

# A NULL MODEL TO EXPLAIN ZOOPLANKTON SPECIES ASSOCIATIONS IN SALINE LAKES OF THE SOUTH AMERICAN ALTIPLANO (14-27°S)

BY

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## ABSTRACT

Zooplankton diversity in shallow salt lakes of the Andean countries in South America is low and distribution is highly dependent on salinity, which varies from moderate to high. At salinities lower than 90 g/l, the halophilic copepod *Boeckella poopoensis* (Marsh, 1906) predominates, whereas above that level the anostracan *Artemia franciscana* (Kellogg, 1912) is the exclusive component of the habitat. This constitutes, however, fragmentary information only. A review of the available literature for Andean saline lakes in Bolivia, Chile, and Peru, confirms that presence and distribution of both species is significantly driven by salinity levels. The results of a species co-occurrence null model analysis, indicates that species associations are not random, and these results are supported by the correlation analysis, which indicates a significant, inverse correlation between species number and salinity, and a significant direct relation of species number with surface of the habitat. The low species diversity characteristically seen in these habitats and their dependence on salinity changes effectuated by weather conditions, provide a good model-system for monitoring weather change.

## RESUMEN

La diversidad del zooplankton en lagos salinos poco profundos de Sudamérica es baja y su distribución depende altamente de la salinidad, la cual varía de moderada a alta. A salinidades menores a 90 g/l predomina el copépodo halofílico *Boeckella poopoensis* (Marsh, 1906), mientras que a salinidades superiores a ese nivel, el anostraco *Artemia franciscana* (Kellogg, 1912) es el componente exclusivo de los hábitats. Esto constituye sin embargo una información parcial. En una revisión de la literatura disponible para lagos salinos Andinos en Bolivia, Chile y Perú se confirma que la presencia y distribución de ambas especies está significativamente regulada por el nivel de la salinidad. Los resultados del modelo nulo de co-ocurrencia de especies indican que las asociaciones de especies no son aleatorias, y estos resultados están respaldados por el análisis de correlación, el cual indica una relación inversa significativa entre número de especies con salinidad, y hubo relaciones directas significativas entre número de especies con la superficie del hábitat. El bajo

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número de especies que es característico de estos hábitats y su dependencia con los cambios de salinidad efectuado por las condiciones climáticas provee un buen modelo de sistema de monitoreo de cambios climáticos.

## INTRODUCTION

The water bodies in the northern Andes mountains are characterized by high salinity values and low species numbers of the local crustacean zooplankton assemblages (Hurlbert et al., 1986; Williams et al., 1995; De los Ríos & Crespo, 2004). These saline lakes in South America are mainly found in arid zones of tropical and subtropical regions of the Andean countries, like Argentina, Bolivia, Chile, and Peru (Williams et al., 1995), which are located at latitudes between 13 and 27° South. These ecosystems are difficult to access for research, and consequently they have been poorly studied (De los Ríos & Crespo, 2004; De los Ríos, 2005). As Hurlbert et al. (1986) pointed out, zooplankton in these water bodies is primarily regulated by the level of salinity. In their first report of the halophilic copepod *Boeckella poopoensis* (Marsh, 1906), those authors (Hurlbert et al., 1986) found *Daphnia* and cyclopoid copepods to be dominant at salinities below 90 g/l, whereas the anostracan *Artemia* was the sole inhabitant at higher salt concentrations. Such a pattern has also been observed in saline lakes of northern Chile, between 22 and 27° South (De los Ríos & Crespo, 2004; De los Ríos, 2005; De los Ríos & Contreras, 2005), but the true generality of this pattern remains uncertain so far. The calanoid, *B. poopoensis* has also been reported in shallow lagoons with moderate to high salinities located at 14-27°S (Argentina, Bolivia, Chile, and Peru) (Bayly, 1993; Echaniz et al., 2006), whilst *Artemia franciscana* (Kellogg, 1912) has been reported from northern Chile (Gajardo et al., 1998) and northern Argentina (Amat et al., 2004). The present study focuses on the pattern of salinity-mediated exclusion between the calanoid copepod and the anostracans, as described by Hurlbert et al. (1986) in shallow salty lagoons. By comparing different datasets, all be these limited, we expect to shed light on the generality of that pattern as well as on the co-occurrence of species that tend to occur at opposite ends of a salinity gradient.

## MATERIAL AND METHODS

In total 27 sites/lakes were compared, located in four countries. These are situated over a range of altitude spanning 850-4600 m a.s.l., and from 14°59'S 70°07'W to 27°05'S 69°10'W, together covering a range of salinity between 0.5 and 300 g l<sup>-1</sup>. The maximum depth ranges between 0-2 and 14 m and their surface areas between 0.9 and 280 km<sup>2</sup>. These data and the numbers of species collected

are shown in table I (cf. Hurlbert et al., 1984, 1986; Williams et al., 1995; Zúñiga et al., 1999; De los Ríos, 2005).

Crustacean community structure was explored using the null model analysis, which tests whether species co-occur less frequently than expected by chance (Gotelli, 2000). Based upon an absence/presence matrix, a “checkerboard score” (“C-score”) is calculated, which represents a quantitative index of co-occurrence (see Tondoh, 2006; De los Ríos, 2008; De los Ríos et al., 2008a). A community is concluded to be structured by competition when its C-score is significantly larger than expected by chance (Gotelli, 2000, 2001). In order to determine whether a particular score is statistically significant, a set of randomizations of the species occurrence data is performed, and a null distribution for the coexistence index is created. Gotelli & Entsminger (2004), Tondoh (2006), and Tiho & Johens (2007) suggested the following three statistical models for creating the randomized communities, with the species placed in rows and the sites in columns:

(1) Fixed-Fixed: in this model, the row and column sums of the matrix are preserved. Thus, each random community contains the same number of species as the original community (fixed column) and each species occurs with the same frequency as in the original community (fixed row).

(2) Fixed-Equiprobable: in this algorithm, only the row sums are fixed, and the columns are treated as equiprobable. This null model considers all the sites (columns) as equally available for all species, which occur in the same proportions as in the original communities.

(3) Fixed-Proportional: this algorithm holds the species occurrence totals the same as in the original community, and the probability that a species at a site (column) is proportional to the column total for that sample.

All three models exhibit fairly reasonable combinations of Type I and Type II error rates, although model #3 has a high Type I error rate (false positives) using the C-score index, but they have differences in their underlying assumptions and behaviour (Gotelli, 2000). The fixed-fixed model is suggested to be most appropriate for island species lists, in which species-area effects are expected, while the fixed-equiprobable model would be most appropriate for standardized samples in a homogeneous environment (Gotelli, 2000). The fixed-proportional algorithm represents an intermediate model, which might be most appropriate in our system, due to habitat heterogeneity as well as differences in depth and width along the range of lakes. Differing results among models can provide insights into community structure. The null model analyses were performed using the software Ecosim version 7.0 (Gotelli & Etsminger, 1997).

In a second step, a Pearson correlation analysis was applied to determine potential associations of species numbers with altitude, surface, salinity, and maximum depth, and this analysis was executed using the software Xlstat 6.0.

## RESULTS AND DISCUSSION

Table I summarizes the sites ( $n = 27$ ) in Bolivia, Chile, and Peru, with the relevant parameters (salinity, etc.) and species presence at each site, upon which the analysis was performed. Sites were observed with one species, that can be the anostracan, *Artemia franciscana* at salinities above 90 g/l, or the calanoid, *Boeckella poopoensis* at salinities lower than 90 g/l, and it appeared possible to find two or more species at sites with salinities lower than 20 g/l (table I). A total of eight species represents the overall diversity observed, and these are not randomly associated. In all simulations of the co-occurrence null model (C-score,  $P < 0.001$ ; table II), remarkably a significant result is observed in the fixed-fixed simulation ( $P < 0.004$ ; table II), because this simulation gives the most robust

TABLE I  
Geographical location, species richness, and salinity for the sites studied in Bolivia, Chile, and Peru

Site	Geographical location (south/west)	Altitude (m a.s.l.)	Surface (km <sup>2</sup> )	Salinity (gr/l)	Maximum depth (m)	Species observed	Reference
Salinas (Peru)	14°59' 70°07'	3840	9.7	251.0	1.0	<i>Artemia franciscana</i> (Kellogg, 1912)	Hurlbert et al., 1986
Collpacocha (Peru)	15°15' 70°03'	3825	1.4	39.0	1.0	<i>Boeckella poopoensis</i> (Marsh, 1906) Cyclopoida indet.	Hurlbert et al., 1986
Parinacochas (Peru)	15°17' 73°42'	3273	67.0	5.6	3.0	<i>Boeckella poopoensis</i> Cyclopoida indet. <i>Daphnia</i> spp.	Hurlbert et al., 1986
Loripongo (Peru)	16°50' 70°55'	4555	33.0	0.5	2.6	<i>Boeckella poopoensis</i> <i>Daphnia</i> spp.	Hurlbert et al., 1986
Loriscota (Peru)	16°52' 70°02'	4552	33.0	10.4	2.6	<i>Boeckella poopoensis</i>	Hurlbert et al., 1986
Uru-Uru (Bolivia)	17°55' 66°27'	3668	280.0	4.4	No data	<i>Boeckella poopoensis</i> Cyclopoida indet. Harpacticoida indet. Ostracoda indet.	Williams et al., 1995
Surire (Chile)	18°48' 69°40'	4200	1.0	102.0	1.0	<i>Artemia franciscana</i>	Zúñiga et al., 1999
Llamara (Chile)	21°18' 69°37'	850	1.0	160.0	0.5	<i>Artemia franciscana</i>	Zúñiga et al., 1999
Loromayu (Bolivia)	22°18' 67°13'	4650	7.5	94.0	No data	<i>Artemia franciscana</i>	Hurlbert et al., 1984

TABLE I  
(Continued)

Site	Geographical location (south/west)	Altitude (m a.s.l.)	Surface (km <sup>2</sup> )	Salinity (gr/l)	Maximum depth (m)	Species observed	Reference
Cañapa (Bolivia)	21°30' 68°01'	4140	0.4	80.0	No data	<i>Artemia franciscana</i>	Hurlbert et al., 1984
Chulluncani (Bolivia)	21°32' 68°05'	4450	2.0	19.0	No data	<i>Boeckella poopoensis</i> <i>Branchinecta</i> spp.	Hurlbert et al., 1984
Hedionda (Bolivia)	21°34' 68°14'	4121	4.4	47.9	0.3	<i>Artemia franciscana</i>	Williams et al., 1995
Ramaditas (Bolivia)	21°38' 68°05'	4117	4.0	47.9	0.2	<i>Boeckella poopoensis</i>	Williams et al., 1995
Colorado (Bolivia)	22°10' 67°47'	4278	52.0	156.4	0.2	<i>Artemia franciscana</i>	Williams et al., 1995
Colorado II (Bolivia)	22°10' 67°47'	4278	1.0	4.4	1.0	<i>Boeckella poopoensis</i>	Williams et al., 1995
Kalina (Perú)	22°32' 67°11'	4530	16.0	65.0	No data	<i>Artemia franciscana</i>	Hurlbert et al., 1986
Verde (Bolivia)	22°48' 67°48'	4315	10.0	49.0	No data	<i>Boeckella poopoensis</i>	Hurlbert 1986
Cejas (Chile)	23°02' 68°13'	2400	1	182.0	14	<i>Artemia franciscana</i>	Zúñiga et al., 1999
Tebenquiche (Chile)	23°07' 68°16'	2400	1	300.0	10	<i>Artemia franciscana</i>	Zúñiga et al., 1999
Gemela Oeste (Chile)	23°14' 68°14'	2400	1	51.4	7.0	<i>Boeckella poopoensis</i>	De los Ríos & Crespo, 2004
Gemela Este (Chile)	23°14' 68°14'	2400	1	41.0	7.0	<i>Boeckella poopoensis</i>	De los Ríos & Crespo, 2004
Miniques (Chile)	23°43' 67°48'	4120	1.6	9.7	5.0	<i>B. poopoensis</i> Cyclopoida indet. <i>Alona pulchella</i> (King, 1853) <i>Daphnia</i> spp.	De los Ríos & Crespo, 2004
Miscanti (Chile)	23°43' 67°48'	4140	13.4	8.9	9.0	<i>B. poopoensis</i> Cyclopoida indet. <i>Alona pulchella</i> <i>Daphnia</i> spp.	De los Ríos & Crespo, 2004
Capur (Chile)	23°54' 67°48'	3950	0.9	3.4	1.5	<i>Boeckella poopoensis</i> Cyclopoida indet. Chydoridae indet.	De los Ríos & Crespo, 2004
Santa Rosa (Chile)	27°05' 69°10'	3760	1	8.0	1.5	<i>Boeckella poopoensis</i> <i>Alona pulchella</i> Chydoridae indet.	De los Ríos & Crespo, 2004

TABLE II

Results of null model analysis of the crustacean zooplankton species in South American shallow saline lakes for the sites studied using a C-score

	Observed index	Mean of simulated index	Standard error of estimate	<i>P</i>
Fixed-fixed	10.583	9.043	3.242	0.004
Fixed-equiprobable	10.583	8.703	1.726	0.034
Fixed-proportional	10.583	7.129	2.760	0.001

result and avoids the type I error, to falsely accept the null hypothesis (Tiho & Johens, 2007). The results thus found indicate an explanation due to the existence of regulating factors, i.e., environmental parameters, and the observations agree with other, similar results for inland water zooplankton assemblages (De los Ríos, 2008; De los Ríos et al., 2008a, b; De los Ríos & Soto, in press). In the present study, all simulations denoted significant effects, indicating the presence of regulating factors (table II). The probable cause would be that in spite of the low species number reported, the sites can have *B. poopoensis* or *A. franciscana*, but not both species (table I). This is a scenario different in comparison to southern Chilean inland waters, where it is possible to find one or more species at practically all studied sites, which would be explained by simulations that denote the absence of regulating factors (De los Ríos, 2008; De los Ríos et al., 2008a, b; De los Ríos & Soto, 2009).

The correlation analysis denoted the absence of a correlation of species number with altitude, maximum depth, or latitude, whereas a direct, significant correlation was established between species number and surface area. Also, a significant, inverse correlation appeared to exist between species number and salinity (fig. 1). The analysis confirms that zooplankton diversity in shallow saline Andean lakes is significantly and inversely correlated with salinity (Williams, 1998; De los Ríos, 2005). At high salinity, the brine shrimps *A. franciscana* or *A. persimilis* Piccinelli & Prosdocimi, 1968, predominate (Williams 1998; De los Ríos, 2005). Indeed, *Artemia* is the typical and more conspicuous inhabitant of hypersaline lakes (Hurlbert et al., 1986; Williams et al., 1995). The lack of coexistence of *Artemia* and *Boeckella poopoensis* has been observed in almost every field observation in the South American altiplano (Hurlbert et al., 1986, 1984; Bayly, 1993; Williams et al., 1995; De los Ríos, 2005). The reason for that would be, that *B. poopoensis* adults predate on *Artemia* nauplii at low salinity (Hurlbert et al., 1986; Williams, 1998), similar to what happens to *Artemia* in North America, where these species are predated upon by other halophilic crustaceans (Williams, 1998). Thus, we conclude that most probably salinity would be the main regulator of zooplankton assemblages at the studied sites (De los Ríos & Crespo, 2004; De los Ríos, 2005), but it would still be necessary establish if the salinity itself and/or the predator-prey

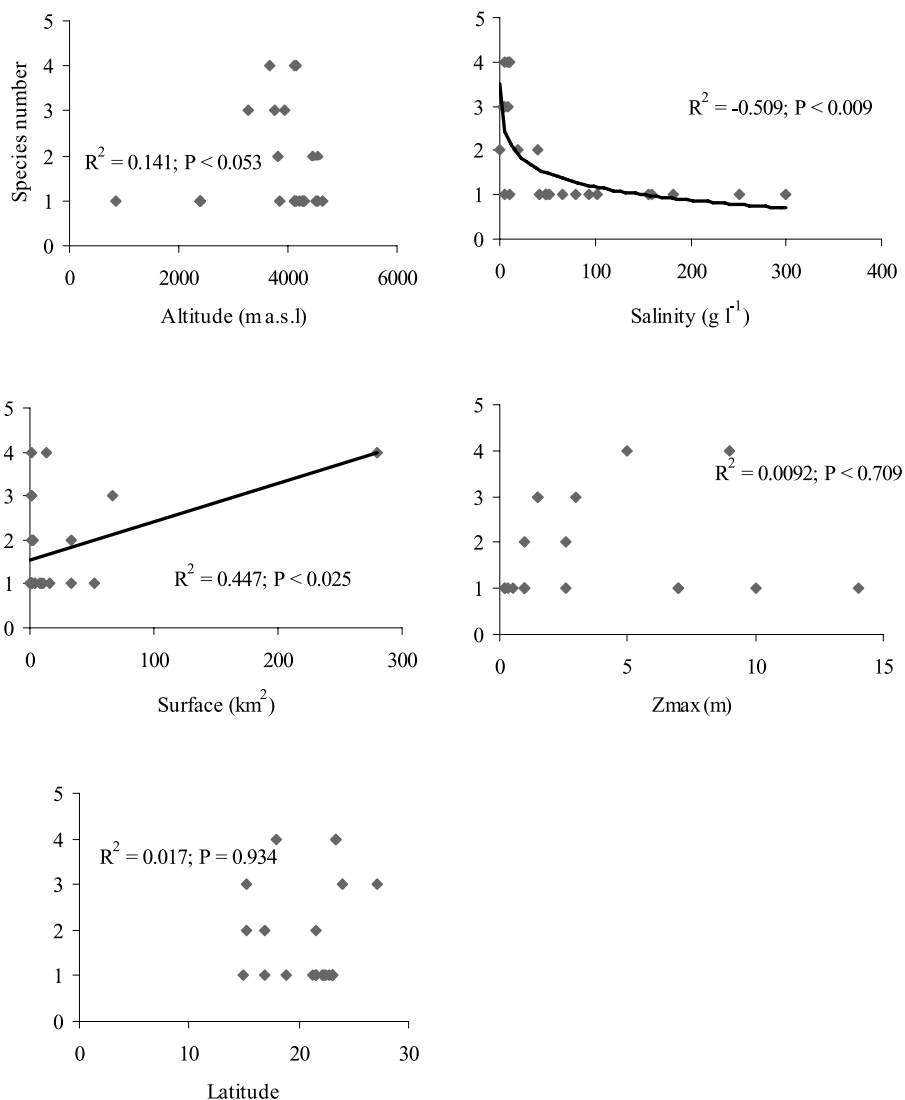


Fig. 1. Correlations between species number and the parameters of the sites considered in the present study. “ $P$ ” values lower than 0.05 denote significant correlation; Zmax, maximum depth.

interactions are the proximate cause of the non-coexistence of *A. franciscana* and *B. poopoensis*.

The correlation between surface area and species number agrees with results observed for zooplankton in northern-hemisphere lakes (Dodson, 1992; Dodson & Silva-Briano, 1996), but this result was not observed before in Chilean lakes (Soto & Zúñiga, 1991; Soto & De los Ríos, 2006; De los Ríos & Soto, 2007). The sites studied had no fish populations, and in this scenario it would be necessary

to study the trophic interactions at the studied sites more comprehensively, because it is necessary to study the role of top-down and bottom-up forces and their consequences with regard to species richness and the abundance of each species (Gliwicz et al., 2001; Gliwicz, 2002). The results obtained in the present study suggest that it is necessary do more ecological studies to understand these ecosystems, and also include the effects of weather changes (i.e., precipitation) on the functioning of these ecosystems.

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#### REFERENCES

- ABATZOPOULOS, T. J., G. V. TRIANTAPHYLLIDIS, N. ROEDAKI, A. D. BAXENAVIS, A. TRAIANTAPHYLLIDIS & P. SORGELOOS, 2003. Elevated salinities may enhance the recovery of hydrated heat-shocked *Artemia franciscana* cysts (international study on *Artemia*, LXV). Belgian Journ. Zool., **133**: 103-109.
- AMAT, F., R. G. COHEN, F. HONTORIA & J. C. NAVARRO, 2004. Further evidence and characterization of *Artemia franciscana* (Kellogg, 1906) populations in Argentina. Journ. Biogeogr., **31**: 1735-1749.
- BAYLY, I. A. E., 1993. The fauna of athalassic saline waters in Australia and the altiplano of South America: comparison and historical perspectives. Hydrobiologia, **267**: 225-231.
- DE LOS RÍOS, P., 2005. Richness and distribution of zooplanktonic crustacean species in Chilean altiplanic and southern Patagonian ponds. Polish Journ. env. Stud., **14**: 817-822.
- —, 2008. A null model for explain crustacean zooplankton species associations in central and southern Patagonian inland waters. An. Inst. Patagonia, **36**: 25-33.
- DE LOS RÍOS, P., P. ACEVEDO, R. RIVERA & G. ROA, 2008. Comunidades de crustáceos litorales de humedales del norte de la Patagonia chilena (38°S): rol potencial de la exposición a la radiación ultravioleta. In: A. VOLPEDO & L. FERNÁNDEZ (eds.), Efectos de los cambios globales sobre la biodiversidad, Programa CYTED Red 406RT0285: 209-218.
- DE LOS RÍOS, P. & P. CONTRERAS, 2005. Salinity level for occurrence of calanoids copepods in shallow ponds in South American altiplano and Chilean Patagonia. Polish Journ. Ecol., **53**: 445-450.
- DE LOS RÍOS, P. & J. CRESPO, 2004. Salinity effects on the abundances of *Boeckella poopoensis* (Copepoda, Calanoida) in saline ponds in the Atacama Desert, northern Chile. Crustaceana, **77**: 417-423.
- DE LOS RÍOS, P., N. RIVERA & M. GALINDO, 2008. The use of null models to explain crustacean zooplankton associations in shallow water bodies of the Magallan region, Chile. Crustaceana, **81**: 1219-1228.
- DE LOS RÍOS, P. & D. SOTO, 2009. Estudios limnológicos en lagos y lagunas del Parque Nacional Torres del Paine (51° S, Chile). An. Inst. Patagonia, **37**: 63-71.
- ECHANIZ, S. A., A. M. VIGNATTI, S. J. DE PAGGI, J. C. PAGGI & A. PILATI, 2006. Zooplankton seasonal abundance of South American saline shallow lakes. Int. Rev. Hydrobiol., **91**: 86-100.



- GAJARDO, G. M., N. COLIHUEQUE, M. PARRAGUEZ & P. SORGELOOS, 1998. International study on *Artemia* VIII. Morphologic differentiation and reproductive isolation of *Artemia* populations from South America. *Int. Journ. Salt Lake Res.*, **7**: 133-151.
- GOTELLI, N. J., 2000. Null models of species co-occurrence patterns. *Ecology*, **81**: 2606-2621.
- , 2001. Research frontiers in null model analysis. *Global Ecol. Biogeogr.*, **10**: 337-343.
- GOTELLI, N. J. & G. L. ENTSMINGER, 2004. ECOSIM: Null models software for ecology, Version 7.0. Acquired Intelligence Inc. and Kelsey-Bear, Jericho, VT 05465. Via: <http://garyentsminger.com/ecosim.htm>
- HURLBERT, S. H. & J. O. KEITH, 1979. Distribution and spatial patterning of flamingos in the Andean altiplano. *The Auk*, **96**: 328-324.
- HURLBERT, S. H., W. LOAYZA & T. MORENO, 1986. Fish-flamingo-plankton interactions in the Peruvian Andes. *Limnol. Oceanogr.*, **31**: 457-468.
- HURLBERT, S. H., M. LÓPEZ & J. KEITH, 1984. Wilson's phalarope in the central Andes and its interaction with the Chilean flamingo. *Rev. Chilena Hist. nat.*, **57**: 47-57.
- TIHO, S. & G. JOSENS, 2007. Co-occurrence of earthworms in urban surroundings: a null model analysis of community structure. *European Journ. Soil Biol.*, **43**: 84-90.
- TONDOH, J. E., 2006. Seasonal changes in earth worm diversity and community structure in central Côte d'Ivoire. *European Journ. Soil Biol.*, **42**: 334-340.
- TRIANAPHYLLIDIS, G. V., T. J. ABATZOPOULOS & P. SORGELOOS, 1998. A review of the biogeography of the genus *Artemia* (Crustacea, Anostraca). *Journ. Biogeogr.*, **25**: 213-226.
- WILLIAMS, W. D., 1998. Salinity as a determinant of the structure of biological communities in salt lakes. *Hydrobiologia*, **381**: 191-201.
- WILLIAMS, W. D., T. R. CARRICK, I. A. E. BAYLY, J. GREEN & D. B. HERBST, 1995. Invertebrates in salt lakes of the Bolivian altiplano. *Int. Journ. Salt Lake Res.*, **4**: 65-77.
- ZÚÑIGA, O., R. WILSON, F. AMAT & F. HONTORIA, 1999. Distribution and characterization of Chilean populations of the brine shrimp *Artemia* (Crustacea, Branchiopoda, Anostraca). *Int. Journ. Salt Lake Res.*, **8**: 23-40.