Revista Chilena de Historia Natural
81: 185-203, 2008

Finding patterns of distribution for freshwater phytoplankton, zooplankton and fish, by means of parsimony analysis of endemicity

Encontrando patrones de distribución para fitoplancton, zooplancton y peces dulceacuícolas por medio de análisis de parsimonia de endemismos

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ABSTRACT

During the last decades, limnological studies on Chilean systems have contributed to know the species composition and main environmental variables of many water bodies distributed over a wide latitudinal interval, from 18º to 53º S. However, we still lack of a comprehensive view about the structure and functioning of regional freshwaters. In this work we review the available information about pelagic biota from Chilean basins, in order to reveal patterns of species distribution and their possible association with environmental variables. We built presence-absence matrices for phytoplankton, zooplankton and fish over lakes and basins. From this database, we performed parsimony analysis of endemicity as a tool for determining fundamental distribution patterns of freshwater biota. Also, we assessed the relationship between species occurrences and some available site-related variables. Our results indicated that latitude exerted the strongest influence on species distribution, although altitude, longitude, and area also exerted significant effects for some groups. On the other hand, our results suggest a relationship between the degree of vagility of the groups and the degree of metacommunity structuring, related to the number of endemicity areas.

Key words: limnology, lakes, plankton, biogeography, Chile, CCA.

RESUMEN

Durante las últimas décadas, los estudios limnológicos en sistemas chilenos han contribuido al conocimiento de la composición de especies y de las principales variables ambientales de muchos cuerpos de agua distribuidos sobre un amplio intervalo latitudinal, desde los 18º a los 53º S. Asimismo, aún carecemos de una visión comprensiva acerca de la estructura y funcionamiento de las aguas dulces regionales. En este trabajo revisamos la información sobre la biota pelágica de las cuencas de Chile, con el propósito de revelar patrones de distribución de especies y su posible asociación con variables ambientales. Construimos matrices de presencia-ausencia para fitoplancton, zooplancton y peces en lagos y cuencas. Desde esta base de datos realizamos análisis de parsimonia de endemismo, como medio para determinar patrones fundamentales de distribución de la biota dulceacuícola. También, determinamos la relación entre la presencia de especies y algunas variables relevantes de los sitios. Nuestros resultados sugieren que la latitud ejerce una fuerte influencia en la distribución de especies, aunque también la altitud, longitud y el área ejercen efectos significativos en algunos grupos. Por otro lado, los resultados sugieren una relación entre el grado de vagilidad de los grupos y el grado de estructuración de la metacomunidad, relacionada con el número de áreas de endemismos.

Palabras clave: limnología, lagos, plancton, biogeografía, Chile, CCA.

INTRODUCTION

Understanding patterns of biodiversity and community structure on a given region, as much as developing guidelines for conservation of biota and environmental care, requires knowledge about patterns of distribution and abundance of entire taxonomic groups. In southern latitudes, data about freshwater biota are often scarce, incomplete, and dispersed. Particularly in Chile, the field of limnology is still in an early stage from the viewpoint of scientific development, and accordingly, most ecologically oriented work on freshwaters habitats has been mainly descriptive and comparative, with modest progress in experimental or theoretical research.

In spite of several decades of valuable descriptive work, regional information about freshwater biota is fragmented and biased, both geographically and taxonomically. As a consequence, we lack of basic knowledge about patterns of distribution and biodiversity, which contrasts sharply with the abundance and variety of freshwater bodies found in the country. Chilean freshwaters exhibit a wide spectrum of physical features associated to strong gradients of climate, lithology, topography and vegetation cover, in agreement with their broad latitudinal range and the strong influences from high Andes and Pacific Ocean.

Here we intend for the first time to review the available information about key components of pelagic biota from Chilean freshwaters, in order to reveal patterns of species distribution and their possible association with environmental variables.

Parsimony analysis of endemicity (PAE) is a powerful biogeographical tool, useful for determining distributional patterns of species and for identifying biodiversity hotspots (Garrafoni et al. 2006). For these reasons, PAE can help for building up a comprehensive view on some aspects of the structure freshwater biota, as well as for guiding conservation planning. Originally developed by Rosen (1988), PAE aims to classify areas by most parsimonious solutions based on the shared presence of species (Nihei 2006). This allows for the identification of areas with non-random distributional congruence among different species (Morrone 1994).

In this work we review the available information about distribution of freshwater phytoplankton, zooplankton, and fish species from mainland Chile. We use the compiled data for finding out basic distribution patterns for the analyzed biota through (a) testing whether the distribution of species across lakes and basins can be statistically explained by the environmental variables at hand, and (b) identifying areas of endemism for each of the groups of interest.

MATERIAL AND METHODS

Database

We attempted to review all published information (in both indexed and not-indexed journals) about species distribution of phytoplankton, zooplankton and fish from Chilean freshwaters. We were able to find 41 articles with reliable data, and three additional papers containing environmental information needed for our analyses. The published data spanned from year 1973 to 2006. We studied 55 lakes located between 18.25° and 53.46° S, although most of them concentrate between 32.54° and 46.5° S (Fig. 1).

From this dataset we constructed presence/absence matrices for each taxon (available upon request), with species as columns and sites as rows. Lakes and basins were treated separately as sites. For phytoplankton (found in 22 lakes), we constructed matrices for the three major taxa Bacillariophyceae (diatoms, 18 lakes), Chlorophyceae (green algae, 18 lakes), and Cyanophyceae (blue-green algae, 16 lakes). For zooplankton (52 lakes), we analyzed separately the three major taxa Cladocera (41 lakes), Copepoda (47 lakes), and Rotifera (31 lakes). Fish were treated as a single taxon and only data by basins were available.

In order to avoid anecdotic records, we did not considered lakes below percentile 10 of species richness, within each taxonomic group. For species names, we maintained the nomenclature contained in the original references.

We also reviewed the available environmental information associated to each site. For lakes, we recorded area, latitude, longitude, and altitude. Most of these data were obtained from the published information. For lakes Pichilafquen, Quillehue, and Chiguay, geographic coordinates were taken from Google Earth (http: //earth.google.com). Surface area for lakes Pichilafquen, Quillehue, Chiguay, Atravesado, Bonita, Huilipilun, La Posada, Patos Bravos, and Lynch were measured with the software Image Tool 3.0 (http: //ddsdx.uthscsa.edu/dig/itdesc.html) from images obtained with Google Earth.

A total of 40 basins were defined according to the official website of Dirección General de Aguas (http: //www.dga.cl), from which we also obtained their surface area and perimeter. For determining the characteristic geographic coordinates of each basin, we followed the following protocol. For exhorreic basins between 22.47° and 48.20° S, basin coordinates were defined as those of the middle point of their main river. For coastal basins between 31.78° and 38.25° S, basin latitude was defined as the mean of those of the two rivers that limit the basin; and longitude was defined as that of the shoreline at the basin latitude. Basins between 42.54° and 53.83° S present a large region of flooded land, and their coordinates correspond to that of the middle point of the entire area. This same procedure was used for basins Altiplanica and Budi. Chilean basins were also grouped into seven hydrographic zones, following official terms (http: // www.igm.cl). Matrices with phytoplankton and zooplankton by basins were constructed from the information of species occurrences in the lakes that belong to each basin.

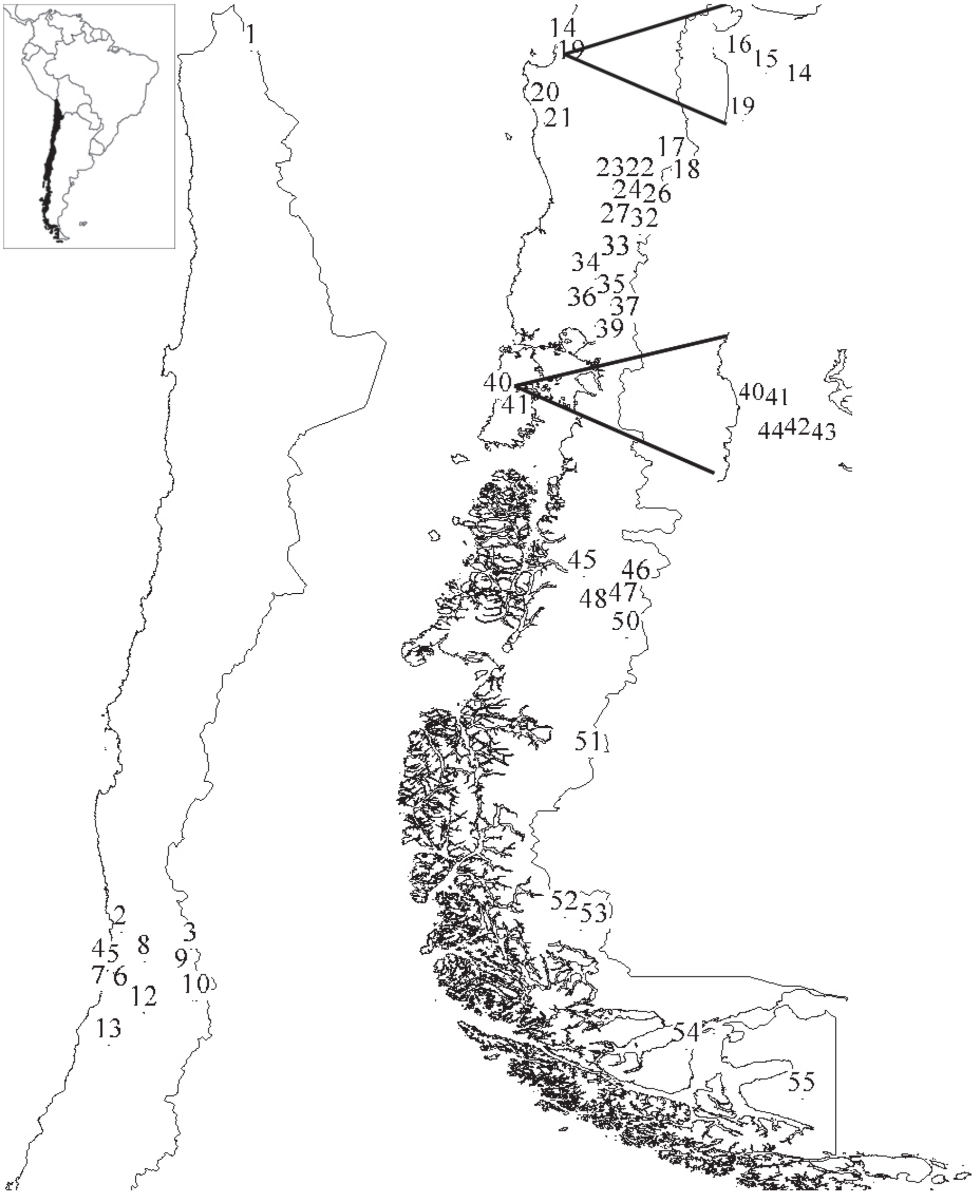

Fig. 1: Map of mainland Chile, indicating the 55 lakes used in the analyses.

Mapa de Chile continental, indicando los 55 lagos usados en los análisis.

Multivariate statistics

In order to establish the possible relationship between the presence/absence of several taxa in both Chilean lakes and basins and their environmental variables described below, we performed a multivariate direct gradient analysis, specifically a canonical correspondence analysis (CCA, Ter Braak 1986). CCA extracts continuous axes of variation from species occurrence in the light of known environmental variables (EV), by imposing the constraint that axes are linear combinations of EV. Hence, the relationship between species occurrences and EV are assumed to be linear. In order to determine whether these relationships are statistically significant, we performed Monte Carlo permutation tests with 1,000 runs (Manly 1991). The results of statistically significant CCA are displayed using biplot diagrams of sites (symbols) and EV (vectors). Both CCA and permutation tests were done using the package CANOCO v. 4.5 (Ter Braak & Smilauer 2002).

Parsimony analysis of endemicity

We performed parsimony analysis of endemicity (PAE, Rosen 1988, Morrone 1994) in order to determine possible areas of endemism. The analysis was based on a data matrix with species (characters) as columns and basins as rows (OGU's). The character states were coded as presence/absence (1/0) of the species on sites. For these analyses we used basins instead lakes as sites, in order to minimize the effect of incomplete sampling of species across lakes. A hypothetical basin without any species presence was used for rooting the tree. Data were analyzed with the software PAUP* 4.0b10 (Swofford 2001), using the heuristic search algorithm, randomizing the OGU's entries with 100 replicates. All characters were treated as ordered (Wagner parsimony). The strict consensus tree was calculated, that conserves the most robust grouping of localities and minimizes the influence of widely distributed species (Morrone 1994). A clade defined by at least two species was considered to be an endemicity area (Morrone 1994). We also performed PAE for a matrix that included all species and basins, where a clade defined by at least two species of each taxon was considered to be an endemicity area.

RESULTS

Multivariate statistics

Seven CCA were statistically significant (Monte Carlo permutation test, $P < 0.05$, Table 1), from a total of 17 studied groups. Total zooplankton, copepods, rotifers, and fish consistently exhibited significant associations with the studied EV. In Fig. 2-4 we show biplots summarizing the relationship between the freshwater biota (symbols, classified according to hydrographic Chilean zones) and EV (vectors).

In general terms, latitude represented the main gradient for all groups considered here. This gradient followed the north-to-south succession through the hydrographic zones, crossing the three main climatic regions of Chile: arid, Mediterranean and temperate. Considering the analyses based on lakes, the second gradient was dominated by altitude, except for rotifers where surface area was the main factor. On the other hand, the second gradient in basins-based analyses was dominated by either longitude (total zooplankton, copepods) or surface area (rotifers, fish). Note that for rotifers, surface area covaried with perimeter of the basin.

Results of CCA accounting for the distribution of total zooplankton on lakes indicated that the two first axes represent 80.6 % of total variance (Fig. 2A). The first axis was mainly correlated with latitude ($r = -0.91$) whereas second axis was correlated with altitude ($r = 0.75$). In CCA by basins (Fig. 2B), the first two axes represented 62.5 % of total variance; the first axis was mainly correlated with latitude ($r = -0.80$) and second axis was correlated with longitude ($r = 0.75$).

In CCA of copepod distribution on lakes (Fig. 3A), the first axis was mainly correlated with latitude ($r = -0.82$) and the second axis was correlated with altitude ($r = 0.80$). In CCA by basins (Fig. 3C), the two first axes represented 70.5 % of total variance. The first axis was mainly correlated with latitude ($r = -0.58$) whereas second axis was correlated with longitude ($r = 0.88$).

TABLE 1

Monte Carlo's test of significance of all canonical axes with 1,000 permutations. Canonical correspondence analysis made from both lakes and basins along the continental Chile; NS indicates P > 0.05

Prueba de significación de Monte Carlo para todos los ejes canónicos con 1.000 permutaciones. Análisis de correspondencia canónica realizado para lagos y cuencas a lo largo de Chile continental; NS indica P > 0,05

Variable	Lakes		Basins	
	F-ratio	P-value	F-ratio	P-value
Total phytoplankton	1.251	NS	1.852	NS
Bacyllariophyceae	1.150	NS	1.544	NS
Chlorophyceae	1.302	NS	1.959	NS
Cyanophyceae	1.073	NS	1.754	NS
Total zooplankton	1.816	0.017	1.418	0.012
Cladocera	1.779	NS	0.982	NS
Copepoda	2.479	0.001	1.922	0.002
Rotifera	1.508	0.021	1.384	0.039
Fish	-	-	1.797	0.037

Multivariate analyses testing association of rotifer distribution on lakes and EV (Fig. 3B) showed that the two first axes represent 62.4 % of total variance, where the first axis was mainly correlated with latitude (r = 0.90) while the second axis was correlated with surface area (r = 0.60). In CCA by basins (Fig. 3D), the first two axes represented 60.8 % of total variance; the first axis was mainly correlated with latitude (r = -0.75) and second axis with area (r = -0.44).

Finally, in CCA of fish (Fig. 4) the first axis was mainly correlated with latitude (r = 0.83) whereas second axis was correlated with surface area (r = 0.35).

The analysis of the total information (i.e. a single matrix with all taxa and basins included) did not provided additional information, showing that latitude and area constituted the main driving gradients for the biota analyzed here.

Parsimony analysis of endemicity

Based on the analyzed information, endemicity areas were identified for all taxonomic groups with the exception of blue-green algae. Green algae (Chlorophyceae, Fig. 5A and 8A), exhibited two partially overlapping endemicity areas. The first clade (defined by *Closterium acutum* and *Sphaerocystis schroeteri*) is located between 19.913º and 51.247º S, and was formed by three joint basins (AA, AB, AC, see Table A-1 in the appendix) and four disjoint basins (A, N, S, and AL). The second clade defined for green algae (*Ankistrodesmus falcatus*, *Scenedesmus quadricauda* and *Staurastrum polymorphum*) is located between 33.317º and 39.015º S, and comprised four basins, inside which there were two sub-areas of endemicity: L, Z and R, T. For diatoms (Bacillariophyceae, Fig. 5B and 8B) we observed two endemicity areas. The first clade (defined by *Aulacoseira granulata*, *Cocconeis placentula*, and *Synedra rumpens*) comprised three disjoint basins (19.913º and 42.542º S) A, N, and AD. The second clade (*Melosira granulata*, and *Surirella guatimalensis*) extends between 33.317º and 51,247º S and was composed by 10 basins (L, R, M, S, T, Z, AB, AC, AL, and AA).

Rotifers exhibited two endemicity areas. The first clade (defined by species *Keratella valga* and *Lepadella ovalis*) was built by two adjacent basins (J-K, 32.664º to 32.735º S), while the second (*Kellatera cochlearis*, *Conochilus unicornis*, *Hexarthra fennica* and *Polyarthra vulgaris*, 33.317º to 42.542º S) was represented by a group of nine basins that included two continuous sub-areas comprising basins L-M-N and the region from basin Z till AC plus the island AD, respectively (Fig. 6A and 9A). Copepods exhibited three endemicity areas. The first clade (*Tumeodiaptomus diabolicus* and *Tropocyclops prasinus meridionalis*) is a large group of eight basins located between 33.711º and 42.542º S, inside which there was a continuous sub-area composed by basins Z, AA, AB, and AC. A second endemicity area for copepods (*Parabroteas sarsii* and *Eucyclops Serrulatus*) locates between 45.313º and 47.468º S and it was defined by the union of AH and AI. The last area (*Diaptomus diabolicus* and *Mesocyclops longisetus*) extends from 32.427º to 34.114º and corresponded to the disjoint basins J-L-N (Fig. 6B and 9B). The last zooplankton group, Cladocera, presented a single large endemicity area (defined by species *Diaphanosoma chilense* and *Daphnia ambigua*) covering basins A, L, M, N, V, Z, AA, AB, and AD, inside which there was a continuous sub-area composed by basins Z, AA, AB, located between 39.015º and 40.334º S (Fig. 6C and 9C).

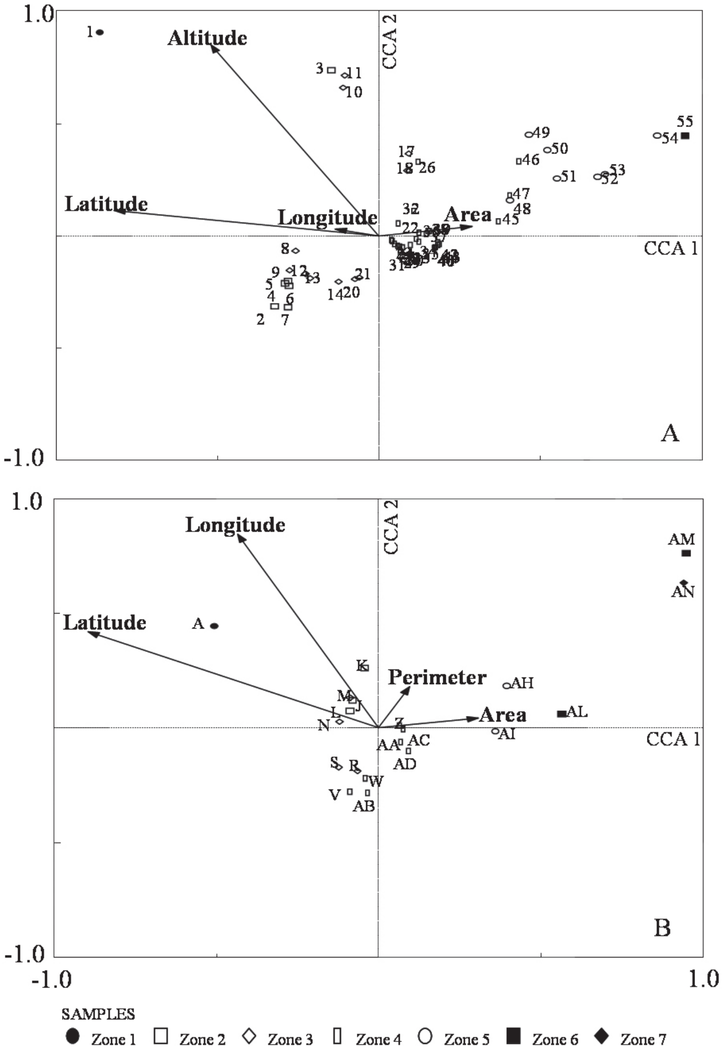

Fig. 2: Summary results of canonical correspondence analysis for total zooplankton. (A) by lakes, the two first axes represent 80.6 % of total variance; (B) by basins, the two first axes represent 62.5 % of total variance.

Resumen de resultados del análisis de correspondencia canónica para zooplancton total. (A) por lagos. Los dos primeros ejes representan el 80,6 % del total de la varianza; (B) por cuencas, los dos primeros ejes representan el 62,5 % del total de la varianza.

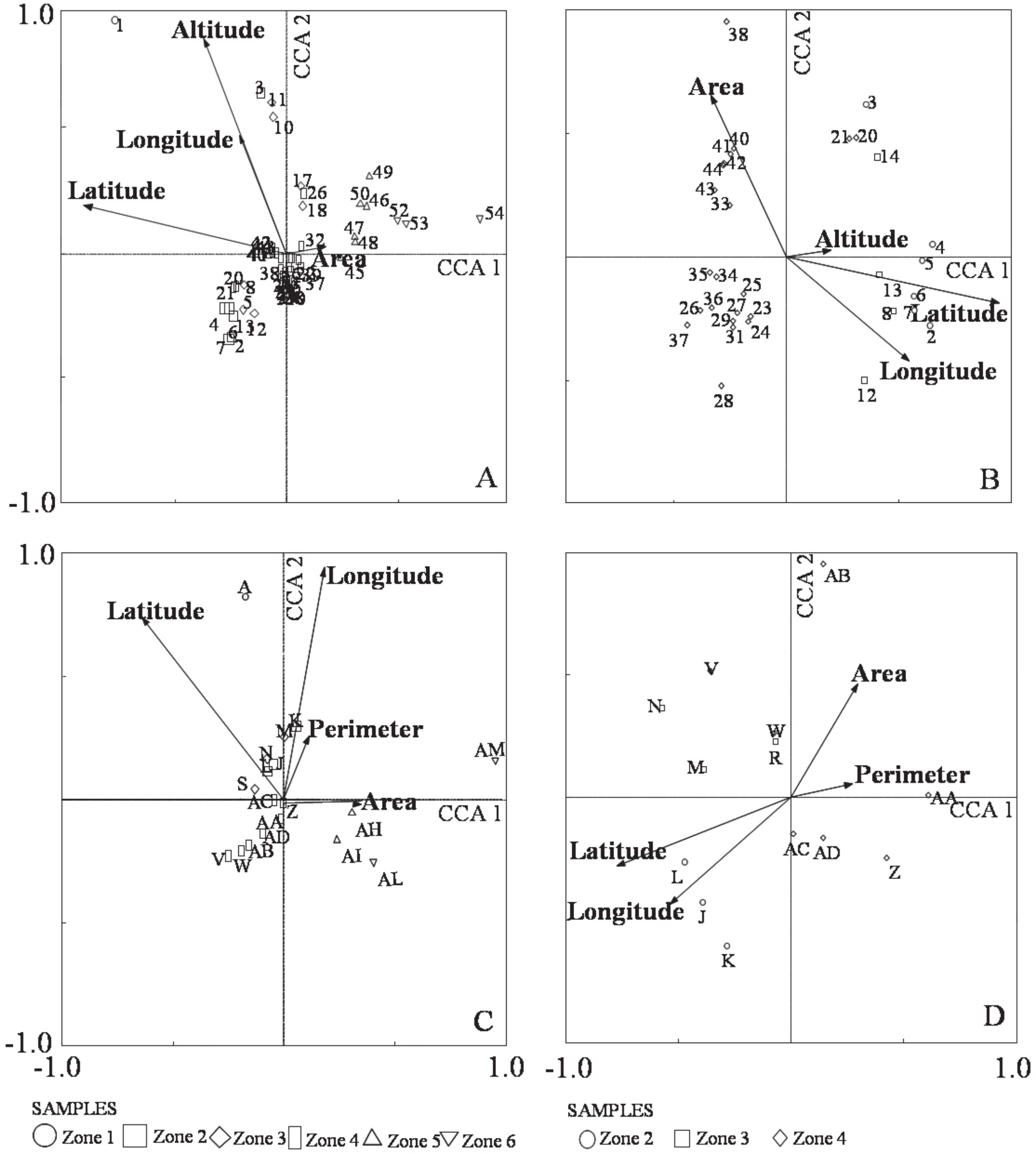

Fig 3: Summary results of canonical correspondence analysis for copepods (A and C) and rotifers (B and D). (A) Copepods by lakes, the two first axes represent 74.2 % of total variance; (B) rotifers by lakes, the two first axes represent 62.4 % of total variance; (C) copepods by basins, the two first axes represent 70.5 % of total variance; (D) rotifers by basins, the two first axes represent 60.8 % of total variance. Note that the perimeter and the area are autocorrelated in (D).

Resumen de resultados de análisis de correspondencia canónica para copépodos (A y C) y rotíferos (B y D). (A) Copépodos por lagos, los dos primeros ejes representan 74,2 % del total de la varianza; (B) rotíferos por lagos, los dos primeros ejes representan el 62,4 % del total de la varianza; (C) copépodos por cuencas, los dos primeros ejes representan 70,5 % de la varianza; (D) rotíferos por cuencas, los dos primeros ejes representan el 60,8 % del total de la varianza. Note que el perímetro y el área están autocorrelacionados en (D).

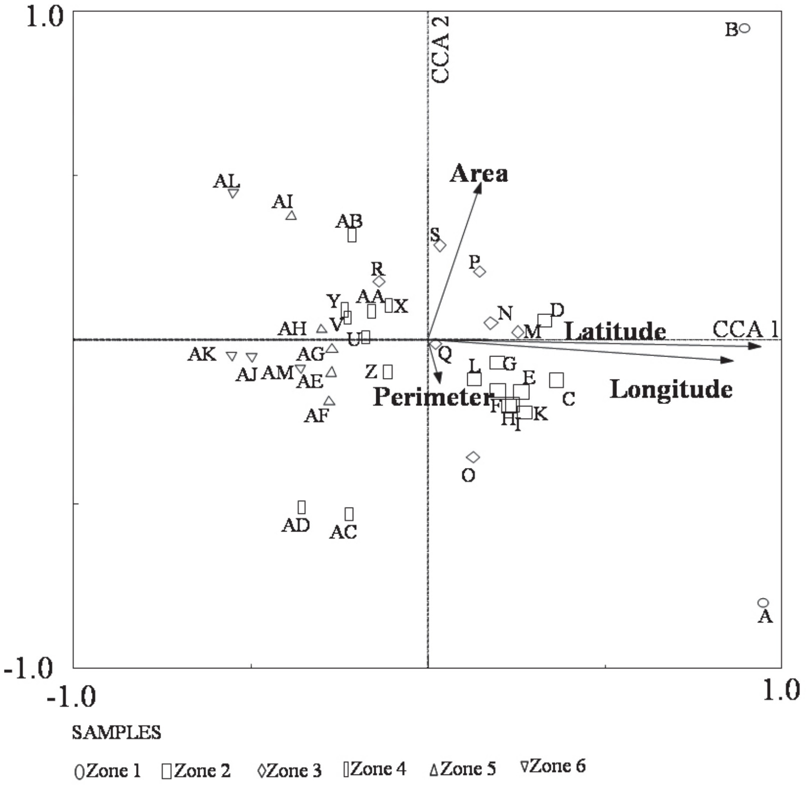

Fig. 4: Summary results of canonical correspondence analysis for fish. The first two axes represent 78 % of total variance.

Resumen de resultados del análisis de correspondencia canónica para peces. Los dos primeros ejes representan 78 % del total de la varianza.

Four endemicity areas were defined for fish (Fig. 7 and 10). The first clade (*Cyprinus carpio* and *Trichomycterus areolatus*) is located between 30.685° and 39.885° S and included a continuous region from basin K (Aconcagua) until X (Imperial), plus the basins D and AA. Nine basins that include a continuous geographical region formed by the group AB, AC, AD, AE, AF, composed the second clade (*Aplochiton zebra* and *Aplochiton taeniatus*). Basins C and E represented the third clade (formed by *Mugil cephalus*, *C. carpio*, and *Oncorhynchus mykiss*). The fourth clade corresponded to a single basin (L, coastal Aconcagua-Maipo) that was defined by the species *Cheirodon interruptus*, *Basilichthys australis*, *Cyprinus carpio*, *Gambusia holbrooki*, and *Cnesterodon decemmaculatus*.

If we consider only the native fish species for the identification of endemicity areas, the first clade would loss basin D and it would be defined by *Diplomystes chilense*, *Basilichthys australis*, *Percichthys melanops*. In the same vein, the third and fourth endemicity areas would disappear.

The analysis of the total information (all taxa included) showed four endemicity areas. A first area appeared in all groups analyzed (basins Z-AD). The second area (L, N) was already defined for plankton groups, the area M, S appeared for green algae, and the fourth area AL was defined for green algae, diatoms, and copepods. The number of retained trees was 7717, with a length of 819. Consistency Index of this tree was 0.37, and Retention Index was 0.46.

Our results revealed that basin AB (Bueno), N (Rapel), Z (Toltén), AA (Valdivia), and L (Coasta Aconcagua-Maipo) form part of endemicity areas for all groups studied here, excluding blue-green algae. Basins AC (Basin/Island Bueno-Puelo), and M (Maipo) form part of endemicity areas for five out of six groups (excluding blue-green algae).

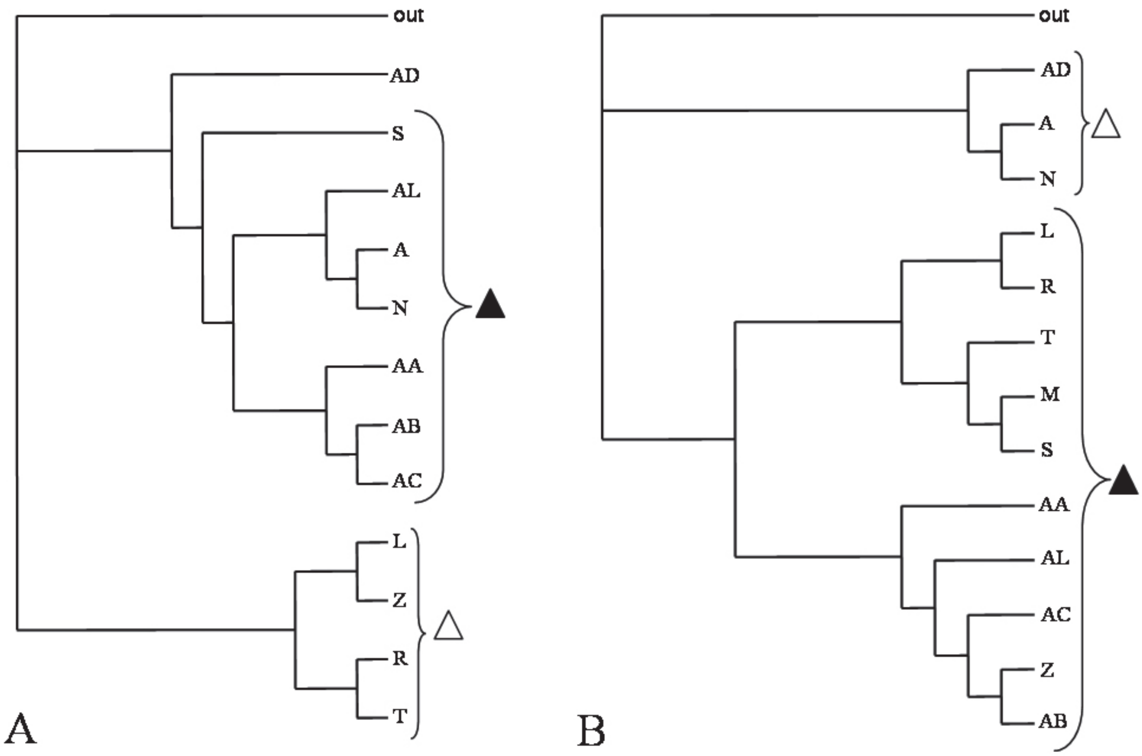

Fig. 5: Most parsimonious PAE trees for phytoplankton, by basins. (A) Chlorophyceae: number of trees = 30, length = 133, Consistency Index = 0.4511, Retention Index = 0.3707; (B) Bacillariophyceae: number of trees = 4, length = 222, Consistency Index = 0.4595, retention Index = 0.4258; Cyanophyceae did not present endemicity areas. For each group, symbols were associated to endemicity areas (denoted by brackets), same that will be depicted and described in Fig. 8.

Árboles PAE más parsimoniosos para fitoplancton, por cuencas. (A) Chlorophyceae: número de árboles = 30, largo = 133, índice de consistencia = 0,4511, índice de retención = 0,3707; (B) Bacillariophyceae: número de árboles = 4, largo = 222, índice de consistencia = 0,4595, índice de retención = 0,4258; Cyanophyceae no presentó áreas de endemismo. Para cada grupo se asociaron símbolos a las áreas de endemismo (indicadas por llaves) que serán presentados y descritos en la Fig. 8.

PAE performed for lakes (not shown here) exhibited more confuse results, although they show agreement with the basin-based analyses regarding the main endemicity areas.

DISCUSSION

Our CCA results revealed that neither phytoplankton nor cladocerans exhibit a distribution trend that could be explained by the environmental variables considered here. On the other hand, latitude was the main factor explaining species distribution of total zooplankton, copepods, rotifers, and fish. Altitude/longitude constituted also an important gradient for total zooplankton and copepods, while lake surface did so for rotifers. Since this work only assessed general distributional trends of a regional freshwater biota, mechanisms generating the observed patterns are still unknown. Nevertheless, previous works emphasize that phytoplankton distribution is often driven by dispersal, while distribution of fish is driven by vicariance. This relates to the relative vagility of the two groups, with zooplankton locating midway between phytoplankton and fish. This agrees with the lack of significance in CCA results for algae.

Phytoplankton dispersal mechanisms are largely passive ones. Passive dispersal of algae rest on airborne transport operating at distances, while foretic movements mediated mostly by beetles, dragonflies and waterbirds are important mechanisms over shorter distances. Furthermore, local dispersal also occurs by means of drift among rivers and

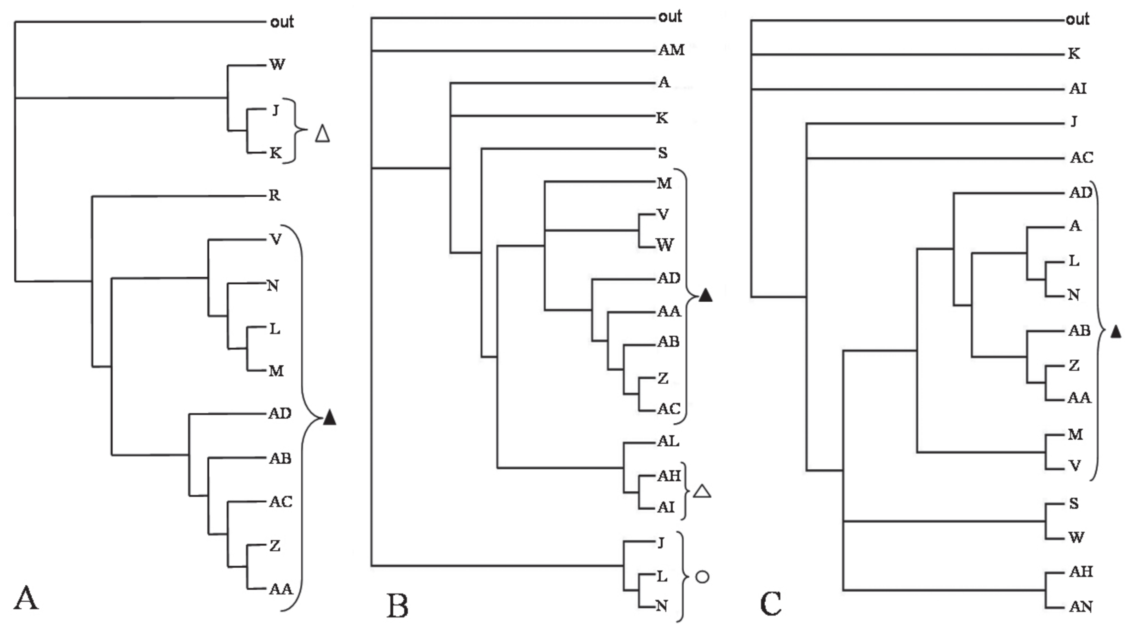

Fig. 6: Most parsimonious PAE trees for zooplankton, by basin. (A) Rotifera: number of trees = 21, length = 111, Consistency Index = 0.4505, Retention Index = 0.4602; (B) Copepoda: number of trees = 10, length = 45, Consistency Index = 0.4667, Retention Index = 0.662; (C) Cladocera: number of trees = 20, length = 40, Consistency Index = 0.5, Retention Index = 0.6825. Symbols for each clade correspond to those of Fig. 9.

Árboles PAE más parsimoniosos para zooplancton, por cuencas. (A) Rotifera: número de árboles = 21, largo = 111, índice de consistencia = 0,4505, índice de retención = 0,4602; (B) Copepoda: número de árboles = 10, largo = 45, índice de consistencia = 0,4667, índice de retención = 0,662; (C) Cladocera: número de árboles = 20, largo = 40, índice de consistencia = 0,5, índice de retención = 0,6825. El uso de los símbolos para cada clado se corresponde con la Fig. 9.

streams (Kristiansen 1996). On the other hand, dispersal mechanisms of zooplankton are often associated to resting stages (ephippia in cladocerans, diapausing eggs in rotifers, and criptobiosis in rotifers and copepod nauplii). Similar to algae, passive dispersal of zooplankton resting stages occurs mediated by wind, drift, and foretic transport through invertebrates and waterbirds (Bilton et al. 2001, Bohonak & Jenkins 2003, Havel & Shurin 2004). Dispersal determines at a large extent the distributional patterns of algae, rotifers and cladocerans; but distribution of copepods - being less vagile- is often determined by both vicariance and dispersal mechanisms (Rayner & Heeg 1994). On the other hand, fish disperse by active means and therefore their movements depend on the connectivity of the riparian network, as well as their life-history strategies. This explains the importance of vicariance for the current distribution of freshwater fish species (Anderson 1998, McDowell 2002, Cunha Ribeiro 2006).

Our results from endemicity analyses show that highly vagile groups due to their passive dispersal mechanisms such as algae, rotifers and cladocerans, exhibit at most two endemicity areas over the studied region. Intermediate levels of vagility associated to copepods agree with the finding of intermediate number of endemicity areas for this group, which are distributed along a latitudinal gradient. Fish exhibit the minimal relative vagility, and consistently they show the largest number of endemicity areas along the north-south gradient.

As a cautionary note, consider that some endemicity areas may have been defined by species that, in global sense, are widely distributed. Nevertheless, species that define endemicity areas within a region have a restricted area therein.

The results of our analyses reveal that latitude strongly influence distribution of some groups inhabiting Chilean freshwaters, and relative vagility among groups seems to influence the degree of metacommunity structure. Previous studies also support latitudinal patterns of distribution. For example, Henio (2001) found latitudinal gradient in species distribution of macrophytes, beetles, dragonflies, and stoneflies in the north hemisphere; Chengalath & Koste (1989, see also Segers 1996) found latitudinal variation in distribution patterns of rotifers in the circumpolar region; and Weckstroèm & Korhola (2001) found similar trends for diatoms in Fennoscandia.

In spite of the fact that dispersal abilities of organisms, particularly of planktonic ones, are important determinants of their current distribution (Fenchel et al. 1997, Finlay 2002, Fenchel & Finlay 2004), establishment on a given site strongly depends on the success of species in the front of abiotic constraints and natural enemies, as well as on their ability for exploiting local resources. On the other hand, new species can also appear by speciation mechanisms other than vicariance (Maidana et al. 2005, Pedrós-Alió 2006).

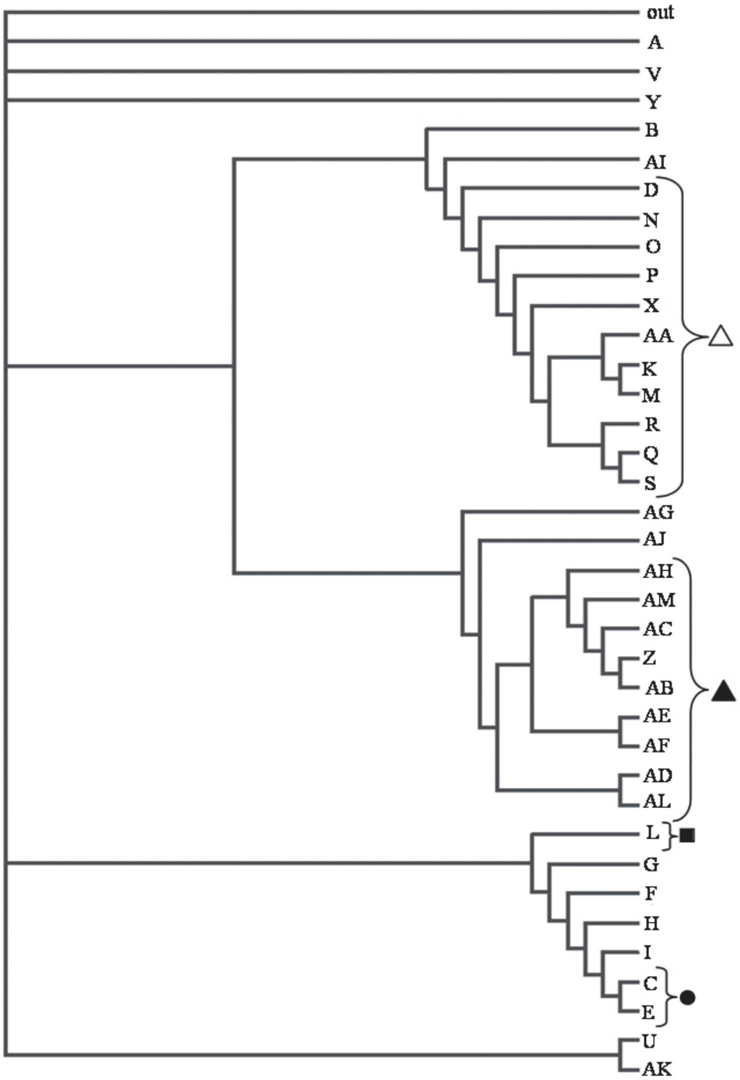

Fig. 7: Most parsimonious PAE trees for fish: number of trees = 705, length = 142, Consistency Index = 0.3028, Retention Index = 0.6610. Symbols for each clade correspond to those of Fig. 10.

Árboles PAE más parsimoniosos para peces: número de árboles = 705, largo = 145, índice de consistencia = 0,3028, índice de retención = 0,6610. El uso de los símbolos para cada clado se corresponde con la Fig. 10.

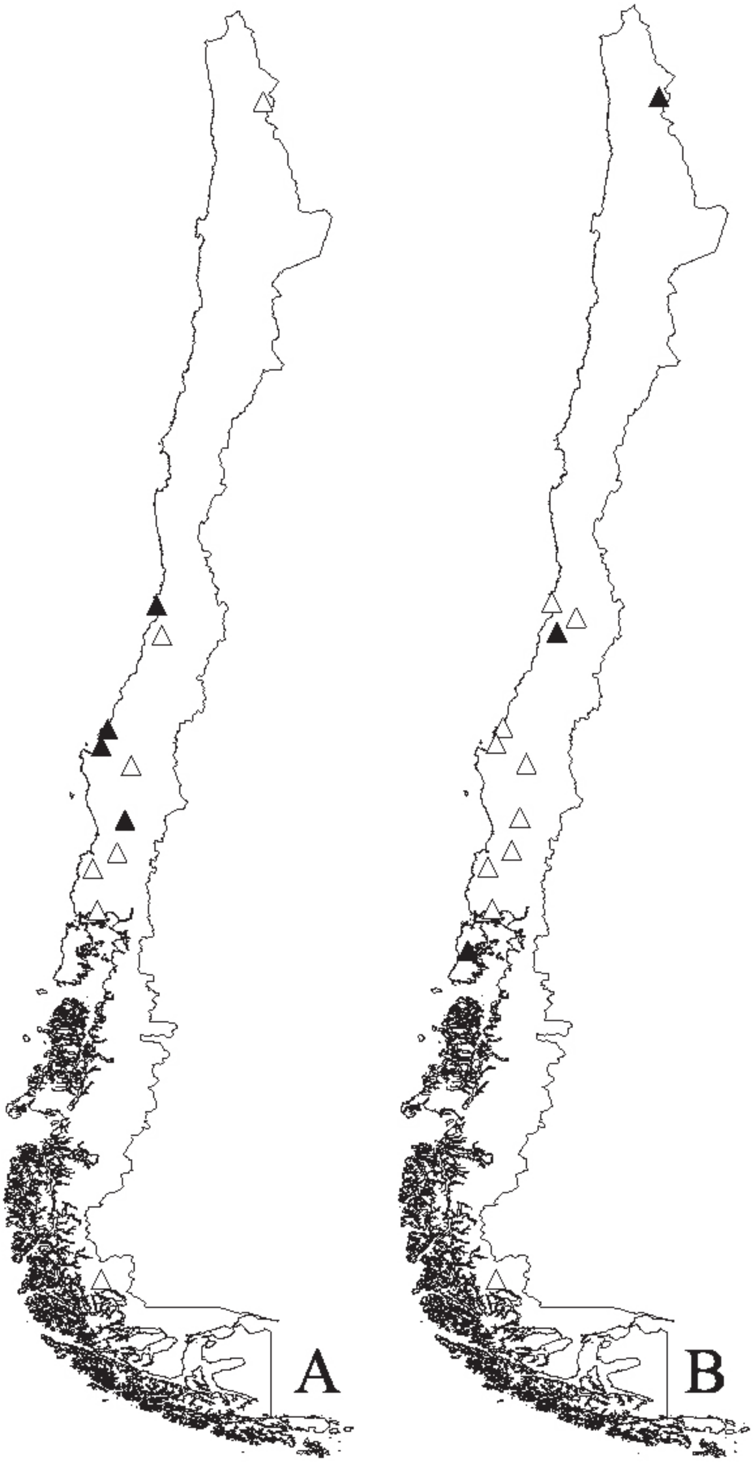

Fig. 8: Endemicity basins for phytoplankton. Different symbols correspond to different endemicity areas, according to Fig. 5. (A) Chlorophyceae: clades 1 and 2 are represented respectively by black and white triangles; (B) Bacillariophyceae: clades 1 and 2 are represented respectively by white and black triangles.

Cuencas de endemismo para fitoplancton. Símbolos diferentes representan diferentes áreas de endemismo. (A) Chlorophyceae: clados 1 y 2 representados respectivamente por triángulos negros y blancos; (B) Bacillariophyceae: clados 1 y 2 representados respectivamente por triángulos blancos y negros.

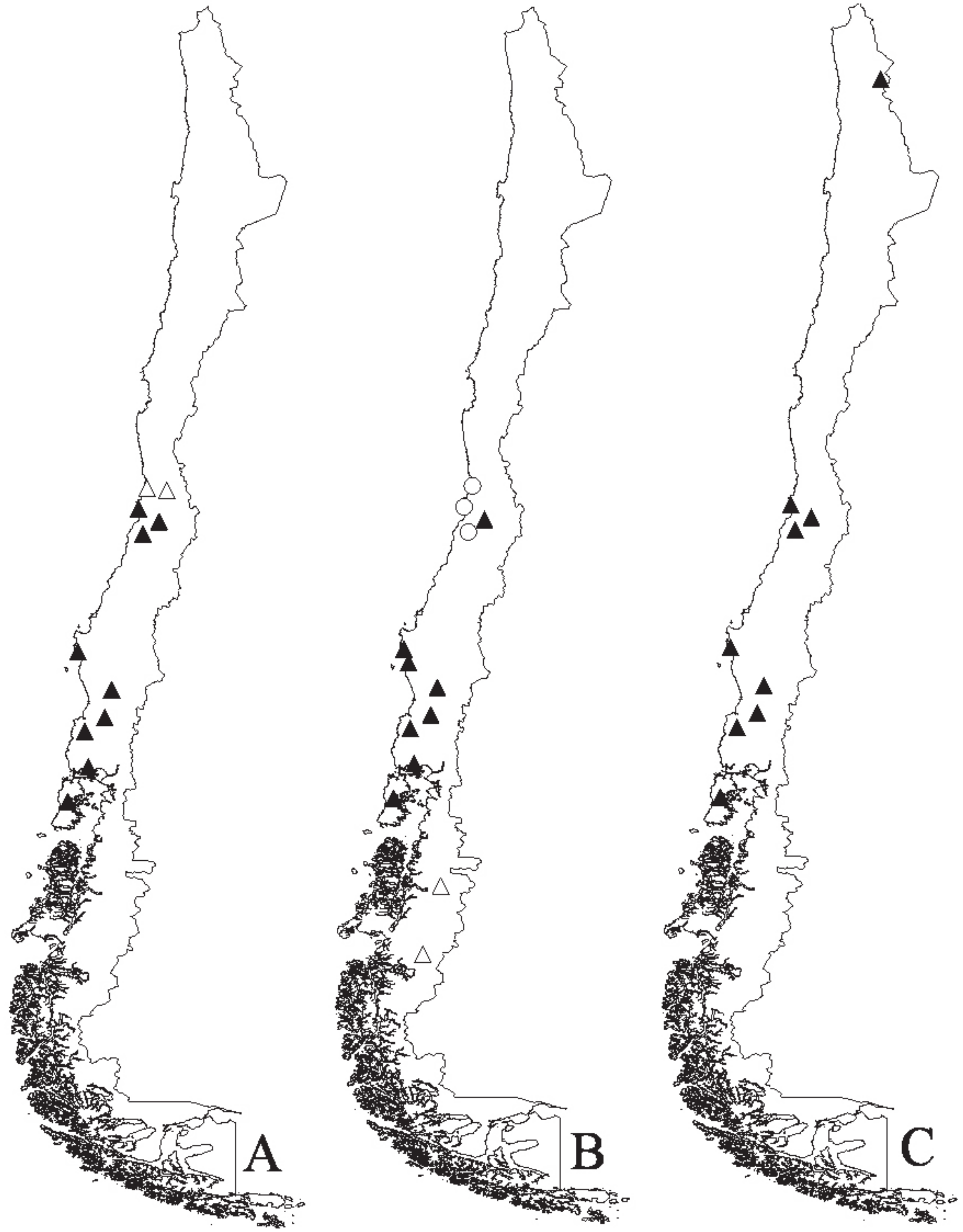

Fig. 9: Endemicity basins for zooplankton. (A) Rotifera: clades 1 and 2 are represented respectively by white and black triangles; (B) Copepoda: clades 1, 2, and 3 are represented respectively by black triangles, white triangles, and white circles; (C) Cladocera: black triangles show the only clade.

Cuencas de endemismo para zooplancton. (A) Rotifera: clados 1 y 2 representados respectivamente por triángulos blancos y negros; (B) Copepoda: clados 1, 2, y 3 representados respectivamente por triángulos negros, triángulos blancos y círculos blancos; (C) Cladocera: triángulos negros muestran un único clado.

Fig. 10: Endemicity basins for fish: clades 1-4 represented respectively by white triangles, black triangles, black circles, and a black square.

Cuencas de endemismo para peces; clados 1-4 representados respectivamente por triángulos blancos, triángulos negros, círculos negros, y un cuadrado negro.

In this way, local physical and chemical conditions of waters bodies such as light penetration, pH, nutrients availability, and lake morphometry among others, might exert significant effects on species richness and distribution (Gutiérrez-Aguirre & Suárez-Morales 2001, Duggan et al. 2002). Unfortunately, we lack of such information for the bulk of systems analyzed here, and consequently we were not able to test their influence. Nevertheless our results may serve as a start point for future research on metacommunity structure of regional freshwaters, as well as for focal hypothesis testing. Latitude is associated with climate and soil composition, which partially determine basin and lake morphometry, water chemistry, and temperature. Organisms' biology influences their life histories as well as dispersal abilities and hence colonization probabilities. At the same time, environmental features interacting with biological traits influence the structure and dynamics of populations and communities, which in turn affects local persistence. Therefore, from the rough relationships between freshwater biota and environmental variables shown here, future research on local systems could advance towards revealing the actual ecological mechanisms driving distributional patterns of species occurrences. Finally, our analysis also identified geographic areas of endemicity for each of the groups considered, and the species that define them. These results should be considered for decision making in the field of natural reserve design and conservation planning.

ACKNOWLEDGMENTS

We thank J.L. Fajardo for collecting an important amount of basal information. We also thank I. Vila, V. Montecino and L. Zúñiga for providing literature difficult to find. This work was supported by the Millennium Institute of Ecology and Biodiversity (ICM PO2-051), and grants CONICYT-PBCT ACT 34/2006 and MULT-05-04/2 from Dirección de Investigación of Universidad de Chile. Sergio Scott acknowledges financial support by MECESUP UCO-214 doctoral fellowship.

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Associate Editor: Horacio Zagarese
Received September 5, 2007; accepted November 17, 2007

APPENDIX 1

Lakes and basins analyzed, with their corresponding labels, hydrographic zone (I to VII from north to south), and references(*)

Lagos y cuencas analizados, con su correspondiente rótulo, zona hidrográfica (I a VII de norte a sur), y referencias(*)

Label		Basin	Lake	Zone	References
1	A	Altiplánica	Chungará	I	1-2-15-21-28
	B	Loa		I	
	C	Elqui		II	
	D	Limarí		II	
	E	Choapa		II	
	F	Coastal Choapa - Limarí		II	
	G	Quilimarí		II	
	H	Petorca		II	
	I	La Ligua		II	
2	J	Coastal La Ligua - Aconcagua	Catapilco	II	2-21
3	K	Aconcagua	Del inca	II	2-21-29
4	L	Coastal Aconcagua - Maipo	El plateado	II	2-21-31-32
5		Coastal Aconcagua - Maipo	Peñuelas	II	2-18-21-24
6		Coastal Aconcagua - Maipo	Lo Orozco	II	2-21
7		Coastal Aconcagua - Maipo	El peral	II	2
8	M	Maipo	Rungue	III	2-24
9		Maipo	Huechún	III	21
10		Maipo	Yeso	III	2-21
11		Maipo	Negra	III	2-21
12		Maipo	Aculeo	III	2-21-25-27
13	N	Rapel	Rapel	III	1-2-21-22
	O	Mataquito		III	
	P	Maule		III	
	Q	Itata		III	
14	R	Coastal Itata - Bío Bío	Lo Méndez	III	19-20
15	S	Bío Bío	Chica de San Pedro	III	19-20-26
16		Bío Bío	Grande de San Pedro	III	13-16
17		Bío Bío	Icalma	III	25
18		Bío Bío	Galletué	III	25
19	T	Coastal/islands Bío Bío - Carampangue	La Posada	IV	19-20
	U	Carampangue		IV	
20	V	Coastal Lebu - Paicaví	Lanalhue	IV	2-21-25
21	W	Coastal/isles Paicaví - Region boundary	Lleu-lleu	IV	2-21-25
	X	Imperial		IV	
	Y	Budi		IV	
22	Z	Toltén	Caburgua	IV	2-3-7-25
23		Toltén	Huilipilún	IV	2-31
24		Toltén	Pichilafquén	IV	2-21-31
25		Toltén	Villarrica	IV	2-3-9-21-25-31

APPENDIX 1 (continuation)

Label		Basin	Lake	Zone	References
26		Toltén	Quillehue	IV	2-21-31
27	AA	Valdivia	Calafquén	IV	2-21-25-31
28		Valdivia	Pellaifa	IV	2-21-25-31
29		Valdivia	Panguipulli	IV	2-21-25-31
30		Valdivia	Neltume	IV	2-21-25
31		Valdivia	Rinihue	IV	2-3-4-7-21-25-31
32		Valdivia	Pirehueico	IV	2-21-25
33	AB	Bueno	Ranco	IV	2-3-8-10-14-21-23-25-31
34		Bueno	Puyehue	IV	2-6-21-23-25-27-31
35		Bueno	Rupanco	IV	2-12-17-21-23-25-31
36		Bueno	Bonita	IV	2-21-31
37	AC	Basin/island Bueno - Puelo	Todos los Santos	IV	2-21-23-25-31
38		Basin/island Bueno - Puelo	Llanquihue	IV	2-5-21-23-25-31
39		Basin/island Bueno - Puelo	Chapo	IV	25
40	AD	Chiloé Island and surrounding	Cucao	IV	30
41		Chiloé Island and surrounding	Huillinco	IV	30
42		Chiloé Island and surrounding	Tarahuín	IV	30
43		Chiloé Island and surrounding	Natri	IV	30
44		Chiloé Island and surrounding	Tepuhueico	IV	30
	AE	Yelcho		V	
	AF	Palena and coastals - Region boundary		V	
	AG	Coastal/islands Palena - Aysén		V	
45	AH	Aysén	Riesco	V	25
46		Aysén	Polux	V	2-25
47		Aysén	Atravesado	V	2-25
48		Aysén	Elizalde	V	2-21-25
49	AI	Baker	Chiguay	V	2-21-25-29
50		Baker	General Carrera	V	2-25
51		Baker	Los Cisnes	V	29
	AJ	Pascua		VI	
	AK	Atlantic slope		VI	
52	AL	Coastal Seno Andrew - R Hollemberg	Nordenskjold	VI	25
53		Coastal Seno Andrew - R Hollemberg	Toro	VI	11-25
54	AM	Coastal Laguna Blanca, Seno Otway, Jerónimo channel, Magallanes	Patos Bravos	VI	21
55	AN	Tierra del Fuego	Lynch	VII	2

(*) 1: Andrew et al. (1989); 2: Araya & Zúñiga (1985); 3: Campos (1984); 4: Campos et al. (1987a); 5: Campos et al. (1988); 6: Campos et al. (1989); 7: Campos et al. (1987b); 8: Campos et al. (1992a); 9: Campos et al. (1983); 10: Campos et al. (1982); 11: Campos et al. (1994); 12: Campos et al. (1992b); 13: Cruces et al. (2001); 14: Domínguez & Zúñiga (1979); 15: Domínguez (1973); 16: Domínguez & Casanova (1989); 17: Donoso & Phinney (1988); 18: Olgín & Domínguez (1995); 19: Parra et al. (1976); 20: Parra & González (1975); 21: Ruiz & Bahamonde (1989); 22: Ruiz & Bahamonde (2003); 23: Schmid-Araya (1993); 24: Schmid-Araya & Zúñiga (1992); 25: Soto & Zúñiga (1991); 26: Urrutia et al. (2000); 27: Valero-Garcés et al. (2002); 28: Vila & Pardo (2003); 29: Villalobos (1994); 30: Villalobos et al. (2003); 31: Zúñiga & Domínguez (1977); 32: Zúñiga et al. (1985). Data for fish distribution were obtened from Acuña et al. (2005); Arratia (1981); Arratia (1983); Berra et al. (1995); Campos (1973); Campos (1985); Campos et al. (1996); Campos et al. (1998); Chang et al. (1978); Dyer (2000a); Dyer (2000b); Habit (2005); Habit et al. (2002); Habit et al. (2003); Habit et al. (2006); Keller & Soto (1998); Parra et al. (2003); Pequeño (1997); Rubílar (1994), Rubilar & Abad (1990); Vila et al. (1999a), (1999b); Villwock & Sienknecht (1996); Zunino et al. (1999)