are characterized by their low species number (Woelfl, 2007; De los Ríos-Escalante, 2013), which situation is markedly opposed to that found in Northern Hemisphere lakes (Gillooly & Dodson, 2000). The detailed studies performed on the community structure based on observations in Patagonian lakes (39–51°S) revealed the existence of a dominance of calanoids (De los Ríos-Escalante, 2010). This condition was interpreted as being probably due to the marked oligotrophy, as reported in the first limnological descriptions (Soto & Zúñiga, 1991; Woelfl, 2007; Kamjunke et al., 2009; De los Ríos-Escalante, 2010, 2016). Similar results have been reported for Argentinean Patagonian lakes (Modenutti et al., 1998). However, until now no integrative studies have been performed yet.

In Chile, there are many inland water bodies, which include saline lakes in the north, reservoirs in the central zones, lakes in the central-southern regions, and shallow subsaline lagoons and ponds in the extreme southern area (Soto & Zúñiga, 1991; De los Ríos-Escalante, 2010, 2013). In general, a direct association was found between the numbers of crustacean zooplankton species and the chlorophyll concentration for different kinds of water bodies present on the continental Chilean territory (Soto & Zúñiga, 1991; De los Ríos-Escalante, 2013).

From a limnological viewpoint, in central Chile (33–39°S) there are many small lakes with a different kind of trophic status that show a direct association between the chlorophyll concentration and the number of species (De los Ríos-Escalante, 2013). Also, under mesotrophic and eutrophic conditions, the calanoid copepods decrease in abundance (De los Ríos-Escalante, 2010). A different situation is encountered in Patagonian lakes (39–51°S), which are characterized by their glacial origin, their large surface area, and their greater depth. Originally, these lakes are oligotrophic, which we find mainly at southern latitudes (De los Ríos-Escalante, 2010), but in lakes located in northern Patagonia (39–41°S), such lakes can have an oligo-mesotrophic status due to human intervention, i.e., when in their surrounding catchment basins native forest has been replaced by towns and industrial zones (De los Ríos-Escalante et al., 2017). Then, in this scenario, under the condition of an oligotrophic status calanoid copepods are dominant, mainly *Tumeodiaptomus*

diabolicus Brehm, 1935, between 39–41°S, *Boeckella gracilipes* Daday, 1902, between 40–51°S, and *B. michaelsoni* Mrázek, 1901, which tends to predominate over *B. gracilipes* at latitudes south of 45°S (De los Ríos-Escalante, 2010), whereas under an oligo-mesotrophic status the calanoids are gradually replaced by cladocerans and by cyclopoid copepods (Woelfl, 2007; De los Ríos-Escalante, 2010).

The purpose of the present study is to review the literature of central and southern Chilean lakes (33–51°S) with the aim at determining potential regulatory factors of calanoid dominance in the zooplankton communities.

MATERIAL AND METHODS

Data from the literature on central Chilean and Chilean Patagonian lakes were analysed in the present study. We referred to Schmid-Araya & Zúñiga (1992), Campos et al. (1994a, b), Villalobos (1999), Soto & De los Ríos (2006), and De los Ríos-Escalante et al. (2017) (see table I, fig. 1). Variables considered were data of latitude, surface area, maximum depth ($Z_{\max}$), chlorophyll *a* (Chl *a*) concentration and the percentage of calanoids, considering the relation between calanoid abundance and total crustacean zooplankton abundance (i.e., the sum of calanoids, cyclopoids, cladocerans, and nauplii found). Data of saline and subsaline lakes from northern and southern Chile were not considered, due to the potential noise effect of salinity (De los Ríos-Escalante, 2010). Next, a Principal Component Analysis (PCA) was applied to the data obtained, using the software R and the package HSAUR (R Development Core Team, 2009; Everitt & Hothorn, 2016).

In a second step, data from Llanquihue Lake (41°S) obtained between 2001 and 2003, were retrieved from the literature (table I, fig. 1; De los Ríos-Escalante et al., 2017). The data considered were values of total dissolved nitrogen, orthophosphate, and chlorophyll concentrations, as well as the percentages of daphniid cladocerans and calanoid copepods as a percentage of total crustacean zooplankton (calanoids, cyclopoids, cladocerans, and nauplii) as the main zooplankton grazers (Soto & Zúñiga, 1991; Gillooly & Dodson, 2000). These last two serial data were transformed to arcsine square root in order to obtain a normal distribution (Zar, 1999). Next, the data were subjected to a multiple regression analysis using the software R and the package HSAUR (R Development Core Team, 2009; Everitt & Hothorn, 2016).

RESULTS

The results obtained revealed the presence of a significant and direct association between calanoid copepods and latitude ($R^2 = 0.731$; $P < 0.05$; table II), and

a significant, inverse relationship of calanoid copepods with the chlorophyll concentration ($R^2 = -0.873$; $P < 0.05$; table II), as well as a significant, inverse correlation between chlorophyll concentration and latitude ($R^2 = -0.814$; $P < 0.05$; table II). The main variables contributing to axis 1 were latitude, chlorophyll “a” concentration, and calanoid percentage, whereas the main contributor variables for axis 2 were surface, maximum area, and maximum depth (table III). The PCA results revealed that lakes Sarmiento and Del Toro have a high calanoid dominance, occupy the southernmost location, and show a low chlorophyll *a* concentration (fig. 2, table I), whereas Llanquihue Lake has a relatively moderate calanoid percentage and chlorophyll concentration, a large surface, and a comparatively great depth (fig. 2, table I). Another group was composed of the pools Escondida, Los Palos, Melliza Este, and Melliza Oeste, joined by Riesco Lake, waterbodies that all have a moderate surface area and a moderate maximum depth, as well as a variable calanoid percentage and also a variable chlorophyll concentration (fig. 2, table I). Finally, the reservoirs Peñuelas and Runge have a high chlorophyll concentration, show an absence of calanoids, have only a small surface area, and also a limited depth, in combination with their northern location (fig. 2, table I).

TABLE I

Geographical location, surface area, maximum depth ($Z_{\max}$), chlorophyll *a* concentration (in $\mu\text{g/l}$) and percentage of calanoids (on the basis of total crustacean zooplankton: calanoids, cyclopoids, and cladocerans) for all lakes considered in the present study; and soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN), and chlorophyll *a* concentrations (in $\mu\text{g/l}$) and daphniid and calanoid percentages for sites in Llanquihue Lake

	Geographical location	Surface (km ²)	$Z_{\max}$ (m)	SRP	DIN	Chl <i>a</i>	% Calanoids	% Daphniids
Peñuelas	33°00'S 70°53'W	19.00	15			77.6	0.00	
Runge	33°10'S 71°29'W	0.48	14			38.9	0.00	
Llanquihue	41°08'S 72°50'W	870.00	317			2.0	72.73	
Los Palos	45°19'S 72°42'W	7.32	59			1.2	99.29	
Escondida	45°39'S 72°20'W	6.70	68			0.6	1.63	
Riesco	45°49'S 72°40'W	14.70	130			1.0	98.33	
Del Toro	51°03'S 72°38'W	196.00	300			0.4	85.06	
Sarmiento	51°12'S 72°37'W	86.00	312			0.3	85.71	
Melliza Este	51°03'S 72°57'W	0.13	16			5.3	49.41	
Melliza Oeste	51°03'S 72°57'W	0.12	25			3.2	69.46	
Sites in Llanquihue lake								
Llanquihue	41°14'S 72°02'W			1.80	10.50	15.95	43.19	56.34
Puerto Chico	41°19'S 72°58'W			1.00	2.79	6.50	0.00	33.33
Puerto Phillippi	41°13'S 72°02'W			2.10	18.51	8.75	35.22	55.07
Puerto Rosales	41°17'S 72°51'W			30.20	181.10	12.70	66.67	33.34
Ensenada	41°12'S 72°35'W			1.00	4.00	1.95	72.73	13.60
Puerto Octay	40°58' S 72°54'W			2.10	6.50	8.20	99.70	0.10
Volcanes Bay	41°08'S 72°34'W			1.00	3.50	7.40	99.70	0.10
Venado beach	41°12'S 72°49'W			1.00	3.10	3.90	99.00	0.01

Fig. 1. Map with sites included in the present study. Left, lakes along the Chilean territory: 1, Peñueñas; 2, Runge; 3, Llanquihue; 4, Los Palos; 5, Escondida; 6, Riesco; 7, Del Toro; 8, Sarmiento; 9, Gemela Este; 10, Gemela Oeste. Right, sites in Llanquihue Lake: 11, Llanquihue town; 12, Puerto Chico; 13, Puerto Phillippi; 14, Puerto Rosales; 15, Ensenada; 16, Puerto Octay; 17, Volcanes Bay; 18, Venado beach. [Source: Google Earth, 2016.]

The results from Llanquihue Lake revealed that Multiple Regression Analysis yielded an inverse association between the percentages calanoids and daphniids, and a direct correlation with the concentration of dissolved inorganic nitrogen.

TABLE II

Results of correlation analysis between calanoid percentage with latitude, maximum depth (m), surface area (km²) and chlorophyll *a* concentration ($P < 0.05$ denotes significant associations)

	Latitude (S)	Surface area	$Z_{\max}$	Chl <i>a</i>
% Calanoids	0.731 ($P = 0.043$)	0.120 ($P = 0.539$)	0.454 ($P = 0.110$)	-0.873 ($P = 0.030$)
Chl <i>a</i>	-0.814 ($P < 0.001$)	-0.198 ($P = 0.584$)	-0.443 ($P = 0.199$)	
$Z_{\max}$	0.334 ($P = 0.33$)	0.667 ($P = 0.350$)		
Surface area	-0.097 ($P = -0.100$)			

TABLE III
Percentage contribution of variables for axes 1 and 2 of the PCA performed for data of all lakes considered in the present study

	Axis 1	Axis 2
Latitude (S)	0.4809	−0.3578
Surface area (km ²)	0.1979	0.7426
Z _{max} (m)	0.3950	0.5146
Chl <i>a</i>	−0.5444	0.1582
% Calanoids	0.5263	−0.1747

The regression equation describing this association was determined as:

$$Y = 100.9812 + 0.1458X_1 - 1.6475X^2,$$

where *Y* = percentage calanoids, *X*₁ = dissolved inorganic nitrogen concentration, *X*₂ = percentage daphniids with a Multiple *R*-squared of 0.734 and *P* = 0.0364.

Fig. 2. Results of the PCA for variables studied that have been included in the present study. See text for further explanation.

DISCUSSION

The results obtained would confirm the first preliminary observations of Soto & Zúñiga (1991), who proposed that the oligotrophy of these inland waters would constitute the main cause of the calanoid abundance and the low species number of crustacean zooplankton in zooplankton assemblages in the Chilean Patagonian large and deep lakes. This pattern was confirmed in recent studies (Woelfl, 2007; Kamjunke et al., 2009; De los Ríos-Escalante, 2010, 2016). The present study is the first that included central Chilean lakes, which would be expected to have a different pattern in comparison to Patagonian lakes, where the main regulating factors would be the chlorophyll concentration, and where the greater maximum depth would play a protective role against exposure towards natural ultraviolet radiation (Marinone et al., 2006; De los Ríos-Escalante, 2010). The direct relationship between chlorophyll concentration and calanoid relative abundance would be explained due to the marked decrease of chlorophyll concentration at southern latitudes that would be correlated with an increase of the mixing depth (Soto, 2002). In this scenario, the calanoid copepods would be more tolerant to ultraviolet in oligotrophic environments, i.e., by avoiding exposure through migrating to deeper strata, such as has been observed for Patagonian lakes, and this would thus explain the main dominance of this group in zooplankton communities (De los Ríos & Soto, 2005, 2006, 2007; Marinone et al., 2006). Similar conditions would appear from the results obtained in New Zealand's lakes and lagoons (Jeppensen et al., 1997, 2000).

This pattern of calanoid abundance and oligotrophy in zooplankton assemblages was described for Argentinean Patagonian lakes as well (Modenutti et al., 1998; Reissig et al., 2006; Hylander et al., 2012). Under pristine, native conditions, the calanoids in these lakes would have a key role as grazers on mixotrophic ciliates that are the main primary producers in these ecosystems (Modenutti et al., 1998; Woelfl, 2007; Kamjunke et al., 2009; De los Ríos-Escalante & Woelfl, 2017). In this scenario, i.e., under such oligotrophic conditions, in these Patagonian lakes we find a marked dominance of *Boeckella gracilipes*, which gradually decreases at more southern latitudes. There, from 46°S onward, this species is gradually being replaced by *B. michaelsoni*, although both species can coexist. *B. michaelsoni* is dominant south of 51°S (Menu-Marque et al., 2000; De los Ríos-Escalante, 2010).

Under the conditions of a transition from oligotrophy to mesotrophy, the calanoids decrease in abundance, and daphniid cladocerans and cyclopoid copepods appear in the zooplankton communities (Woelfl, 2007; Kamjunke et al., 2009; De los Ríos-Escalante, 2010). In comparison, this pattern is the opposite of that found in Canadian lakes, where daphniids are dominant in zooplankton assemblages (Gillooly & Dodson, 2000), and that same pattern is also frequently met

with in all North American lakes, where it is possible to find daphniids in high abundance and with large-sized bodies at high latitudes (Hoffmann & Dodson, 2005; Dodson et al., 2009). The studies of North American lakes included pristine lakes as well as lakes altered through human influence, and direct correlations were found between chlorophyll concentrations and the abundance of daphniid cladocerans, as well as with species richness (Gillooly & Dodson, 2000; Hoffmann & Dodson, 2005; Dodson et al., 2009). However, the introduction of salmonids in Argentinean and Chilean lakes generated effects in zooplankton communities that have been preliminarily studied: this introduction would have an effect on phytoplankton abundance due to cascade effects, because the salmonids can predate on zooplanktivorous fishes, which by consequence generates an increase in zooplankton grazing activity (Soto & Zúñiga, 1991; Reissig et al., 2006; Soto & De los Ríos, 2006; De los Ríos-Escalante, 2015). A different situation is found in North American lakes that have salmonids as native fauna, and where there are complex trophic webs with high species richness and a high abundance of daphniid cladocerans (Gillooly & Dodson, 2000; Hoffmann & Dodson, 2005).

This first integrative study included two representative central Chilean waterbodies, i.e., Rungue and Peñuelas, but nevertheless, it would be necessary to do more integrative studies that include saline and subsaline lakes in the northern and southern extreme regions of Chile, as well as the central Chilean lakes and reservoirs that have not been studied in sufficient detail, yet. Only then may we expect to better understand the actual structures in the community patterns of crustacean zooplankton, with the aim of understanding potential biogeochemical effects on surrounding ecosystems, whenever changes are brought about (or are intended to be brought about) through human influence. Under such conditions of sufficient knowledge, we may be able to predict what these effects could be and how we can cope with those results.

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REFERENCES

- CAMPOS, H., D. SOTO, W. STEFFEN, G. AGÜERO, O. PARRA & L. ZÚÑIGA, 1994a. Limnological studies in Lake del Toro, Chilean Patagonia. *Arch. Hydrobiol.*, **99**(Suppl. 1/2): 199-215.
- CAMPOS, H., D. SOTO, W. STEFFEN, G. AGÜERO, O. PARRA & L. ZÚÑIGA, 1994b. Limnological studies in Lake Sarmiento, a subsaline lake from Chilean Patagonia. *Arch. Hydrobiol.*, **99**(Suppl. 1/2): 217-234.

- DE LOS RÍOS-ESCALANTE, P., 2010. Crustacean zooplankton communities in Chilean inland waters. *Crust. Monogr.*, **12**: 1-109.
- DE LOS RÍOS-ESCALANTE, P., 2013. Crustacean zooplankton species richness in Chilean lakes and ponds (23°-51°S). *Lat. Am. J. Aqu. Res.*, **41**: 600-605.
- DE LOS RÍOS-ESCALANTE, P., 2015. Fish predation effects on body length of planktonic cladocerans and copepods in Chilean lakes. *Crustaceana*, **88**: 1193-1199.
- DE LOS RÍOS-ESCALANTE, P., 2016. Null models for study rotifers and crustacean zooplankton species richness in Chilean Patagonian lakes. *Act. Limnol. Brasiliensia*, **28**: e11.
- DE LOS RÍOS-ESCALANTE, P., D. SOTO, P. ACEVEDO & R. SANTANDER MASSA, 2017. Zooplankton communities in bays with different trophic status in Llanquihue lake (41°S, Chile). *Brazilian J. Biol.*, **77**: 469-475.
- DE LOS RÍOS-ESCALANTE, P. & S. WOELFL, 2017. Use of null models to explain crustacean zooplankton assemblages in north Patagonian lakes with presence or absence of mixotrophic ciliates (38°S, Chile). *Crustaceana*, **90**: 311-319.
- DE LOS RÍOS, P. & D. SOTO, 2005. Survival of two species of crustacean zooplankton under to two chlorophyll concentrations and protection or exposure to natural ultraviolet radiation. *Crustaceana*, **78**: 163-169.
- DE LOS RÍOS, P. & D. SOTO, 2006. Effects of the availability of energetic and protective resources on the abundance of daphniids (Cladocera, Daphniidae) in Chilean Patagonian lakes (39°-51°S). *Crustaceana*, **79**: 23-32.
- DE LOS RÍOS, P. & D. SOTO, 2007. Crustacean (Copepoda and Cladocera) species richness in Chilean Patagonian lakes. *Crustaceana*, **80**: 285-296.
- DODSON, S. I., A. L. NEWMAN, S. WILL-WOLF, M. L. ALEXANDER, M. P. WOODFORD & S. VAN EGEREN, 2009. The relationship between zooplankton community structure and lake characteristics in temperate lakes (northern Wisconsin, USA). *J. Plankt. Res.*, **31**: 93-100.
- EVERITT, B. S. & T. HOTHORN, 2016. A handbook of statistical analysis using R (1st ed.). <https://cran.r-project.org/web/packages/HSAUR/HSAUR.pdf> [visited 13 July 2016].
- GILLOOLY, J. F. & S. I. DODSON, 2000. Latitudinal patterns in the size distribution and seasonal dynamics of New World freshwater cladocerans. *Limnol. Ocean.*, **45**: 25-30.
- HOFFMANN, M. D. & S. I. DODSON, 2005. Land use, primary productivity, and lake area as descriptors of zooplankton diversity. *Ecology*, **86**: 225-261.
- HYLANDER, S., M. S. SOUZA, E. BALSEIRO, B. MODENUTTI & L. A. HANSSON, 2012. Fish mediated trait compensation in zooplankton. *Funct. Ecol.*, **26**: 608-615.
- JEPPENSEN, E., T. L. LAURIDSEN, S. F. MITCHELL & C. W. BURNS, 1997. Do zooplanktivorous fish structure the zooplankton communities in New Zealand lakes? *New Zealand J. Mar. Freshwat. Res.*, **31**: 163-173.
- JEPPENSEN, E., T. L. LAURIDSEN, S. F. MITCHELL, K. CHIRSTOFFERSSEN & C. W. BURNS, 2000. Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *J. Plankt. Res.*, **22**: 951-968.
- KAMJUNKE, N., B. VOGT & S. WÖLFL, 2009. Trophic interactions of the pelagic ciliate *Stentor* spp. in north Patagonian lakes. *Limnologica*, **39**: 107-114.
- MARINONE, M. C., S. MENU MARQUE, D. AÑÓN SUÁREZ, M. C. DIÉGUEZ, A. P. PÉREZ, P. DE LOS RÍOS, D. SOTO & H. E. ZAGARESE, 2006. UVR radiation as a potential driving force for zooplankton community structure in Patagonian lakes. *Photochem. Photobiol.*, **82**: 962-971.
- MENU-MARQUE, S., J. J. MORRONE & C. LOCASCIO DE MITROVICH, 2000. Distributional patterns of the South American species of *Boeckella* (Copepoda, Centropagidae): a track analysis. *J. Crust. Biol.*, **20**: 262-272.
- MODENUTTI, B. E., E. G. BALSEIRO, C. P. QUEIMALIÑOS, D. A. AÑÓN SUÁREZ, M. C. DIEGUEZ & R. J. ALBARIÑO, 1998. Structure and dynamics of food webs in Andean lakes. *Lakes and Reserv. Res. Manag.*, **3**: 179-189.

- R DEVELOPMENT CORE TEAM, 2009. R: a language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna, Austria).
- REISSIG, M., C. TROCHINE, C. QUEIMALIÑOS, E. BALSEIRO & B. MODENUTTI, 2006. Impacts of fish introduction on planktonic food webs in lakes of the Patagonian Plateau. *Biol. Cons.*, **132**: 437-447.
- SCHMID-ARAYA, J. M. & L. R. ZUÑIGA, 1992. Zooplankton community structure in two Chilean reservoirs. *Arch. Hydrobiol.*, **123**: 305-325.
- SOTO, D., 2002. Oligotrophic patterns in southern Chile lakes: the relevance of nutrients and mixing depth. *Rev. Chilena Hist. Nat.*, **75**: 377-393.
- SOTO, D. & P. DE LOS RÍOS, 2006. Trophic status and conductivity patterns as regulators in daphnids dominance and zooplankton assemblages in lakes and ponds of Torres del Paine National Park. *Biologia Bratislava*, **61**: 541-546.
- SOTO, D. & L. R. ZUÑIGA, 1991. Zooplankton assemblages of Chilean temperate lakes: a comparison with North American counterparts. *Rev. Chilena Hist. Nat.*, **64**: 569-581.
- VILLALOBOS, L., 1999. Determinación de capacidad de carga y balance de fósforo y nitrógeno de los lagos Riesco, Los Palos, y Laguna Escondida en la XI región. Technical Report Fisheries Research Foundation — Chile, FIP-IT/97-39. [In Spanish.]
- WOELFL, S., 2007. The distribution of large mixotrophic ciliates (*Stentor*) in deep north Patagonian lakes (Chile): first results. *Limnologica*, **37**: 28-36.
- ZAR, J. H., 1999. Biostatistical analysis: 1-165. (Prentice-Hall, Upper Saddle River, NJ).

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