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RESEARCH

# Seaweed cultivation under threat: the impact of epiphytes on *Gracilaria chilensis* cultivation in Chile

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## Abstract

The cultivation of *Gracilaria chilensis* ("pelillo") is an important aquaculture industry in Chile, but the growth of epiphytic algae threatens its productivity. This study investigates the spatio-temporal dynamics of epiphytic algae in *G. chilensis* farms in the Pudeto and Maullín rivers, Los Lagos Region, Chile, from 2017 to 2021. Seasonal sampling assessed epiphyte biomass, taxa richness, and their impact on the seaweed's growth. A total of 21 species of epiphytes were identified, with 14 found within the sampling quadrats and seven outside. Significant seasonal fluctuations in wet biomass and taxa richness were observed, with the highest epiphyte load recorded during the summer months, particularly in the Pudeto river. Here, the epiphyte load was consistently higher than Maullín's, which showed no significant annual changes in 2017 but a notable increase in epiphyte biomass by 2021, even during winter. Canonical Correspondence Analysis (CCA) revealed that environmental factors, such as salinity, significantly influenced epiphytic assemblages. Lower salinity sites promoted *Chaetomorpha linum*, *Grateloupia* sp., and *Ulva* sp., while more marine conditions supported *Polysiphonia* sp. and *Ulva* sp. These findings highlight the need for targeted management strategies to mitigate epiphyte proliferation, ensuring the sustainability of *G. chilensis* farming. Effective intervention measures, including improved farming practices and environmental monitoring, are critical to reducing economic losses and maintaining the viability of this important aquaculture resource.

**Keywords** Cultivation · Chile · Epiphyte · *Gracilaria* · Rhodophyta · Seaweed culture

## Introduction

The commercial culture of seaweed (i.e., macroalgae) has increased worldwide over the past two years (FAO 2024). Compared to terrestrial plants, the "domestication of the oceans" (Duarte et al. 2007), particularly the culture of seaweeds, has recently emerged in human history. Seaweed is mainly cultivated for high-value food products, agar-type polysaccharides, carrageenan, and alginate extraction (Aroca et al. 2020). Due to the growing development of seaweed aquaculture, epiphytism is a common phenomenon in marine and brackish environments, altering the production and interactions of the macroalgae (Ingle et al. 2018). Epiphytes may be other non-wanted algal species, viruses, bacteria, and fungi. They can attract grazers such as crabs, lobster, shrimp, fish, and turtles, which may have positive (increasing the biodiversity of the ecosystems) and negative (decreasing the biomass yield) impacts.

*Gracilaria chilensis* (ex *Agarophyton chilensis*; Gracilariales, Rhodophyta), commonly and locally known as "pelillo," is the only species of macroalgae that is cultivated in Chile for the production of agar–agar used in the global food and pharmaceutical industry (Buschmann et al. 2001). This seaweed has a high rate of vegetative propagation (Alveal 1986) and the ability to form an extensive system of underground thalli (Santelices and Ugarte 1987), making it easy to cultivate in soft seabeds. The presence of epiphyte species of green algae, such as *Enteromorpha* sp., *Ulva* sp., and *Rhizoclonium* sp., has negatively impacted the productivity and commercial value of the local and world market of "pelillo". Epiphytism is generally seasonal, impacting production during summer, the most critical season for biomass

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production. Even though there have been reports of green algae in "pelillo" cultures in the Los Lagos Region, there are many gaps relating to this epibiont organism's morphology, growth, and reproduction (Aroca et al. 2020).

*Gracilaria chilensis* production through cultivation in the country began in the 1980 s and has been maintained uninterrupted over four decades, turning Chile into one of the world's leading producers of raw materials for agar (Buschmann et al. 2008). On average, Chile produces more than 60,500 tonnes of this seaweed, of which 31% of this production originates from harvests from farming centers, while the remaining 69% is from shore harvesting (Subsecretaria de Pesca y Acuicultura 2024). The Los Lagos Region's participation in artisanal landings and harvests from farming centers contributes to the average figures of close to 85% of the national total, which shows the importance of the resource for artisanal fishing and small-scale aquaculture in the region.

The "*pelillo*" farming is mainly located in three districts, which in order of productive importance are Ancud (50%), Maullín (31.8%) and Puerto Montt (7.7%). The extraction and cultivation of this seaweed are consolidated economic activities in the Los Lagos region, which concentrates on average 84% of the national landings of this seaweed (Subsecretaria de Pesca y Acuicultura 2024). During 2013, 2014, 2015, 2020, and 2021, the presence of *Rhizoclonium* sp. was recorded in culture farms of *G. chilensis* in the northern sector of Maullín river. These green algae covered large river extensions, causing losses of up to 93.9% of spring and summer "pelillo" causing an economic and social detrimental effect. A similar situation is observed in the Pudeto River (Ancud), where the purchase is suspended at times of the year, causing economic difficulties for the producers and the whole commercialization network. Because of these events, the rivers of Maullín and Pudeto were declared a plague area by the Chilean Subsecretary of Fisheries and Aquaculture (Res. Ex. N°2424–2024, SUBPESCA, Ministerio de Economía).

This study aims to identify and characterize the spatial and temporal abundance of epiphytic algae in the *G. chilensis* crops in the Pudeto and Maullín rivers in the Los Lagos Region.

## Methods

### Study area and sampling

Biological samples were carried out during the spring of 2017 in the estuarine portion of the Maullín and Pudeto rivers in the Los Lagos Region, Chile (Fig. 1). The Maullín River extends for 9 km to the Lepihue locality, the farthest

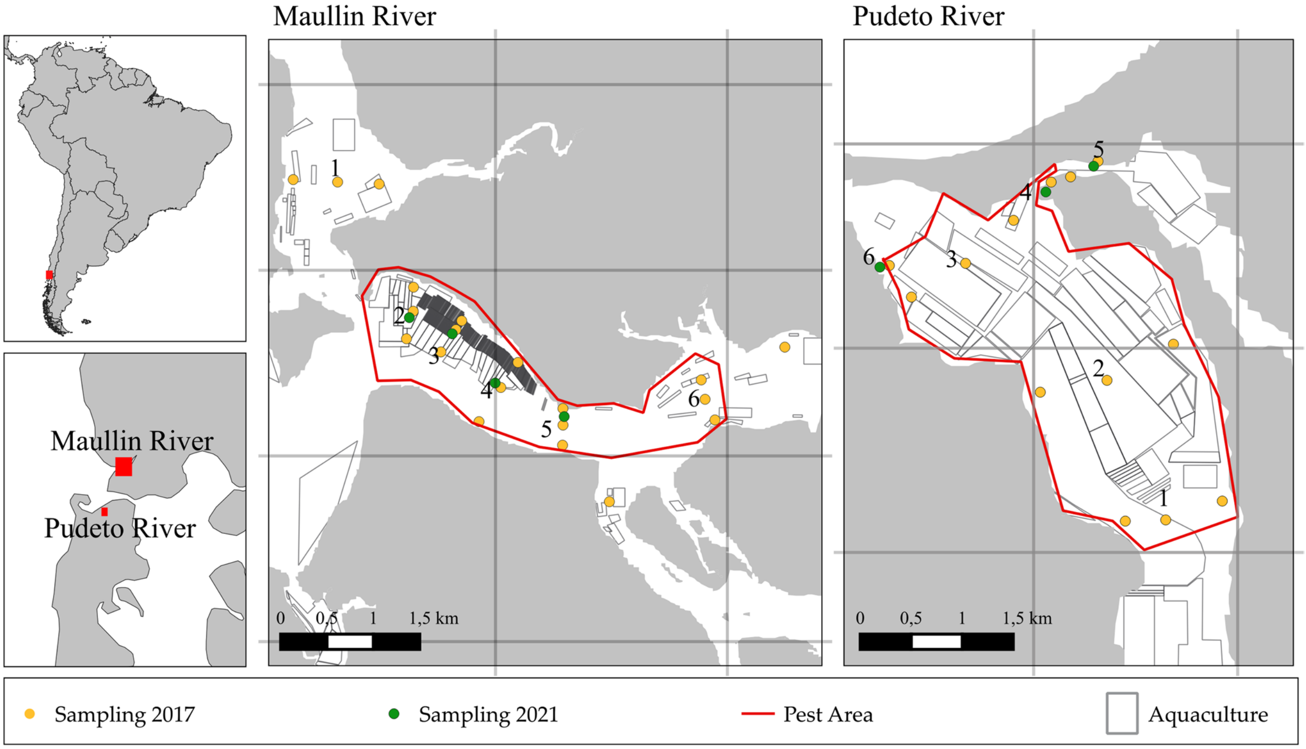


**Fig. 1** The area from which the study was conducted in Southern Chile. Sampling points in 2017 (yellow circles) and 2021 (green circles) in Maullín and Pudeto rivers within the polygon declared as a pest area for *Rhizoclonium* spp. (red line). The aquaculture area is also displayed in grey squares

*G. chilensis* farming area from the sea. In the case of the Pudeto River, the limit is 7 km from the sea in the locality of Pupelde Cove, where the seaweed farming ends. Both localities are characterized by a soft substrate composed of sand and mud. In Maullín River, we had seven sampling points; three samples were taken for each site in the northern, central, and southern shores (Fig. 1). In Pudeto River, we had six sampling points along the west, east and central part of the river (Fig. 1). Samples were transported in moistened paper towel to the Laboratory of Macroalgae from the Universidad Arturo Prat in Puerto Montt and kept in cooler boxes.

## Epiphytes species identification

We only considered the epiphytes attached to *Gracilaria*. To establish a complete species list for both sampling localities, the epiphyte taxa found in the area that did not occur within the quadrats of the sampling protocol were also considered. These records, however, were not included in the comparative statistical analyses. We used key morphological and cytological characters to identify the epiphytic algae (Boedeker et al. 2016; Aroca et al. 2020) at different taxonomic levels. We characterized morphological general characteristics such as colour, shape, size, substrate adhesion, ramification, reproductive structures, etc. For cytological measurement, we calculated the length and width of 30 cells using AxionVision software (Rel. 4.8) using a 10 × magnifying lens. Photographs were taken using a Canon camera (EOS Rebel T5) with Canon Utilities software incorporated in an inverted Zeiss Primovert microscope.

## Temporal variability of algae biomass and epiphytic of G. chilensis

To estimate the temporal variability of the richness and biomass of epiphytic algae, seasonal sampling was carried out starting in spring 2017 and ending in spring 2018. For comparison purposes of epiphytism in different years, we repeated the sampling in Maullín and Pudeto in 2021 in some sites (Fig. 1).

For both the Pudeto and Maullín rivers, a destructive sampling of 9 quadrats was carried out, removing all the algal material contained within the 1 $m^2$ quadrat. The material collected from each quadrat was weighed, and a random subsample of 250 g was subsequently taken and placed in bags labelled with the corresponding quadrat number. Finally, the bags were stored in a cooler and transported to the laboratory, where the proportion of epiphytic algae biomass relative to the biomass of *G. chilensis* was determined.

## Epiphytes load capacity in *G. chilensis*

The different epiphytic species from the subsamples were separated and identified under a stereoscopic microscope. Subsequently, the algae of each species were dried at 60 °C until reaching their dry weight, which was recorded. Epiphyte richness was calculated as the total number of different taxa identified in the subsample of 250 g of *Gracilaria*. We also calculated the specific load as the proportion of the dry weight of each epiphytic algal species in relation to the dry weight of the *G. chilensis* subsample.

## Sampling design and data analyses

We conducted a general characterization of "pelillo" across space and time using the total wet biomass obtained from the average of the quadrates of each season. Seasonal and spatial variability in specific epiphytes load, taxa richness, and wet biomass were tested using multifactorial analyses by Generalized Linear Models (GLM). Specific epiphytes load and wet biomass fitted to a negative binomial distribution, while taxa richness fitted to a quasipoisson distribution. The whole model included three factors: "season" (fixed, four levels including summer, autumn, winter and spring), "localities" (fixed, two levels for Pudeto and Maullín, crossed with season), "sites" (fixed, including seven levels for the stations within Maullín and six levels for the stations within Pudeto, nested with localities). Therefore, the sampling design for total wet biomass of *G. chilensis*, and for the specific load and epiphytes richness, the sampling design was: 4 (seasons-fixed) × 2 (localities – fixed) × 7 (Maullín sites – fixed) or 6 (Pudeto sites – fixed) × 9 quadrats = 504 samples for Maullín and 432 samples for Pudeto.

Consequently, we analysed deviance and used Tukey post hoc for pairwise comparison. A comparison of epiphyte load between the years 2017 and 2021 at the sites we were able to resample was performed using the non-parametric U Mann-Witney test. All GLMs and the Mann-Witney test were performed using the packages "MASS" and "emmeans" in R environment (R Core Team 2024).

The relationships between the epiphyte's assemblage structure and environmental variables (temperature, salinity, and turbidity) were investigated using a canonical correspondence analysis (CCA). This analysis coordinates the community structure of epiphyte assemblages based on the variance constrained by the selected environmental factors.

Permutational Analysis of Variance PERMANOVA (Anderson 2005) was used to test the seasonal changes in epiphyte composition. We ran PERMANOVA with 14 variables (i.e., taxa). The statistical processing was performed by transforming the data (fourth root), which was analysed by Bray–Curtis dissimilarities matrices with 9999 permutations. The complete model was the same as the GLM described above. Finally, we calculated the contribution of each taxon per season in assemblage structures by SIMPER routine (Clarke 1993). In this procedure, the data were transformed to the fourth square root to reduce the contribution of the more abundant macroalgae compared to that of the less conspicuous macroalgae. SIMPER list was cut off when the accumulated contribution of species reached 90%. All PERMANOVA, Simper, and CCA were done using the packages "vegan" in R environment v4.2.2 (R Core Team 2024).

## Results

### Characterization of macroalgae assemblage composition

Morphological and cytological criteria allowed the epiphyte identification at the highest possible taxonomic level. For example, in *Ulva* specimens, we identified three morphotypes (laminar *Ulva* sp.1, filamentous *Ulva* sp.2 and tubular *Ulva* sp.3) based on their structure (Supplementary material Figure S1). Overall, the taxa richness during the entire study period was 21 taxa (Table 1). Among them, 7 species were detected only outside the quadrats and 14 within the quadrats (Table 1). The summer season was the only period in which we detected all the epiphytes (Table 1).

### Wet biomass, taxa richness, and specific load of epiphytes

The deviance analysis of wet biomass showed significant fluctuations between seasons and localities (Table 2 and Fig. 2). The seasonal fluctuations of *G. chilensis* were significant mainly between summer and the rest of the seasons (Table 2, Fig. 2). Some sites within each locality showed greater seasonal variations than others (e.g., Pud_6 and Mau_7).

Overall, the deviance analysis revealed a significant interaction between Season and Sites (Locality) (Table 2). In turn, sites showed that the magnitude of seasonal changes for taxa richness and specific load of epiphytic macroalgae varied at each locality and site (Fig. 3 and 4, respectively). For example, sites Pud_2 - 5 exhibited significant differences in taxa richness compared to summer and the other seasons ($p < 0.05$). However, these seasonal differences were not observed in most sites in Maullín (Fig. 3B) ($p > 0.05$). A similar trend was observed in the epiphytic macroalga's specific load, where the seasonal variation's magnitude varied regarding localities and sites. For example, site Pud_4 - 6 showed significant differences between summer and winter, while sites in Maullín did

**Table 1** Absence and presence of each taxon per season of the epiphyte assemblage in Pudeto and Maullín rivers

| *Epiphytes* | *Autumn* | *Winter* | *Spring* | *Summer* |
|---|---|---|---|---|
| *Asterfilopsis furcellata* | x | x |  | x |
| *Callithamnion* sp. | x |  | x | x |
| *Callophylis variegata* | x |  | x | x |
| *Ceramium* spp. | x | x | x | x |
| *Chaetomorpha linum* |  |  | x | x |
| *Chondracanthus chamissoi* | x | x |  | x |
| *Desmarestia ligulata* | x |  | x | x |
| *Grateloupia* spp. | x |  | x | x |
| *Sarcothalia crispata* | x |  | x | x |
| *Macrocystis pyrifera* |  | x | x | x |
| *Polysiphonia* spp. | x | x | x | x |
| *Ulva* sp.1 | x | x | x | x |
| *Ulva* sp.2 |  |  | x | x |
| *Ulva* sp.3 |  |  | x | x |
| Chlorophyceae *indet.** | x | x |  | x |
| Rhodophyta *indet.** | x | x | x | x |
| Ochrophyta *indet.** | x | x | x | x |
| Hydrozoa *indet.** | x | x | x | x |
| Bryozoa *indet.** | x | x | x | x |
| Decapoda *indet.** | x | x | x | x |
| *Mytilus chilensis** | x | x | x | x |

* indicates taxa that were recorded only outside of the sampling quadrants. sp.: taxa identified with a morphological criterion; spp.: taxa identified at genus level; indet.: indeterminate

**Table 2** GLM results for wet biomass of macroalgae, epiphytes taxa richness, and specific load. Pr (< Chi) indicates the *P* value

| Variable | Source of Variability | Df | LR Chisq | Pr (< Chi) |
|---|---|---|---|---|
| Wet Biomass | Season | 3 | 134.04 | **** |
|  | Locality | 1 | 3.59 |  |
|  | Season × Locality | 3 | 22.22 | **** |
|  | Sites (Locality) | 11 | 327.17 | **** |
|  | Season × Sites(Locality) | 33 | 142.3 | **** |
| Taxa Richness | Season | 3 | 99.681 | **** |
|  | Locality | 1 | 76.611 | **** |
|  | Season × Locality | 3 | 24.071 | **** |
|  | Sites (Locality) | 11 | 164.578 | **** |
|  | Season × Sites (Locality) | 33 | 99.263 | **** |
| Specific load | Season | 3 | 20.274 | **** |
|  | Locality | 1 | 126.546 | **** |
|  | Season × Locality | 3 | 5.712 |  |
|  | Sites (Locality) | 11 | 71.202 | **** |
|  | Season × Sites (Locality) | 33 | 67.5 | **** |

The asterisk (*) indicates significant differences: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

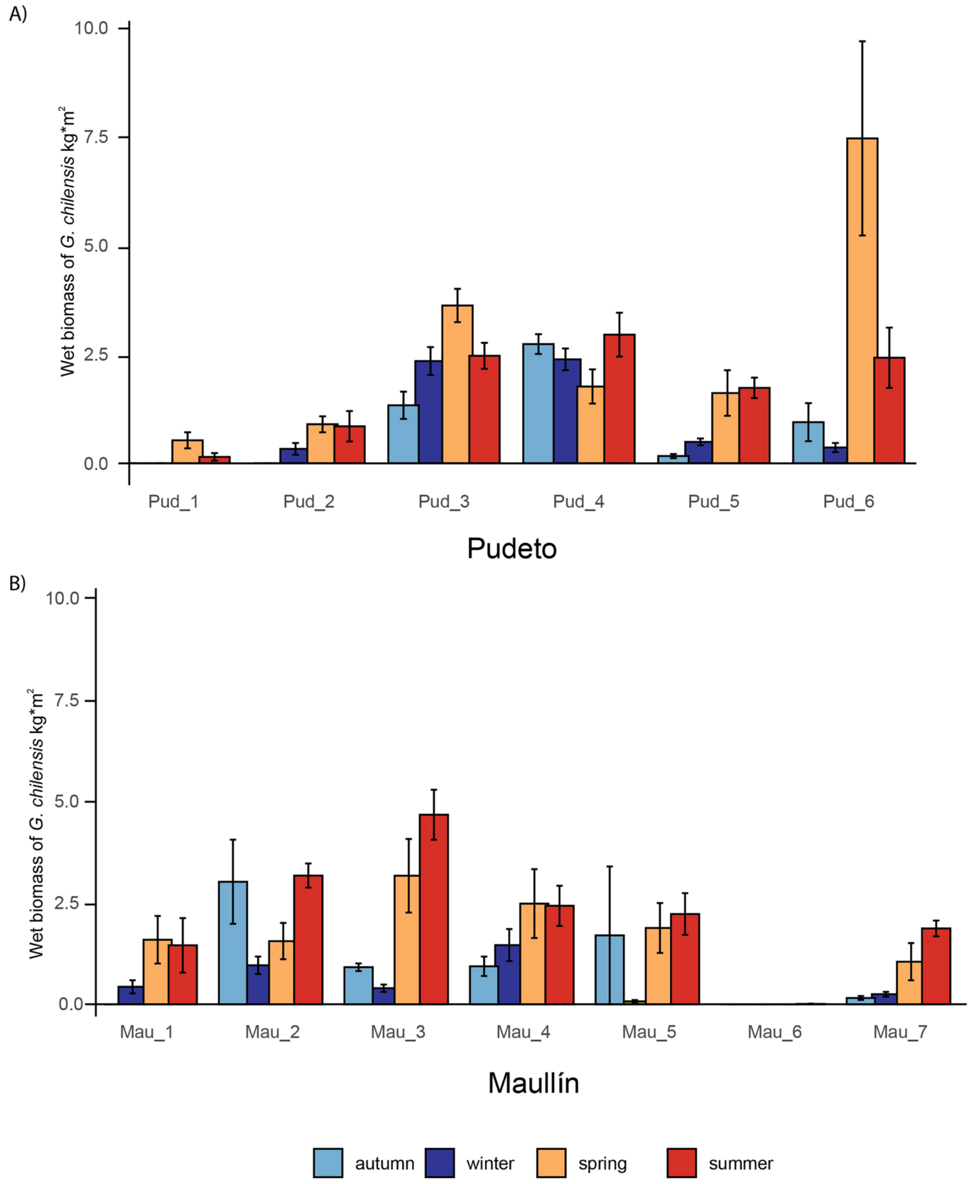


**Fig. 2** Wet biomass during autumn, winter, spring, and summer for (A) Pudeto and (B) Maullín rivers for each sampling point. Wet biomass is expressed in kg of *Gracilaria chilensis* per m$^2$. The bars represent the standard deviation (SD)

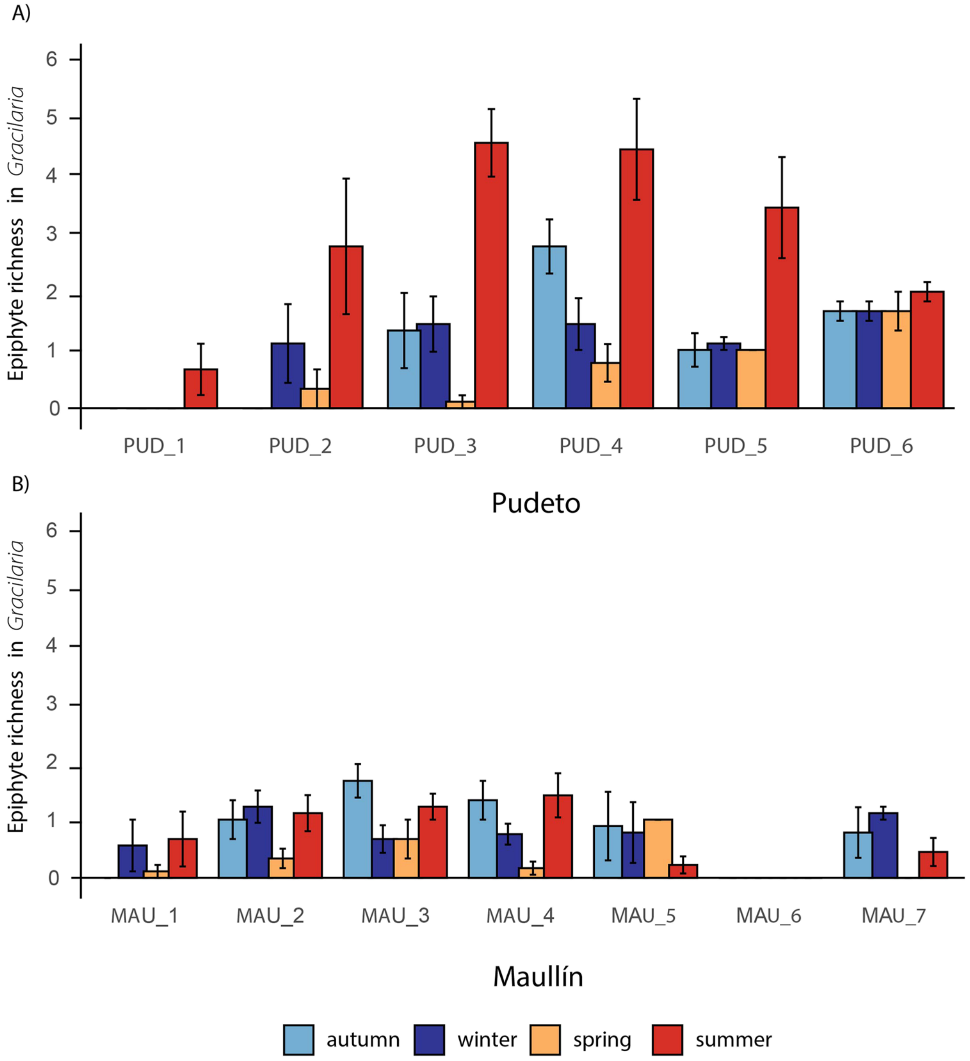
not register significant differences during the study period (Fig. 3B).

Although no variation was detected in the specific load of epiphytes in Maullín during 2017, there was a significant increase between 2017 and 2021 for the summer and winter seasons in some sites (Fig. 5, $p < 0.001$). For example, we detected a significant increase in Mau_2,4,5 sites in the winter period and Mau_4,5 in the summer of 2021 (Fig. 5). While in Pudeto, an increase in epiphyte load was observed at sites Pud_5 and Pud_6, during the autumn season of 2021. We highlight these results, as there was a significant increase in epiphyte biomass during 2021 in Maullín and Pudeto, and more importantly, this increase was observed in autumn and winter (Fig. 5).

### Influence of environmental factors on epiphytic macroalgae

During the summer season, the CCA analysis revealed strong correspondence between the studied environmental factors and the presence of two groups of taxa (Fig. 6). Together, both axes of the CCA analysis explained more than 55% of the variability of epiphytic macroalgal assemblages (Fig. 6). The assemblages that were associated with sites with less salinity (negatively correlated with higher salinity) had a higher specific load of the epiphytes *Chaetomorpha linum*, *Grateloupia* sp., *Ceramium* sp. and *Ulva* sp.2 (Fig. 6). Assemblages that were associated with more marine conditions (positively correlated with higher salinity) had a higher specific load of the epiphytes *S. crispata*, *Ulva* sp.3,

**Fig. 3** Epiphyte richness during autumn, winter, spring, and summer in (A) Pudeto and (B) Maullín rivers for every sampling point. Epiphyte richness is expressed as the total number of different taxa identified in the subsample of *Gracilaria*. The bars represent the standard deviation (SD)



*Callithamnion* sp., *Polysiphonia* sp. and *Ulva* sp.1. (Fig. 6). The PERMANOVA results supported the influence of the temporal and spatial variability on the effects of the seasonal changes and horizontal stress gradients on community structure, as the interactive effect of both factors was significant (Table 3, $p < 0.05$). However, significant differences in community composition between localities were detected only in the spring and summer seasons.

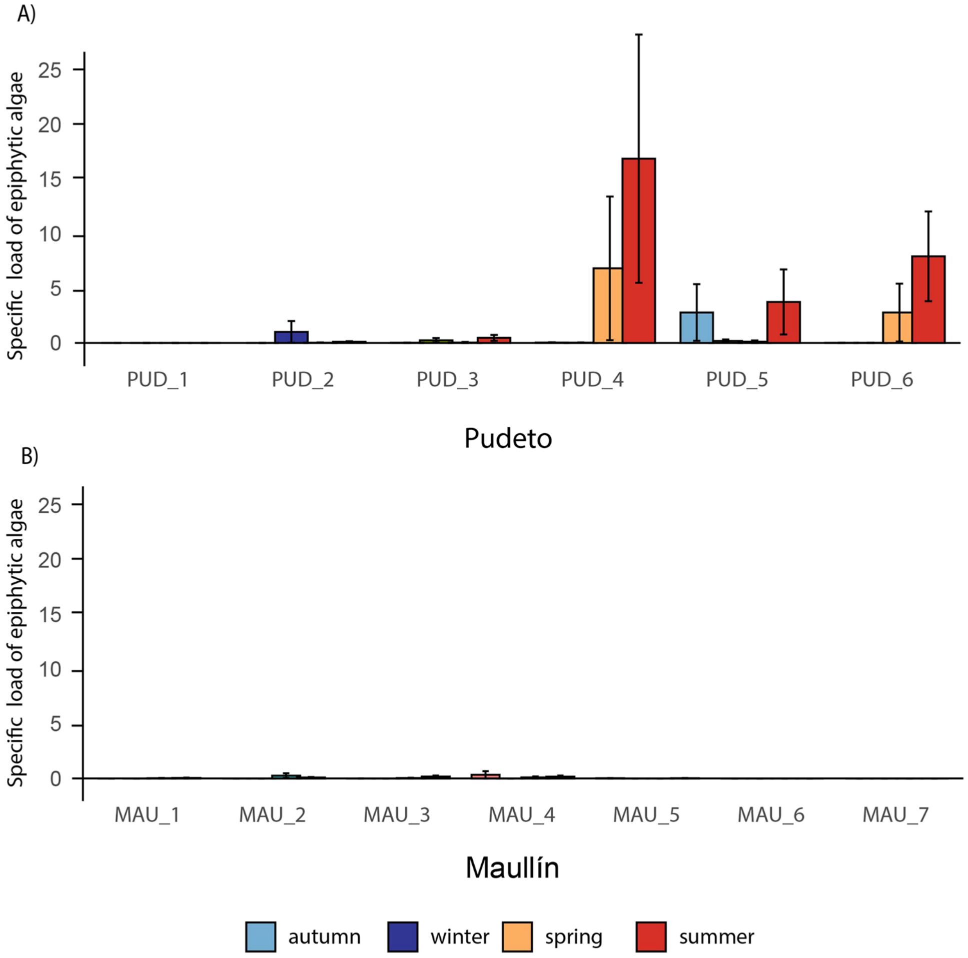
SIMPER analysis showed that the epiphytic community structure is composed of 10 taxa that explain 90% of the dissimilarity between the localities during the Spring and summer season (Supplementary Material S2). The taxa that contribute most to spring dissimilarity (> 50%) were *Callithamnion* sp., *C. linum*, and *Polysiphonia* sp1. (Supplementary Material S1). Meanwhile, during summer, the taxa that contribute most to the dissimilarity (> 50%) were *Ceramium* spp., *Callithamnion* sp., *C. linum*, and *Ulva* sp.2.

When comparing the composition of epiphyte assemblages between 2017 and 2021, PERMANOVA analysis only detected significant differences at the Maullín locality. The SIMPER analysis showed that for both summer and winter seasons the algae that contributed most to the similarity of the assemblage was the taxon *C. linum* (> 70%) (Fig. 7).

## Discusion

This study provides a detailed description and analysis of the richness and abundance patterns of epiphytic algae associated with *Gracilaria chilensis* ("pelillo"), a highly exploited species in the Los Lagos region of southern Chile. The results reveal significant seasonal variations in macroalgal epiphyte assemblage, with the highest richness and abundance observed during summer, and the lowest during autumn and winter. During the spring and summer, the increase of daylight hours and light intensity raises temperature, and nutrient concentration affects algae metabolism directly or indirectly (Rivers and Peckol

**Fig. 4** Specific epiphyte load during autumn, winter, spring, and summer in (A) Pudeto and (B) Maullín rivers for every sampling point**.** Specific epiphyte load is expressed as the proportion of the dry weight of each epiphyte algal species per unit of *G. chilensis* (g). The bars represent the standard deviation (SD)



1995). Increasing temperature and inorganic nutrients, such as nitrate concentration, promotes the proliferation of epiphytic green algae (Wang et al. 2020; Kim et al. 2021). These dynamics align with previous studies on micro- and macroalgal assemblages in the channels and fjords of the Magellan Sub-Antarctic Ecoregion, particularly in Robalo Bay (Ojeda et al. 2019), Otway Sound and the Strait of Magellan (Rosenfeld et al. 2018), and Puerto Montt (Kuschel and Buschmann 1991). In other cold temperate coasts, the seasonality of macroalgal biomass can vary significantly depending on environmental factors specific to the local context (Gunnarsson and Ingolfsson 1995; Paruelo et al. 1998; Bertness et al. 2006; Raffo et al. 2014; Ojeda et al. 2019). For example, in high-latitude regions of the Northern Hemisphere, macroalgal coverage tends to increase during winter and decrease in summer. This pattern is primarily influenced by irradiance and nutrient availability changes, rather than higher temperatures (Gunnarsson and Ingolfsson 1995). In the Magellan channels and fjords ecoregion, the highest richness and biomass of macroalgae are observed during summer. This variation can be attributed to multiple factors, including light availability, photoperiod, nutrient concentration, sea surface temperature, relative humidity, and species composition (Ojeda et al. 2019). Species composition, in particular, plays a crucial role, as it significantly influences the seasonal variation in macroalgal richness and biomass (Gunnarsson and Ingolfsson 1995; Rosenfeld et al. 2018; Ojeda et al. 2019). For instance, when macroalgal assemblages are dominated by ephemeral species such as *Ulva* spp., seasonal fluctuations in richness and biomass tend to be more pronounced (Rosenfeld et al. 2018; Ojeda et al. 2019). Our data indicate that the epiphyte assemblages associated with *Gracilaria* are primarily composed of ephemeral algae, including *C. linum*, *Polysiphonia* spp., *Ceramium* spp., and *Ulva* spp., which reach their highest biomass during spring and summer. The associated macroalgal epiphytes may affect *Gracilaria* growth and biomass, since they can cause the collapse of the host population via shading, increased breakage and reduced nutrient uptake (Ralph et al. 2006).

Dense and prolonged aggregations of epiphytes, primarily ephemeral algae, have frequently been linked to coastal eutrophication processes (Hauxwell et al. 2001; Holmer and

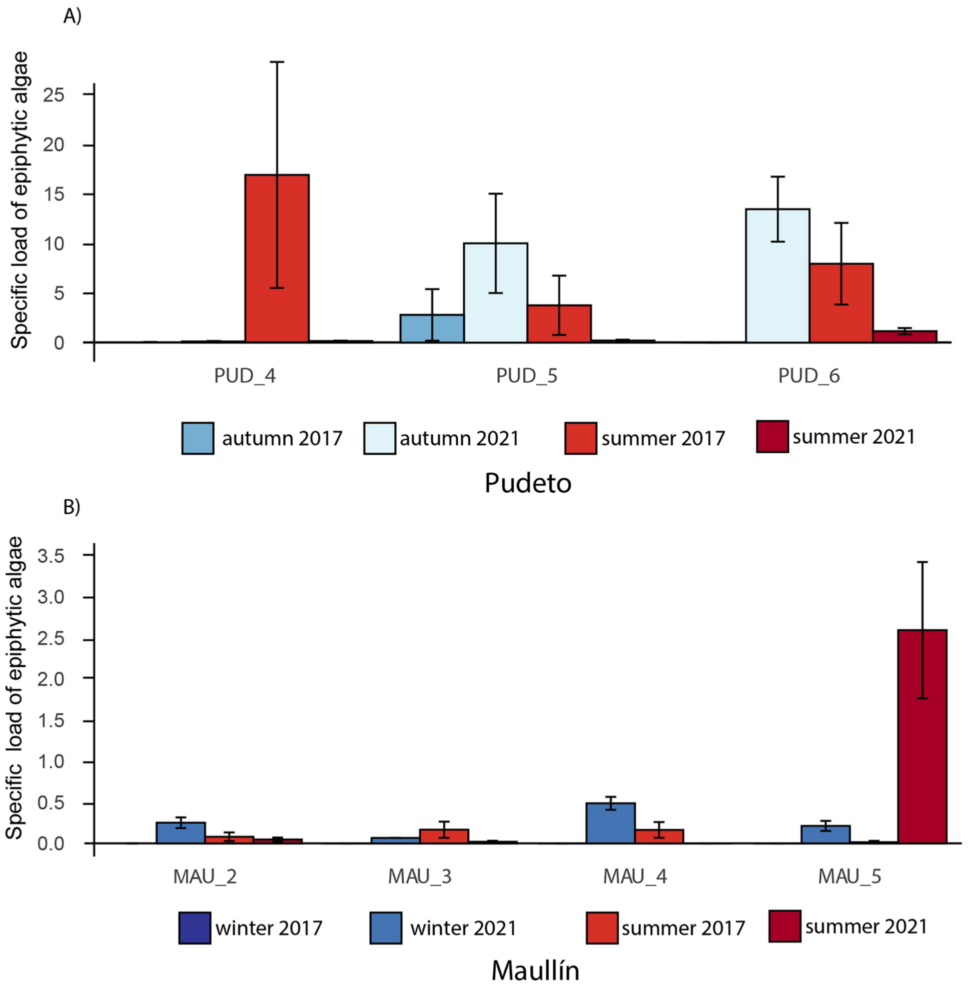


**Fig. 5** Comparative proportion of epiphytism in *Gracilaria chilensis* in 2017 and 2021 from both rivers. A) autumn and summer of 2017 and 2021 for Pudeto, and (B) summer and winter of 2017 and 2021 for Maullín. The bars represent the standard deviation (SD)

Nielsen 2007). However, the coverage of these algae can exhibit significant temporal and spatial variability (Rasmussen et al. 2013). Our findings reveal that in 2017 the epiphyte load in Maullín was generally low and nearly absent during winter, consistent with observations from Puerto Montt (Kuschel and Buschmann 1991). In contrast, by 2021 in the Maullín River, we observed a 20% increase in epiphyte load during winter and a 60% increase during summer in the proportion of epiphytism on *G. chilensis*. This result is particularly significant, as it indicates a notable rise in epiphyte load during a period when epiphytes were previously absent in *Gracilaria* populations. The marked increase in epiphytism at specific Maullín sites between 2017 and 2021 is attributed to the rise in the biomass of *C. linum*. Unlike *Ulva* spp., whose abundance is severely limited in winter due to low salinity, temperature, and irradiance (Zhang et al. 2014), *C. linum* is a bloom-forming macroalga with traits that allow it to persist and proliferate year-round. *Chaetomorpha linum* can capitalize on elevated nutrient concentrations during winter, storing phosphorus to support high growth rates during the summer period, (Lavery and McComb 1991; Xie et al. 2024). *Rhizoclonium* sp. has been officially recorded as the only epiphytic species responsible for plagues in *G. chilensis* farms (Res. Ex. N°2424–2024, SUBPESCA, Ministerio de Economía) in Maullín. Although this may be true, during 2021 we detected a significant increase of *C. linum*, indicating that there has probably been an underestimation of other morphologically similar epiphytic species that could cause green tides.

Another noteworthy result is that Pudeto exhibited a higher epiphyte richness and a more significant proportion of epiphytism throughout the year compared to Maullín. In the Maullín river, *G. chilensis* cultivation is conducted through direct seeding of algal clumps on the soft bottom, using semi-autonomous diving techniques supported by a shovel. In contrast, cultivation in the Pudeto river employs 5 mm ropes to which algae clusters naturally adhere along hundreds of meters. These ropes are anchored to the riverbed with small stakes and aligned with the current within aquaculture concessions. It has been documented that farming practices have significantly altered the life-history traits of *G. chilensis*, including low genetic diversity in vegetatively propagated crops (Guillemin et al. 2008), which may respond differently to physicochemical variables. For

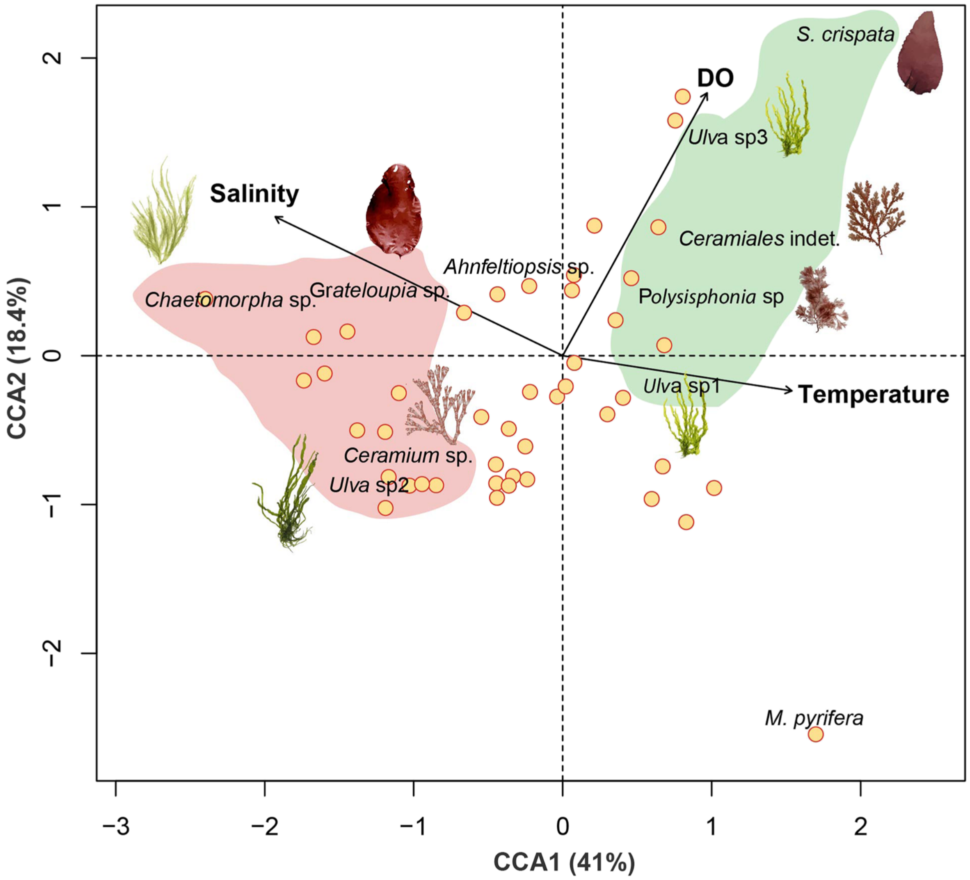


**Fig. 6** Canonical correspondence analysis (CCA) biplot between epiphytes structure assemblage and environmental parameters at Pudeto and Maullín rivers during summer

**Table 3** PERMANOVA results for seasonal variation of epiphytes composition

| Variable | Source of Variability | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|---|
| Composition | Season | 3 | 8133 | 2711 | 7.0397 | 0.0001 |
| | Locality | 1 | 6641.8 | 6641.8 | 6.5747 | 0.0006 |
| | Season × Locality | 3 | 10198 | 1019.8 | 4.7915 | 0.0001 |
| | Sites (Locality) | 11 | 7480.9 | 2493.6 | 6.4753 | 0.0001 |
| | Season × Sites (Locality) | 33 | 11615 | 387.16 | 1.8192 | 0.0001 |
| | Res | | 84279 | 212.83 | | |
| | Total | | 126160 | | | |

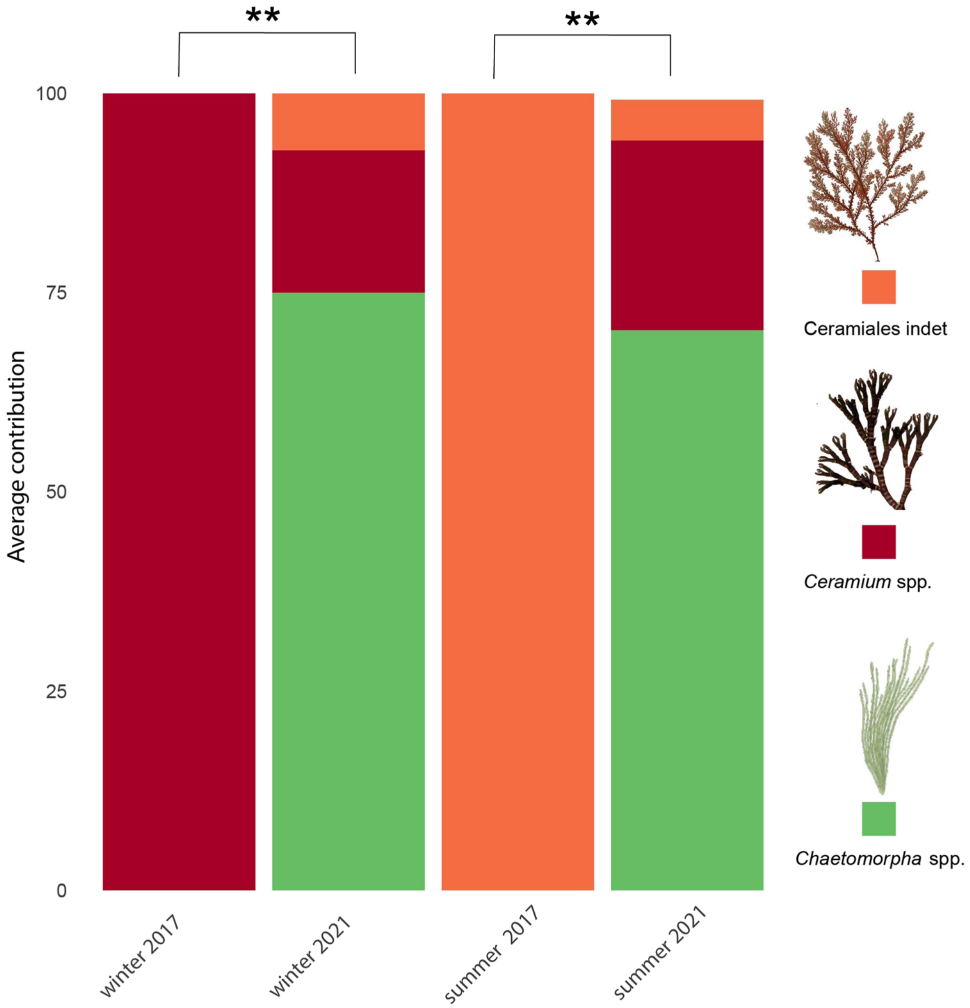
The asterisk (*) states significant differences: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

example, Gallegos Sánchez et al. (2018) farmed populations of *G. chilensis* are less sensitive to salt stress and can grow across a wider salinity range compared to natural populations. Similarly, Usandizaga et al. (2019) demonstrated that farmed populations exhibit growth rates that are less sensitive to temperature variation than their wild counterparts. Our results are in the same direction, in that the farming practice of *G. chilensis* in the Pudeto river by vegetative propagation produces monoclonal populations of *Gracilaria* with a smaller genetic diversity than the wild population, making them more vulnerable to environmental changes. Salinity and temperature play a critical role in shaping the composition and distribution of marine and estuarine organisms. Epiphytic algae were not the exception (Aroca et al. 2020). In this study, we detect that salinity was a critical environmental factor in driving the epiphyte species composition in both rivers, with distinct differences in epiphyte communities occurring along the salinity between the more estuarine conditions of the Pudeto river and the higher salinity conditions in the Maullín river.

## Ecological and economic implications

Epiphyte loads reduce the growth of *G. chilensis*, potentially leading to lower biomass and reduced economic returns for local farmers. The cultivation of *G. chilensis* plays a fundamental role

**Fig. 7** Percentage contribution SIMPER of epiphytes composition assemblage for the winter and summer months in 2017 and 2021 in Maullín River. The contribution limit was 90% of the total composition assemblage. The significance of the differences was inferred through Wilcoxon tests, and p-values (P) are displayed. ** P < 0.001



in the communities of the coastal sectors of Pudeto and Maullín studied, with 16 and 357 active farming centers, respectively (Avila et al. 2019). However, the seasonality of cultivation, with income concentrated in spring and summer and low prices for "pelillo" and issues with epiphytes, has diminished interest in this activity. Alternatives such as using stranded seaweed to produce biofertilizers and biorefineries have been explored, demonstrating their potential to generate added value (McHugh 2003; Tang et al. 2009; Prasad et al. 2010; Zhang et al. 2013; Sarkar et al. 2018). To counteract this trend, it is crucial to promote innovative initiatives that enhance the value of cultivated *G. chilensis* and encourage value-added uses for epiphytic algae.

Farmers affected by epiphytism have reduced production, facing significant economic losses. This situation has worsened over time as the phenomenon has spread, increasing the number of affected areas, similar to what has been observed in China with the"green tides"(Liu et al. 2010; Zhang et al. 2019).

Both rivers (Maullín and Pudeto) are experiencing a progressive accumulation of sediments due to decreased currents caused by human activities such as abandoned road infrastructure and the illegal use of poles to delimit and retain *G. chilensis* algae. These alterations have changed the depth and substrate composition in farming areas, resulting in a significant reduction in productive habitats. Economic uncertainty has driven labour migration, leaving many households, often managed by women, to take on the role of providers partially (Fernández et al. 2024).

It is concerning that no effective mitigation and eradication program exists. While restrictions on seed transport have been implemented, they have not prevented the spread of the pest to new areas. Establishing working groups that include government representatives, universities, and producers is crucial to designing mitigation strategies based on scientific evidence. These measures should be complemented with continuous monitoring programs and adaptive management strategies.

Government efforts have primarily focused on funding monitoring programs to record epiphyte abundance. However, no comprehensive plan has been developed to translate these results into concrete mitigation and eradication measures, limiting their effectiveness in addressing the problem.

## Conclusions

From an ecological and economic perspective, the proliferation of epiphytes threatens the sustainability of *G. chilensis* aquaculture. This can lead to reduced yields, economic instability for local farmers, and potential long-term consequences for the industry. The increasing presence of epiphytes outside their typical seasonal patterns, particularly during winter, suggests that environmental shifts and farming practices may exacerbate the problem.

Given the economic and social importance of cultivating *G. chilensis*, immediate and integrated management strategies are needed. Future efforts should include improved monitoring, mitigation measures, and adaptive farming techniques to control epiphyte proliferation. Collaboration among government agencies, researchers, and local farmers will be crucial to ensuring the long-term sustainability of this vital aquaculture resource.

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## Declarations

**Competing interests** The authors declare no competing interests.

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