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Crustacean Lacustrine Zooplankton Species Patterns along a Latitudinal Gradient in Continental Chile

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ABSTRACT

Crustacean zooplankton communities in Chilean inland waters are typically characterised by low species richness, potentially regulated by trophic status and conductivity. This study examined patterns of species richness along a broad latitudinal gradient (23–51° S), incorporating climatic variables and fish presence. The results indicated non significantly species richness in lakes with fish compared to fishless systems. Non-metric multidimensional scaling (NMDS) and redundancy analysis (RDA) revealed clear community structuring associated with climatic gradients, distinguishing semi-arid northern systems from temperate southern environments. Species richness was lowest in northern saline lakes and in oligotrophic Patagonian lakes with fish, whereas higher richness was observed in low-conductivity systems in southern Patagonia. Although fish presence was associated with reduced species richness, the underlying ecological mechanisms were not directly evaluated and should therefore be interpreted with caution. These findings highlight the

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ARTICLE INFO

Received: 13 February 2026 | Revised: 18 April 2026 | Accepted: 23 April 2026 | Published Online: 17 July 2026
DOI: <https://doi.org/10.30564/re.v8i4.13164>

CITATION

De los Ríos-Escalante, P.R., Correa-Araneda, F., Esse, C., et al., 2026. Crustacean Lacustrine Zooplankton Species Patterns along a Latitudinal Gradient in Continental Chile. *Research in Ecology*. 8(4): 77–87. DOI: <https://doi.org/10.30564/re.v8i4.13164>

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importance of climatic and environmental gradients in structuring zooplankton communities in Chilean inland waters. Similar results were described for Andean lakes from Argentina, due to the similarities in climate and vegetational communities associated with their respective basins, due to geomorphological and geological similarities. Also, from a biogeographical viewpoint, these results are markedly different in comparison to northern hemisphere lakes, because in North American lakes, the predation fish effect affects zooplankton in pelagial environments, and there is a marked food web that involves piscivorous fishes that predate on zooplanktivorous fishes, whereas in Patagonian lakes, the fish predation effect can not be confirmed or rejected.

Keywords: Species Richness; Zooplankton; Latitudinal Gradient; Climate Variations

1. Introduction

Zooplankton assemblages in Chilean inland waters were first described as having low species richness, with a marked dominance of calanoid copepods, particularly in large and deep Patagonian lakes located between 38–51° S. These lakes are characterised by a glacial origin and pronounced oligotrophic conditions^[1–3]. Early studies suggested a potential effect of introduced salmonids on zooplankton community structure, proposing that the original trophic web was relatively simple, with phytoplankton as primary producers, zooplankton as grazers, and native fishes as predators of zooplankton. Under this framework, introduced salmonids would prey upon native fishes, generating a trophic cascade in which zooplankton abundance increases while phytoplankton decreases^[1,4]. Nevertheless, more recent studies have shown that both introduced salmonids and native fishes feed predominantly on benthic invertebrates, and that their effects on zooplankton are less pronounced than those reported for North American lakes^[5].

Along the Chilean continental latitudinal gradient, distinct limnological and climatic zones can be identified. In the extreme north, shallow fishless saline and subsaline lakes are located in the Andean region under arid climatic conditions^[2,3]. In central Chile, there is a transition from desert to shrublands and grasslands, with the presence of reservoirs used for agricultural purposes under a Mediterranean climate. Further south, central-southern Chile exhibits a transition from shrublands to temperate forests, accompanied by a shift from Mediterranean to temperate rainy climates. Within this zone (38–41° S), deep Patagonian lakes have been extensively studied in early limnological research^[3]. South of 41° S, climatic conditions shift towards colder and wetter environments, with a transition

from temperate forests to subpolar shrublands and grasslands, where the southernmost large and deep lakes (up to 51° S) are located^[2,4]. Further south, beyond 51° S, numerous small, shallow, ephemeral and permanent lagoons occur^[2]. Finally, south of 53° S, particularly in Tierra del Fuego and adjacent islands, there is a transition to subpolar grasslands and cold temperate forests, characterised by small lakes and peat bogs^[2,3].

Early comparative studies highlighted a particularly interesting pattern in lakes and fish ponds in Torres del Paine National Park, where the presence of fish was associated with low crustacean zooplankton species richness and dominance of small-bodied taxa, in contrast to fishless ponds^[4,6]. Similar patterns have been reported in comparative studies across different types of lakes and ponds along the Chilean latitudinal gradient, spanning northern to southern regions^[2,3,7,8]. These findings are also consistent with observations from similar latitudinal gradients in Argentina^[9,10].

The aim of the present study is to evaluate patterns of crustacean zooplankton species richness in lacustrine systems along a latitudinal gradient in continental Chile. Based on previous studies, we hypothesise that:

- H1.** *Zooplankton species richness decreases in lakes with fish presence due to top-down control.*
- H2.** *Climatic gradients structure zooplankton communities along the Chilean latitudinal gradient.*
- H3.** *Low-conductivity environments support higher species richness than high-conductivity systems.*

2. Material and Methods

Zooplankton community data were compiled from published literature^[8,11,12]. Study sites were classified into two groups according to fish presence or absence (**Table 1**).

Table 1. Environmental and geographic characterization of the studied lakes.

Lake	Coordinates	LT	Climate	Surface Area (km ²)	Mean Water Temperature (°C)	Mean Conductivity (mS/cm)
Miscanti	23°43' S 67°48' W	0	SA	13.4	13.9	9.0
Miniques	23°43' S 67°48' W	0	SA	1.6	13.8	12.5
Capur	23°54' S 67°48' W	0	SA	0.1	26.0	3.4
Santa Rosa	27°05' S 69°10' W	0	TU	0.1	9.0	10.3
Caburgua	39°16' S 71°58' W	1	TRSD	51.9	13.0	0.1
Villarrica	39°07' S 71°46' W	1	TRSD	175.9	13.2	0.1
Panguipulli	39°41' S 72°15' W	1	TRSD	116.9	11.1	0.1
Riñihue	39°49' S 72°19' W	1	TRSD	77.5	11.5	0.1
Llanquihue	41°07' S 72°50' W	1	RT	870.5	13.3	0.1
Lagunitas	41°30' S 72°56' W	1	RTCI	1.0	11.0	0.1
Trapén	41°30' S 72°06' W	1	RTCI	1.0	14.0	0.2
Mansa	41°27' S 72°54' W	1	RTCI	1.0	10.0	0.1
Riesco	45°39' S 72°20' W	1	RT	14.7	9.1	0.3
Elizalde	45°46' S 72°55' W	1	RT	30.0	6.0	0.2
Jeinimeni	46°52' S 72°54' W	1	CRT	0.4	7.1	0.1
Maldonado	47°15' S 72°31' W	1	MRW	0.2	7.1	0.1
Esmeralda	47°18' S 72°35' W	1	MRW	6.2	7.1	0.1
Melliza Este	51°01' S 72°52' W	1	CRT	0.1	8.1	1.4
Melliza Oeste	51°01' S 72°52' W	1	MRCW	0.1	10.2	1.1
Larga	51°01' S 72°52' W	0	MRCW	0.1	14.2	4.3
Paso de la Muerte	51°01' S 72°52' W	0	MRCW	0.1	11.8	0.5
Redonda	51°01' S 72°52' W	0	MRCW	0.1	11.4	1.4
Juncos	51°01' S 72°52' W	0	MRCW	0.1	16.8	0.4
De los Cisnes	51°01' S 72°52' W	0	MRCW	0.1	16.8	13.2
Del Toro	51°01' S 72°52' W	0	MRW	300.0	12.5	0.0
Arauco	51°58' S 72°02' W	0	SA	0.1	9.0	2.3
Los Palos	52°43' S 71°02' W	0	MRCW	0.1	21.9	0.0
Cabeza de Mar	52°46' S 72°02' W	0	MRCW	0.1	19.3	1.2
Kon Aikén “a”	52°51' S 70°55' W	0	MRCW	0.1	17.1	0.4
Kon Aikén “b”	52°51' S 70°55' W	0	MRCW	0.1	17.1	0.5
Rio Seco	52°06' S 70°53' W	0	MRCW	0.1	17.2	1.2

Note: LT = Lake type; 0 = fishless; 1 = with fish. SA (semi-arid), TU (tundra), TRSD (temperate rainy, summer dry), RT (rainy temperate), RTCI (rainy temperate with coastal influence), CRT (coastal rainy cold), MRW (Mediterranean rainy winter), and MRCW (Mediterranean rainy cold winter).

According to the sampling methodologies described in the source literature, different procedures were applied depending on lake type. In lakes with fish (except Melliza Este and Melliza Oeste), zooplankton samples were collected using vertical hauls from the surface to a depth of 20 m with a plankton net (20 cm diameter, 100 µm mesh size). In contrast, in fishless lakes (including Melliza Este and Melliza Oeste), samples were obtained by filtering 40–80 L of water through a 100 µm mesh.

The reviewed studies consistently reported that maximum zooplankton species richness was observed between October and February, corresponding to the austral spring–summer period. Therefore, data from this seasonal window were considered to ensure comparability among sites. Zooplankton data were standardised as species presence/absence for each site based on the information provided in the cited literature. Taxonomic harmonisation was performed following published taxonomic references^[2,3].

Sites descriptions (**Figure 1**): in the Salar de Atacama basins are recorded these vegetational formations^[13]: Altoandine steppe, shrub-steppe, pre-Pune, desert of Loa River upper basin, and desert of Salar de Atacama. In the Salar de Maricunga, a wetland altoandine was observed, remarking the wetlands of Pantanillo, Las Lajitas streams, Barros Negros, Villalobos stream and Cienaga redonda^[14]. In Southern Chile, from 38° S, it in according to Chilean forestry typology^[15], the predominant forest is Roble-Raulí-Coigüe, Coigüe-Raulí-Tepa, evergreen, Alerce, Lenga, Guaitecas Cipres, and Magallan Coigüe. The vegetational communities are described based on literature^[16], it remarks the presence of Andean resinous forest of *Araucaria araucana*-*Nothofagus dombeyi*, resinous Andean Mediterranean-temperate forests of *Araucaria araucana*-*Festuca scabriuscula*, resinous temperate coastal forests of *Fitzroya cupressoides*, temperate Andine resinous forest of *Fitzroya cupressoides*, resinous temperate coast-

al forest of *Pilgerodendron uvifera*-*Tepualia stipularis*, resinous temperate coastal forests *Pilgerodendron uvifera*-*Astelia pumila*, perennial temperate Andean forest of *Nothofagus dombeyi*-*Saxegothea conspicua*, inner perennial temperate Andean forest of *Nothofagus nitida*-*Podocarpus nubigenus*, perennial temperate Andean forest of *Nothofagus betuloides*-*Desfontainea fulgens*, mixture perennial temperate-antiboreal forest of *Nothofagus betuloides*-*Drimys winteri*, coastal perennial temperate-antiboreal forest of *Nothofagus betuloides*-*Embothrium coccineum*, coastal perennial temperate-antiboreal forest of *Nothofagus betuloides*-*Drimys winteri*, shrub perennial coastal temperate forest of *Pilgerodendron uvifera*-*Nothofagus nitida*, coastal bog temperate of *Donatia fascicularis*-*Oreobolus obtusangulus*, coastal antiboreal bog of *Astelia pumila*-*Donatia fascicularis*, coastal antiboreal bog of *Bolax caespitosus*-*Phyllachne uliginosa*, inner, coastal antiboreal bog of *Sphagnum magellanicum*-*Schoenus antarcticus*.

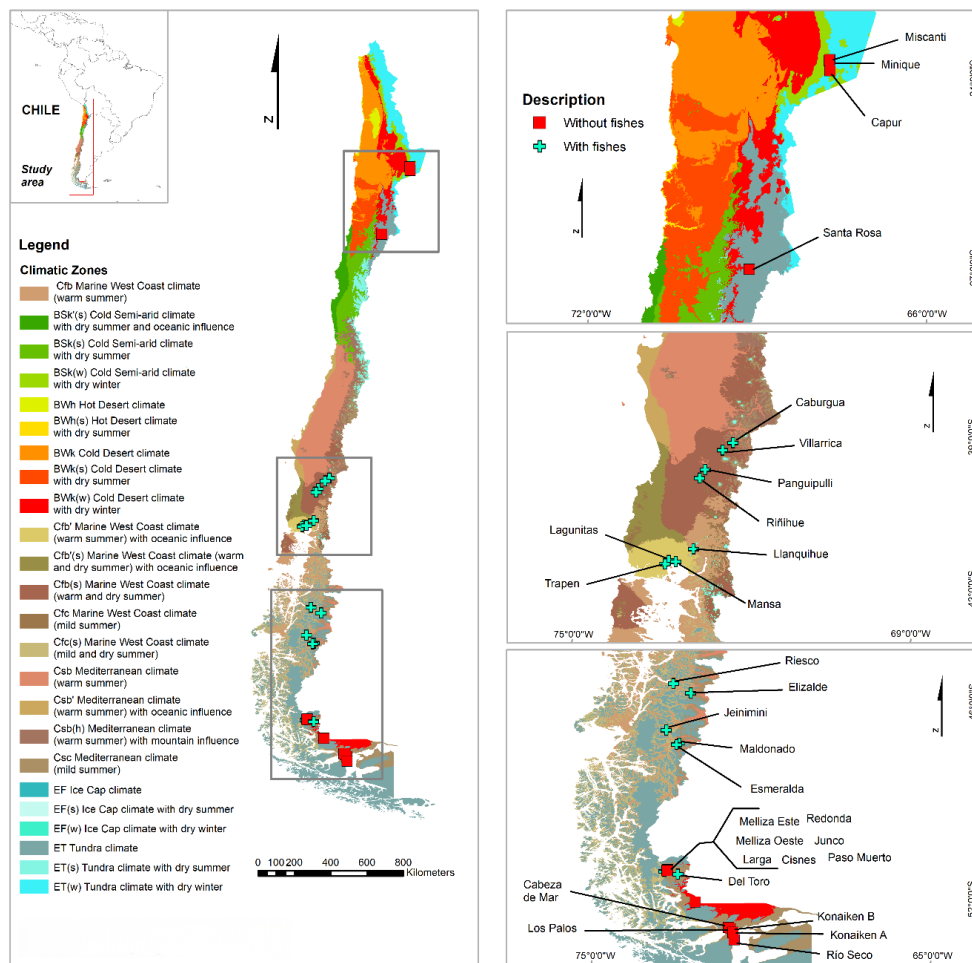


Figure 1. Map of Chile showing the geographic location of the studied lakes, including fishless and fish-containing systems distributed across semi-arid, temperate, Mediterranean, and cold-rainy climatic zones.

Note: Based on the modified Koppen-Geiger system and Sarricolea et al.^[17].

Redundancy analysis (RDA) was applied to the set of climatic variables to evaluate their relative importance in structuring the study sites. This analysis was conducted using R software^[18]. The climatic matrix was obtained from NASA POWER^[19], and included the following variables: PS (surface pressure, kPa), TS (earth skin temperature, °C), T2M (air temperature at 2 m, °C), QV2M (specific humidity at 2 m, g kg⁻¹), RH2M (relative humidity at 2 m, %), WS2M (wind speed at 2 m, m s⁻¹), T2MDEW (dew/frost point at 2 m, °C), T2MWET (wet-bulb temperature at 2 m, °C), GWETTOP (surface soil wetness), T2M_MAX (maximum air temperature at 2 m, °C), T2M_MIN (minimum air temperature at 2 m, °C), PREC (corrected precipitation, mm), UVA (surface UVA irradiance, W m⁻²), and UVB (surface UVB irradiance, W m⁻²). Climatic classification followed Sarricolea et al.^[17], including the categories SA (semi-arid), TU (tundra), TRSD (temperate rainy, summer dry), RT (rainy temperate), RTCI (rainy temperate with coastal influence), CRT (coastal rainy cold), MRW (Mediterranean rainy winter), and MRCW (Mediterranean rainy cold winter).

Statistical analyses were performed to evaluate differences in crustacean zooplankton species richness and community composition across lake types (with vs. without fish) and climatic categories. Species richness (S) was defined as the total number of species recorded per site (**Table 1**). Differences in species richness among groups were assessed using non-parametric Kruskal–Wallis tests due to non-normality and heteroscedasticity of the data. When appropriate, post hoc pairwise comparisons were conducted using Dunn's test with Bonferroni correction.

Community composition was analysed using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity, a metric widely used for ecological community data. Differences among groups (fish presence/absence and climatic categories) were tested using analysis of similarities (ANOSIM) with 999 permutations. To further evaluate the influence of environmental variables on zooplankton community structure, redundancy analysis (RDA) was conducted as a constrained ordination method linking species data to environmental gradients. The statistical significance of the RDA model was assessed using permutation tests (999 permutations). Model performance was evaluated using the coefficient of determination

(R²) and adjusted R². All analyses were conducted in R^[18], primarily using the *agricolae*^[20] and *vegan*^[21] packages.

3. Results

Species richness showed no significant differences between lakes with and without fish (Kruskal–Wallis test: $H = 0.196$, $p = 0.6577$; **Figure 2a**). Similarly, no significant differences in species richness were detected among climatic categories (Kruskal–Wallis test: $H = 7.693$, $p = 0.3604$; **Figure 2b**). Although these differences were not statistically significant, a tendency towards lower richness values was observed in lakes with fish and in high-conductivity systems.

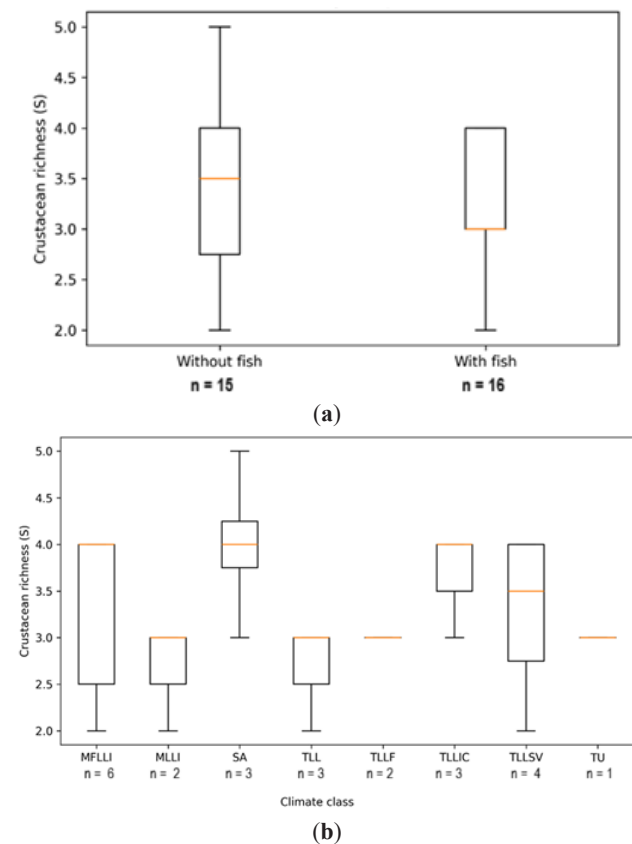


Figure 2. Differences in crustacean zooplankton species richness (S) across environmental categories: (a) Comparison between lakes with and without fish. (b) Comparison among climatic categories.

Note: No significant differences were detected (Kruskal–Wallis tests, $p > 0.05$ in all cases). Boxes represent interquartile ranges, horizontal lines indicate medians, and whiskers represent data dispersion.

The NMDS ordination based on Bray–Curtis dissimilarity revealed clear differences in zooplankton community composition between lakes with and without fish (**Figure**

3). The ordination showed a good fit, with a low stress value indicating an adequate representation of multivariate relationships. Group differences were statistically significant (ANOSIM $R = 0.488$, $p = 0.0002$), suggesting that fish presence is associated with marked shifts in community composition. Similarly, NMDS analysis based on climatic categories revealed a clear structuring of zooplankton communities (Figure 4). Differences among climatic groups were also significant (ANOSIM $R = 0.318$, $p = 0.0012$), indicating that climatic gradients play an important role in shaping community composition.

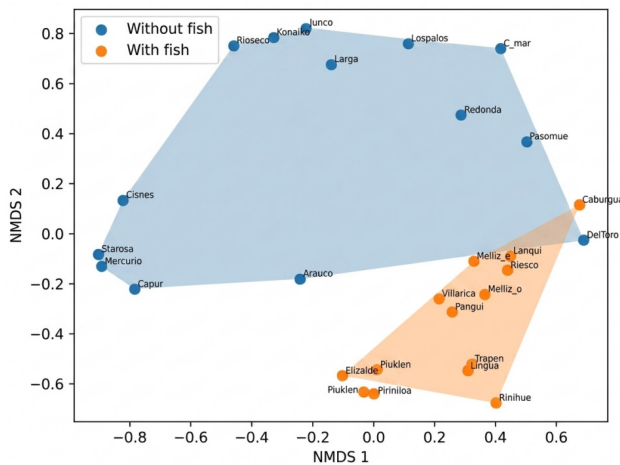


Figure 3. Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity showing differences in zooplankton community composition between lakes with and without fish.

Note: The ordination showed a good fit (low stress value), and group separation was statistically significant (ANOSIM $R = 0.488$, $p = 0.0002$).

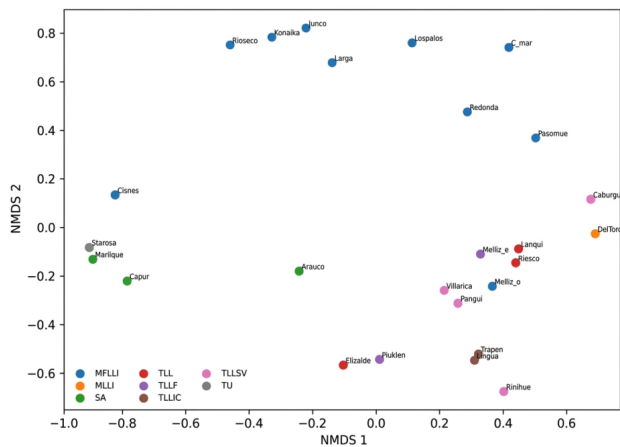


Figure 4. Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity showing zooplankton community structure across climatic categories.

Note: Differences among climatic groups were statistically significant (ANOSIM $R = 0.318$, $p = 0.0012$), indicating the influence of climatic gradients on community composition.

The RDA analysis revealed significant relationships between environmental variables and zooplankton community composition (Figure 5). The global model was statistically significant (pseudo- $F = 3.347$, $p = 0.0005$), explaining a substantial proportion of the variance in the dataset ($R^2 = 0.401$; adjusted $R^2 = 0.281$).

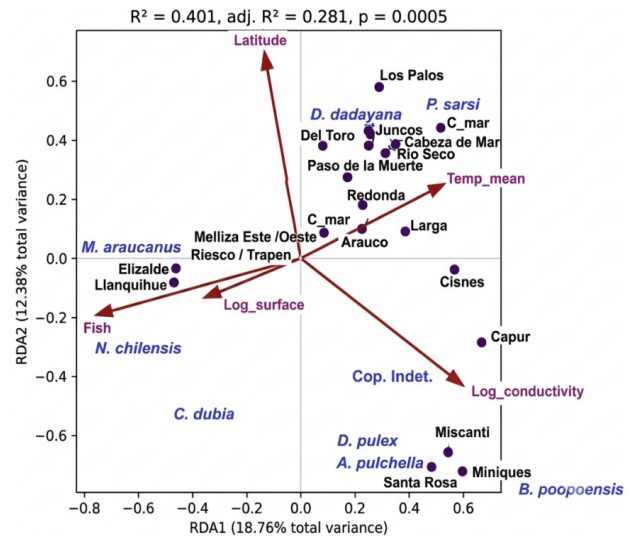


Figure 5. Redundancy analysis (RDA) showing the relationships between environmental variables and zooplankton community composition across Chilean inland waters.

Note: The global model was statistically significant (pseudo- $F = 3.347$, $p = 0.0005$), explaining 40.1% of total variance (adjusted $R^2 = 0.281$). The first two axes explained 31.14% of the variance (RDA1 = 18.76%, RDA2 = 12.38%).

The first two canonical axes explained 31.14% of the total variance (RDA1 = 18.76%, RDA2 = 12.38%), indicating that environmental gradients captured an important component of community structure. The ordination diagram showed a clear grouping of sites along environmental gradients, particularly separating northern saline systems from southern temperate environments, as well as distinguishing lakes with fish and fishless (Figure 5).

Overall, the results indicate that zooplankton community composition is strongly structured by climatic variation along the latitudinal gradient, while species richness shows weaker and non-significant patterns. Nevertheless, both species composition and richness exhibit consistent trends associated with fish presence and environmental conditions.

4. Discussion

The present study revealed clear patterns in crus-

tacean zooplankton species richness and community structure along a broad latitudinal gradient in continental Chile. These patterns appear to be primarily associated with climatic variation and environmental heterogeneity, which are known to influence inland water ecosystems across large spatial scales ^[15,22,23]. The marked differentiation observed between northern semiarid systems and southern temperate environments supports the idea that climatic gradients play a fundamental role in structuring freshwater communities in Chile. This includes the presence of both endemic species and taxa with wide distributions, reflecting distinct biogeographical patterns across the gradient ^[2,3,24].

Species richness was generally low across the studied systems, particularly in northern saline lakes and in large oligotrophic Patagonian lakes with fish presence. In contrast, higher species richness was observed in low-conductivity systems in southern Patagonia, particularly in fishless environments ^[2,3,7,8]. These findings are consistent with previous studies conducted in Chilean and Argentinean lakes, which have reported low diversity in oligotrophic and saline systems, and higher diversity in small, less mineralised water bodies ^[1-3,9,10]. A relevant comparison can be made with Argentinean Andean lakes located along the border with Chile, where similar climatic transitions occur. These gradients range from arid landscapes to Mediterranean shrublands and prairies, followed by temperate forests and ultimately subpolar environments ^[9,10]. Notably, in Argentina, these transitions occur over broader spatial scales, extending further east from the Andes, where tropical and subtropical systems dominate northern regions, and cold, windy subpolar plains with numerous shallow lagoons dominate central and southern areas ^[9].

The NMDS analyses indicated a clear separation of zooplankton communities based on both fish presence and climatic categories, with low stress values indicating a robust ordination. Similarly, the RDA results highlighted the importance of environmental gradients in structuring community composition, with the first two axes explaining a substantial proportion of the total variance. Together, these multivariate analyses support the existence of strong environmental and biogeographical controls on zooplankton assemblages ^[24,25].

In this context, the present study spans a latitudinal gradient of approximately 3,000 km, encompassing substantial variation in climate, landscapes, and limnological conditions, as previously reported for Chile ^[2,3] and Argentina ^[9,10]. Comparisons with studies from the Northern Hemisphere would be valuable; however, few studies have addressed such large-scale gradients across hemispheres. The only available comparative study focused on body size variation in dominant zooplankton groups, reporting a positive relationship between body size and latitude for cladocerans in Northern Hemisphere lakes, and a similar pattern for calanoid copepods, which dominate Southern Hemisphere systems ^[25].

The lower species richness observed in lakes with fish is consistent with patterns reported in other freshwater ecosystems, where fish presence has been associated with reduced zooplankton diversity and shifts in community structure ^[4,6,8,26,27]. These patterns are often attributed to top-down control mechanisms, including selective predation on large-bodied zooplankton ^[4,6]. However, it is important to emphasise that the present study did not directly evaluate trophic interactions or predation processes. Therefore, while the observed patterns are consistent with potential fish effects, the underlying mechanisms should be interpreted cautiously, as previously suggested for Chilean lakes ^[5].

Early studies proposed relatively simple trophic webs in Chilean lakes, with phytoplankton as primary producers, zooplankton as grazers, native fishes as predators of zooplankton, and introduced salmonids preying upon native fishes, forming a trophic structure comparable to that described for North American lakes ^[1]. However, subsequent studies have shown that native fishes predominantly consume littoral invertebrates rather than zooplankton, and are themselves preyed upon by introduced salmonids ^[5]. Although differences in zooplankton body size between systems with and fishless have been reported, the role of fish in structuring zooplankton communities remains insufficiently understood. This is largely due to the lack of direct evidence of predation by juvenile salmonids on zooplankton and the absence of experimental studies addressing these interactions ^[15]. Consequently, while some field observations suggest a potential influence of fish predation on zooplankton communities in Patagonian lakes ^[2,5,7,8],

this hypothesis cannot yet be conclusively supported or rejected and requires further experimental and field-based investigation.

In addition to biotic interactions, abiotic factors such as conductivity and trophic status appear to play a key role in determining species richness. The low richness observed in northern Chilean saline lakes is likely related to high mineral content and environmental harshness, which can limit species establishment and persistence, as reported in studies from the Northern Hemisphere ^[28,29]. Conversely, the higher richness observed in low-conductivity systems in southern Patagonia may reflect more favourable environmental conditions and reduced physiological constraints. Under moderate conductivity and higher chlorophyll concentrations, increased phytoplankton productivity may support more abundant and diverse zooplankton communities in terms of biomass, abundance, and species richness ^[4,6].

Interestingly, the patterns observed in this study differ from those commonly reported in Northern Hemisphere lakes, where species richness is often positively associated with lake size and productivity ^[27–31]. In contrast, the Chilean systems analysed here suggest that environmental constraints such as conductivity and climatic variability may override these general patterns, highlighting the importance of regional context in ecological processes.

From a biogeographical perspective, the relatively high species richness observed in southern Patagonia may indicate favourable conditions for species coexistence and potential colonisation processes ^[2,24]. This region could represent an important area for the diversification and distribution of freshwater zooplankton in southern South America ^[32,33]. The presence of endemic species, particularly in southern Patagonia and northern Andean systems ^[2,3], may further support the idea of regional centres of diversification and dispersal ^[2].

Despite these insights, the present study has several limitations that should be acknowledged. The analyses were based on compiled data from multiple sources ^[8,11,12,34,35], and differences in sampling methods and effort may have influenced the observed patterns. Additionally, the study focused on species richness and community composition, without incorporating abundance data or direct

measurements of ecological interactions. Future research should integrate experimental and long-term observational approaches to better understand the mechanisms underlying zooplankton community structure in Chilean inland waters.

Overall, the results highlight the importance of climatic gradients, environmental conditions, and potential biotic interactions in shaping zooplankton communities across Chile. These findings contribute to a better understanding of freshwater biodiversity patterns in the Southern Hemisphere and emphasise the need for integrative approaches combining ecological, environmental, and biogeographical perspectives ^[2,3]. Further studies based on experimental and field evidence are needed to clarify the role of trophic interactions within zooplankton communities, particularly predator–prey dynamics, as well as the potential influence of fish predation ^[7,8,35].

5. Conclusions

This study demonstrates that crustacean zooplankton communities in Chilean inland waters are structured primarily by large-scale climatic and environmental gradients rather than by differences in species richness alone. Although fish presence was associated with a tendency towards lower species richness, community composition showed much stronger responses to climatic variation and environmental conditions. These findings highlight the importance of considering both biogeographical and ecological processes when interpreting freshwater biodiversity patterns across broad spatial scales. Future studies integrating standardised sampling protocols, abundance data, and experimental approaches will be essential to clarify the relative roles of climate, water chemistry, and trophic interactions in shaping zooplankton communities in southern South American lakes.

Author Contributions

Conceptualization and methodology, P.R.D.I.R.-E.; software, C.E.; investigation, F.C.-A. and M.R.-M.; writing—original draft preparation, P.R.D.I.R.-E. and C.E.; writing—review and editing, P.R.D.I.R.-E. and C.E.; All authors have read and agreed to the published version of

the manuscript.

Funding

The present study was financed by CONICYT-Chile (Doctoral fellowship, Doctoral grant for support of doctoral thesis, and grant to finish doctoral thesis); it was also financed by projects DID-UACH d2001-11, IAI (Enhanced ultraviolet B radiation in natural ecosystems as an added perturbation due to ozone depletion), FONDECYT 1080456, FONDECYT 1231551 (F.C.-A.), FONDECYT Regular 1240447 (ANID-Chile)(C.E.), DGI-UCT CDA 2007-01, Tides Grant Foundation TRF13-03011, and MECESUP UCT 0804 (P.R.D.I.R.-E.).

Institutional Review Board Statement

Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

The data used in this study are available from the corresponding author upon reasonable request.

Acknowledgments

The authors express their gratitude to the National Forestry Corporation (CONAF-Chile) for access authorizations for protected areas, and the Chilean Navy (Directorate of Maritime Territory and Merchant Marine; DIRECTEMAR-Chile, specifically Villarrica Lake Maritime Authority) for logistic support in field work. Finally, the main author expresses their gratitude to M.I. and S.M.A for their valuable suggestions, which improved the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

AI Use Statement

The authors declare that no artificial intelligence (AI) tools were used in the preparation of this manuscript.

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