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USE OF NULL MODELS TO EXPLAIN CRUSTACEAN ZOOPLANKTON ASSEMBLAGES IN WATERBODIES OF ALERCE ANDINO NATIONAL PARK (41°S, CHILE)

BY

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ABSTRACT

The zooplankton assemblages in deep, mostly oligotrophic northern Patagonian lakes are characterized by low species numbers and a marked dominance of calanoid copepods. In the present study, data collected in field work on six water bodies located in Alerce Andino National Park (41°S) were analysed using the Jaccard Index of community similarity and a co-occurrence of null models, and such with the aim of determining potential regulating factors for the observed crustacean assemblages, using a presence-absence matrix. A significant correlation between species number and surface area was found. The null model used species co-occurrence, and the basis of this model is that the species associations observed are random. The results revealed the absence of regulating factors and indicate that the sites are relatively homogeneous, with low species numbers and similar plankton assemblages at all studied sites. This finding is in accordance with similar descriptions for zooplankton assemblages in other Chilean Patagonian lakes.

RESUMEN

Los ensambles zooplanctónicos en lagos del norte de la Patagonia se caracterizan por su bajo número de especies y marcada dominancia de copépodos calanoideos. En el presente trabajo se colectaron datos de seis cuerpos de agua del Parque Nacional Alerce Andino, los cuales se analizaron usando un índice de similitud de comunidades de Jaccard y un modelo nulo de co-ocurrencia y con el mismo se determinaron los factores reguladores potenciales para explicar los ensambles zooplanctónicos usando una matriz de presencia y ausencia de especies. Este modelo nulo usó la co-ocurrencia de especies y parte de la base que las asociaciones de especies son aleatorias. Se observó una asociación significativa entre número de especies y superficie. Los resultados obtenidos indican la ausencia de factores reguladores en la mayoría de los análisis, lo que se debería a que los sitios

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son homogéneos, y al bajo número de especies reportadas las que además presentaron pocas especies repetidas en prácticamente todos los sitios estudiados. Estos resultados coinciden con descripciones similares para ensambles zooplanctónicos para otros lagos y lagunas de la Patagonia chilena.

INTRODUCTION

The zooplankton assemblages in deep, oligotrophic northern Patagonian lakes are characterized by their low species numbers and their marked dominance of calanoid copepods (Soto & Zúñiga, 1991; De los Ríos & Soto, 2006, 2007; De los Ríos-Escalante, 2011). Studies on littoral microcrustaceans in Chilean lakes are restricted to copepods and cladocerans (Araya & Zúñiga, 1985; Soto & Zúñiga, 1991), and it is probable that other crustaceans, like amphipods, are present (González, 2003) as well. Nevertheless, a correlation between total microcrustaceans (littoral and pelagic) and trophic status has not been determined until now (De los Ríos et al., 2007; De los Ríos & Roa, 2010).

However, it is not clear whether there exists a regulating factor for the observed pelagic and littoral microcrustacean assemblages in lakes with a similar trophic status. To study the presence of a regulating factor, ecologists have proposed null models using presence/absence data in order to find out whether the observed distribution pattern is random or not (Gotelli, 2000, 2001; Tondoh, 2006; Tiho & Johens, 2007; Gotelli & Entsminger, 2009). Although null models have mostly been applied to terrestrial ecosystems until now (Tondoh, 2006; Tiho & Johens, 2007), recently they were also extended to be used in microcrustacean communities of inland waters (De los Ríos, 2008; De los Ríos et al., 2008). These null models were based mainly on species co-ocurrence and revealed for shallow southern Patagonian lakes that zooplankton associations there are random, due to the homogeneity of the environmental conditions of the studied sites. They all showed low species numbers and a similar distribution of the taxa over the sites (De los Ríos, 2008; De los Ríos et al., 2008; De los Ríos & Soto, 2009; De los Ríos & Roa, 2010).

The present study was performed in Alerce Andino National Park, a Chilean government protected area, characterized by mountains with *Nothofagus pumilio* (Poepp. & Endl.) Krasser, *N. dombeyi* (Mirb.) Oerst., *N. nitida* (Phil.) Krasser, and *Fitzroya cupressoides* (Molina) Johnst. This park of 39,255 ha has numerous oligotrophic lakes (Steinhart et al., 1999, 2002), four of which can be accessed via mountain roads, while these are also located at least 4 km from the two main entrances to the park. The importance of these water bodies is their condition of being practically unpolluted and pristine, due to the low human intervention (Steinhart et al., 1999, 2002). Thus, the native fauna can be studied under conditions of non-intervention. The aim of the present study was to apply null model analysis in order to explain the composition of the zooplankton assemblages in water bodies of Alerce Andino National Park. Here, we report our first results on six water bodies located in the park.

MATERIAL AND METHODS

The studied site was visited in December 2010 and January 2011. Three lakes and a small wetland were taken into consideration: Lake Sargazo (41°30′S 72°36′W), Lake Chaiquenes (41°34′S 72°32′W), Lake Triangulo (41°36′S 72°28′W), and in addition a small pool located along the way to the Sargazo lake, located at 2 km distance from this lake, as well as two shallow, ephemeral water bodies (locally called "Mallines") associated with grass and shrubs (fig. 1). Vertical hauls were taken in the pelagic zone and in littoral zones with an Apstein net of 20 cm diameter and 80 μm mesh size, and fixed with absolute ethanol. Species identification and quantification were done according to literature descriptions (Araya & Zúñiga, 1985; Reid, 1985; Bayly, 1992; González, 2003). Chlorophyll analysis was performed according to the methods described by Wetzel & Likens (1991). We tested for relationships between species richness and three physical variables (salinity, conductivity, and altitude) using correlation coefficients (Rho-Spearman), calculated in the software SPSS v. 12.

A species absence/presence matrix was constructed, with the species in rows and the sites in columns. First, the Jaccard Index for similarity was obtained to determine potential similarities between sites on the basis of species associations (Gotelli & Graves, 1996); we did this analysis using the software Biodiversity Pro. version 2.0. Secondly, we calculated 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 is 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 (2009) and Gotelli (2000) suggested the following statistically robust 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 (column) as equally available for all species. (3) Fixed-Proportional: in this algorithm the totals of species occurrence are maintained as in the original community, and the probability that a species occurs at a site (column) is proportional to the column total for that sample. The null model analyses were performed using the software Ecosim version 7.0 (Tondoh, 2006; Gotelli & Entsminger, 2007; Tiho & Johens, 2007).

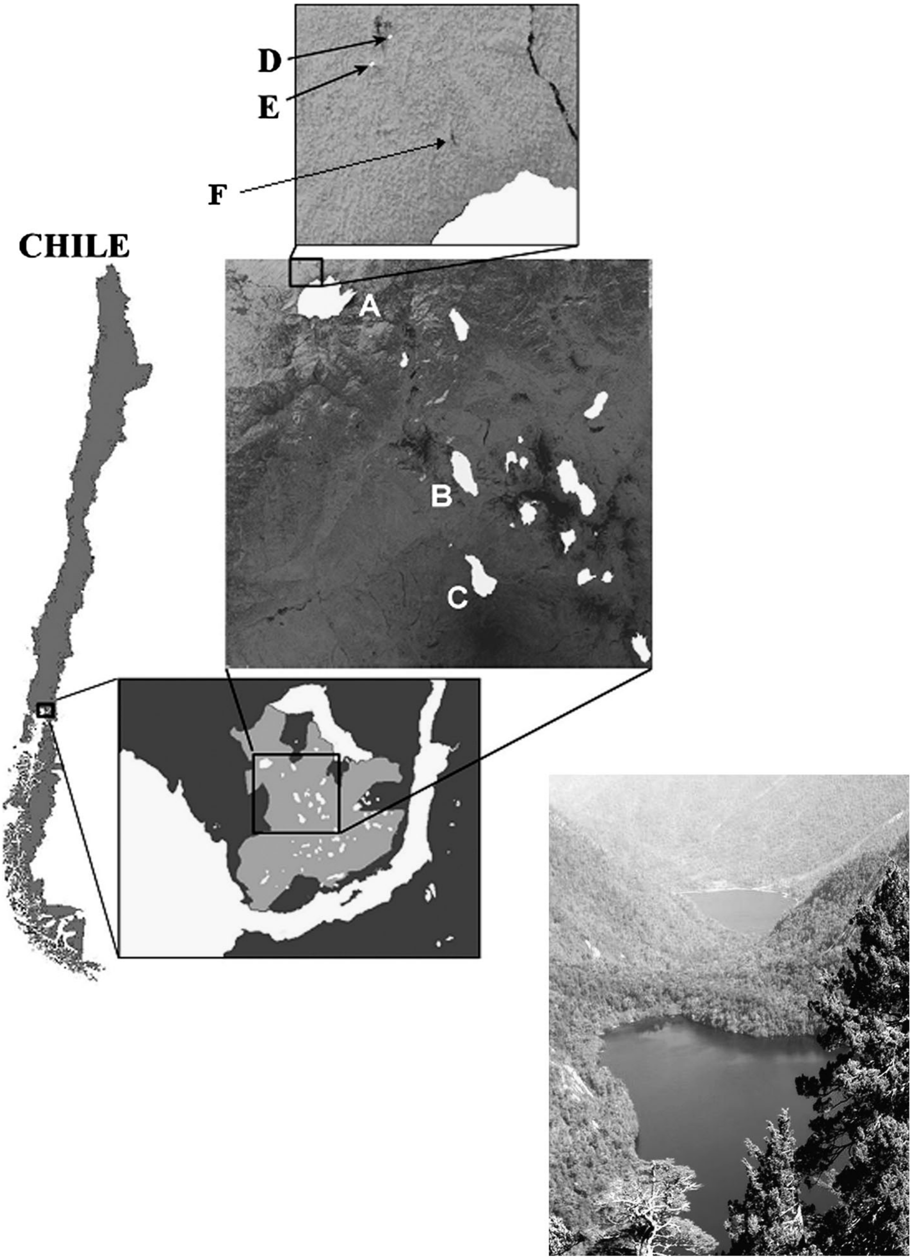

Fig. 1. Map of the sites studied; the lakes are represented in white: A, Sargazo; B, Chaiquenes; C, Triangulo; D, Mallin 1; E, Mallin 2; F, pool close to Sargazo lake; and a photograph showing Lake Triangulo (in the foreground, bottom half of the picture) and Lake Chaiquenes (background, in top half) in situ.

TABLE I

Species of crustacean zooplankton (based on adult specimens only) observed in water bodies of Alerce Andino National Park, and correlation analysis between the species numbers found and the variables considered in the present study

	Sargazo lake	Pool at Sargazo lake way	Mallin 1 at Sargazo lake way	Mallin 2 at Sargazo lake way	Chaiquenes lake	Triangulo lake
Geographical location	41°30′S 72°36′W	41°30′S 72°37′W	41°30′S 72°36′W	41°30′S 72°36′W	41°33′S 72°32′W	41°35′S 72°32′W
Altitude (in m a.s.l.)	354	316	235	235	538	285
Surface area (km^2)	1.397	<0.001	<0.001	<0.001	0.582	0.577
Conductivity (μS/cm)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Total dissolved solids	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
pH	9.23	6.11	7.70	8.10	7.62	8.66
Temperature (°C) at surface	12.6	12.4	17.1	18.5	14.7	18.9
Chlorophyll *a* (μg/L)	0.9	0.9	0.9	0.1	0.6	1.4
CLADOCERA						
Alona sp.	x	x			x	
Simosa exspinosa (De Geer, 1778)			x			x
Scapholeberis spinifera (Nicolet, 1849)	x	x				
COPEPODA						
Boeckella gracilis (Daday, 1902)	x				x	
Tropocyclops prasinus meridionalis Kiefer, 1927	x					
HARPACTICOIDA		x		x		x
AMPHIPODA						
Hyalella simplex Schellenberg, 1943	x		x		x	

Correlation analysis

	R^2	P
Species number — Altitude	0.482	0.334
Species number — Surface area	0.811	0.050
Species number — Conductivity	—	—
Species number — pH	0.234	0.656
Species number — Temperature	−0.833	0.040
Species number — Chlorophyll *a*	0.307	0.554

RESULTS AND DISCUSSION

The studied sites show low chlorophyll concentrations (table I), the crustacean fauna was characterized by the presence of the cladoceran *Alona* sp. at three sites, with the exception of Triangulo lake; *Scapholeberis exspinifera* (Nicolet, 1849) and unidentified Harpacticoida were found in the Pool and in Triangulo lake; whereas *Boeckella gracilis* (Daday, 1902) and *Hyalella simplex* Schellenberg, 1943 were found in lakes Sargazo and Chaiquenes; finally, *Tropocyclops prasinus meridionalis* Kiefer, 1927 was found only in Lake Chaiquenes (table I). To conclude, *S. exspinosa* and *H. simplex* were found in Mallin 1, and Mallin 2 yielded as yet unidentified Harpacticoida (table I).

The correlation analysis only revealed a weakly significant, direct correlation between species number and surface area, and a significant inverse correlation with temperature, whereas species number does not show significant correlations with altitude, conductivity, pH, or chlorophyll concentration (table I). The results of the cluster analysis revealed the existence of a first, quite similar group composed of the Sargazo and Chaiquenes lakes, the next closest water body in the dendrogram is the Pool situated close to Sargazo lake, then Triangulo lake, and, finally, the sites Mallin 1 and Mallin 2 are the sites showing the lowest similarity values, both among all six sites sampled as well as among the two of them (fig. 2).

The co-occurrence analysis revealed for all simulations, that the observed microcrustacean associations were random and no regulating factor was recognizable (table II). The results of the Jaccard Index likewise revealed the existence of a close group comprising the lakes Sargazo and Chaiquenes, both located at 4 km distance from their respective main entrance, whereas the Pool close to Sargazo lake is close to both sites, Triangulo lake is the site furthest away, probably due to the fact that this site is located in one of the remotest areas of the mountain paths (figs. 1, 2), while finally sites Mallin 1 and Mallin 2 are the most different sites in terms of crustacean zooplankton, probably due to the marked differences of both sites in all environmental parameters as compared to the remaining sites (fig. 2).

Our results are similar to those described for the zooplankton communities of shallow lakes in southern Patagonia and of the mountain lakes in northern Patagonia (De los Ríos et al., 2008, 2010; De los Ríos & Soto, 2009; De los Ríos & Roa, 2010; De los Ríos-Escalante, 2011). This is interesting, because our earlier results were obtained in a very different type of lake (large, deep, oligotrophic, soft water), which is dominated by a different species of crustacean zooplankton (in this example: *Boeckella gracilipes* Daday, 1901 is present there, in those deep lakes, instead of *Boeckella gracilis* found in the shallow lakes in the present study; see table I). In contrast, the southern and northern Patagonian mountain lakes are very small (<1 km^2) and very shallow (<5 m), and in the case of the southern Patagonian lakes also cover a large range of electrical conductivity (70-16500 μS cm^{-1}) and trophic states (oligo- to eutrophic) (De los Ríos & Soto, 2009; De los Ríos & Roa, 2010). In both cases, the results of the null model analyses of species associations are probably caused by their low species diversity (De los

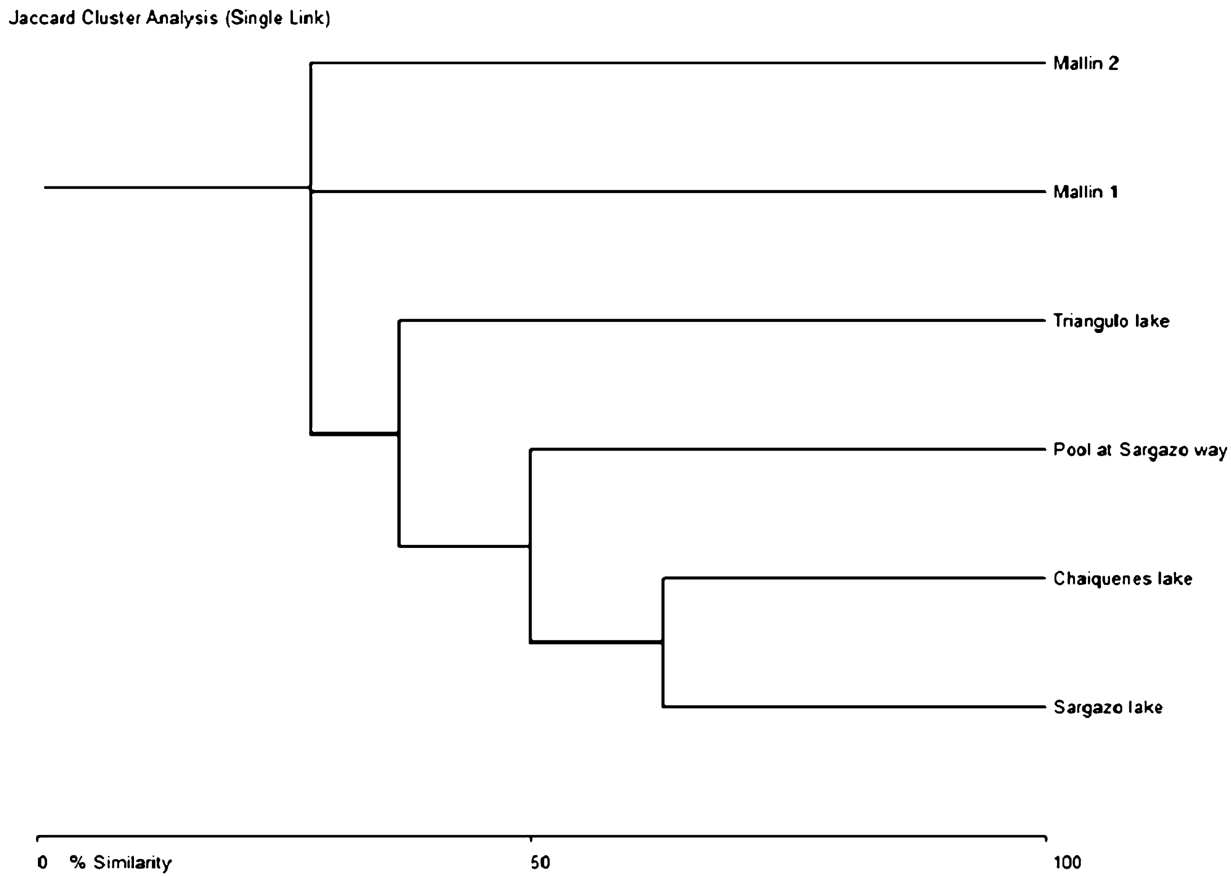

Fig. 2. Dendrogram produced through Jaccard Index cluster analysis performed with Single Linkage, of the similarities found in species composition at the sites studied in the present investigation. See text for further explanation.

TABLE II

Results of microcrustacean assemblages co-occurrence analysis (Null models) for Alerce Andino National Park from December 2010 to January 2011; "*P*" values lower than 0.05 denote significant differences

Simulation	Observed index	Mean index	Standard size effect	*P*
Fixed-Fixed	1.761	1.786	−0.236	0.646
Fixed-Proportional	1.761	1.528	0.506	0.694
Fixed-Equiprobable	1.761	1.815	−0.145	0.627

Ríos et al., 2008; De los Ríos & Roa, 2010) and the marked habitat homogeneity (Tondoh, 2006; Tiho & Johens, 2007). This does not mean that the zooplankton associations are similar in all lakes, but means that the species distribution is random. In this scenario, the descriptions of co-occurrence of species agree with classical descriptions for Chilean Patagonian lakes that are similar with respect to the environmental parameters, specifically their oligotrophy and low mineral concentrations (Soto & Zúñiga, 1991; De los Ríos & Soto, 2006, 2007, 2009). This was also shown for deep Argentinean Patagonian lakes (Modenutti et al., 1998) and for New Zealand lakes (Jeppensen et al., 2000), which are very similar to the Chilean northern Patagonian lakes. The opposite scenario occurred in North American and western European lakes that are characterized by a high species number and marked cladoceran dominance within a wide trophic range (Dodson, 1992; Gillooly & Dodson, 2000). The present study can thus conclude that in spite of the heterogeneity of the sites studied (lakes on the one hand, and shallow water bodies such as "mallines" and ponds, on the other) in this area, the presence of these all water bodies is important for conservation purposes, considering their susceptibility to human impact (Correa-Araneda et al., 2011). In this scenario, the sites studied are interesting for studies considering their unpolluted condition, that would explain their oligotrophic status and low species number, as reported for all water bodies considered in the present study.

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