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RESEARCH

Seasonal life-cycle dynamics of *Macrocystis pyrifera* in a chronically polluted coastal ecosystem

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Abstract

The giant kelp *Macrocystis pyrifera* is a foundational species in marine coastal ecosystems, yet its microscopic life stages are particularly vulnerable to warming and pollution. We examined its seasonal phenology over an annual cycle initiated under the 2023—2024 El Niño warming at Horcón (central Chile), a coastal site strongly influenced by long-term industrial activity. Sori were collected in austral spring and summer to winter, and in vitro cultures were used to quantify settled spores, germination, gametophyte and sporophyte development, sex ratio, fecundity, and reproductive success. Sea surface temperature (SST) data showed strong seasonal contrasts, with warm anomalies in summer-autumn linked to the coastal El Niño, followed by markedly cooler conditions in winter. Winter cultures, after El Niño waned, reached ~ 220,500 spores cm^{-2}, nearly ten times higher than in spring and autumn and twenty times higher than in summer. Germination peaked in winter (96—100% by day 7) but was lower in spring and autumn (53% and 83%, respectively), with no germination further than day 7. Female gametophytes dominated across seasons (≤ 49%) until day 14 of development, while males remained consistently scarce (≤ 20%). Sporophyte development differed markedly: by day 14, autumn reached 34%, spring 2%, and winter none; by day 28, however, winter reached 46%, surpassing the other seasons, though juveniles were smaller due to density effects. The decoupling of male and female gametophytes during winter reduced fecundity and reproductive success despite high settlement. Summer cultures and field restocking collapsed early, underscoring the fragility of *M. pyrifera* under stress. Overall, our findings reveal pronounced seasonal shifts in reproductive dynamics, underscoring the sensitivity of kelps to warming in a coastal pollution site.

Keywords Coastal pollution · Life cycle stages · Phenology · Seasonality · SST · Phaeophyceae

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Introduction

Temperature and pollution are major environmental drivers of seaweed phenology, particularly in kelps. Sea surface temperature (SST) (e.g., Kain 1989; Carballo et al. 2002; Graham et al. 2007; De Bettignies et al. 2018; Arafeh-Dalmau et al. 2019; Spiecker and Menge 2022) and coastal pollution from anthropogenic activities are on the rise and compromise reproductive potential, development, and growth across kelp life stages (e.g., Oyarzo-Miranda et al. 2020; Meynard et al. 2021; Véliz et al. 2025). In fact, the formation and maturation of microscopic life stages (e.g., propagule release, gametophytes, juvenile sporophytes) show different thermal tolerances (Andrews et al. 2014; Becheler et al. 2022; Solas et al. 2024) and sensitivities to metal and pollution (Contreras et al. 2007; Leal et al. 2016; Espinoza-Gonzalez et al. 2021; Veenhof et al. 2023). For example, in *Lessonia spicata* it has been demonstrated that copper and PAHs significantly inhibit gametogenesis and early sporophyte development, with strong dose-dependent effects even at low concentrations (Espinoza-Gonzalez et al. 2021). In *Macrocystis pyrifera*, combined exposure to Cu, Cd, and PAHs strongly inhibited early stages, with spores being the most sensitive. Mixtures showed synergistic effects on settlement but variable responses overall, not predictable from single pollutants (Meynard et al. 2021).

While pollution is usually associated with point-source discharges and its later dispersion is mediated by nonlinear physical processes, the marine environment is distinctively cyclical (Ord and Caceres 2026). Seasonal environmental processes, such as the annual cycle in SST or nitrogen supply by seasonal upwelling are critical for kelp phenology and reproduction (Reed et al. 1996; Fernández et al. 2021). Overall, the reproductive potential of seaweed is strongly coupled with environmental variability and anthropogenic influences.

The giant kelp *M. pyrifera* is found along the coastlines of southern Australia and the temperate coasts of north and south America (Graham et al. 2007). Current climatic trends, particularly warming, have been shown to drive increasingly variable reproductive success, underscoring the vulnerability of *M. pyrifera* populations to SST (Hollarsmith et al. 2020). Its seasonal growth and reproductive cycle have been shown to change over interannual scales by large-scale oceanographic processes such as the El Niño-Southern Oscillation cycle (ENSO, Dayton et al. 1999; Reed et al. 2011). In California, *M. pyrifera* was severely affected by the 1982/83 ENSO in central regions and by the 1997/98 event in the south, with slower recovery after 1982/83 (Edwards 2019). Along the Pacific coast of Baja California, the warm edge of the range of *M. pyrifera* has repeatedly shifted following heatwaves over the past two decades (Arafeh-Dalmau et al. 2019; Cavanaugh et al. 2019). These findings indicate that *M. pyrifera* is highly sensitive to ocean warming, just as it is to marine pollution, with temperature-driven variability strongly affecting its reproductive success and population stability. While large-scale processes like ENSO influence its dynamics, local seasonal conditions appear to play a more dominant role in shaping population responses.

The giant kelp *M. pyrifera* exhibits a complex haplodiplontic life cycle, comprising a macroscopic diploid sporophyte (2n) and microscopic haploid gametophytes (n). The two stages of the life cycle are differentially influenced by seasonal and local environmental processes (Deysher and Dean 1984; Reed et al. 1996, 2011; Meynard et al. 2021; Becheler et al. 2022; Solas et al. 2024). *Macrocystis pyrifera* is a key kelp species that can dominate low intertidal and subtidal habitats along the Southeast Pacific (Aguilera et al. 2019; Avila-Peltroche and Padilla-Vallejos 2020). In Perú, the poleward distribution limit of *M. pyrifera* occurs near Lima (12° S), extending south along the entire Chilean coast. Wild populations are intensively harvested across much of this range (Buschmann et al. 2014; Vásquez 2016; Carbajal Enzian and Gamarra 2018; Ávila-Thieme et al. 2025). Combined with high international demand, harvesting pressure has driven local declines of kelp forests in the Southeast Pacific (Kang et al. 2023). In this context, strengthening the scientific understanding of its biology is essential under current climate trends, particularly given the strong temperature sensitivity of its life cycle, as well as the additional stress imposed by highly contaminated marine environments (Buschmann et al. 2014; Avila-Peltroche and Padilla-Vallejos 2020; Oyarzo-Miranda et al. 2020). This knowledge is critical for identifying optimal restocking windows in areas subjected to high environmental and social pressure. In this context, we examined the phenological responses of *M. pyrifera* using in vitro cultures from sori collected from a location, Caleta Horcón (Valparaíso Region) strongly affected by pollution (Oyarzo-Miranda et al. 2020) during different seasons: elevated SST during the onset of an ENSO event (spring 2023-autumn 2024) versus cooler winter 2024 after its waning (Fig. S1 Supplementary Material). To this end, we quantified settled spores, gametophyte and sporophyte development, sex ratio, fecundity, and reproductive success for every season. Owing to the pollution history of the locality, we hypothesized that spore settlement, and germination would decline under elevated SST, while microscopic life stages would develop across seasons with peaks under optimal physicochemical conditions. Consistent with earlier studies, we expected female gametophytes to show greater thermal resilience than sporophytes (Becheler et al. 2022; Solas et al. 2024). Finally, we briefly discuss our experimental results in relation to kelp restoration initiatives.

Materials and methods

Environmental context, sea surface temperature (SST) data acquisition and processing

Our study location, Caleta Horcón, is a coastal town and cove located adjacent to the industrial zone of Quintero Bay (central Chile) (Contreras-Porcia et al. 2023). We selected the location following its documented contamination history, with copper (Cu) and arsenic (As) in seaweed, urchins, seawater, and sediments exceeding international standards, together with our working relationship with local fishermen who provided access to their coastal resource management areas and *M. pyrifera* individuals (Oyarzo-Miranda et al. 2020; Latorre-Padilla et al. 2021; Véliz et al. 2025). Following the complexity of long-term work with multiple fisher organizations, we did not attempt to use a reference location during our study and instead rely on results from earlier studies in non-polluted locations.

The period from austral autumn 2023 to autumn 2024 was characterized by warm temperature anomalies associated to a coastal El Niño along the southeastern Pacific shores (Martinez-Villalobos et al. 2024). To characterize local environmental conditions, we used NOAA's optimum interpolation sea surface temperature (OISST, 1/4° daily resolution) to quantify long-term temperature anomalies (Richard and Banzon 2008). Daily SST time series were obtained from the Google Earth Engine platform (Gorelick et al. 2017), selecting the grid cell closest to the sampling site. Daily anomalies from the OISST record were then calculated over a 20-year reference period (2005—2025), providing a baseline against which conditions in the days immediately preceding sampling could be evaluated.

To validate the satellite observations, we collected seawater temperature data in Horcón cove during part of the study period using Onset HOBO and compared the record to a long-term in situ climatology from two nearby locations. We did not attempt to calculate anomalies or compare the local and OISST records following the limited duration our field dataset (less than 1 year) owing to the temporary loss of the Horcón instrument (December 2023-March 2024) and subsequent loss (winter 2024) of a reference thermometer located nearby. Further details on data collection and processing are provided elsewhere (Fig. S1; Aravena et al. 2014; Véliz et al. 2025).

Sori sample collection

Seasonal sampling of reproductive biomass was conducted near Horcón (Playa El Tebo; 32°43′34.52″S, 71°30′11.58″W; see Véliz et al. (2025)) during austral spring 2023 and the summer to winter of 2024. Reproductive sori of *M. pyrifera* were randomly collected from 10—15 individuals per season to ensure representative sampling. We cleaned the blades to reduce and eliminate epiphytes and microorganisms following Contreras-Porcia et al. (2025) using sequential rinses in 4% ethanol, distilled water, and 1 µm filtered seawater, and then gently dried. Samples were transported in darkness at 10-14 °C in ice-cooled containers to the LEBMA laboratory (www.lebma.cl, last accessed: March 2026).

Release of spores

Sori were selected by trimming blades and removing epiphytic sections, then desiccated for 1 h under white light in a laminar flow hood. They were subsequently incubated in 2-L Schott bottles filled to their full capacity (2 L) with 0.22 µm filtered seawater. The bottles were kept closed and maintained at 15-17 °C for 12 h to induce spore release. During incubation, they were wrapped in aluminum foil to ensure darkness and protect the reproductive tissue.

Culture and maintenance

We measured spore density in triplicate from suspended cultures with a Neubauer chamber and adjusted to 10,000 spores mL^{-1}. From this suspension, 20 mL were inoculated into six sterile 100 mm Petri dishes per season. Cultures were maintained for 28 days at 13-14 °C, 30-50 µmol photons m^{-2} s^{-1}, and a 12:12 h light–dark cycle in 1 µm filtered seawater enriched with von Stosch medium (8 mL L^{-1}) that was renewed weekly after an initial change after 48 h. Antibiotics (ampicillin, penicillin, streptomycin; 0.25 g L^{-1}) and GeO_2 (1 g mL^{-1}) were added to cultures to minimize contamination. Then, we recorded microscopic life stages at 24 h, and on days 2, 7, 14, 21, and 28 using an inverted microscope (Eclipse Ts2, Nikon). Spore settlement (spores adhering to the bottom surface of Petri dishes without evidence of germination tube) and germination (spores with a germination tube) were assessed in twelve 0.5 mm^2 fields per dish, while gametophytes and juvenile sporophytes were quantified in twelve 1 mm^2 fields. Each stage was expressed as a percentage of the total observed, and final sporophyte density was calculated as individuals per cm^2.

We assessed sex ratio from the proportion of male to female gametophytes following Oppliger et al. (2011):

$$\text{Sex ratio}(\%) = \frac{MG}{MG + FG} \cdot 100$$

where MG represents male gametophytes and FG represents female gametophytes.

Fecundity and reproductive success were estimated according to Lee and Brinkhuis (1986):

$$\text{Fecundity}(\%) = \frac{TS+FGO}{TS+FGO+FGwO} \cdot 100$$

$$\text{Reproductive success}(\%) = \frac{TS}{TS+FGO+FGwO} \cdot 100$$

where TS represents total sporophytes, FGO represents female gametophytes with oogonia, and $FGwO$ represents female gametophytes without oogonia. These three metrics allowed us to track the timing and relative frequency of each developmental stage throughout the culture period.

Statistical analysis

All data, except final sporophyte density are expressed as percentages. We tested for normality and variance homogeneity assumptions using Shapiro–Wilk and Bartlett's tests using raw or transformed data. If normality and homoscedasticity were met, we used one-way or repeated-measures two-way ANOVA to assess the effects of season, time (days), and their interaction on the percentage of settled spores, and final sporophyte density. Tukey's HSD was used for *post-hoc* comparisons. When homoscedasticity assumptions were not met, for life-stage, sex ratio, fecundity, and reproductive success, we used generalized linear mixed models (GLMMs) with a beta distribution and significance based on χ^2 tests (Crawley 2013). Percentages were transformed into proportions to avoid extreme values (0 or 1) (Smithson and Verkuilen 2006). "Days and season" were treated as fixed factors and "Petri dishes" as random factor. We used *post-hoc* analyses to estimate marginal means (EMMs) with the 'emmeans' package (Version 1.11.2; Lenth et al. 2025), with Tukey adjustment. All statistical analyses were performed in R software (version 4.3.0; R Development Core Team 2024).

Results

Sea temperature patterns

The analysis of satellite-derived SST anomaly patterns indicated that the first austral spring sampling in 2023 occurred under relatively neutral to slightly negative conditions (Fig. 1). In contrast, the second sampling during austral summer 2024 was preceded by predominantly positive anomalies throughout the previous month. Subsequent samplings in austral autumn and especially winter 2024 were characterized by markedly colder conditions (Fig. 1). These patterns highlight that the experiment took place under rather atypical thermal regimes, with pronounced extremes during the opposite ends of the seasonal cycle. Moreover, in situ records showed a comparable seasonal trend, with higher SST during austral summer and autumn and lower values

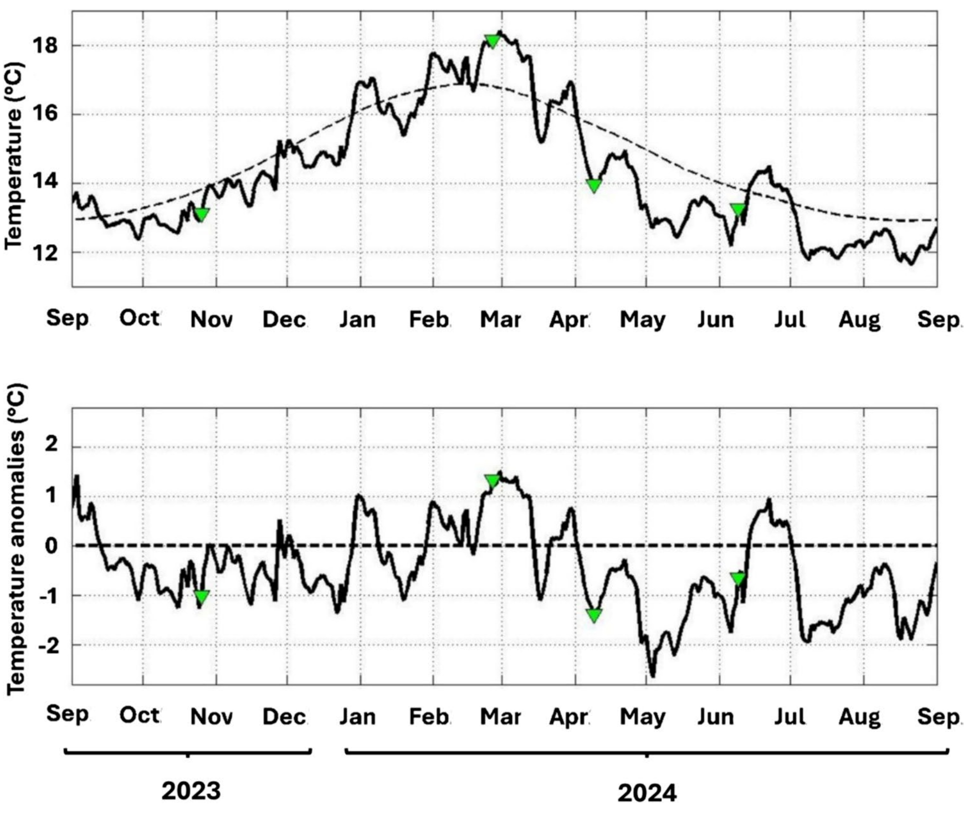


Fig. 1 Daily long-term SST data for Horcón, Chile, during the sampling period (September 2023-August 2024). The upper panel shows observed SST values (solid line) with overlaid on the long-term climatology (dashed line), while the lower panel depicts standardized SST anomalies, calculated as the difference between daily values and the 20-year climatological mean, divided by the 20-year climatological standard deviation. Green triangles indicate the specific days when we conducted field collections of reproductive material

in winter and spring. The departure of our field-based SST observations and climatology were in good agreement with the OISST pattern showing large positive anomalies during summer and negative anomalies during fall (Fig. 1, Fig. S1, Supplementary material).

Settled spores

Significant differences were found on settled spores of *M. pyrifera* between seasons (one-way ANOVA, $F_{3,20} = 276.6$, $p < 0.001$). Overall, we observed higher number of *M. pyrifera* spores settled specially in winter 2024 at 24 h of culture (Mean ± SD; 220,514 ± 28,000 spores cm^{-2}). Moreover, in summer 2024 the settled spores reached the lowest values in comparison to other seasons (Fig. 2).

Throughout the culture period, spore settlement was highest on day 2 in spring (~40%). In autumn, settlement reached only ~20% (Fig. 3), whereas in winter it was close to 0%. After day 7, no more settled spores were observed (Fig. 3). It is noteworthy that during spring, summer, and autumn, a substantially greater field effort was required to collect sporophylls with mature sori, whereas in winter such material was more readily available in the environment. Additionally, in summer, microscopic life stages declined sharply after day 7; therefore, these cultures were excluded from subsequent analyses.

Spore germination

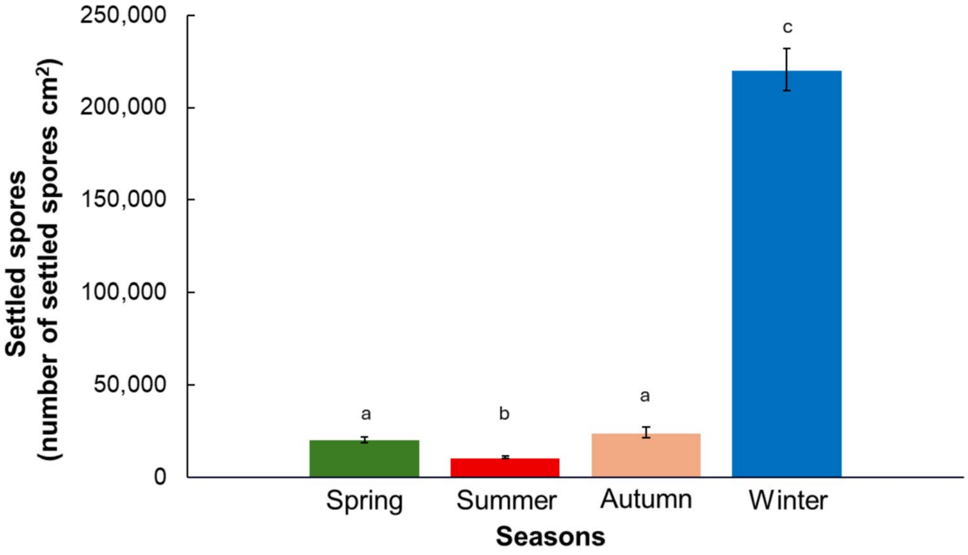
Significant differences were found for spore germination of *M. pyrifera* between days ($\chi^2 = 263.06$, $p < 0.001$) and seasons ($\chi^2 = 454.48$, $p < 0.001$). Also, a significant interaction was found between days and seasons ($\chi^2 = 191.45$, $p < 0.001$) (Fig. 3). Spore germination on day 2 was significantly higher in winter up to 95% in comparison with spring (53%) and autumn (83%) (Fig. S2 Table S1A1 and A2 Supplementary Material). Furthermore, spore germination on day 7 showed a similar pattern with highest values in winter (100%), whereas no germination was observed after day 14 (Fig. 3 Table S1A1 and A2 Supplementary Material).

Gametophyte development

Significant differences were found for the female gametophytes of *M. pyrifera* between days ($\chi^2 = 335.26$, $p < 0.001$) and seasons ($\chi^2 = 127.52$, $p < 0.001$) (Table S1A1 and A3, Supplementary Material). Furthermore, significant interactions were found between both factors ($\chi^2(6) = 59.66$, $p < 0.001$). In general, female gametophyte development was higher on day 7 and 14 reaching values of 49% and 44% in winter in comparison with days 7 and 14 of spring where the gametophyte development was ~29% and ~3%, respectively, and autumn with ~29% and ~10%, respectively. By days 21 and 28, female gametophytes were lower in spring (~7%) and winter (~2%) while it was absent in autumn 2024 (Fig. 3).

For male gametophytes, significant differences were found for gametophyte development between days ($\chi^2 = 40.13$, $p < 0.001$), and seasons ($\chi^2 = 43.51$, $p < 0.001$) (Table S1A1 and A3, Supplementary Material). In this case, a significant interaction was also found between days and seasons ($\chi^2 = 79.92$, $p < 0.001$). In more detail, on day 7 male gametophytes development was ~20% in spring and autumn and lower in winter (~5%). On the other hand, on day 14 male gametophytes development was relatively similar between seasons (~5—10%) increasing on day 21 to ~10—20% in spring and winter, respectively, while its marginally decreased to 18% in autumn. On day 28, male

Fig. 2 Number of *Macrocystis pyrifera* spores settled on 24 h of cultivation at Horcón during spring, and summer, autumn and winter. Different letters denote significant differences among seasons. Each bar show mean ± standard error (n = 6)



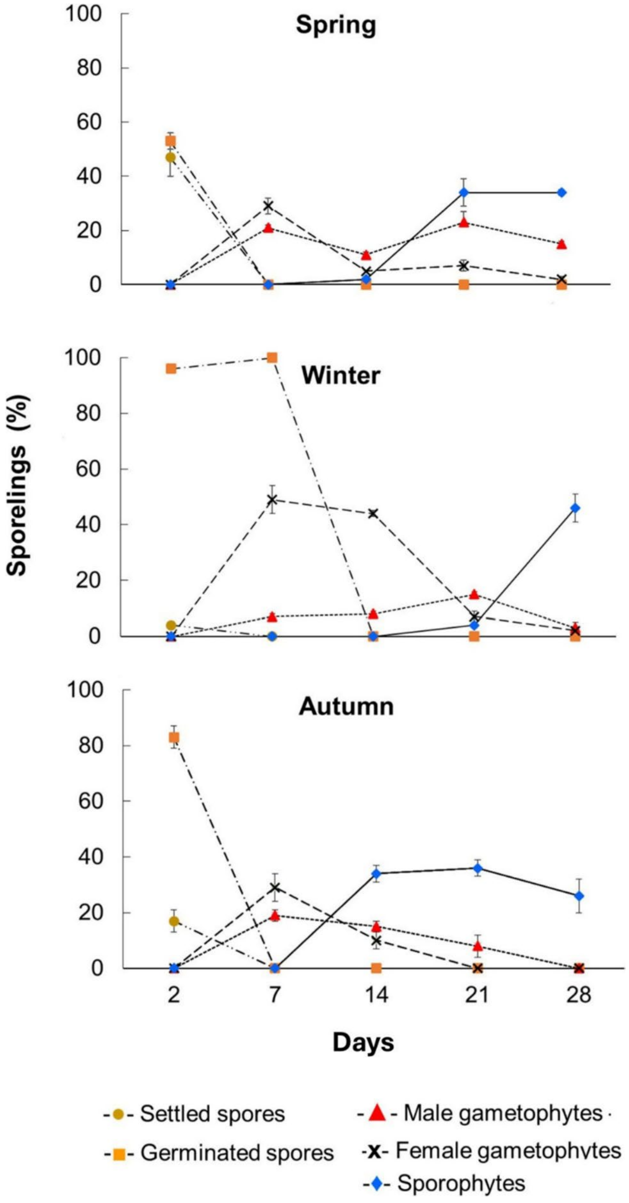


Fig. 3 Life-cycle stages (sporelings %) of *Macrocystis pyrifera* during spring, autumn, and winter. Percentages of settled spores, germinated spores, male and female gametophytes, and sporophytes were recorded after 2, 7, 14, 21, and 28 days of culture. Values represent mean ± standard error (n = 6)

gametophytes were higher in spring (~ 15%) and near to 0% in autumn and winter (Fig. 3).

Sporophyte development

Significant differences were found for sporophyte development of *M. pyrifera* between days ($\chi^2 = 39.637$, $p < 0.001$) and seasons ($\chi^2 = 15.49$, $p < 0.001$). Besides, a significant interaction was found between days and seasons ($\chi^2 = 156.74$, $p < 0.001$) (Table S1B1 and B3, Supplementary Material). Overall, on day 14, sporophytes were higher in autumn (~ 34%), lower in spring (~ 2%) and absent in winter, while on day 21 sporophytes increased in spring (~ 35%) and stayed similar in autumn. Differently, on day 28 sporophytes were higher in winter (45%), and relatively similar between spring and autumn (~ 30-40%) (Fig. 3). Finally, the cumulative number of juvenile sporophytes on day 28 was significantly higher in the winter 2024 culture than in spring 2023 and autumn 2024 (one-way ANOVA, $F_{2,15} = 72.25$, $p < 0.001$), which did not differ significantly from each other (Fig. 4).

Sex ratio

Significant differences were found for sex ratio of *M. pyrifera* between days ($\chi^2 = 9.33$, $p = 0.025$) and seasons ($\chi^2 = 9.55$, $p < 0.001$). Moreover, a significant interaction was found between days and seasons ($\chi^2 = 26.64$, $p < 0.001$) (Table S1B1 and B3, Supplementary Material). In general, on day 7 and 14, sex ratios were lower in winter reaching values of ~ 10% in comparison to spring and autumn which were around ~ 40 and ~ 60%, respectively. Interestingly, on day 21 the sex ratio was relatively similar between spring and winter (70-80%) while it was lower in autumn (~ 60%) (Fig. 5). Finally, on day 28, lower sex ratio was observed in autumn (Fig. 5). This difference resulted from a more rapid decline of female gametophytes in autumn 2024, with both sexes almost absent by day 28 (Fig. 3).

Fecundity success

Significant differences were found for the fecundity of *M. pyrifera* between days ($\chi^2 = 315.23$, $p < 0.001$) and season ($\chi^2 = 126.72$, $p < 0.001$). Also, a significant interaction was found between days and seasons ($\chi^2 = 95.47$, $p < 0.001$) (Table S1B2 and B4, Supplementary Material). On day 14, the lower fecundity was found in winter (~ 8%) in comparison with spring (~ 65%) and autumn (~ 80%). Moreover, on days 21 the fecundity was slightly higher in autumn (~ 95%) in comparison with spring and winter (~ 80%) (Fig. 6). On day 28, fecundity success was highest across all seasons.

Reproductive success

Significant differences were found for the reproductive success of *M. pyrifera* between days ($\chi^2 = 293.73$, $p < 0.001$), and seasons ($\chi^2 = 453.30$, $p < 0.001$). Besides, a significant interaction was found between both factors ($\chi^2 = 41.24$, $p < 0.001$) (Table S1B2 and B4, Supplementary Material).

On day 14, the reproductive success of *M. pyrifera* was delayed in winter and lower in spring (~ 9%). Contrarily, the reproductive success on day 14 reached ~ 65% in autumn.

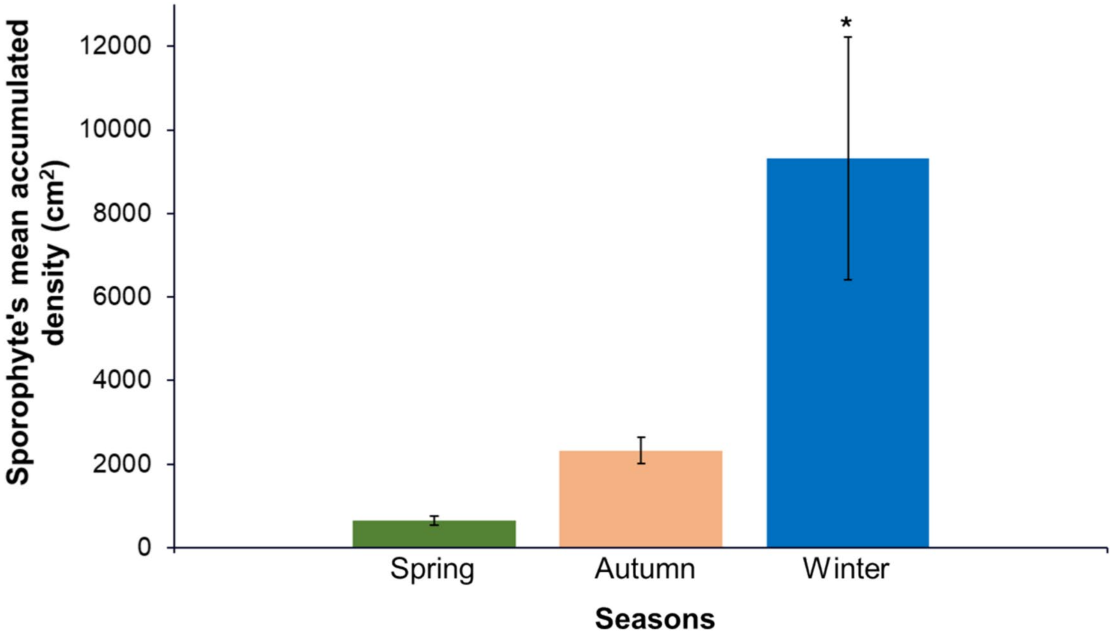
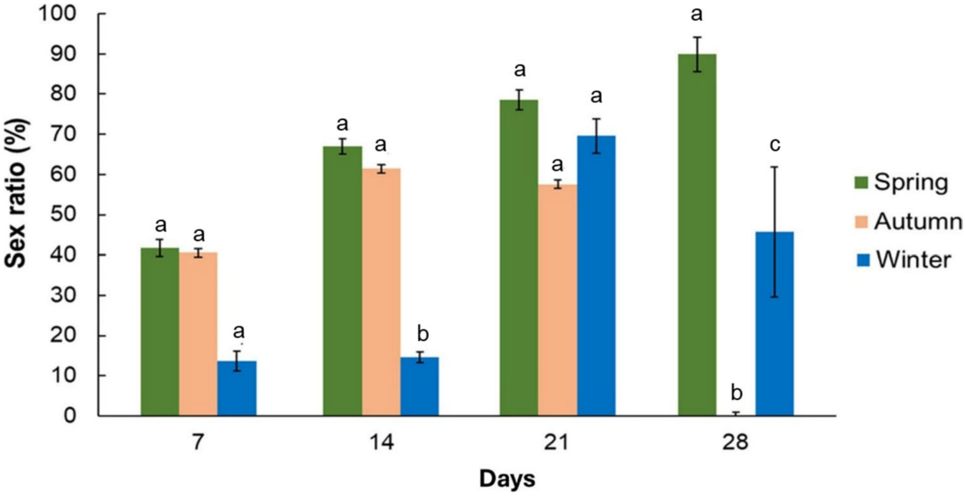


Fig. 4 Accumulated number of *Macrocystis pyrifera* sporophytes at day 28 of cultivation at Horcón during spring, autumn 2024, and winter. * indicates significant differences among seasons. Bars show mean ± and standard error (n = 6)

Fig. 5 Sex ratio (%) of *Macrocystis pyrifera* based on male gametophytes during spring, autumn, and winter. Zero values indicate undifferentiated gametophyte stages. Bars show mean ± SE (n = 6). Different letters indicate statistically significant differences among seasons ($p < 0.05$)



On day 21, the reproductive success increased in winter and spring to 6% and 48%, respectively, whereas in autumn it reached ~ 99%. Finally, on day 28, the reproductive success increased to ~ 90% and ~ 65% in spring and winter, while it remained similar to day 21 in autumn (Fig. 7).

Discussion

In this study we demonstrate that extremes of the seasonal cycle influence the microscopic phenology of giant kelp *Macrocystis pyrifera* from a location with a history of pollution, revealing pronounced heterogeneity in its reproductive and recruitment dynamics. We recorded the highest settlement and germination during winter, whereas summer cultures collapsed early. Female gametophytes dominated, males remained scarce, and reproductive success was reduced despite high settlement. Thus, seasonal extremes strongly shape the microscopic phenology of *M. pyrifera* in polluted environments, driving marked variability in reproduction and recruitment. Kelp forests are increasingly degraded by environmental and anthropogenic pressures worldwide (Buschmann et al. 2014; Arafeh-Dalmau et al. 2019; Véliz et al. 2025). Therefore,

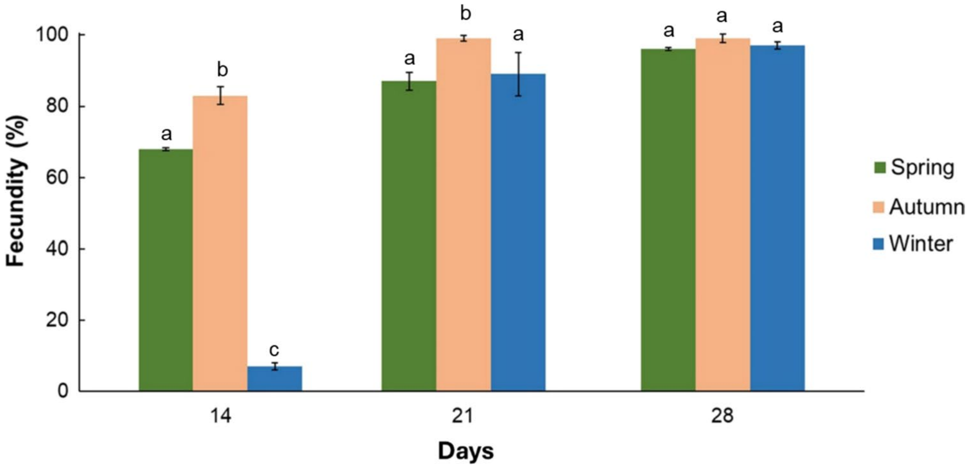


Fig. 6 Fecundity (%) of *Macrocystis pyrifera* at Horcón during spring, autumn and winter. Bars represent mean ± SE (n = 6). Different letters indicate statistically significant differences among seasons ($p < 0.05$)

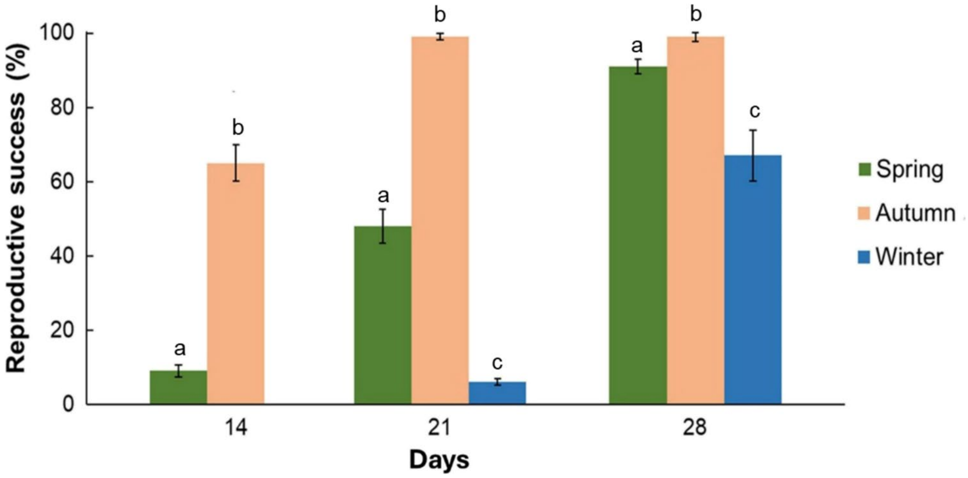


Fig. 7 Reproductive success (%) of *Macrocystis pyrifera* at Quintay and Horcón during spring, autumn, and winter. Bars show mean ± SE (n = 6). Different letters indicate statistically significant differences among seasons ($p < 0.05$)

it is imperative to understand their phenological dynamics, as detailed in the present study, making their restoration both an urgent priority and a key opportunity for sustainable aquaculture (Feehan et al. 2021; Eger et al. 2024).

Our results demonstrate that the development of the different life-history stages of *M. pyrifera* exhibits a pronounced seasonal pattern and is strongly dependent on both temporal dynamics and the progression of preceding stages. For instance, the decline in gametophyte abundance occurred concomitantly with an increase in sporophyte recruitment, suggesting a stage-dependent transition within the life cycle. These patterns were particularly evident during winter, when the reduction in gametophyte abundance, especially in female gametophytes, coincided with enhanced sporophyte development (Fig. 3). This phenological pattern is consistent with previous studies across multiple latitudes in Chile, which have shown that low temperatures act as a trigger for zoospore release, germination, and early sporophyte growth (Buschmann et al. 2004, 2006). In upwelling ecosystems, low temperatures also exhibit an inverse correlation with nitrate concentration, another key factor influencing the life cycle of *M. pyrifera* (Nielsen and Navarrete 2004; Palacios et al. 2013; Rodriguez et al. 2016).

Experimental studies show that gametophytes from Peruvian and Chilean populations can survive at 24 °C, with greater tolerance at lower latitudes, whereas sporophytes generally exhibit high mortality under similar conditions (Becheler et al. 2022; Solas et al. 2024). Nevertheless, survival often comes at the cost of reduced fertility or parthenogenesis, while selfing further decreases fitness, restricting the persistence of small and isolated populations (Raimondi et al. 2004). That juvenile sporophytes at Horcón were notably smaller during the cold ocean conditions during winter 2024 compared to spring 2023 and autumn 2024, probably reflected density-dependent effects linked to higher settlement rates instead of a temperature effect. These experimental results can help explain the contrasting field outcomes observed at Horcón. Elevated SSTs during El Niño, reduced upwelling, chronic industrial pollution, and limited reproductive material likely converged to constrain reproductive output and transplant survival. This aligns with the long-term degradation of the site, where historically extensive kelp forests have declined to sparse, fragmented stands. During our study, summer SST exceeded 17 °C for over a month, surpassing thermal thresholds for *M. pyrifera*, which likely contributed to the collapse of cultures and field restocking observed under these conditions (Fig. S3 Supplementary Material). Finally, a seasonal pattern is also consistent with observations of adult sporophyte phenology, where peak population growth occurs in spring and reaches maximum in summer, reflecting the development, release, and settlement of microscopic life stages during the preceding winter, as observed in our study (Almanza and Buschmann 2013; Gonzalez-Aragon et al. 2025). Comparisons with nearby sites and other kelps highlight the role of local environmental context and suggest species-specific variation in physiological and ecological tolerance. At Quintay, *L. spicata* maintained stable reproductive success despite the 2023 warming (Véliz et al. 2025). In contrast, at Horcón, reproductive success was reduced, with lower densities and elevated stress markers relative to non-polluted sites, emphasizing the compounding impact of industrial pollution on kelp resilience (Oyarzo-Miranda et al. 2020; Véliz et al. 2025). Today, the interplay of climate variability, anthropogenic pressures, and biological constraints thus emerges as a key determinant of *M. pyrifera* dynamics in central Chile, highlighting both the fragility and the limited recovery potential of remnant populations in historically polluted environments.

Understanding the factors governing the successful growth and development of kelps is therefore critical for advancing evidence-based management, aquaculture, and restoration strategies (Morris et al. 2020). Restoration outcomes are ultimately shaped by the broader social and management contexts in which they occur (Abelson et al. 2016; Morris et al. 2020). In Chile, thousands of people depend on kelp harvesting, which sustains the livelihoods of artisanal fishers and contributes significantly to both local and national economies (Vásquez 2008; Vásquez et al. 2012). Here, our results are critical for informing kelp restoration as they identify ecological windows of opportunity for successful recruitment and recovery. Reproductive tissue should ideally be collected following prolonged periods of reduced sea surface temperature (SST), which typically coincide with the onset of seasonal upwelling. These conditions are associated with increased nutrient availability, enhanced water column mixing, and reduced thermal stress (Chavez et al. 2008; Largier 2020), all of which favor gametogenesis and subsequent early developmental stages. Restocking of *M. pyrifera* sporophytes should therefore be conducted while upwelling conditions persist, maximizing recruitment success and early sporophyte performance.

The implementation and effectiveness of restoration strategies in *M. pyrifera* are further shaped by the coexistence of different management regimes. The *M. pyrifera* fishery operates under two management regimes, Territorial Use Rights for Fisheries (TURFs) and Regional Management Plans (MPs), which differ in governance structure, enforcement, and user participation. Within TURFs, non-transferable, area-based use rights are granted to organized small-scale fisher associations, allowing for direct user control over harvesting and local enforcement, and are associated with higher performance. In contrast, MPs are formal regulatory frameworks that define the rules governing resource extraction, with more limited user control and weaker enforcement, in some cases operate as de facto open-access systems, and are associated with lower performance (BCN 2024; Gelcich et al. 2010; Gonzáles-Roca et al. 2021; 2023; Ávila-Thieme et al. 2025). In this context, the seasonal patterns determined in our study identify the windows opportunity for restauration. However, the capacity to implement and sustain these actions is likely to vary across management regimes. TURFs, as Caleta Horcón, may provide more favorable conditions for aligning restoration efforts with ecological dynamics, whereas in MP or open-access areas, limited enforcement and higher harvesting pressure may constrain it. Previous studies in the Chilean subtidal kelp *Lessonia trabeculata*, has evidenced that TURFs sites have faster recovery than MPs, highlighting the role of local fisheries management to restoration (Pérez-Matus et al. 2025). Therefore, aligning seasonal reproductive dynamics with restoration actions needs to consider the heterogeneity across management regimes and is an important next step.

Conclusion

This study shows that *Macrocystis pyrifera* from a chronically polluted coastal site exhibits strong seasonal variability in its microscopic life stages, which are tightly coupled with temperature fluctuations. Winter conditions following the 2023-2024 coastal El Niño promoted the higher spore production and early developmental, highlighting the sensitive to temperature. These results identify key ecological windows for restoration, indicating that interventions should be aligned with period of reduced SST. Integrating ecological and governance dimensions is essential to improve long-term kelp restoration and support coastal livelihoods. This study provides a practical ecological basis to improve restoration of *M. pyrifera* in impacted coastal systems.

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Data availability All data generated or analyzed during this study are available within the published article and its supplementary materials.

Declarations

Competing interest The authors declare no competing interests.

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