

Latin American Journal of Aquatic Research

E-ISSN: 0718-560X

lajar@ucv.cl

Pontificia Universidad Católica de Valparaíso Chile

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Latin American Journal of Aquatic Research, vol. 43, núm. 1, 2015, pp. 186-200
Pontificia Universidad Católica de Valparaíso
Valparaíso, Chile

Available in: http://www.redalyc.org/articulo.oa?id=175036979016



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Research Article

Landscape composition as a determinant of diversity and functional feeding groups of aquatic macroinvertebrates in southern rivers of the Araucanía, Chile

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ABSTRACT. Changes in land use which directly or indirectly affect freshwater fauna constitute one of the principal anthropic factors which have caused world biological diversity to disappear rapidly during recent decades. This fauna includes aquatic benthic macroinvertebrates, organisms presenting temporal and spatial variation due to a variety of factors, one of which is the diverse food resources available in the rivers. To assess the effect of anthropic activities on this fauna, the distribution, abundance and characterisation of the functional feeding groups of aquatic macroinvertebrates were analysed, together with the physical and chemical variables in the environments of four coastal river basins of southern south-central Chile. A total of 104 taxa of macroinvertebrates were recorded, the principal component of the community being the Diptera (26 taxa). The abundance and richness of taxa were greater in summer and lower in winter. The most abundant species belong to the order Ephemeroptera and Plecoptera. Macroinvertebrates were affected by different land use: stations with less anthropic activity and greater altitude had higher macroinvertebrates abundance, while the lowest abundance was found at the lowest stations. The functional feeding groups which were most abundant spatially and temporally were the collector-gatherers and the shredders. The physical and chemical water quality variables proved to be of exceptional quality in all the stations. These results suggest that policies governing changes in land use in central and southern Chile should take into account the dramatic alterations that these changes impose on the macroinvertebrates community. Policies for biodiversity conservation should therefore focus on these small but important organisms in the north Patagonian region of South America, which is a hotspot of world diversity.

Keywords: diversity, macroinvertebrates, functional feeding groups, land use, Chile.

Composición del paisaje como determinante de la diversidad y de grupos funcionales alimentarios de macroinvertebrados acuáticos en ríos de la Araucanía, Chile

RESUMEN. Los cambios en el uso de suelo que afectan directa o indirectamente la fauna dulceacuícola, son uno de los principales factores antropogénicos por los cuales la diversidad biológica mundial está desapareciendo a elevadas tasas durante las últimas décadas. Dentro de esta fauna se encuentran los macroinvertebrados bentónicos acuáticos, organismos que varían temporal y espacialmente debido a diversos factores, uno de los cuales son los diversos recursos alimentarios disponibles en los ríos. Para esto, se analizó la distribución, abundancia, y caracterización de los grupos funcionales alimentarios de macroinvertebrados, y las variables físicas y químicas de cuatro cuencas costeras del centro-sur de Chile. Un total de 104 taxa de macroinvertebrados fueron registrados, siendo los dípteros (26 taxa) el componente principal de la comunidad. La abundancia y riqueza de taxa fue más conspicua en verano y menor en invierno. Las especies más abundantes correspondieron al orden Ephemeroptera y Plecoptera. Los macroinvertebrados fueron afectados por los diferentes usos de suelo: estaciones con menor actividad antropogénica y mayor altura tuvieron la mayor abundancia de macroinvertebrados, mientras que lo contrario ocurrió para la estación de menor altura. Los grupos funcionales alimentarios de recolectores y fragmentadores fueron los más abundantes espacial y tempo-

Corresponding editor: Sergio Palma

ralmente. Las variables físicas y químicas del agua, presentaron una calidad excepcional en todas las estaciones. Estos resultados sugieren que las políticas de cambio de uso de suelo en la zona centro-sur de Chile, deberían considerar los cambios dramáticos que causan sobre la comunidad de macroinvertebrados. Las políticas de conservación de biodiversidad, deberían enfocarse a estos pequeños pero importantes organismos en una zona *hotspot* de diversidad mundial como es la región norpatagónica de Sudamérica.

Palabras clave: diversidad, macroinvertebrados, grupos funcionales alimentarios, uso de suelo, Chile.

INTRODUCTION

Among the world's biogeographical regions, the ecosystems of the Andean region are among the most diverse on Earth (Udvardy, 1975; Myers et al., 2000; Olson et al., 2001; Morrone, 2006). The watersheds of these ecosystems have been affected in recent years by disturbances of anthropic origin, which directly or indirectly affect the functioning of aquatic systems (Barletta et al., 2010). Important environmental stressors are those generated by productive activities such as agriculture, deforestation, plantations of exotic species, industry and mine waste pollution (Roldán, 1999). Although these activities are recognised as the principal generators of the local economies of developing countries (Barbier, 2004), in many cases no control or management measures are applied for the protection of biological communities, and as a result biodiversity is disappearing rapidly (Mittermeier et al., 2011).

Benthic macroinvertebrates are one of the most important components of freshwater ecosystems. These are mainly immature stages of insects, most of which spend at least one stage of their life cycle in aquatic systems before emerging in the adult state (Hauer & Resh, 2006). This fauna plays an important role in aquatic systems since they are of vital importance in the nutrient cycle, acting as decomposers of organic matter, forming part of food chains and transferring energy to higher links; this makes them useful as bioindicators of organic pollution, etc. (Wallace & Webster, 1996). The seasonal and spatial distribution of these invertebrates in watercourses has been extensively debated (Summerville & Crist, 2003; Sporka et al., 2006). One area of discussion is the analysis of their life cycles; another concern is the principal factors which determine their diversity in lotic systems, i.e., disturbances to water flow, substrate structurecomposition, physical and chemical factors in the water and high variations in the ecotone (Wais, 1987; Evans & Norris, 1997; Bradley & Ormerod, 2001; Huttunen et al., 2012). The latter generates a great diversity of habitats, offering macroinvertebrates a wide range of food supply and thus allowing functional feeding groups (FFGs) to vary throughout the course of a river (Vannote et al., 1980).

The south-central region of Chile belongs to the Mediterranean forest biome (Olson et al., 2001), it possesses a great diversity of natural ecosystems. In particular, its coastal forests harbour great biological diversity, making it a world biodiversity hotspot (Myers et al., 2000; Valdovinos, 2006). A wide variety of ecosystems are also found in this geographical zone, such as plains, wetlands and mountain ranges, which contain the densest and most diverse evergreen forests of southern South America (Villagrán, 1991; Peña-Cortés et al., 2009). Historically this territory has experienced high levels of anthropic activity (Peña-Cortés et al., 2011) causing changes to the ecological landscape, especially the south-central region of Chile, which is one of the zones most affected by deforestation of native forest and its replacement by exotic species such as Pinus spp. and Eucalyptus spp. (4.1% annual loss of native forests) (Altamirano & Lara, 2010).

The purpose of this study is to relate the diversity of macroinvertebrates and functional feeding groups across different land uses in contrasting seasons of the year. The results of the study will also provide a taxonomic database of freshwater macroinvertebrates, which may be used in future conservation and biomonitoring studies in a zone of high biological diversity.

MATERIALS AND METHODS

Study area

The study area corresponded to four basins on the Pacific slope of the Araucanía, Chile (37°35'-39°37'S). The climate of this region is oceanic with Mediterranean influence, with an average annual precipitation between 1,200 and 1,600 mm (Di Castri & Hajek, 1976). The atmospheric data for temperature, rainfall and wind speed were also recorded, from the Climatological Yearbook 2010 for the city of Temuco (DGAC, 2011). The geomorphology varies from mountain systems to marine abrasion platforms. The maximum and minimum altitudes of the basins are 870 to -2 m above sea level (Peña-Cortés et al., 2011). Eleven sampling stations were selected and classified into six groups according to the land use of coastal basins of southern Chile (Peña-Cortés et al., 2009) (see Table 1). Based on the sizes of the four basins, the following stations were selected: one in the Danquil

Table 1. Altitude, type of vegetation and land use in the 11 sampling stations located in the coastal zone of the Araucanía Region (Chile) during the study period (based on Peña *et al.*, 2009). *Co: Coihue (*Nothofagus dombeyi*), Ra: Raulí (*Nothofagus alpina*), Te: Tepa (*Laureliopsis philippiana*), Ro: Roble (*Nothofagus obliqua*), Ca: Canelo (*Drimys winteri*), Myrt: Myrtaceae.

| Sampling station | Altitude (masl) | Type of vegetation | Land use |
|------------------|-----------------|-------------------------------|---|
| 1 | <50 | Dune-type | Beaches, forest plantation and herbaceous vegetation which advances into the dunes. |
| 2 | Up to 100 | Marshy, Ca, Myrt | Mixed use, dominant matrix arable and livestock farming. Regeneration and swamp forest. |
| 3, 4 | 100-250 | Evergreen, Ro-Ra-Co, Ca, Myrt | Mixed use, dominant matrix arable and livestock farming. Recent forest plantation and swamp forest. |
| 5, 6 | 200-400 | Evergreen, Ro-Ra-Co | Mixed use, arable and livestock farming matrix, dominant. Forest plantation and native forest. |
| 7, 8 | 400-600 | Evergreen, Ro-Ra-Co | Mixed use, arable and livestock farming matrix, forest plantation and dominant native forest. |
| 9, 10, 11 | >600 | Evergreen, Co-Ra-Te, Ro-Ra-Co | Native forest predominates. |

basin (Station 1), one in the Boyeco basin (Station 2), three in the Moncul basin (Stations 4, 6 and 8) and six in the Queule basin (Stations 3, 5, 7, 9, 10 and 11). All eleven studied streams are 3rd (St. 1, 4, 5 and 8), 4th (St. 2, 6, 7, 9 and 10) and 5th (St. 3 and 11) order, after Strahler (1957) (Fig. 1, Table 1).

Benthic macroinvertebrates sampling

The samples of freshwater benthic macroinvertebrates were collected by seasons (summer: January, autumn: April, winter: July and spring: November 2010). At each sampling station three replicates were taken with a Surber sampler (900 cm², 500 µm pore size) from riffles (the most common habitat type). The samples were fixed in situ with 90% ethanol and subsequently taken to the Benthos Laboratory of the Institute of Marine and Limnological Sciences, Universidad Austral de Chile, where they were separated and identified to the lowest possible taxonomic level under microscope and stereoscopic microscope. macroinvertebrates were then classified into seven Functional Feeding Groups (FFGs): shredders, collector-gatherers, collector-filterers, scrapers, predators, detritivores and parasites, using the criteria of Merrit & Cummins (1996), Miserendino & Pizzolon (2003) and Pérez et al. (2004).

Water sampling

Water samples were collected together with the macroinvertebrate samples during the morning (8-11 am); they were deposited in bottles and taken to the Analytical Chemistry Laboratory of the Institute of Chemistry and Natural Resources, Universidad de Talca, for determination of the following parameters: bio-chemical oxygen demand, suspended solids, dissolved oxygen, chlorides, sulphates, dissolved solids, nitrates and phosphates. All the methods of analysis were carried out according to the standard methods for the examination of water and waste-water (APHA, 2005). In addition, temperature, pH and conductivity were measured in situ. The physical and chemical variables were analysed to obtain a measurement of water quality for each sampling station, using the methodology employed by Fierro et al. (2012) according to the secondary environmental quality standard for the protection of Chilean continental waters (CONAMA, 2004).

Statistical analysis

Two way ANOVA analyses, with sampling stations and seasons as categorical variables as treatments, and abundance or species richness as response variables followed by *post hoc* tests when significant (Tukey test

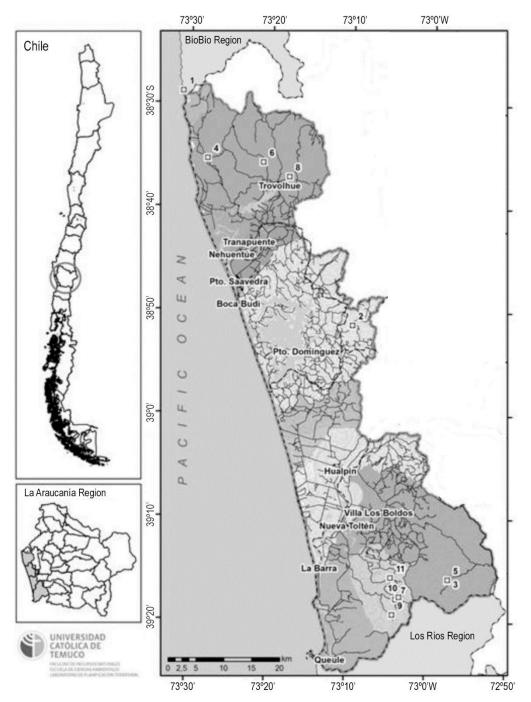


Figure 1. Study area showing the locations of the 11 sampling stations in the four river basins of the coastal zone of the Araucanía Region (Chile) during the study period.

P < 0.05) were used to assess differences in sampling stations uses and seasons. These analyses were conducted using the software package Statistica v7.0.

In addition, the biological data were compared considering the data of mean macroinvertebrates density (means for each season) per station. In order to avoid over estimating the abundance of infrequent taxa,

the data were first transformed to \log_{10} (x+1) to construct the Bray-Curtis similarity matrix (Bray & Curtis, 1957), from which a dendrogram was constructed using group average as criterion (999 permutations). The Simprof test was used on the dendrogram to identify statistically significant groups (P < 0.05). The similarity matrix was also analyzed

using a non-metric multidimensional scaling analysis (nMDS) as the ordination method, representing the similitude of the sampling stations in two dimensions, based on the abundance and composition of the macroinvertebrates communities.

The BIOENV (Bioenvironmental, Clarke Ainsworth, 1993) analysis was used to determine possible associations between the environmental variables and the biological data, using Spearman correlation. This analysis used the Bray-Curtis similitude data based on the abundance and richness of benthonic macroinvertebrates (transformed to $\log x+1$) and the physical and chemical parameters (land use, altitude, lotic order, temperature, conductivity, total dissolved solids, pH, dissolved oxygen biochemical oxygen demand, phosphates, nitrates, apparent colour, chlorides and sulphates); these data were first transformed to log_{10} (x+1) to normalise them. This analysis allowed us to evaluate the physical and chemical variables that were significantly related to the structure of the biota.

The structure of the macroinvertebrate community was analysed using Margalef's index, Pielou's evenness index and the Shannon-Weaver index (with base "e"). To represent the proportional abundance of each FFG, the cumulative values of the four seasons were used. All the above analyses were performed using PRIMER V.6 software (Clarke & Warwick, 1994).

RESULTS

Environmental parameters

Precipitation within the study area varied between 14.6 and 170.6 mm in April and June 2010 respectively; the minimum mean air temperature was 6.1°C in July and the maximum 14.7°C in January 2010. Finally, the wind varied between 3 and 11 knots in April-May and June 2010 respectively.

Following the secondary environmental quality standard for the protection of Chilean continental waters all the physical and chemical analyses indicated exceptional water quality for all stations sampled throughout the year (Table 3).

Macroinvertebrates community

A total of 104 taxa of aquatic benthic macroinvertebrates were collected; the dominant taxa were immature phases of insects throughout the study area and all year round. The most representative orders were Diptera (26 taxa), Trichoptera (19 taxa), Ephemeroptera (17 taxa), Plecoptera (15 taxa) and Coleoptera (8 taxa) (Appendix 1). The greatest abundance and richness of taxa across all sampling stations occurred in

summer, with 24,112 ind m⁻² (80 taxa, the most abundant species was *Meridialaris diguillina* (Leptophlebiidae, Ephemeroptera) with 5,004 ind m⁻²), followed by autumn with 22,363 ind m⁻² (79 taxa, the most abundant was *Limnoperla jaffueli* (Gripopterygidae, Plecoptera) with 3,533 ind m⁻²), spring with 14,907 ind m⁻² (63 taxa, *Andesiops torrens* (Baetidae, Ephemeroptera) was the most abundant species with 1,821 ind m⁻²) and winter with 9,141 ind m⁻² (64 taxa, the most abundant was again *L. jaffueli* with 2,406 ind m⁻²) (Appendix 1).

The highest mean density value during the whole year was recorded at land use native forest (station 10, Queule basin), especially during summer where peak abundance was found: 5,505 ind m⁻²; while the least abundant was recorded at forest plantation and herbaceous vegetation (station 1, Danquil basin), especially during autumn, where the lowest abundance was recorded: 399 ind m⁻² (Table 1, Fig. 2).

Significant differences in taxon richness (P < 0.001) and abundance (P < 0.001) of macroinvertebrates were found among sampling stations (land uses) and seasons (Table 2). According to the analysis of the classification and ordination of seasons based on abundance data in Appendix 1, which indicated five groups. Sites with more anthropic activities having significantly lower richness and abundance than the rest, and sampling stations located in dominant native forest having higher richness than mixed land use (native forest, forest plantation and livestock farming). This agreed with their spatial locations in the basins, namely stations 1 (Danguil basin), 2 (Boyeco basin) and 4 (Moncul basin), which were at the lowest altitude (<250 masl) and more affected by anthropic activity (Table 1, Fig. 3). In addition, station 10 (native forest predominate) presented the largest number of taxa (66), while the lowest number was obtained at station 1 (40 taxa), which coincided with Margalef's index of species richness. According to Pielou's evenness index (J) for the distribution of abundance for each taxa, all the stations presented dominant taxa (values greater than 0.55). Finally the Shannon-Wiener index values (H') ranged between 2.16 for station 5 (mixed use) and 2.91 for station 10 (Table 4).

Seasonally, Shannon-Weaver diversity values ranged between 2.82 and 1.21; maximum values were recorded at station 10 in autumn and spring, while minimum values were recorded at stations 2 and 5 (mixed land use), both in winter. Most stations showed values greater than 0.55 for Pielou's evenness index (J), indicating presence of dominant taxa; only three stations showed values less than 0.55: station 2 and 5 in winter and station 7 in spring. The highest values of Margalef's index of species richness were recorded in station 10 throughout the year (data not shown).

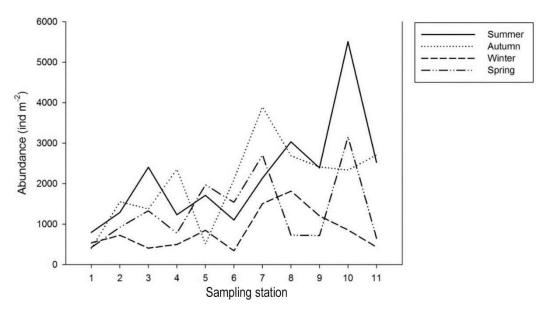


Figure 2. Seasonal variation in the abundance of macroinvertebrates recorded in the 11 sampling stations in the coastal zone of the Araucanía.

Table 2. F and *P*-values from two-way ANOVA of abundance and richness.

| Parameter | Sea | ason | Sta | ation | Season x Station | | | |
|-----------|--------|---------|-------|---------|------------------|---------|--|--|
| | F | P | F | P | F | P | | |
| Abundance | 51.340 | < 0.001 | 18.76 | < 0.001 | 6.15 | < 0.001 | | |
| Richness | 30.86 | < 0.001 | 19.21 | < 0.001 | 2.23 | < 0.001 | | |

The BIOENV procedure showed a strong relationship between community macroinvertebrate distribution and the measured environmental variables. The variables that best explained the multivariate relationships between the biotic and abiotic matrices were land use, altitude, temperature, suspended solids and nitrates, with a highly significant Spearman correlation ($\rho = 0.730$; P < 0.008).

Functional Feeding Groups (FFGs)

According to the FFGs, 31 taxa were assigned to collector-gatherers, 25 to predators, 18 to collector-filterers, 14 to shredders, 10 to grazers, 4 to detritivores and 2 to parasites (Appendix 1).

The most representative FFGs of all land use were collector-gatherers, which were dominant in eight stations: station 1 with 46.9% of the total community; station 3 with 56.4%; station 6 with 55.8%; station 7 with 48.4%; station 8 with 51.2%; station 9 with 56.1%; station 10 with 36.7% and station 11 with 54.4% of the total community. Shredders were somewhat dominant

in station 2 with 36.8% of the total community and station 5 with 44.9%; finally collector-filterers were dominant only in station 4 (41.6%). The predators presented consistently abundances below 25%, detritivores less than 5%, scrapers less than 2% and finally parasites less than 1% (Fig. 4).

Among seasons, collectors were dominant in summer, autumn and spring with 53.8%, 45.6% and 39.9% relative abundance, respectively. In winter two FFGs were dominant; the shredders (35.3%) and the collectors (34.2%). The representation of the other FFGs was less than 20% (Fig. 5).

DISCUSSION

Our main objective was to investigate the invertebrate community composition between different landscape compositions. This is a very significant factor influencing the freshwater macrofauna, affecting their abundance, spatial distribution, community parameters, etc. (Standford, 2006). We found a high taxonomic

total dissolved solids, SS: suspended solids, DO: dissolved oxygen, BOD5: biochemical oxygen demand, PO₄-3: phosphate, NO³: nitrate; CL: chlorides; SU: **Table 3.** Average (± SD) physical and chemical parameters of the water in the 11 sampling stations located in the coastal zone of the Araucanía Region. TDS: sulphates.

| OC SU | $g L^{-1}$) (mg L ⁻¹) | | | | | $11.2 \pm 2.3 1.0 \pm 0.3$ | | | | | $11.3 \pm 1.7 1.3 \pm 0.3$ | |
|--------------------|------------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------------------|-----------------|-----------------|-----------------|----------------|-----------------------------|-----------------|
| NO ³⁻ | | | | | | 40.6 ± 16.9 11.2 | | | | | | |
| PO ₄ -3 | | | | | | 71.7 ± 31.6 40 | | | | | | |
| BOD5 | | | | | | 1.8 ± 0.1 | | | 7.7 | 0.1 | | 7.4 |
| DO | $(mg L^{-1})$ | 10.9 ± 1.1 | 10.6 ± 1.3 | 8.2 ± 5.0 | 10.7 ± 1.1 | 8.3 ± 5.1 | 11.0 ± 1.2 | 10.9 ± 1.0 | 11.1 ± 1.2 | 11.2 ± 1.1 | 11.0 ± 1.3 | 10.6 ± 0.8 |
| SS | $(mg L^{-1})$ | 7.5 ± 3.9 | 12.7 ± 5.5 | 5.5 ± 4.9 | 8.6 ± 5.4 | 4.3 ± 1.6 | 5.8 ± 1.2 | 2.4 ± 1.9 | 7.0 ± 8.6 | 1.8 ± 0.8 | 3.0 ± 1.3 | 6.3 ± 3.3 |
| Пч | пд | 6.8 ± 0.3 | 6.9 ± 0.2 | 6.7 ± 0.1 | 6.7 ± 0.3 | 6.8 ± 0.2 | 6.9 ± 0.3 | 6.8 ± 0.1 | 6.8 ± 0.3 | 7.0 ± 0.3 | 6.7 ± 0.3 | 6.8 ± 0.1 |
| LDS | $(mg L^{-1})$ | 49.4 ± 17.6 | 37.9 ± 19.5 | 24.1 ± 12.4 | 29.4 ± 14.9 | 23.6 ± 11.8 | 35.0 ± 12.9 | 24.1 ± 12.9 | 27.1 ± 13.5 | 18.0 ± 9.3 | 16.1 ± 8.3 | 26.4 ± 13.8 |
| Conductivity | $(\mu S \text{ cm}^{-1})$ | 57.8 ± 1.0 | 53.4 ± 1.7 | 34.1 ± 2.1 | 40.9 ± 0.3 | 33.4 ± 1.3 | 40.2 ± 2.6 | 33.9 ± 0.9 | 44.2 ± 9.3 | 24.7 ± 0.8 | 22.8 ± 1.3 | 37.3 ± 1.9 |
| Temperature | (°C) | 10.4 ± 3.1 | 10.6 ± 3.6 | 12.3 ± 3.2 | 10.3 ± 3.0 | 12.4 ± 3.8 | 10.8 ± 3.2 | 11.3 ± 2.7 | 11.0 ± 3.4 | 10.4 ± 4.0 | 10.5 ± 3.6 | 11.0 ± 2.7 |
| Stations | Stations | 1 | 7 | ю | 4 | 5 | 9 | 7 | ∞ | 6 | 10 | 11 |

diversity of aquatic benthic macroinvertebrates in coastal basins of south central Chile, consistent with the exceptional quality of the water sampled in the rivers.

In the basins located in the coastal zone of the Araucanía Region, macroinvertebrate assemblages were mainly affected by basin-related variables (land use, altitude) and water (temperature, suspended solids and nitrates). Similar trends were found in other studies (Miserendino & Masi, 2010; Egler et al., 2012) which indicate that macroinvertebrate fauna can be altered by land use practices (e.g., agriculture, forest plantations). Macroinvertebrates showed significant differences between stations and seasons responding to this gradient; sites with strong anthropogenic pressures had lower abundances than low impacted sites. The Queule basin, specifically station 10 (high altitude), presented the greatest richness and abundance of the whole study area, due to the high proportion of native forest, roble (Nothofagus obliqua), raulí (N. alpina) and coihue (N. dombeyi), and the low proportion of the matrix consisting of farmland and forestry plantation (Peña-Cortés et al., 2009). In the opposite situation, the stations 1 (Danquil basin), 2 (Boyeco basin) and 4 (Moncul basin), reflected in the cluster analysis which assigned them to separate groups with specific species ensembles. These stations were characterised by low altitude and by being subjected to strong pressures of use, e.g., for agricultural, forestry and tourism activities (Peña-Cortés et al., 2009). The geomorphological slopes at these stations are almost zero, and therefore there are zones with greater deposits (i.e., potamon environments). This agrees with the findings of Brown & Brussock (1991) and Buffagni & Comin (2000) who reported lower richness and abundance in the macroinvertebrate community on pools habitats. The lowest values for Shannon's diversity index were obtained at station 5 (Queule basin), specifically in autumn when only 23 taxa and 510 ind m⁻² were recorded. This was due in part to disturbance of the bed by the construction of a bridge, which increased the concentration of suspended solids in the water; according to Suren et al. (2005) and Billota & Brazier (2008) this is one of the principal factors influencing the presence of aquatic biota. However this situation was reversed in the later samples, evidence of rapid recovery of the habitat, possibly by colonisation from tributaries (Rice et al., 2001).

Some taxa, especially families, tend to present wide geographical distributions, since they tolerate greater changes in the environment and are therefore generally less sensitive to pollution (e.g., organic) (Winterbourn et al., 1981). The species Meridialaris diguillina (Leptophlebiidae), Limnoperla jaffueli (Gripopterygidae) and Andesiops torrens (Baetidae) were the most

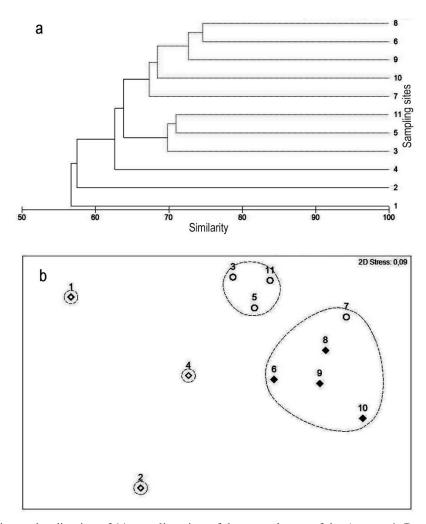


Figure 3. Classification and ordination of 11 sampling sites of the coastal zone of the Araucanía Region, through a) cluster analysis and b) non-metric multidimensional scaling (nMDS), obtained from a Bray & Curtis dissimilarity matrix of abundance data (ind m^{-2}). The groups were defined using the Simprof test (P < 0.05). Axes appear without legend because they are relative scales.

Table 4. Number of taxa (S), total population abundance (ind m^{-2}) ($n \pm SD$), richness of species according to Margalef (d), Pielou's Evenness index (J) and Shannon-Weaver Diversity index (H') of the macroinvertebrates in the 11 sampling stations in the coastal zone of the Araucanía Region averaged across all seasons.

| Station | S | n | d | J | Η´ |
|---------|----|------------------|-------|--------|-------|
| 1 | 40 | 2154 ± 181 | 5.081 | 0.7262 | 2.679 |
| 2 | 42 | 4479 ± 371 | 4.877 | 0.691 | 2.581 |
| 3 | 45 | 5514 ± 818 | 5.107 | 0.646 | 2.458 |
| 4 | 52 | 4857 ± 819 | 6.008 | 0.697 | 2.754 |
| 5 | 48 | 5037 ± 693 | 5.513 | 0.558 | 2.160 |
| 6 | 50 | 5079 ± 745 | 5.742 | 0.689 | 2.694 |
| 7 | 60 | 10239 ± 1016 | 6.389 | 0.669 | 2.740 |
| 8 | 47 | 8256 ± 1028 | 5.101 | 0.658 | 2.532 |
| 9 | 48 | 6719 ± 856 | 5.333 | 0.686 | 2.654 |
| 10 | 66 | 11877 ± 1941 | 6.928 | 0.696 | 2.917 |
| 11 | 41 | 6312 ± 1206 | 4.571 | 0.591 | 2.195 |

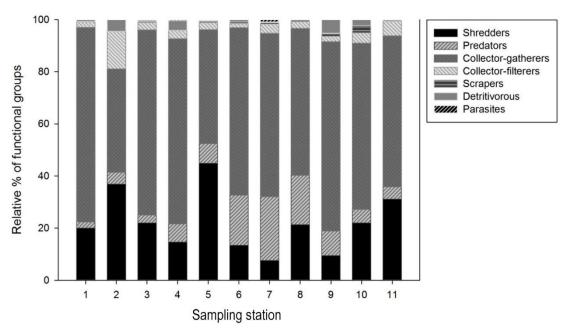


Figure 4. Station variation in the relative abundance of the functional feeding groups recorded in the 11 sampling stations in the coastal zone of the Araucanía Region.

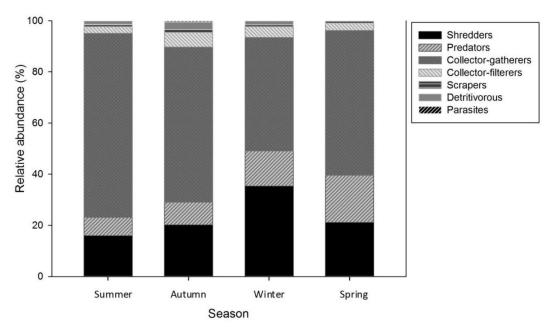


Figure 5. Average seasonal variation in the relative abundance of the different Functional Feeding Groups (FFGs) recorded in the 11 sampling stations located in the coastal zone of the Araucanía Region.

abundant throughout the study area. These same taxa have been described as a principal component of the macroinvertebrate community in central and southern rivers of Chile (Campos *et al.*, 1984; Habit *et al.*, 1998; Guevara-Cardona *et al.*, 2006; Fierro *et al.*, 2012), and indeed in other South American rivers (Miserendino, 2001; Miserendino & Pizzolon, 2003; Molina *et al.*, 2008; Kleine *et al.*, 2011). All these situations occurred

in undisturbed rivers with lotic and *rhithron* environments (*i.e.*, sectors with great slope, high current velocities, stable low temperatures, high concentration of oxygen, etc.), properties that would tend to favour the presence of these taxa.

Various authors (e.g., Linke et al., 1999; Huttunen et al., 2012) propose performing at least one year of sampling in order to avoid underestimating taxon

richness for use in bio-assessments. This is because the macroinvertebrate community changes not only due to anthropic effects, but also due to seasonal and/or biological changes. The seasonal changes are mainly the result of different life cycles (*i.e.*, univoltine or bivoltine) which are correspondingly synchronized (Cayrou & Céréghino, 2005).

In the study area, the physical and chemical variables of the water presented no great variations attributable to anthropic activities in the basins, so any variation in the macroinvertebrates was due especially to their own seasonality (Figs. 2-5), with a greater abundance present in summer than in winter. Similar results were reported by Marchant (1988) in Australia and by Miserendino & Pizzolon (2003) in Argentina, with the highest abundance occurring in summer and the lowest in winter. The temperature and the hydrological regime have been mentioned as dominant factors in the seasonal structuring of the macroinvertebrate community (Hawkins & Sedell, 1981; Statzner & Higler, 1986; Beltrán et al., 2011), meaning that in dry seasons (low water) macroinvertebrates have greater possibilities of colonising the river area, since the habitat becomes homogenised and their densities and specific richness can increase (Poff & Ward, 1989; Poff et al., 1997; Reynaga & Dos Santos, 2013). In rainy seasons such as winter, when the water flow increases due to the high level of precipitation, macroinvertebrates are transported downstream by dramatic drifts (Lancaster, 2008; Gualdoni & Oberto, 2012). Furthermore, the increased flow causes the habitat to fragment, producing heterogeneous zones within the same river, which would favour certain FFGs (Newbury & Bates, 2006).

Seasonal differences were observed in FFGs. The collector-gatherers were more conspicuous in summer, autumn and spring (>39%), while in winter they shared dominance with the shredders (34% and 35% respectively). The shredders are responsible for processing and reducing allochthonous detritus (e.g., leaves and remains of wood) to small particles (<1 mm), which are subsequently "collected" as food by the collector-gatherers; both groups use leaves as a substrate for adherence and refuge (Cummins, 1974; Bird & Kaushik, 1985; Cummins et al., 1989). This group colonises the leaves which fall into rivers and accumulate there in small reservoirs, so their abundance will depend on the season when the forest leaves fall (Lake et al., 1985). In our study, the shredders were most abundant during rainy seasons, which is when the highest leaf fall occurs of both deciduous (i.e., roble and raulí) and evergreen species (i.e., coihue, tepa, Eucalyptus) in the study area. This same situation was recorded by Miserendino &

Pizzolon (2004) in southern Argentina; they recorded scrapers and shredders in higher abundance in autumn and winter seasons (literfall period), where fine and coarse organic matter was more abundant, Later, when wind and precipitations decrease (Fig. 2), the input of allochthonous organic matter tends to diminish; consequently the abundance of shredders decreases while that of collector-gatherers starts to increase, reaching its peak in the drier seasons (Roeding & Smock, 1989).

According to the continuum river concept, low order rivers should contain mainly collector-gatherers and shredder organisms (Vannote et al., 1980). This situation has been found both in this study and in other places, e.g., Winterbourn et al. (1981) in New Zealand, Figueroa et al. (2000) in Chile and Callisto et al. (2001) in Brazil. Nevertheless, this is not a generalized pattern, since Miserendino & Pizzolon (2003) in Argentinean Patagonia, Lake et al. (1985) in Australia and Duncan & Brusven (1985) in Alaska recorded only collectors as the most abundant group in their study areas. Despite this difference, the marked dominance of collectorgatherers and shredders in the study area shows that these two groups play an important role in processing organic matter in coastal rivers of low-medium order $(3^{rd}, 4^{th} \text{ and } 5^{th})$ of this region.

Any disturbance in the land use in these basins has the potential to affect the biodiversity of aquatic ecosystems, due to the close relation between the terrestrial and aquatic components (Clarke et al., 2008). As a result, the diversity of fauna inhabiting these ecosystems continues to be threatened worldwide (Moss, 2000; Vieira et al., 2008). One of the most diverse groups found in these ecosystems is aquatic benthic macroinvertebrates, which have been greatly reduced and in some cases become extinct throughout the world (Lydeard et al., 2004, Poole & Downing, 2004; Strayer, 2006). Conservation strategies in aquatic systems in South America, and Chile in particular as a biodiversity hotspot, must therefore give special consideration to aquatic invertebrate fauna. This study therefore contributes to a better knowledge of the spatial distribution of benthic macroinvertebrates of these ecosystems.

ACKNOWLEDGEMENTS

The authors would like to thank Raúl Arriagada and Eduardo Fernández for their help in field work, and Dr. Lafayette Eaton for his help checking this manuscript. This study was financially supported by FONDECYT Projects 1080317 and 1110798. P. Fierro receives funding from a grant from the Comisión de Ciencia y Tecnología de Chile (CONICYT) for Master's degree studies in Chile.

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Appendix 1. List of taxa of macroinvertebrates recorded in the 11 sampling stations (mean of 4 seasons). The population abundance (ind m⁻²) and Functional Feeding Group (FFG) for each taxa are also indicated. S: shredders, CG: collectorgatherers, CF: collector-filterers, SC: scrapers, P: predators, D: detritivorous and PA: parasites.

| | Sampling station | | | | | | | | | | | |
|---|------------------|---------|------------|------------|------------|-----------|----------|-----------|-----------|----------|-----------|-----------|
| | FFG | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Plecoptera | | | | | | | | | | | | |
| Austronemoura chilena | S | 30 | 9 | 0 | 39 | 0 | 15 | 3 | 9 | 5 | 24 | 6 |
| Neofulla sp. | S | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| Diamphipnoa helgae | S | 0 | 0 | 3 | 3 | 0 | 3 | 24 | 21 | 5 | 51 | 9 |
| Diamphipnopsis samali | S | 3 | 0 | 9 | 0 | 6 | 0 | 123 | 3 | 90 | 852 | 9 |
| Inconeuria porteri | P | 3 | 21 | 3 | 15 | 0 | 0 | 9 | 6 | 10 | 57 | 12 |
| Kempnyella genualis | P | 6 | 0 | 0 | 3 | 9 | 0 | 12 | 0 | 24 | 0 | 3 |
| Pictetoperla gayi | P | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| Klapopteryx armillata | S | 0 | 54 | 3 | 0 | 12 | 33 | 309 | 81 | 177 | 1128 | 81 |
| Penturoperla barbata | S | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| Ceratoperla schwabei | S S | 0 | 0 | 3 | 0 | 0 | 3 570 | 0 | 0 | 0 | 0 | 3 |
| Limnoperla jaffueli | S | 312 | 1008 15 | 750 0 | 186 294 | 2226 0 | 9 | 210 12 | 1173 3 | 313 5 | 336 48 | 1419 0 |
| Antarctoperla michaelseni Notoperlopsis femina | S | 15 | 3 | 444 | 30 | 3 | 6 | 87 | 435 | 21 | 111 | 378 |
| Pelurgoperla personata | S | 48 | 561 | 0 | 135 | 12 | 6 | 0 | 0 | 9 | 15 | 63 |
| Neuroperlopsis patris | S | 3 | 0 | 0 | 21 | 0 | 33 | 6 | 36 | 15 | 21 | 0 |
| Ephemeroptera | 5 | J | V | V | 21 | v | 55 | Ü | 50 | 15 | | V |
| Andesiops peruvianus | CG | 450 | 573 | 414 | 312 | 690 | 273 | 438 | 594 | 152 | 528 | 645 |
| Andesiops torrens | CG | 117 | 6 | 126 | 87 | 69 | 846 | 2322 | 747 | 1230 | 2238 | 234 |
| Chiloporter eatoni | P | 0 | 0 | 9 | 0 | 42 | 3 | 21 | 15 | 14 | 48 | 18 |
| Chaquihua bullocki | P | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| Hapsiphlebia anastomosis | CG | 0 | 0 | 21 | 6 | 9 | 66 | 159 | 330 | 55 | 0 | 6 |
| Meridialaris diguillina | CG | 225 | 39 | 1266 | 609 | 747 | 1005 | 906 | 2058 | 1728 | 993 | 2181 |
| Meridialaris chilooense | CG | 96 | 63 | 0 | 0 | 15 | 0 | 342 | 0 | 0 | 0 | 3 |
| Nousia sp. | CG | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Nousia maculata | CG | 0 | 174 | 15 | 63 | 63 | 30 | 6 | 36 | 0 | 54 | 0 |
| Nousia delicata | CG | 0 | 0 | 0 | 0 | 0 | 0 | 102 | 6 | 14 | 36 | 9 |
| Penaphlebia sp. | CG | 21 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Penaphlebia chilensis | CG | 12 | 237 | 12 | 81 | 24 | 228 | 12 | 111 | 443 | 207 | 0 |
| Penaphlebia vinosa | CG | 0 | 0 | 0 | 0 | 0 | 36 | 0 | 0 | 0 | 0 | 0 |
| Massarttellopsis irrarazavali | CG | 0 | 0 | 0 | 0 | 3 | 0 | 246 | 0 | 0 | 0 | 0 |
| Siphonella gutatta | CG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 3 | 0 |
| Caenis chilensis | CG | 0 | 0 | 0 | 3 | 0 | 0 | 0 9 | 0 | 0 | 0 | 0 |
| Murphyella needhami | CF | 0 | 0 | 0 | U | 0 | 3 | 9 | 0 | 26 | 111 | U |
| Trichoptera | CG | 0 | 42 | 0 | 93 | 9 | 9 | 3 | 0 | 38 | 33 | 39 |
| Ecnomidae indeterminate Austrotinodes sp. | CG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Hydrobiosidae indeterminate | P | 6 | 12 | 9 | 177 | 27 | 57 | 15 | 177 | 0 | 33 | 24 |
| Rheochorema sp. | P | 0 | 0 | 6 | 0 | 21 | 0 | 18 | 0 | 0 | 0 | 33 |
| Hydroptilidae indeterminate | SC | 0 | 0 | 12 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hydroptila sp. | CG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 | 0 |
| Metrichia sp. | CG | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 6 | 3 | 0 | 0 |
| Neotrichia sp. | CG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 15 | 0 |
| Neotrichia chilensis | CG | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| Polycentropus sp. | P | 0 | 0 | 0 | 0 | 0 | 6 | 3 | 0 | 0 | 6 | 0 |
| Parasericostoma sp. | S | 3 | 0 | 0 | 3 | 3 | 0 | 9 | 0 | 0 | 27 | 0 |
| Smicridea sp. | CF | 21 | 522 | 18 | 18 | 81 | 30 | 9 | 123 | 70 | 198 | 9 |
| Smicridea annulicornis | CF | 0 | 93 | 42 | 69 | 21 | 12 | 147 | 0 | 0 | 33 | 168 |
| Leptoceridae indeterminate | SC | 0 | 3 | 3 | 3 | 0 | 3 | 3 | 3 | 0 | 6 | 0 |
| Oecetis sp. | SC | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 |
| Brachysetodes sp. | SC | 0 | 0 | 0 | 0 | 6 | 0 | 18 | 27 | 9 | 111 | 0 |
| Triplectides sp. | S | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Eosericostoma sp. | CG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Dolophilodes sp. | S | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| Coleoptera | D | , | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Coleoptera indeterminate | P | 6 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| Austrolimnius sp. | CG | 0 75 | 0 | 0 1104 | 15 270 | 0 | 0 | 3 | 3 | 0 94 | 0 189 | 0 |
| Austrolimnius sp. | CG CG | 75 0 | 6 0 | 1194 12 | 12 | 162 3 | 315 | 366 0 | 330 0 | 0 | 3 | 318 |
| Luchoelmis sp. Tychepsephenus felix | SC | 0 | 3 | 6 | 0 | 6 | 36 | 24 | 12 | 73 | 3 141 | 9 |
| Haliplidae indeterminate | SC | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Haliplus sp. | SC | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 |
| Gyrinidae indeterminate | P | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| OJIIII auc III acteriiii iate | | U | J | J | U | U | J | J | 9 | J | 0 | 5 |

Continuation

| | FFG Sampling station | | | | | | | | | | | |
|---------------------------------|----------------------|-----|-----|-----|------|-----|-----|------|------|-----|------|-----|
| | TTU | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Diptera | | | | | | | | | | | | |
| Stilobezzia sp. | P | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 3 | 0 | 3 | 0 |
| Alluadomyia sp. | P | 0 | 3 | 9 | 6 | 15 | 6 | 39 | 12 | 42 | 12 | 3 |
| Tipulidae indeterminate | P | 3 | 3 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 21 | 0 |
| Tipula sp. | P | 0 | 0 | 0 | 3 | 0 | 0 | 75 | 6 | 93 | 15 | 0 |
| Hexatoma sp. | P | 3 | 6 | 30 | 12 | 45 | 432 | 2190 | 1176 | 133 | 183 | 39 |
| Atherix sp. | P | 0 | 75 | 0 | 3 | 12 | 51 | 0 | 114 | 245 | 108 | 0 |
| Limonia sp. | P | 18 | 12 | 42 | 84 | 48 | 378 | 45 | 45 | 39 | 87 | 15 |
| Empididae indeterminate | P | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 |
| Hemerodromia sp. | CG | 3 | 21 | 36 | 6 | 6 | 12 | 45 | 3 | 5 | 0 | 0 |
| Psychodidae indeterminate | CG | 0 | 0 | 3 | 3 | 0 | 0 | 6 | 0 | 0 | 3 | 0 |
| Blephabericeridae indeterminate | SC | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| Simulium sp. | CF | 24 | 24 | 90 | 42 | 21 | 24 | 162 | 84 | 29 | 111 | 162 |
| Gigantodax sp. | CF | 0 | 0 | 0 | 15 | 9 | 3 | 27 | 3 | 9 | 0 | 6 |
| Arauchnephioides sp. | CF | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dicrotendipes sp. | CF | 0 | 0 | 0 | 27 | 18 | 0 | 0 | 0 | 0 | 0 | 0 |
| Corynoneura sp. | CG | 42 | 6 | 132 | 0 | 57 | 30 | 165 | 21 | 257 | 42 | 138 |
| Thienemaniella sp. | CG | 15 | 0 | 12 | 12 | 123 | 111 | 660 | 57 | 128 | 450 | 0 |
| Pentaneura sp. | CG | 12 | 3 | 15 | 42 | 33 | 9 | 162 | 48 | 38 | 9 | 6 |
| Paratrichocladius sp. | CG | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 |
| Rheotanytarsus sp. | CG | 0 | 3 | 162 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 |
| Tanytarsus sp. | CG | 39 | 0 | 69 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| Eukiefierella sp. | CG | 186 | 222 | 273 | 1305 | 111 | 57 | 108 | 171 | 58 | 690 | 27 |
| Orthocladius sp. | CG | 231 | 366 | 90 | 423 | 24 | 84 | 243 | 54 | 611 | 1767 | 24 |
| Lopescladius sp. | CG | 69 | 3 | 51 | 54 | 30 | 147 | 120 | 75 | 15 | 252 | 33 |
| Coelotanypus mendax | CG | 0 | 0 | 9 | 6 | 0 | 0 | 3 | 3 | 0 | 15 | 0 |
| Symbiocladius wygodzinskyi | PA | 0 | 0 | 12 | 0 | 12 | 0 | 9 | 0 | 0 | 0 | 3 |
| Odonata | ъ. | | | 2 | | | | | | _ | | |
| Neogomphus sp. | P | 0 | 0 | 3 | 0 | 21 | 0 | 0 | 0 | 5 | 0 | 0 |
| Megaloptera | | | | | | | | | | _ | - | |
| Protochauliodes sp. | P | 3 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 5 | 6 | 6 |
| Decapoda | | | | | | | | | | | | |
| Aegla sp. | P | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 |
| Aegla araucaniensis | P | 0 | 15 | 54 | 36 | 129 | 30 | 48 | 0 | 8 | 15 | 135 |
| Aegla manni | P | 0 | 54 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Isopoda | 00 | | | 2 | | , | 0 | | | | 2 | |
| Heterias exul | CG | 0 | 0 | 3 | 15 | 6 | 0 | 0 | 0 | 0 | 3 | 0 |
| Amphipoda | 00 | 2 | 2 | 0 | 0 | 0 | | 0 | 0 | 0 | 10 | 0 |
| Hyalella sp. | CG | 3 | 3 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 18 | 0 |
| Hyalella costera | CG | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Paracorophium hartmannorum | CG | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Trombodiforme | n | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 10 | , |
| Hydracarina | P | 3 | 0 | 0 | 0 | 9 | 3 | 0 | 0 | 9 | 12 | 6 |
| Araneae | n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| Araneae indeterminate | P | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Collembola | CC | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| Collembola indeterminate | CG | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Prosobranchia | 00 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 20 | 0 |
| Littoridina cumingi | SC | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 30 | 0 |
| Bassomatophora | 90 | 0 | 0 | 0 | 2 | 21 | 0 | 0 | 0 | 0 | 42 | 2 |
| Chilina dombeyana Tubificida | SC | 0 | 0 | 0 | 3 | 21 | 0 | 0 | 0 | 0 | 42 | 3 |
| | D | 12 | 120 | 20 | 174 | 6 | 20 | 21 | 1.5 | 216 | 10 | 24 |
| Tubifex sp. | D | 12 | 129 | 30 | 174 | 6 | 39 | 21 | 15 | 346 | 48 | 24 |
| Haploxatida | D | 0 | (2) | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Naididae indeterminate | D | 0 | 63 | 0 | 6 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lumbriculida | Ъ | 0 | 2 | | 0 | ^ | 2 | 0 | 2 | 2 | 222 | 2 |
| Lumbriculidae indeterminate | D | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 222 | 3 |
| Tricladida | D | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dugesia sp. | D | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Temnocephalida | D A | 0 | 2 | 0 | 10 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 |
| Temnocephala chilensis | PA | 0 | 3 | 0 | 18 | 0 | 0 | 84 | U | 0 | 0 | 0 |