ZOOPLANKTON OF THE HIGHLAND BOGS OF PUTANA, A DESERT WETLAND OF THE HIGH PUNA, NORTHERN CHILE

BY

ANDRÉS MUÑOZ-PEDREROS[1,3]), PATRICIO DE LOS RÍOS-ESCALANTE[1]) and PATRICIA MÖLLER[2])

[1]) Núcleo de Estudios Ambientales NEA, Escuela de Ciencias Ambientales, Facultad de Recursos Naturales, Universidad Católica de Temuco, Casilla 15-D, Temuco, Chile

[2]) Programa de Humedales, Centro de Estudios Agrarios y Ambientales CEA, Casilla 164, Valdivia, Chile

ABSTRACT

The Atacama "puna" (high-altitude plateau) is situated among the high peaks of the Andes at over 4000 m a.s.l. This ecosystem covers parts of north-eastern Chile, north-western Argentina, south-eastern Peru, and mid-western Bolivia. The puna brings together several types of wetlands, such as salt-flats, lakes, rivers, high marshes, and highland bogs. Highland bogs are peatlands associated with endorheic basins. The object of this study was to analyse the specific composition and structure of the zooplankton of the bogs of the Putana River, on the Altiplano of northern Chile. In 2012, zooplankton samples were taken for qualitative and quantitative analysis at nine stations of the bog. Nine taxa of zooplanktonic crustaceans were recorded. The species richness is higher than records in other high Andean wetland at a similar altitude, although the species found have been reported for other high Andean wetlands and Andean lakes in Chile and from neighbouring countries.

Key words. — High altitude wetland, high altitude peatlands, zooplaktonic crustacean of river bogs, Altiplano

RESUMEN

La puna de Atacama se extiende sobre los 4.000 m.s.m., en las altas cumbres de Los Andes. Este ecosistema abarca parte del noreste de Chile, noroeste de Argentina, sureste de Perú y mitad occidental de Bolivia. La puna reúne varios tipos de humedales, como salares, lagunas, ríos, vegas de altura y bofedales. Los bofedales son turberas andinas asociadas a cuencas endorreicas. El objetivo de este trabajo fue analizar la composición específica y estructura del zooplancton de los bofedales del río Putana, en el Altiplano del norte de Chile. En 2012 se tomaron muestras de zooplancton para análisis análisis cuali y cuantitativo en nueve estaciones en el bofedal. Se registraron nueve taxa de crustáceos zooplanctónicos. La riqueza de especies es mayor que la encontrada en otro humedal alto andino a similar altitud, aunque las especies encontradas se han reportado para otros humedales alto andinos y lagos andinos de Chile y de países vecinos.

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[3]) Corresponding author; e-mail: amunoz@uct.cl

INTRODUCTION

The Atacama "puna" (high-altitude plateau) is situated among the high peaks of the Andes at over 4000 m a.s.l. and was formed by recent volcanic activity that filled the valleys separating the mountain ranges with ash and lava. The puna forms an elongated area from north to south, covering parts of north-eastern Chile, north-western Argentina, south-eastern Peru, and mid-western Bolivia. In Chile it extends from 17°30′ to 28°S, and westward from the country's eastern border for a width varying between 20 and 70 km (García, 1967). The puna in the Antofagasta Region is called the "puna salada" (salt puna) (Troll, 1968).

It contains various types of wetlands, such as salt-flats, lakes, rivers, high marshes, and highland bogs. The latter form a floral and plant complex presenting clearly defined zones, ranging from those with running water to zones presenting drier conditions. They present a remarkable floral wealth, which has been diminished through intensive grazing by camelids and sheep (Gajardo, 1994). Highland bogs are high altitude peatlands associated with endorheic basins and with plant formations dominated by graminids (*Oxychloe andina* Phil. and *Distichia muscoides* Nees & Meyen) consisting of clumps of grasses and reeds. They are peaty meadows originally formed under water, consisting mainly of plants of the families Cyperaceae and Juncaceae, often growing in compact clumps or cushions, and occurring in marshy areas of the altiplano and the puna. Bogs develop where there is running water with a higher oxygen concentration and a lower concentration of salts, as opposed to the more abundant stagnant saline waters known as marshes, into which other puna wetlands develop (DGA, 2004). Palaeo-ecological investigations suggest that some bogs are recent features of the landscape, having developed over the last 3000 years or less (Earle et al., 2003). These bogs are unique habitats, extremely fragile due to their dependence on water, sensitive to climate change, and vulnerable to the human alterations resulting from mining activity in the region. They also support grazing, on which the indigenous peoples depend (Squeo et al., 2006).

The size of the bogs ranges from less than one hectare to hundreds of hectares and they are found from approximately 18°30′S in the north of Chile, at the southern limit of the Wet Puna eco-region, across the dry puna to around 31°S at the southern limit of the Southern Andean Steppe eco-region (Squeo et al., 2001). They appear as green oases on the bottoms of valleys, in superficial basins, and in other low-relief features in the landscape.

The object of this study was to analyse the specific composition and structure of the zooplankton of the bogs of the Putana River, located in the altiplano, at a site which is considered a priority site for biodiversity conservation in northern Chile.

MATERIAL AND METHODS

Study area

The study area is the Putana River bog (22°32′07″S 68°02′12″W) at 4600 m a.s.l. It forms part of the Putana River sub-basin, which provides the majority of the water from its spring system in the Andes Range to the Río Grande-San Pedro system, which drains the Atacama Salt Flat. The highest points are the Tocorpuri Mountains (5808 m a.s.l.) and the Putana Volcano further south (5809 m a.s.l.). The principal tributaries of the Putana River (from north to south) are the Quebrada La Torta, the Blanco or Tocorpuri River, the Quebrada San Lucrecio, and the Incahuasi River (fig. 1). The whole of the NW and SE sectors of the Putana sub-basin consists of little-eroded volcanic formations, partly developed since the last ice-age (Late Pleistocene-Holocene). These volcanoes and lava-flows partially overlie the ignimbrites of the Tatio formation, which extend eastwards; they are drained by the Quebrada Agua Brava which starts in Bolivia (MOP, 2007). The central sector of this sub-basin drains from east to west over a surface of slight to moderate slopes, formed by the ignimbrites of the Tatio formation. The change in gradient in this sector has resulted in the deposition of material, and bogs have
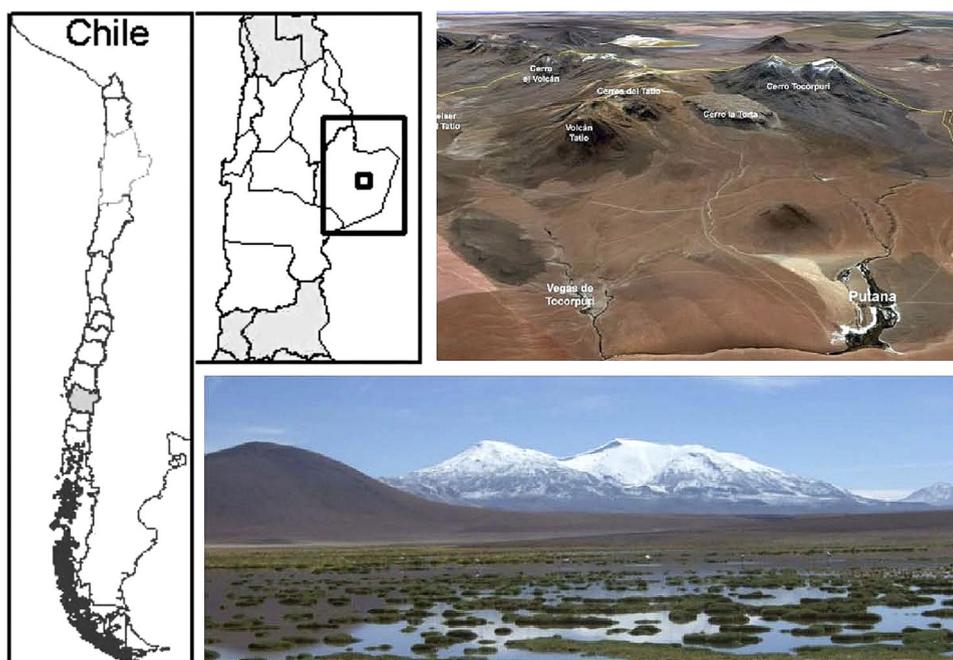

Fig. 1. Study area in the Putana River Bog, northern Chile. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/15685403.

developed on the extensive alluvial deposits, mainly sand, in the interfluvial zones between Quebrada La Torta, the Tocorpuri River, and the Incahuasi River.

The climate is high steppe (BSH), associated with the altiplano or puna (Köppen, 1948; Fuenzalida, 1965). The principal characteristics are low temperatures (annual mean 2°C) and a high thermal range (more than 20°C). According to the climatic information compiled by SGA-GND (2007), the average annual precipitation in the area is 159 mm, of which ca. 14 mm fall in winter and ca. 144 mm in summer. The precipitation is determined partly by the altitude, but also by a tropical convection system that produces summer rain in the altiplano in the form of short, localized showers, generally of low intensity (less than 20 mm/day); this phenomenon is known as the "altiplano winter". As a result, there is little run-off and therefore little erosion, so that the relief formations have developed very little. However, above 3500 m a.s.l., where the soil is formed of volcanic material, erosion has caused long, deep ravines ("quebradas"). There are great annual variations in precipitation, with series of very dry years. Abnormally high rainfall events exceed the capacity of the underdeveloped drainage network, resulting in flooding, which has modelled the geomorphology significantly. The erosive action of the run-off water in the watercourses is seasonal, filling many beds that remain dry for much of the year. The frequency of flooding is generally every six to eight years (MOP, 2007). Local morphodynamics are also affected by agents like wind, snow, and temperature changes, which degrade and fragment the rocks by physical-mechanical effects in conjunction with frost weathering, thermoclastism, and exfoliation. In general, the geomorphology of the area is now evolving slowly, with the exception of extreme climatic events that activate greater- or smaller-scale processes on a seasonal basis (e.g., the altiplano winter). However, the existing relief was strongly influenced by erosion in the Quaternary, when large-scale phenomena of material transport and deposition, excavation of deep quebradas, and active volcanism strongly modelled the landscape, which contains imposing units and forms inherited from the past.

The area forms part of the Andean volcanic belt of the Late Cenozoic, consisting of a huge pile of interstratified andesitic to rio-dacitic lavas, covered by large deposits of ignimbrites (welded tuffs) varying in age from the Late Miocene to the Quaternary. Glaciation during the Pleistocene produced significant erosion in some volcanic centres, giving rise to moraines and peri-glacial deposits which today are found above 4000 m a.s.l. The emission centres of lava and ash display a clear structural control, since their distribution coincides with the principal fault and/or alignment systems which characterize this sector of the Andes, with north-south orientation (Lahsen, 1982).

The vegetation and associated water-fowl were described in a simultaneous investigation in the study area (Muñoz-Pedreros et al., unpublished), which

found a community of hydrophilous herbaceous plants named *Oxychloe andina*-community, in which the representative species is *Oxychloe andina* Phil., accompanied by various species of the genus *Deyeuxia* (*D. breviaristata* Wedd., *D. chrysanta* J. Presl, *D. curvula* Wedd., *D. eminens* J. Presl, *D. velutina* Nees & Meyen), *Junellia minima* (Meyen) Moldenke, *Zameioscirpus atacamensis* (Phil.) Dhooges & Goetgh., *Lilaeopsis macloviana* (Gand.) AW Hill, *Mimulus glabratus* Kunth., *Azolla filiculoides* Lamk., *Lemna minor* L., and *Myriophyllum quitense* Kunth. It is a generally hydrophilous community, since the species of which it is composed are typical of marshes or water bodies (Hoffmann et al., 1998). Gajardo (1994) says that this community is high Andean altiplano steppe, forming a bog. Twenty bird species were recorded, the most abundant being *Lophonetta specularioides* (King, 1828), *Chloephaga melanoptera* (Eyton, 1838), *Fulica gigantea* Eydoux & Sauleyet, 1841, and *Anas georgica* Gmelin, 1789.

Methodology

In March 2012 (late southern summer) samples were taken in the western area of the bog (fig. 1). Samples of zooplankton were taken at nine stations for qualitative and quantitative analysis by filtering 30 litres of surface water per station, using a conventional conical net with 50 μm mesh, with the methods described by Soto & De los Ríos (2006); the material was fixed in situ with alcohol 75%. The observations on, and taxonomic identification and measurements of, the specimens were carried out under a compound microscope and a stereo-microscope, with the identification following the relevant specialized literature (e.g., Araya & Zúñiga, 1985; Reid, 1985; Bayly, 1992; González, 2003). Counts were based on aliquots (4), applying Cassie's formula (Edmonson & Winberg, 1971), with 10% error, in 1 and 5 cm^3 Sedgwick Rafter chambers for micro-zooplankton (naupliar and rotifer forms) and macro-zooplankton (cladocerans, copepodites, and adult copepods) respectively, or total counts when abundance was very low.

The data were analysed first by a correlation analysis of the abundances of the species reported and the parameters considered in the present study. Next, a hierarchical agglomerative cluster analysis using the Bray-Curtis index was applied to determine possible similarities between the groups (diversity sensu Magurran, 1998). For both these analyses, the Biodiversity Pro version 2.0 software (McAleece et al., 1997) was used. The next step was to calculate a Checkerboard score (C-score), which is a quantitative index of occurrence that measures the extent to which species co-occur less frequently than expected by chance (Gotelli, 2000). A community can be considered to be structured by competition when the C-score is significantly larger than expected by chance (Gotelli, 2000). Thirdly, we compared co-occurrence patterns with null expectations via simulation. Gotelli &

Entsminger (2007) and Gotelli (2000) suggest the following robust statistical null models: (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 samples (columns) as equally available for all species. (3) Fixed-Proportional: in this algorithm the species occurrence totals are maintained as in the original community, and the probability of a species occurring at a site (column) is proportional to the column total for that sample. These null model analyses were performed using the Ecosim version 7.0 software (Gotelli & Entsminger, 2007). Finally, a niche-sharing null model was applied using Pianka's and Czekanowski's overlap indices with retained niche breadth, and reshuffled zero states using the Ecosim version 7.0 software (Gotelli & Entsminger, 2007). The Ecosim program also determines whether measured overlap values differed from what would be expected in random sampling of the species data. Ecosim performs Monte Carlo randomizations to create pseudo-communities, and then statistically compares the patterns of these randomized communities with those in the real data matrix (Gotelli & Entsminger, 2007). In this analysis, all values of the general matrix were randomized 1000 times and the niche breadth was retained for each species. In other words, the algorithm retained the amount of specialization for each species (Gotelli & Entsminger, 2007).

RESULTS AND DISCUSSION

A species composition of nine taxa of zooplanktonic crustaceans was recorded (table I); the species associations are random, which would be due the fact that there is a large number of recurring species at the sampling sites, as is confirmed by the niche segregation analysis, which shows that there are no differences (table II) and by the Bray-Curtis similarity analysis (fig. 2). The mean alpha diversity is five species for all stations sampled, and the beta diversity is low, since the cluster analysis shows a high similarity between stations (>75%), resulting in a low change of species from one station to another (fig. 2).

The species richness is higher than that documented by Muñoz-Pedreros et al. (2013) for the high Andean Lake Lejía (eight versus five), also located in the high Andean puna south of the Putana bogs, at a similar altitude (4300 m a.s.l.). The species shared with Lake Lejía are *Macrothrix atahualpa* Brehm, 1936 (= *Macrothrix palearis* Harding, 1955) and *Diacyclops andinus* Locascio de Mitrovich & Menu-Marque, 2001, both also described for Chungará Lake (Araya

TABLE I
Species (ind./l) recorded in the Putana River Bog, northern Chile

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6	Station 7	Station 8	Station 9
BRANCHIOPODA									
Alonella excisa (Fischer, 1854)	0.0	2.6	0.2	0.4	0.0	3.8	4.8	0.2	1.4
Alona sp.	0.4	4.6	0.6	0.4	0.2	10.0	1.0	3.0	0.2
Daphnia sp.	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.0	0.0
Macrothrix atahualpa Brehm, 1936	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
COPEPODA									
Diacyclops andinus Locascio de Mitrovich & Menu-Marque, 2001	0.6	0.8	0.0	0.2	0.6	2.0	4.0	1.0	0.4
OSTRACODA indet.	8.0	0.4	0.4	10.0	2.6	17.2	24.6	6.4	0.4
AMPHIPODA									
Hyalella fossamanchini Cavalieri, 1959	0.2	0.6	0.0	0.4	0.0	0.0	0.2	0.0	0.2
Hyalella kochi Gonzalez & Wattling, 2001	0.2	0.2	0.0	0.0	0.0	0.2	0.2	0.0	0.0
Hyalella juveniles	2.0	1.6	0.0	0.2	0.0	0.8	0.4	0.2	0.0

TABLE II

Results of the null species co-occurrence models and niche segregation in the Putana River Bog, northern Chile

	Observed index	Mean index	Standard effect size	P
Fixed-Fixed	0.750	0.862	−1.161	0.960
Fixed-Proportional	0.750	1.292	−1.369	0.911
Fixed-Equiprobable	0.750	1.429	−1.843	0.961
Pianka	0.000	0.000	0.000	<0.999
Czekanowski	0.000	0.000	0.000	<0.999

& Zúñiga, 1985; De los Ríos-Escalante, 2010a) and shallow high Andean lakes in neighbouring countries of Chile (Locascio de Mitrovich et al., 2005; De los Ríos & Gajardo, 2010). Other taxa shared with Lejía Lake are *Alona* sp. and Ostracoda. The greater species richness is given by the occurrence of *Alonella excisa* (Fisher, 1854), *Hyalella fossamanchini* Cavalieri, 1959, *Hyalella kochi* Gonzalez & Watling, 2001, and juvenile *Hyalella* spp., as well as taxa with a wide geographical distribution in low salinity habitats in high Andean environments, such as *Daphnia* spp. (De los Ríos-Escalante, 2010; Kotov et al., 2010; De los Ríos-Escalante & Kotov, in press). Similar results were observed for the Loa River by De los Ríos et al. (2010).
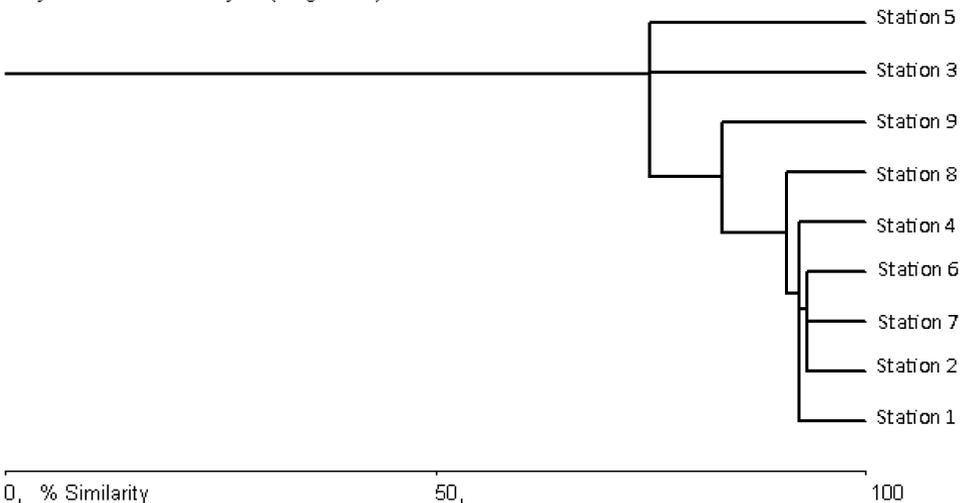

Fig. 2. Similarity dendrogram of the sites considered in the present work, generated through Bray-Curtis cluster analysis and Single Linkage.

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