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Distribution of the cladoceran *Bosmina huaronensis* Delachaux, 1918 and niche differentiation among populations from different biogeographic regions

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ABSTRACT - Described from a high-altitude lake in Peru, *Bosmina huaronensis* Delachaux, 1918 has been recorded in diverse kinds of water bodies in South and North America, suggesting that this species has high environmental tolerance and a wide niche breadth. The present study surveyed the occurrence records of *B. huaronensis* from 55 localities and, using multivariate analysis, investigated the niche differentiation among populations from different biogeographic regions, based on altitude and seven climatic variables. The first two principal components (PC) explained 73% of the overall variance. PC1 was related to annual mean temperature, precipitation of driest quarter, and annual precipitation. PC2 was related to temperature seasonality and precipitation of wettest quarter. The PCA diagram showed three population groups, occupying different climate niches: (1) tropical highlands; (2) Neotropical lowlands; (3) temperate zones of both hemispheres. These results point to the need for further evaluation of these populations under morphological, genetic and ecological aspects.

Key words: Anomopoda, biogeography, Bosminidae, climatic variables

Introduction

Bosmina huaronensis Delachaux, 1918 is a member of the zooplanktonic community from water bodies in a different trophic state (e.g. Menu-Marque and Marinoni, 1986; Zanata, 2005; Di Genaro, 2010). Described from a high-altitude lake in Peru (Lake Huaron, about 4,640 m a.s.l.), it has been recorded in diverse kinds of water bodies in South and North America (e.g. Paggi, 1979; De Melo and Hebert, 1994). In the South American tropical zone, Green (1995) only found *B. huaronensis* in lakes placed above 3,800 m a.sl. However, many records include South American ponds, lakes, reservoirs, and rivers in subtropical and temperate lowlands (e.g. Paggi, 1979; Velho *et al.*, 2000; Serafim Junior *et al.*, 2006; Rocha *et al.,* 2011).

The niche is considered an abstract multidimensional space, in which a set of biotic and abiotic conditions allow a species to maintain a viable population (Hutchinson, 1957; Schnitzler *et al.*, 2012). Considering the variety of water bodies where *B. huaronensis* occurs – in terms of geographic location, size, water flow, and trophic state – this species seems to have high tolerance and a wide niche breadth. On the other hand, it could be hypothesized that dominant clones in different populations differ in their ecological niche.

Principal Component Analysis (PCA) is considered a useful tool for investigating niche differences, as it provides the means to explain the variance magnitudes related to environmental variables, which represent the environmental niche (Janžekovič and Novak 2012). For this purpose, it is desirable to have a robust data set, including as many environmental variables as possible, a condition not reached for *B. huaronensis*, as for many other organisms.

In the absence of a more complete data set, altitude and climatic variables, now easily available from global climate databases, have been used for niche differentiation studies for a variety of organisms and objectives (e.g. Knouft *et al*., 2006; Ibarra-Cerdeña *et al*., 2009; Batista and Gurgel-Gonçalves, 2009; Kamilar and Muldoon, 2010; Giannini *et al.,* 2011; Schnitzler *et al.,* 2012).

The present study aims to survey the occurrence records of *B. huaronensis* and investigate the niche differentiation among populations from different biogeographic regions, based on altitude and climatic variables.

Table 1. Occurrence records of *Bosmina huaronensis* and their biogeographic classification, using Morrone's criteria (2006).

	Occurrence record	Coordinates	Biogeographic Classification	Source
AN01	Pond in Amarillo, Texas, USA	35.218°N, 101.852°W	Neartic region	De Melo and Hebert 1994
AN02	Lyman Lake, Arizona, USA	34.364°N, 109.374°W	Neartic region	Waterflea.Org database
AN03	Santa Anna Reservoir, Hidalgo State, Mexico	20.208°N, 98.208°W	Mexican transition zone	De Melo and Hebert 1994
AN04	La Goleta, Mexico	20.070°N, 99.556°W	Mexican transition zone	Global Barcode database
AS01	Lake Huaron, Peru	11.030°S, 76.428°W	South-American transition zone	Delachaux, 1918
AS02	Lake Junin, Peru	11.024°S, 76.118°W	South-American transition zone	Valdivia-Villar, 1988
AS03	Lake Arapa, Peru	15.155°S, 70.109°W	South-American transition zone	Valdivia-Villar, 1988
AS04	Lake Titicaca, Peru	15.796°S, 69.383°W	South-American transition zone	Paggi, 1979
AS05	Lake Titicaca, Bolivia	16.225°S, 68.764°W	South-American transition zone	Uéno, 1967
AS06	Pools in Cochabamba, Bolivia	17.278°S, 66.213°W	South-American transition zone	Coronel *et al*., 2007
AS07	Lake near Yala, Jujuy, Argentina	24.113°S, 65.484°W	South-American transition zone	Paggi, 1979
AS08	Lake Paranoá, Federal District, Brazil	15.733°S, 47.882°W	Neotropical region	present study
AS09	Três Irmãos Reservoir, São Paulo, Brazil	20.694°S, 51.100°W	Neotropical region	Zanata, 2005; Rocha *et al*., 2011
AS10	Três Irmãos Reservoir, São Paulo, Brazil	20.851°S, 50.555°W	Neotropical region	Rocha *et al*., 2011
AS11	Nova Avanhandava Reservoir, S.Paulo, Brazil	21.156°S, 50.139°W	Neotropical region	Zanata, 2005; Rocha *et al*., 2011
AS12	Lake in Birigui, São Paulo, Brazil	21.241°S, 50.397°W	Neotropical region	Rocha *et al*., 2011
AS13	Promissão Reservoir, São Paulo, Brazil	21.320°S, 49.737°W	Neotropical region	Zanata, 2005; Rocha *et al*., 2011
AS14	Bariri Reservoir, São Paulo, Brazil	22.168°S, 48.731°W	Neotropical region	Rocha *et al*., 2011
AS15	Lake Areia que Canta, São Paulo, Brazil	22.315°S, 48.052°W	Neotropical region	Rocha *et al*., 2011
AS16	Barra Bonita Reservoir, São Paulo, Brazil	22.529°S, 48.523°W	Neotropical region	Zanata, 2005; Rocha *et al*., 2011
AS17	Garças Reservoir, São Paulo, Brazil	23.647°S, 46.624°W	Neotropical region	Di Genaro, 2010
AS18	Itaipu Reservoir, Brazil	25.031°S, 54.379°W	Neotropical region	Velho *et al*., 2000
AS19	Lake Blanca, Formosa, Argentina	25.162°S, 58.143°W	Neotropical region	Paggi, 1979
AS20	Iraí Reservoir, Paraná, Brazil	25.405°S, 49.096°W	Neotropical region	Ghidini *et al*., 2009
AS21	Pozo Negro, Iguaçu River, Argentina	25.602°S, 54.387°W	Neotropical region	José de Paggi, 2002
AS22	Puerto Macuco, Iguaçu River, Argentina	25.648°S, 54.458°W	Neotropical region	José de Paggi, 2002
AS23	Lake in Formosa, Argentina	26.170°S, 58.162°W	Neotropical region	Paggi, 1979
AS24	El Cadillal Reservoir, Tucuman, Argentina	26.608°S, 65.217°W	Neotropical region	Paggi, 1979
AS25	Itajai-Açu River, Santa Catarina, Brazil	26.905°S, 49.017°W	Neotropical region	Serafim-Junior *et al*., 2006
AS26	Lake near Itati, Corrientes, Argentina	27.268°S, 58.251°W	Neotropical region	Paggi, 1979
AS27	Rio Dulce, Santiago del Estero, Argentina	27.504°S, 64.854°W	Neotropical region	Paggi, 1979
AS28	Río Hondo Res., Santiago del Estero, Argentina	27.522°S, 64.888°W	Neotropical region	waterflea.org database
AS29	Lake in Corrientes, Argentina	28.536°S, 56.033°W	Neotropical region	Paggi, 1979
AS30	Lake Guabiyú, Santa Fe, Argentina	28.761°S, 59.149°W	Neotropical region	Paggi, 1979
AS31	Lake Itapeva, Rio Grande do Sul, Brasil	29.488°S, 49.912°W	Neotropical region	Cardoso and Motta Marques, 2004
AS32	Ditch near La Gallareta, Santa Fe, Argentina	29.585°S, 60.384°W	Neotropical region	Paggi, 1979
AS33	Pond at São Simão, Rio Grande do Sul, Brazil	30.952°S, 50.708°W	Neotropical region	present study
AS34	Salto Grande Reservoir, Entre Rios, Argentina	31.116°S, 58.050°W	Neotropical region	José de Paggi, 2002
AS35	La Virgen Stream, Entre Rios, Argentina	31.250°S, 57.917°W	Neotropical region	José de Paggi, 2002
AS36	Lake Paiva, Santa Fe, Argentina	31.275°S, 60.618°W	Neotropical region	Paggi, 1979
AS37	San Roque Reservoir, Cordoba, Argentina	31.370°S, 64.462°W	Neotropical region	Paggi, 1979
AS38	Lake near Santo Tomé, Argentina	31.668°S, 60.768°W	Neotropical region	Paggi, 1979
AS39	Paraná River, Santa Fe, Argentina	31.715°S, 60.516°W	Neotropical region	Paggi, 1979
AS40	Los Mollinos Reservoir, Cordoba, Argentina	31.842°S, 64.528°W	Neotropical region	Paggi, 1979; waterflea.org database
AS41	Cordoba Reservoir, Argentina	32.179°S, 64.405°W	Neotropical region	waterflea.org database
AS42	Río Tercero Reservoir, Cordoba, Argentina	32.213°S, 64.478°W	Neotropical region	Paggi, 1979, Escalante, 1988
AS43	Paraná River, Buenos Ayres, Argentina	34.303°S, 58.515°W	Neotropical region	Paggi, 1979
AS44	Stream near Colonia, Uruguay	34.457°S, 57.791°W	Neotropical region	Paggi, 1979
AS45	Lake Ton-Ton, Uruguay	34.851°S, 56.033°W	Neotropical region	Conde and Sommaruga, 1998
AS46	Lake Don Tomás, La Pampa, Argentina	36.622°S, 64.314°W	Neotropical region	Echaniz *et al*., 2008
AS47	Lake Los Padres, Buenos Ayres, Argentina	37.936°S, 57.731°W	Neotropical region	González-Sagrario and Balseiro, 2010
AS48	Valle Fértil Reservoir, San Juan, Argentina	30.634°S, 67.483°W	Andean region	Paggi, 1979
AS49	Ameghino Reservoir, Chubut, Argentina	43.792°S, 66.451°W	Andean region	Menu-Marque and Marinoni, 1986
AS50	Lake Musters, Chubut, Argentina	45.419°S, 69.177°W	Andean region	Menu-Marque and Marinoni, 1986
AS51	Lake Colhue Huapi, Chubut, Argentina	45.497°S, 68.767°W	Andean region	Menu-Marque and Marinoni, 1986

Material and Methods

Occurrence records of *B. huaronensis* were obtained from literature and internet databases (Tab. 1). Two original records from Brazil were also included: a pond at São Simão Beach, Mostardas, Rio Grande do Sul state, 14m a.s.l (col. LMAEL, Jan.01.2002) and Lake Paranoá, Brasília, Federal District, c. 1,000m a.s.l (col. LMAEL, Feb.19.2012). When literature did not provide geographical coordinates, they were obtained from Google Earth, and only verifiable locations were included in the analysis.

The niche differentiation among *B. huaronensis* populations was investigated by conducting a principal components analysis (PCA), which also was used to identify climatic variables potentially important in the geographic distribution. The abiotic variables (19 climate and one topographic) were obtained from the WorldClim database (http://www.worldclim.org/) at 5 arc-minutes resolution. The "extract value by point" function in DIVA 7.5.0 (Hijmans *et al.*, 2001) was used to obtain the climate and altitude data for each locality.

Before conducting the PCA, a correlation matrix among all variables was constructed; this allowed the degree of multicollinearity in our dataset to be minimized by removing highly correlated variables ($r > 0.8$). Using this criterion, 12 variables were removed from the initial dataset, and the PCA included the following eight variables: altitude, annual mean temperature, mean diurnal range, temperature seasonality, mean temperature of driest quarter, annual precipitation, precipitation of wettest quarter, and precipitation of driest quarter. The data were log10-transformed to standardize data for PCA. Statistics were performed using PAST (Hammer *et al.*, 2001).

To better explore the possible aggregation of occurrence records, these were classified by biogeographic regions and transition zones (Tab. 1), following Morrone's criteria (2006).

Results

The data collected in the present study indicated that *B. huaronensis* is reported from 55 localities in South and North America (Tab. 1), ranging about 45° S to 35° N.

In the multivariate analysis, the first and second principal components explained 44.9 and 28.1% of the overall variance, respectively. The climatic variables most associated with the distribution of occurrence records along axis 1 of the PCA diagram were annual mean temperature, precipitation of driest quarter, and annual precipitation (Tab. 2). Altitude had the strongest negative relation with axis 1. For axis 2, the most related variables were temperature seasonality and precipitation of wettest quarter.

The ordination of occurrence records in the PCA diagram (Fig. 1) showed that populations from the biogeographic regions aggregate in three groups. The first group was represented by the records from South American and Mexican transition zones, including Lake Huaron (AS01), the type locality. The second one was formed by Neotropical populations. Nevertheless, there is an overlapping area between groups 1 and 2, represented by records AS24, AS27, AS28, AS37, AS40, AS41, and AS42 (Fig. 1; for exact localities, see Tab. 1). Finally, the third group aggregated the populations from Andean and Nearctic regions. One of the Neotropical records, from Lake Paranoá (AS08), was placed outside of the 90% density ellipses.

Table 2. PC1 and PC2 loadings from principal components analysis of environmental variables for populations of *Bosmina huaronensis*.

Environmental variable (log-transformed)	PCA 1	PCA 2
Altitude	-0.7110	0.5093
Annual Mean Temperature	0.7648	-0.3033
Mean Diurnal Range	-0.6719	0.0910
Temperature Seasonality	0.0904	-0.8838
Mean Temperature of Driest Quarter	0.6997	-0.3066
Annual Precipitation	0.7493	0.6217
Precipitation of Wettest Quarter	0.5206	0.7871
Precipitation of Driest Quarter	0.8502	0.0872

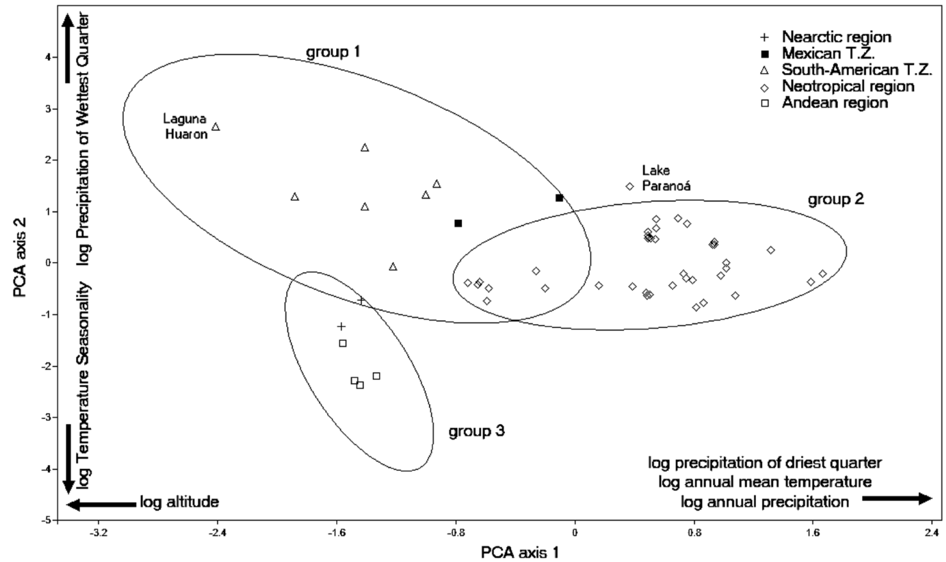

Figure 1. Principal component analysis (PCA) of environmental variables and geographic distributions of *Bosmina huaronensis*, with 90% density ellipses. The first component explains 44.9% of the variation and the second component 28.1%. T.Z means transition zones.

Discussion

According to the surveyed records, *B. huaronensis* has a wide distribution range, including tropical and temperate zones of the American continent, from both hemispheres. In its range, this species occurs in a variety of water bodies, located at different altitudes and under diverse climate regimes.

The current distribution of species results from the interaction of large spatio-temporal processes (e.g. speciation, dispersal, climatic and geographic developments) and small-scale processes (e.g. competition, predation, local disturbances). The former processes act on a regional scale and govern species availability, but the local processes act as definite filters (Winkler and Kampichler, 2000).

The present study investigated *B. huaronensis* distribution only on regional approach, once only climatic and geographic aspects were considered. To better understand the processes acting on this species local distribution, it is also important to consider limnological variables and aspects of zooplankton community structure. However, this approach was outside the scope of this paper.

Despite this limitation, based on altitude and climate variables considered here, the occurrence localities of *B. huaronensis* were gathered into three groups (Figure 1). Group one represents the tropical high-altitude water bodies, located in the Central Andes and Central Mexico. Populations of *B. huaronensis* in these regions occur at low annual mean temperature, temperature seasonality, and precipitation, which is concentrated in the wettest quarter. As the type locality belongs to this group, this climatic niche should be considered the most typical for the species.

The second group, represented by Neotropical records, corresponds to localities in tropical and subtropical lowlands (below 1,000 m a.s.l.). The climate niche of this group is characterized by low temperature seasonality and high annual mean temperatures and precipitation in the wettest quarter. The overlapping area between groups 1 and 2 corresponds to localities on the eastern side of the Andes, with lower precipitation in the driest quarter. It could represent a transitional niche between the former two groups, but, alternatively, it could mean that the Morrone regions and transition zones are not the best criterion under which to investigate *B. huaronensis* distribution.

High temperature seasonality and low annual mean temperature and precipitation characterize the occurrence records of the third group, located in temperate zones of both hemispheres.

As presented here, *B. huaronensis* populations were found under different climate regimes, supporting the idea that the dominant clones in each one occupy a different ecological niche. Many authors have showed clones of cladoceran species differing with regard to their physiological, reproductive, behavioral, and ecological traits (e.g. Reede and Ringelberg, 1995; Dodson *et al.*, 1997; Innes and Singleton, 2000; Michels and De Meester, 2004; Forasacco & Fontvieille, 2010; Lehto and Haag, 2010). Such differences, therefore, allow the occupation of different niches and enable the dominance of certain clones subjected to a particular climate regime.

Nevertheless, the possibility should not be excluded that these groups of populations could represent a complex of species. In recent years, new cladoceran species have been recognized as deep morphological and genetic comparisons between populations from different regions were conducted (e.g. De Melo and Hebert, 1994; Kappes and Sinsch, 2002; Nilssen *et al.*, 2007; Elías-Gutiérrez and Valdez-Moreno, 2008; Belyaeva and Taylor, 2009; Kotov *et al.*, 2009; Sinev and Elmoor-Loureiro, 2010; Van Damme *et al.*, 2011). Therefore, *B. huaronensis* populations should be compared in their morphology, genetics and ecology in order to access their taxonomic status.

In particular, the population from Lake Paranoá should be better investigated. For about 30 years, the planktonic community of Lake Paranoá has been studied, and this species has never been reported before (Elmoor-Loureiro *et al.*, 2004; Mendonça-Galvão, 2005; Batista, 2007; see Padovesi-Fonseca *et al.*, 2001 for previous records). Additionally, it represents the first record from Central Brazil (Elmoor-Loureiro, 2000) and, in general morphology, the individuals do not differ from the species description (Paggi, 1979). However, at a similar latitude (11° to 17°S), *B. huaronensis* had previously been reported only above 3,000m a.s.l. (Delachaux, 1918; Uéno, 1967; Paggi, 1979; Valdivia-Villar, 1988; Coronel *et al.*, 2007), while Lake Paranoá is located at about 1,000m a.s.l. Such geographic uniqueness corresponds to a particular climate (Köppen's Aw, tropical savanna climate, with well defined wet and dry seasons), which is reflected in the PCA diagram, where the Lake Paranoá record is located outside of the 90% density ellipses (Figure 1). Although the possibility that this result arises from gaps in sampling effort cannot be discarded, a more detailed morphological comparison between Lake Paranoá and the typical population is recommended.

The present paper showed that *B. huaronensis* has a wide distribution in the Americas and that its populations occupy three different climate niches: tropical at high altitudes, tropical and subtropical in lowlands, and temperate. Comparative morphological, genetic, and ecological studies are needed to evaluate the taxonomic status of these population groups.

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