



# Natural biocontrol of a *Porphyra* sp. pest on farmed *Gracilaria chilensis* by a pythiosis outbreak

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## Abstract

*Gracilaria chilensis* (a.k.a. pelillo) is the most produced seaweed in Chile and Latin America, yet its cultivation has historically faced lots of pest-associated constraints that threaten its profitability and sustainability. Pests show temporal cycles of recruitment, growth and death/senescence, variation normally linked with sharp changes in environmental factors occurring in estuarine areas where *Gracilaria* is cultivated. Here we report the appearance of a bladed Bangiales species epiphytic on long-line farmed *Gracilaria* and identified as *Porphyra*. This species recruits to cover up to 50–72% of *G. chilensis* early in a suspended set-up in spring, until a filamentous fungal-like organism colonizes *Porphyra* blades, infecting a wide proportion of its tissue. After this outbreak, *Porphyra* recruits collapse, disappearing in few weeks from farmed *Gracilaria*. Observations of diseased individuals, and subsequent isolation and marker-assisted taxonomy of the pathogen, provide evidence for the identification of this organism as *Pythium porphyrae*, the aetiological agent for the red rot disease in commercial nori/gim in Asia. This is the first reported case for *P. porphyrae* in Chile and the Southeastern Pacific as well as for a disease-driven natural biocontrol of a *Gracilaria* pest alga, suggesting an unknown -yet considerable- cryptic biodiversity acting as natural regulators of natural pests during a *Gracilaria* cultivation cycle.

**Keywords** Algal parasite · Epiphyte · Oomycete · *Pythium porphyrae* · Red rot disease

## Introduction

*Gracilaria* production has become a significant component of the global aquaculture industry. With its versatile applications in food, pharmaceuticals, cosmetics, and biofuel, *Gracilaria* cultivation has expanded worldwide (Ferdouse et al. 2018). Several countries have emerged as key players in *Gracilaria* production, including China, Indonesia, the Philippines, Vietnam, and Chile (Mantri et al. 2023). As global demand for seaweed products continues to rise, the production of *Gracilaria* is poised to play an increasingly

vital role in meeting these growing needs while promoting economic development and environmental sustainability. Concomitantly, *Gracilaria* also represent a valuable resource for local communities, as its farming is carried out mainly by local fishermen, contributing directly or indirectly to meet at least five independent United Nations SDGs goals (goals 1, 5, 8, 12 and 14; see <https://sdgs.un.org/goals>).

*Gracilaria chilensis* (a.k.a. pelillo) is the most produced seaweed in Chile via aquaculture (Buschmann et al. 2017). Chilean farmers have adopted both traditional direct “off-bottom” planting (Buschmann et al. 1995) and innovative farming methods, utilizing coastal ponds (Santelices and Doty 1989), long-lines (Westermeier et al. 1993), indoor (Caroca-Valencia et al. 2023) and integrated multi-trophic systems (Abreu et al. 2009) to grow this seaweed. Historically, pelillo farming in Chile has faced recurrent pest outbreaks which stagnate the expansion of the Chilean industry (Mendez et al. 2024). Pests such as epiphytic organisms, fouling species, grazers, and pathogens can compete with *Gracilaria* for resources, inhibit its photosynthetic efficiency, and cause physical damage to the seaweed fronds (Buschmann et al. 1997; Leal et al. 2020). As a result, the

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affected *G. chilensis* may exhibit stunted growth, decreased reproductive output, and increased susceptibility to diseases (Fletcher 1995). Moreover, pest and disease outbreaks can escalate rapidly, spreading between farms or wild stocks, exacerbating the ecological impact and posing a significant biosecurity risk to the surrounding marine environment (Murúa et al. 2023).

A poorly studied aspect on seaweed farming is the interaction of cultivated stocks with local ecosystems, for example pest ecology. In terms of *Gracilaria* pests, there is some knowledge of algal pests being controlled by grazers such as polychaetes controlled by foraging seabirds (Martínez-Curci et al. 2023). Nevertheless pathogen-mediated biocontrol is much as unclear as the general knowledge of algal disease in Latin America (Murúa et al. 2021). In recent observations within a *G. chilensis* suspended system, we identify a fungal-like outbreak that unexpectedly acts as a natural biocontrol agent, effectively suppressing a prevalent seaweed pest population of *Porphyra*. We identified the oomycete species responsible for such pest control, their interactions with the targeted pest, and the potential implications for sustainable *Gracilaria* farming. By exploring the ecological factors contributing to the fungal outbreak and its impact on pest populations, we hope to gain valuable insights into the natural biocontrol mechanisms in seaweed farming systems. This research not only highlights the potential of utilizing natural agents for pest management but also offers prospects for developing eco-friendly strategies to enhance the resilience and productivity of *Gracilaria* cultivation.

## Materials and methods

### Sampling

A suspended *Gracilaria chilensis* set-up was installed in Cariquilda estuary (41.624°S; 73.591°W; Fig. 1A) in spring 2022 (28–09-2022), in order to evaluate epiphyte succession of pests on a biweekly basis. Five 5 m long long-lines (n=5) seeded at ca. 120 g m<sup>-1</sup> were installed superficially (1 m depth). From every long-line, 30 cm were harvested biweekly for *Gracilaria* biomass and pest load estimations. In particular, we focused on epiphytic *Porphyra* (Fig. 1B), which was estimated by i) its coverage on 50 randomly harvested *Gracilaria* filaments measured linearly on a millimeter paper and ii) the epiphyte weight in terms of 100 g of its basiphyte. As a matter of fact, both proxies are correlated (R<sub>2c</sub> = 0.999; p = 0.003; Fig. 2A), and coverage will be used for *Porphyra* abundance hereafter. Additionally, fifteen *Porphyra* individuals per sample were dissected for the estimation of the prevalence of the fungal-like disease.

Statistical analyses were carried out using R (R Core Team 2018). To demonstrate a potential link between

coverage and weight of *Porphyra* recruits, data were fit to a generalised linear mixed model (GLMM) with Poisson error structure using the {glmer} function of the “lme4” package, where long-line measured and time (n° week) were set-up as random effects (Bates et al. 2015). Likewise, to assess the association *Pythium* prevalence and *Porphyra* coverage or week, another GLMM was performed with Poisson error structure and long-line as random effect model. Pairwise comparisons were done applying a Tukey test on the GLMM models using the library “lsmeans” (Lenth 2016). Both conditional (r<sub>2c</sub>, fixed, and random effects) and marginal (r<sub>2m</sub>, fixed-factors effects) goodness of the fits were calculated to estimate the impact of our random effects (Johnson 2014).

### Oomycete isolation

*Porphyra* blades symptomatic for the red rot disease were acquired from our *Gracilaria* farm facility by 10–11-2022. These samples were carefully stored in 50 mL Falcon tubes in a cooled container with ice packs and transported to the FICOPAT lab (UACH) in Puerto Montt, Chile. To isolate the pathogen, we placed infected tissues (ca. 3 mm diameter each) on 1.7% corn meal agar (CMA BBL) plates, prepared in filtered (0.2 µm) and autoclaved seawater from the estuary with a salinity of 25 PSU. Additionally, before pouring the agar, we supplemented with 200 mg mL<sup>-1</sup> of penicillin and streptomycin sulphate to prevent bacterial contamination (Atami et al. 2009).

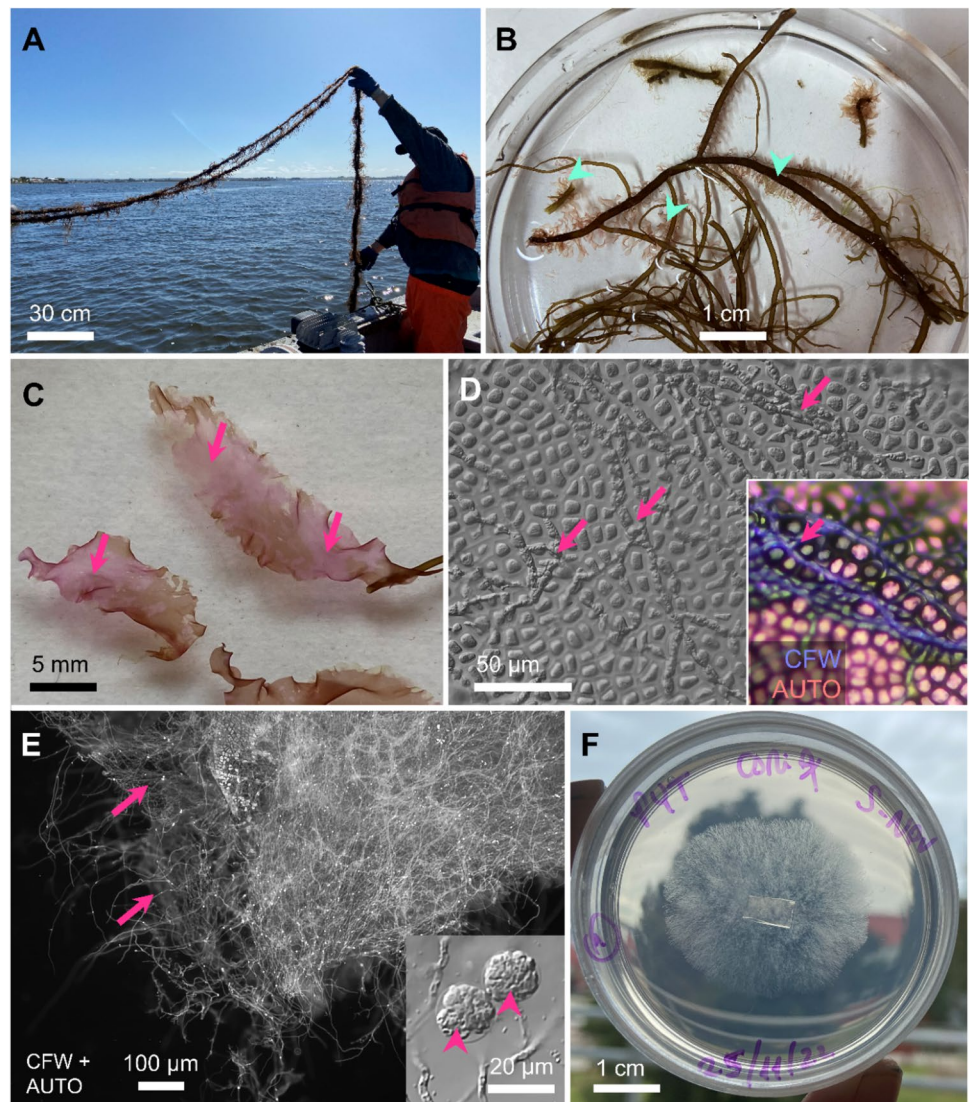
The agar dishes were sealed using Parafilm and then incubated at 12 °C in darkness. They were monitored daily for hyphal growth. After 14 days incubation, single hyphal tips were excised out the agar cultures and transferred to a fresh CMA in Petri dishes, to establish pure cultures. As these visible mycelia grew, we aseptically subcultured single hyphal tips by transferring them to Petri dishes with fresh medium. This process was repeated several times until the cultures were completely free of any visible bacterial or protist contamination.

### Microscopy and molecular diagnoses

Microscopical observations of diseased *Porphyra* and oomycete isolates were performed on fresh material. Samples were mounted using a Calcofluor white (CFW) solutions (0.02 mg mL<sup>-1</sup> in seawater; Gachon et al. 2017), observed and imaged on a Zeiss Microscope Axioscope 5 DIC and epifluorescence microscope with a Axiocam 202 Color digital camera, under a Colibri 3 Illumination System.

For molecular diagnoses, samples were DNA-extracted using a commercial kit (GeneJet DNA extraction kit, Thermofisher). PCRs were performed to amplify 18S (primer pairs F139/R1233 complemented with EUK422-445/EUK1422-1440\_R and TK18Sfwd/ TK18Srev,

**Fig. 1** Identification of the red rot disease agent *Pythium porphyrae* on *Gracilaria*-epiphytic *Porphyra* sp. A: *Gracilaria chilensis* farmed on a suspended long-line in the Cariquilda estuary. B: macroscopic view of *Gracilaria* filaments colonized by *Porphyra* recruits (arrowheads). C: *Porphyra* sp. symptomatic for a Pythiosis (a.k.a. red rot disease in case of Bangiales, arrows). D: upon magnification, necrotic areas show the infection by filamentous fungal like structures, which introduce within *Porphyra* tissues and cells. Inset: after calcofluor white staining (CFW), pathogen cells can be easily spotted inside the host tissue under UV light. AUTO: Chlorophyll autofluorescence. E: in older cultures, *P. porphyrae* overgrew *Porphyra* blades (arrows) and cover most of the tissues. Inset: *Pythium* sporangia (arrowheads) in heavily infected tissues. F: A *Pythium porphyrae* isolate growing in CMA culture media



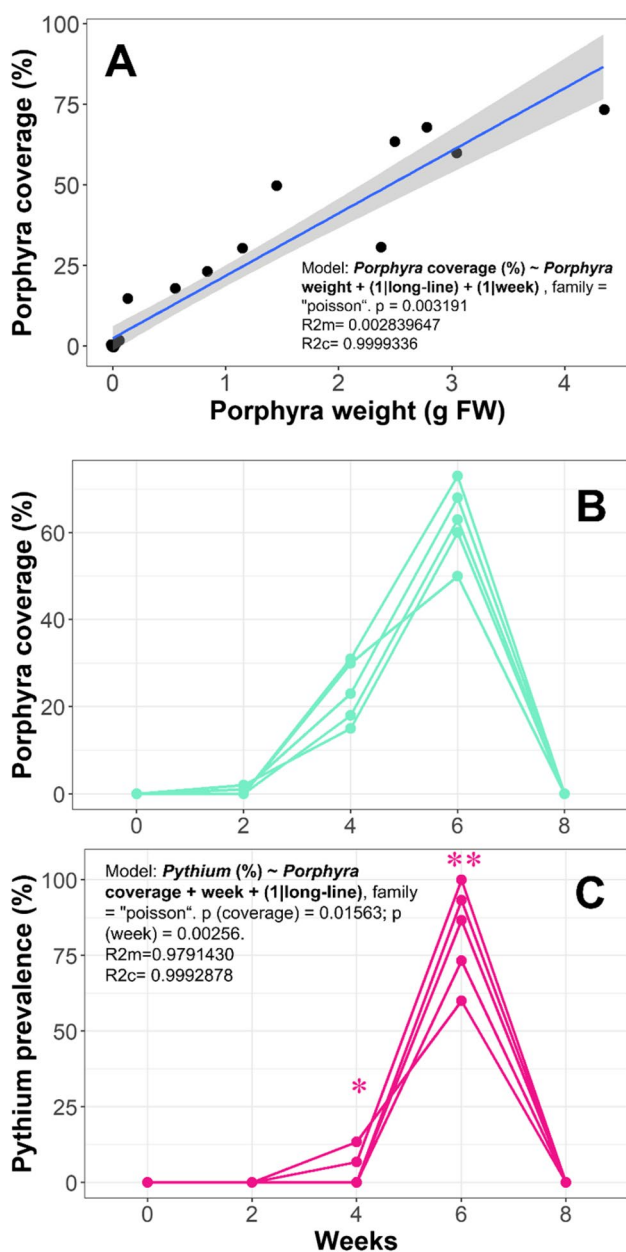
annealing = 55 °C), COI (primers TKCOIfwd -TKCOIrev, annealing = 55 °C) and COII (primers COX2-For3 – COX2-Rev3, annealing = 55 °C) regions (Sekimoto et al. 2007, 2008; Wang et al. 2014; Gachon et al. 2017; Klochkova et al. 2017b), using reagent concentrations established in Murúa et al. (submitted), and sequenced by Sanger (Macrogen). Phylogeny reconstructions were inferred by aligning *Pythium* clade I and II sequences available in NCBI in addition to those newly generated by this study (accessions: PP481400/PP481401 for 18S, PP503415 for COI and PP493240/PP493240 for COII). Alignments were performed using MAFFT (Katoh and Standley 2013) and modelled for phylogeny reconstruction using RAxML version 8.2.11 with 1000 bootstrap replications (Stamatakis 2014) and MrBayes version 3.2.6 using default settings four MCMC chains (Ronquist et al. 2012), implemented in Geneious v11 (Kearse et al. 2012). Analyses were made for each gene separately.

## Results

Once the *Gracilaria* set-up was installed (Fig. 1A), *Porphyra* recruitment started right away after two weeks and progressively increased to reach a peak after 6 weeks of cultivation (50–72%) (Figs. 1B, 2B). At the 8th week, there was a collapse of epiphytic *Porphyra* on *Gracilaria* thalli, with no visible recruits or elongated *Porphyra* from previous months.

Concomitantly, *Porphyra* started to show changes in coloration over the course of cultivation. Whilst 2-week-old *Porphyra* looked dark red, 4- and 6-weeks old specimens show irregular pink areas across the thalli, of variable irregular areas (Fig. 1C). Under the microscope, such areas evidenced an intracellular hyphal organism infecting the host cells (Fig. 1D), which contained a cellulosic/quintinated





**Fig. 2** Variations of *Porphyra* epiphytic load and *Pythium* prevalence during a *Gracilaria chilensis* suspended set-up. **A:** both *Porphyra* coverage and weight are strongly correlated, after a Generalised linear mixed model including the long-line sampled and the week as random effects. **B:** *Porphyra* abundance variation in 8-week *Gracilaria* farming. **C:** *Pythium* prevalence variation (% diseased *Porphyra* specimens) over the same 8-week course. Both weeks and *Porphyra* coverage were significant for the GLMM model fit

cell walls and caused necrosis in neighbouring host cells. In very infected host tissues (ca. 6 weeks old), such hyphae emerged and formed extra-tissular complexes that included sporangia of 15–20  $\mu\text{m}$  diameter in their tips (Fig. 1E). The prevalence of diseased *Porphyra* follows the same pattern of rise and fall of its recruitment (Fig. 2C), with symptomatic

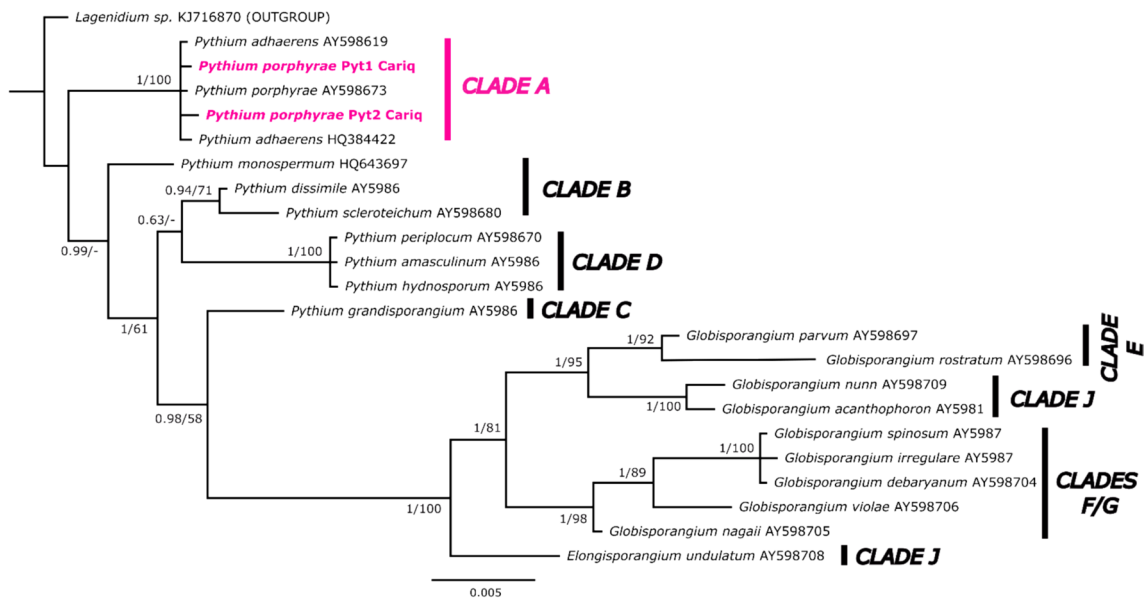
individuals detected after 4 weeks (up to 12%), reaching a peak of infection (60–100%) at 6 weeks, and no records at 8 weeks.

The symbionts were culturable in solid medium (CMA medium; Fig. 1F). We obtained two fungal-like strains from infected *Porphyra* (Pyt1 Cariq and Pyt2 Cariq), which were subjected to molecular phylogeny. Both isolates were identical for 18S sequences and differed in only two bases for COII nucleotide sequences. The phylogenetic analyses, under both RAxML and MrBayes, showed that Chilean samples formed a well-supported clade within *Pythium* clade A, using 18S, COI and COII (Figs. 3, 4 and 5). Within this clade, our isolates share monophyly with *Pythium chondricola*, *P. porphyrae*, and to a lesser extent *P. adhaerens*. Members of *P. porphyrae* includes specimens from Japan, China, Korea and New Zealand, suggesting a cosmopolitan distribution of the species.

## Discussion

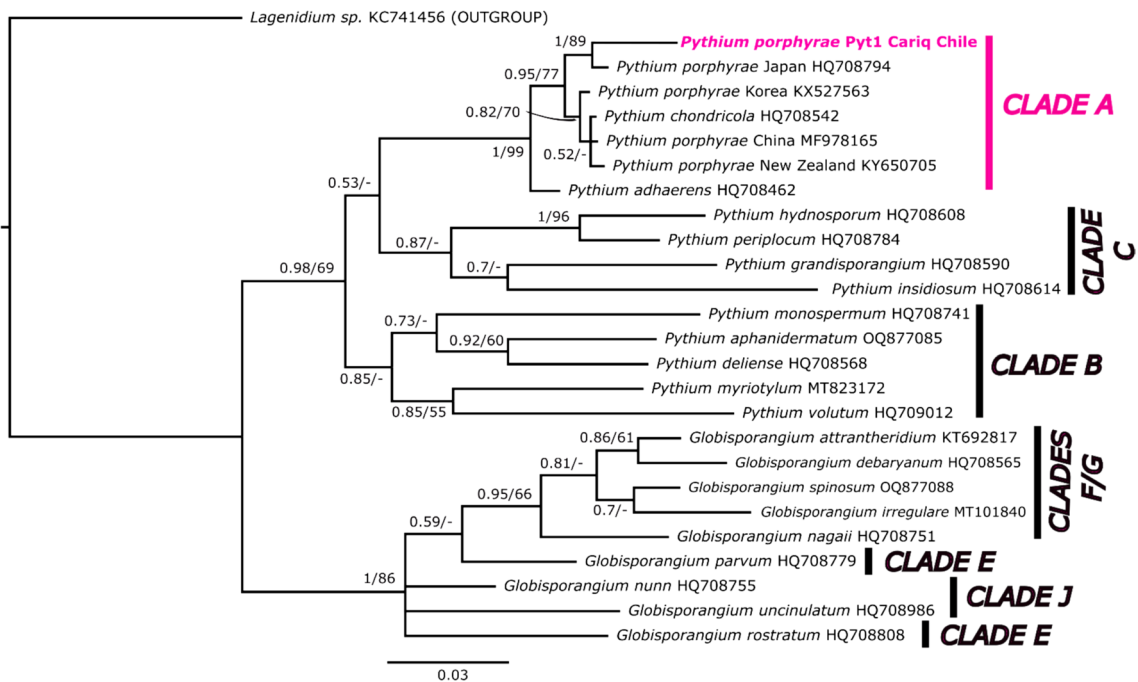
Pest outbreaks are keystone factors regulating profitability and sustainability in seaweed aquaculture (Brakel et al. 2021; Murúa et al. 2023). In *G. chilensis* farms, pests such as worms (Polychaeta), ceramialean blooms or green tides have historically had significant consequences on both the cultivated seaweed, the overall aquaculture operations, and the social acceptability of surrounding settlements (Mantri et al. 2023). For instance, these outbreaks end up with *Gracilaria* reduced biomass, mixed with contaminants (e.g., pests), stunted morphologies and sometimes diminished biochemical quality; thus, economic detriment for farmers (Fletcher 1995). Furthermore, major decomposing pest drifts may lead to human health problems. Such consequences underscore the importance of effective pest identification and management strategies, including early detection, proper sanitation measures, and the implementation of biosecurity protocols (Mendez et al. 2024). By preventing and mitigating the impact of pest outbreaks, farmers can safeguard the health and productivity of seaweed farms, ensuring the sustainability and success of valuable seaweed aquacultural species (Cottier-Cook et al. 2021, 2022).

In Chile, *G. chilensis* has been extensively farmed in systems with direct attachment to substrata (Buschmann et al. 1995). Nevertheless, suspended lines have drawn some attention, as the cultivable areas can be expanded from tidal-affected regions towards offshore. Suspended systems had suggested a lower epiphytic load than direct attachment (Westermeyer et al. 1993), in contrast to abundant filamentous red and brown seaweeds that are very common in traditional systems (Leonardi et al. 2006). Nonetheless, a different bathymetrical level potentially incorporates new ecological interactions. For example, *Porphyra* species had



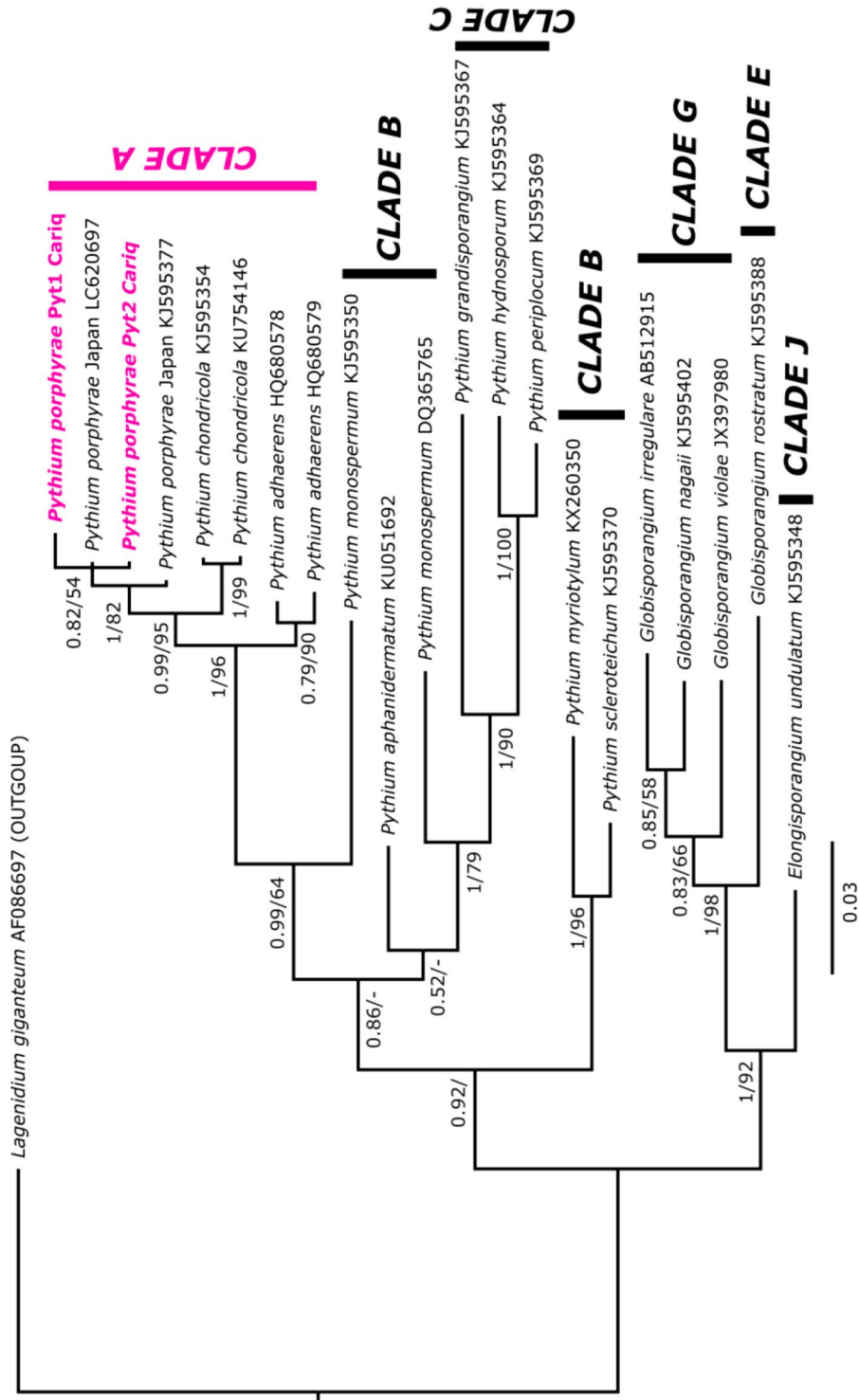
**Fig. 3** Bayesian phylogenetic tree reconstruction of Chilean *Pythium porphyrae* (in bold pink within the tree) and available *Pythium* SSU rDNA sequences. The tree contains a total of 23 sequences and 1834 nucleotide positions. Support values given are posterior probabilities (MrBayes)/

bootstrap support (RAxML). MrBayes settings: chain length 1.000.000, subsample frequency 1.000, burn in of 10%. The scale bar indicates the number of substitutions per site



**Fig. 4** Bayesian phylogenetic tree reconstruction of Chilean *Pythium porphyrae* (in bold pink within the tree) and available *Pythium* COI mtDNA sequences. The tree contains a total of 26 sequences and 682 nucleotide positions. Support values given are posterior probabilities (MrBayes)/

bootstrap support (RAxML). MrBayes settings: chain length 1.000.000, subsample frequency 1.000, burn in of 10%. The scale bar indicates the number of substitutions per site



**Fig. 5** Bayesian phylogenetic tree reconstruction of Chilean *Pythium porphyrae* (in bold pink within the tree) and available *Pythium* COII mtDNA sequences. The tree contains a total of 22 sequences and 615 nucleotide positions. Support values given are posterior probabilities (MrBayes)/bootstrap support (RAxML). MrBayes settings: chain length 1,000,000, subsample frequency 1,000, burn in of 10%. The scale bar indicates the number of substitutions per site

not been recognized in off-bottom systems as a significant epiphytic pest affecting *Gracilaria* farms (Candia et al. 2006). Nevertheless, in our study *Porphyra* was one of the most abundant epiphytes in suspended systems during 2022 and 2023 (unpublished). It is unknown how *Gracilaria* would be affected in terms of growth, survival or biochemical quality (e.g. agar composition) in case *Porphyra* would keep growing, although due to its superficial attachment (type 1–2 after Leonardi et al. 2006), it is presumed a significant competitive interaction only when blades are considerably larger. On the other hand, *G. chilensis* was not observed affected by *P. porphyrae*. Despite its initial abundance, *Porphyra* co-existence in *Gracilaria* farms is rather ephemeral, suggesting an outward disruption source during *Porphyra* recruitment and settlement during the initial weeks.

In this system we report a third party: a fungal-like organism inhabiting *Porphyra*, whose prevalence was directly linked with the demise of *Porphyra* recruits. Identified as *Pythium porphyrae* after marker-assisted taxonomy, the facultative parasitic oomycete caused pink lesions and massive mortality in *Porphyra* blades, resembling red rot disease symptoms (Klochkova et al. 2017a). Our molecular data suggests that Chilean *Pythium* is very similar genetically to those found on *Pyropia plicata* in New Zealand (Diehl et al. 2017) and *Porphyra* and *Pyropia* spp. in China, Korea and Japan (Kawamura et al. 2005; Kim et al. 2014; Qiu et al. 2019). Our phylogenetic analyses also suggest the conspecificity between *P. porphyrae* and *P. chondricola* (Diehl et al. 2017), with neither morphological nor genetic dissimilarity except for COII, which are rather different between them (Robideau et al. 2011; Lee and Lee 2022). Both species have been isolated primarily from algae (Lee et al. 2015), and can 100% identical using other sequences such as ITS1 (Lévesque and De Cock 2004). More powerful techniques (e.g., phylogenomic, phenomics) will be requested in order to pinpoint the specific genetic and phenotypic differences between both traits and to know whether they are currently under a speciation process.

The three-party interaction described here raises important questions about the utilization of microbes in seaweed pest biocontrol. Because of the fragility and dynamisms of the aquatic environment, it is highly non recommendable to use chemical methods for pest control as in terrestrial agriculture (Pawan Kumar et al. 2023). Managing pest suppression by the addition of specific microorganisms or complete microbial communities resulted as an eco-friendly alternative of controlling unwanted organisms (O’Hanlon et al. 2012). In forestry, it is increasingly common the use of native entomopathogenic fungi, bacteria and viruses for the natural biocontrol of insect pests (Dara et al. 2019). In aquatic systems, seaweed fitness has been improved by other accompanying organisms. For example, some mesograzers increased *Gracilaria foliifera* fitness by eating epiphytes that

compete with their host (Brawley and Adey 1981). Similarly, amphipods reduced epiphytic biomass from the seaweed *Sargassum filipendula* (Duffy 1990). As bioengineers, *Gracilaria* also increase the invertebrate biodiversity in the farming area, increasing worm pests that are controlled by migratory birds (Martínez-Curci et al. 2023). In our study we describe a microorganism regulating a macroalgal pest management of a commercially important seaweed. In spite of its potential use for biocontrol in *Gracilaria* aquaculture, its use must be carefully assessed in terms of suitability and environmental impacts.

In contrast to long-lasting pests, *Porphyra* was quickly controlled by the naturally-occurring *P. porphyrae*, counteracting *Porphyra* prevalence to non-detectable levels and indirectly aiding farmed *Gracilaria*. Nevertheless, *P. porphyrae* has been described as a significant biosecurity threat on *Pyropia* and *Porphyra* farms in Asia (Badis et al. 2020). For the first time, we report this parasite in Chilean waters, proposing a widespread distribution alongside subantarctic ecosystems. These records add up to latest records of another pathogenic oomycete of Bangiales, such as *Olpidiopsis* (sensu lato) *porphyrae* in the Southeastern Pacific (Murúa et al. submitted). Both parasites affect farmed and cultivated specimens, whose impact in natural populations or incipient *Pyropia* aquaculture is yet to be assessed.

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**Author contributions** Original concept (LM, PM); field collections and sampling (LM, DJP); strain isolation and laboratory culturing (LM); microscopy (PM); phylogenetic analyses (PM, LM); drafting the manuscript (LM); editing the manuscript (All authors).

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**Data availability** Data obtained in the experiments herein can be available upon request.

## Declarations

**Competing interests** The authors have no competing interest to declare.

## References

- Abreu MH, Varela DA, Henríquez L, Villarroel A, Yarish C, Sousa-Pinto I, Buschmann AH (2009) Traditional vs. integrated multi-trophic aquaculture of *Gracilaria chilensis* C. J. Bird, J. McLachlan & E. C. Oliveira: Productivity and physiological performance. *Aquaculture* 293:211–220
- Atami H, Muraosa Y, Hatai K (2009) Halioticida Infection found in wild Mantis Shrimp *Oratosquilla oratoria* in Japan. *Fish Pathol* 44:145–150

- Badis Y, Han JW, Klochkova TA, Gachon CMM, Kim GH (2020) The gene repertoire of *Pythium porphyrae* (Oomycota) suggests an adapted plant pathogen tackling red algae. *Algae* 35:133–144
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Soft* 67:1–48
- Brakel J, Sibonga RC, Dumilag RV, Montalescot V, Campbell I, Cottier-Cook EJ, Ward G, Le Masson V, Liu T, Msuya FE, Brodie J, Lim P, Gachon CMM (2021) Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture. *Plants People Planet* 3:337–349
- Brawley SH, Adey WH (1981) The effect of micrograzers on algal community structure in a coral reef microcosm. *Mar Biol* 61:167–177
- Buschmann AH, Westermeier R, Retamales CA (1995) Cultivation of *Gracilaria* on the sea-bottom in southern Chile: a review. *J Appl Phycol* 7:291–301
- Buschmann AH, Retamales CA, Figueroa C (1997) Ceramialean epiphytism in an intertidal *Gracilaria chilensis* (Rhodophyta) bed in southern Chile. *J Appl Phycol* 9:129–135
- Buschmann AH, Camus C, Infante J, Neori A, Israel Á, Hernández-González MC, Pereda SV, Gomez-Pinchetti JL, Golberg A, Tadmor-Shalev N, Critchley AT (2017) Seaweed production: overview of the global state of exploitation, farming and emerging research activity. *Eur J Phycol* 52:391–406
- Candia A, Galleguillos F, Nuñez M, Aroca GE (2006) Avances en el mejoramiento productivo del “pelillo”. Proyecto FDI – CORFO 01CR3PT-13. Instituto de Fomento Pesquero, Puerto Montt
- Caroca-Valencia S, Rivas J, Araya M, Núñez A, Piña F, Toro-Melgado F, Contreras-Porcía L (2023) Indoor and outdoor cultures of *Gracilaria chilensis*: Determination of biomass growth and molecular markers for biomass quality evaluation. *Plants* 12:1340
- Cottier-Cook EJ, Nagabhatla N, Asri A, Beveridge M, Bianchi P, Bolton J, Bondad-Reantaso MG, Brodie J, Buschmann A, Cavarubias J, Campbell I, Chopin T, Critchley AT, De Lombaerde P, Doumeizel V, Gachon CMM, Hayashi L, Hewitt CL, Huang J, Hurtado AQ, Kambey CSB, Kim GH, Le Masson V, Lim P, Liu T, Malin G, Matoju I, Montalescot V, Msuya FE, Potin P, Puspita M, Qi Z, Shaxson L, Sousa-Pinto I, Stentiford GD, Suyo GD, Yarish C (2021) Ensuring the sustainable future of the rapidly expanding global seaweed aquaculture industry – a vision. 1). Ensuring the sustainable future of the rapidly expanding global seaweed aquaculture industry – a vision. United Nations University Institute on Comparative Regional Integration Studies and Scottish Association for Marine Science Policy Brief
- Cottier-Cook EJ, Cabarubias JP, Brakel J, Brodie J, Buschmann AH, Campbell I, Critchley AT, Hewitt CL, Huang J, Hurtado AQ, Kambey CSB, Lim PE, Liu T, Mateo JP, Msuya FE, Qi Z, Shaxson L, Stentiford GD, Bondad-Reantaso MG (2022) A new Progressive management pathway for improving seaweed biosecurity. *Nat Commun* 13:7401
- Dara SK, Montalva C, Barta M (2019) Microbial control of invasive forest pests with entomopathogenic fungi: A review of the current situation. *InSects* 10:341
- Diehl N, Kim GH, Zuccarello GC (2017) A pathogen of New Zealand *Pyropia plicata* (Bangiales, Rhodophyta), *Pythium porphyrae* (Oomycota). *Algae* 32:29–39
- Duffy JE (1990) Amphipods on seaweeds: partners or pests? *Oecologia* 83:267–276
- Ferdouse F, Holdt SL, Smith R, Murúa P, Yang Z (2018) The global status of seaweed production, trade and utilization. FAO Globefish Research Program, FAO, Rome
- Fletcher RL (1995) Epiphytism and fouling in *Gracilaria* cultivation: an overview. *J Appl Phycol* 7:325–333
- Gachon CMM, Strittmatter M, Badis Y, Fletcher KI, West PV, Müller DG (2017) Pathogens of brown algae: culture studies of *Anisolpidium ectocarpii* and *A. rosenvingei* reveal that the Anisolpidiales are uniflagellated oomycetes. *Eur J Phycol* 52:133–148
- Johnson PCD (2014) Extension of Nakagawa & Schielzeth’s  $R^2$  GLMM to random slopes models. *Meth Ecol Evol* 5:944–946
- Katoh K, Standley DM (2013) MAFFT Multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biol Evol* 30:772–780
- Kawamura Y, Yokoo K, Tojo M, Hishiike M (2005) Distribution of *Pythium porphyrae*, the causal agent of red rot disease of *Porphyra* spp., in the Ariake Sea. *Japan Plant Dis* 89:1041–1047
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28:1647–1649
- Kim GH, Moon K-H, Kim J-Y, Shim J, Klochkova TA (2014) A reevaluation of algal diseases in Korean *Pyropia* (*Porphyra*) sea farms and their economic impact. *Algae* 29:249–265
- Klochkova TA, Jung S, Kim GH (2017a) Host range and salinity tolerance of *Pythium porphyrae* may indicate its terrestrial origin. *J Appl Phycol* 29:371–379
- Klochkova TA, Kwak MS, Kim GH (2017b) A new endoparasite *Olpidiopsis heterosiphoniae* sp. nov. that infects red algae in Korea. *Algal Res* 28:264–269
- Kumar P, Kumar R, Thakur K, Mahajan D, Brar B, Sharma D, Kumar S, Sharma AK (2023) Impact of pesticides application on aquatic ecosystem and biodiversity: A review. *Biol Bull Russ Acad Sci* 50:1362–1375
- Leal PP, Ojeda J, Sotomayor C, Buschmann AH (2020) Physiological stress modulates epiphyte (*Rhizoclonium* sp.)-basiphyte (*Agarophyton chilense*) interaction in co-culture under different light regimes. *J Appl Phycol* 32:3219–3232
- Lee SJ, Lee S-R (2022) Rapid detection of red rot disease pathogens (*Pythium chondricola* and *P. porphyrae*) in *Pyropia yezoensis* (Rhodophyta) with PCR-RFLP. *Plant Dis* 106:30–33
- Lee SJ, Hwang MS, Park MA, Baek JM, Ha D-S, Lee JE, Lee S-R (2015) Molecular identification of the algal pathogen *Pythium chondricola* (Oomycetes) from *Pyropia yezoensis* (Rhodophyta) using ITS and *cox1* markers. *Algae* 30:217–222
- Lenth RV (2016) Least-squares means: the R package lsmeans. *J Stat Soft* 69:1–33
- Leonardi PI, Miravalles AB, Faugeton S, Flores V, Beltrán J, Correa JA (2006) Diversity, phenomenology and epidemiology of epiphytism in farmed *Gracilaria chilensis* (Rhodophyta) in northern Chile. *Eur J Phycol* 41:247–257
- Lévesque CA, De Cock AWAM (2004) Molecular phylogeny and taxonomy of the genus *Pythium*. *Mycol Res* 108:1363–1383
- Mantri VA, Kambey CSB, Cottier-Cook EJ, Usandizaga S, Buschmann AH, Chung IK, Liu T, Sondak CFA, Qi Z, Lim PE, Van Nguyen N (2023) Overview of global *Gracilaria* production, the role of biosecurity policies and regulations in the sustainable development of this industry. *Rev Aquacult* 15:801–819
- Martínez-Curci NS, Fierro P, Navedo JG (2023) Does experimental seaweed cultivation affect benthic communities and shorebirds? *Appl Extensive Aquaculture Ecol Appl* 33:e2799
- Mendez C, Bustamante DE, Calderon MS, Gauna C, Hayashi L, Robledo D, Tapia-Larios C, Campbell I, Westermeier R, Murúa P (2024) Biosecurity baseline for a sustainable development of seaweed aquaculture in Latin America. *Mar Policy* 159:105933
- Murúa P, Muñoz L, Bustamante D, Gauna C, Hayashi L, Robledo D, Gachon CMM (2021) Actualización de patógenos de algas en Latinoamérica. Presented at the XI Congreso Nacional de Micro y Macroalgas, 4iD, Puerto Montt, 61 p
- Murúa P, Garvetto A, Egan S, Gachon CMM (2023) The re-emergence of phycopathology: when algal biology meets ecology and biosecurity. *Annu Rev Phytopathol* 61:13.1–13.25



- O'Hanlon KA, Knorr K, Jørgensen LN, Nicolaisen M, Boelt B (2012) Exploring the potential of symbiotic fungal endophytes in cereal disease suppression. *Biol Control* 63:69–78
- Qiu L, Mao Y, Tang L, Tang X, Mo Z (2019) Characterization of *Pythium chondricola* associated with red rot disease of *Pyropia yezoensis* (Ueda) (Bangiales, Rhodophyta) from Lianyungang, China. *J Oceanol Limnol* 37:1102–1112
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Robideau GP, De Cock AW, Coffey MD, Voglmayr H, Brouwer H, Bala K, Chitty DW, Désaulniers N, Eggertson QA, Gachon CM, Hu CH, Küpper FC, Rintoul TL, Sarhan E, Verstappen EC, Zhang Y, Bonants PJ, Ristaino JB, Lévesque CA (2011) DNA barcoding of oomycetes with cytochrome *c* oxidase subunit I and internal transcribed spacer. *Mol Ecol Resour* 11:1002–1011
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and model choice across a large model space. *Systematic Biol* 61:539–542
- Santelices B, Doty MS (1989) A review of *Gracilaria* farming. *Aquaculture* 78:95–133
- Sekimoto S, Hatai K, Honda D (2007) Molecular phylogeny of an unidentified Haliphthoros-like marine oomycete and Haliphthoros milfordensis inferred from nuclear-encoded small- and large-subunit rRNA genes and mitochondrial-encoded *cox2* gene. *Mycoscience* 48:212–221
- Sekimoto S, Yokoo K, Kawamura Y, Honda D (2008) Taxonomy, molecular phylogeny, and ultrastructural morphology of *Olpidiopsis porphyrae* sp. nov. (Oomycetes, straminipiles), a unicellular obligate endoparasite of *Bangia* and *Porphyra* spp. (Bangiales, Rhodophyta). *Mycol Res* 112:361–374
- Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313
- Wang Y, Tian RM, Gao ZM, Bougouffa S, Qian P-Y (2014) Optimal eukaryotic 18S and universal 16S/18S ribosomal RNA primers and their application in a study of symbiosis. *PLoS ONE* 9:e90053
- Westermeier R, Gómez I, Rivera P (1993) Suspended farming of *Gracilaria chilensis* (Rhodophyta, Gigartinales) at Cariquilda River, Maullín, Chile. *Aquaculture* 113:215–229

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