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RESEARCH

Influence of environmental seasonality and marine pollution on the phenology of the kelp *Lessonia spicata* (Phaeophyceae)

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Abstract

This study examines the phenological response of *Lessonia spicata* to environmental variability and anthropogenic stress. Two central Chilean sites with contrasting pollution levels were selected: Horcón (high impact) and Quintay (low impact). Sori were collected in spring 2023 and autumn 2024 to assess reproductive effort, followed by a 28-day culture period. Weekly observations recorded spore settlement, germination, sex ratio, fecundity, reproductive success, and sporophyte density. The results indicate that the reproductive effort reached a maximum in autumn at both sites (> 50%), with season having a significant effect; the lowest values were recorded in Quintay during spring (< 30%). Early development varied by site and season, with sustained growth in Quintay cultures and early gametophyte loss in the Horcón autumn cultures. Sex ratio varied significantly between sites but not seasons. By day 21, Horcón autumn cultures showed complete loss of gametophytes, while Quintay maintained a stable ~ 50% ratio. Fecundity also displayed a significant site-season interaction, showing a maximum in Horcón during autumn (> 90%). Sporophyte formation followed the same tendency, reaching 100% in Horcón by days 21 and 28. This apparent success likely resulted from early bleaching that eliminated most gametophytes, allowing only viable individuals to be fertilized, potentially inflating success estimates. Sporophyte density was significantly lower in autumn, especially in Horcón where necrosis and degradation were evident. Our results suggest that anthropogenic contamination affects *L. spicata* phenology and may compromise long-term persistence. Pollution, in combination with seasonal dynamics and environmental drivers, such as temperature and nutrient variability, could potentially influence the timing and success of key life cycle stages.

Keywords Phaeophyceae · Marine contamination · Life cycle · Kelps · Phenology · Reproductive effort · Seasonality · Spore development

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Introduction

The term heavy metals is commonly used to refer to a group of metals and metalloids that can become toxic when present in high concentrations, often acting as environmental pollutants (Tchounwou et al. 2012; Walker et al. 2012; Kumar 2024). These elements can originate from natural sources, such as volcanic activity or the weathering of mineral-rich rocks, as well as from anthropogenic activities, including mining, fossil fuel combustion, industrial discharges, urban runoff, and agricultural practices. Among these, human activities are particularly significant in increasing both the concentration and bioavailability of heavy metals in ecosystems, thereby amplifying their ecological and health risks (Walker et al. 2012; Saravanan et al. 2024). The rise in specific contaminants within marine ecosystems has prompted an intensification of ecotoxicological research aimed at evaluating their impacts across multiple biological levels: individuals, populations, communities, and entire ecosystems (Eklund and Kautsky 2003; Kumar 2024; Saravanan et al. 2024). Among these contaminants, heavy metals are of particular concern due to their persistence and bioaccumulation potential. Marine pollution has been shown to adversely affect seaweed by impairing key physiological processes such as growth, reproduction, and cellular homeostasis. These disruptions compromise the ecological functions that seaweeds perform, ultimately affecting the stability and resilience of marine ecosystems that depend on them as primary producers, habitat providers, and nutrient cyclers (Nor 1987; Nielsen et al. 2003; Ansari et al. 2004; Naser 2013; Oyarzo-Miranda et al. 2020; Espinoza-González et al. 2021; Latorre-Padilla et al. 2021; Meynard et al. 2021; Gayó et al. 2022; El-Sharkawy et al. 2025).

The Quintero-Puchuncaví industrial park (32°46′23.5″ S, 71°29′35.20″ W) (Fig. 1) is one of the most heavily impacted coastal zones in Chile. Located within Quintero Bay, this area hosts major industrial activities, primarily a copper smelter and a coal-fired power plant complex. The region has experienced long-term environmental degradation, including chronic atmospheric deposition since 1964 and hydrocarbon discharges into the coastal environment (Salmani-Ghabeshi

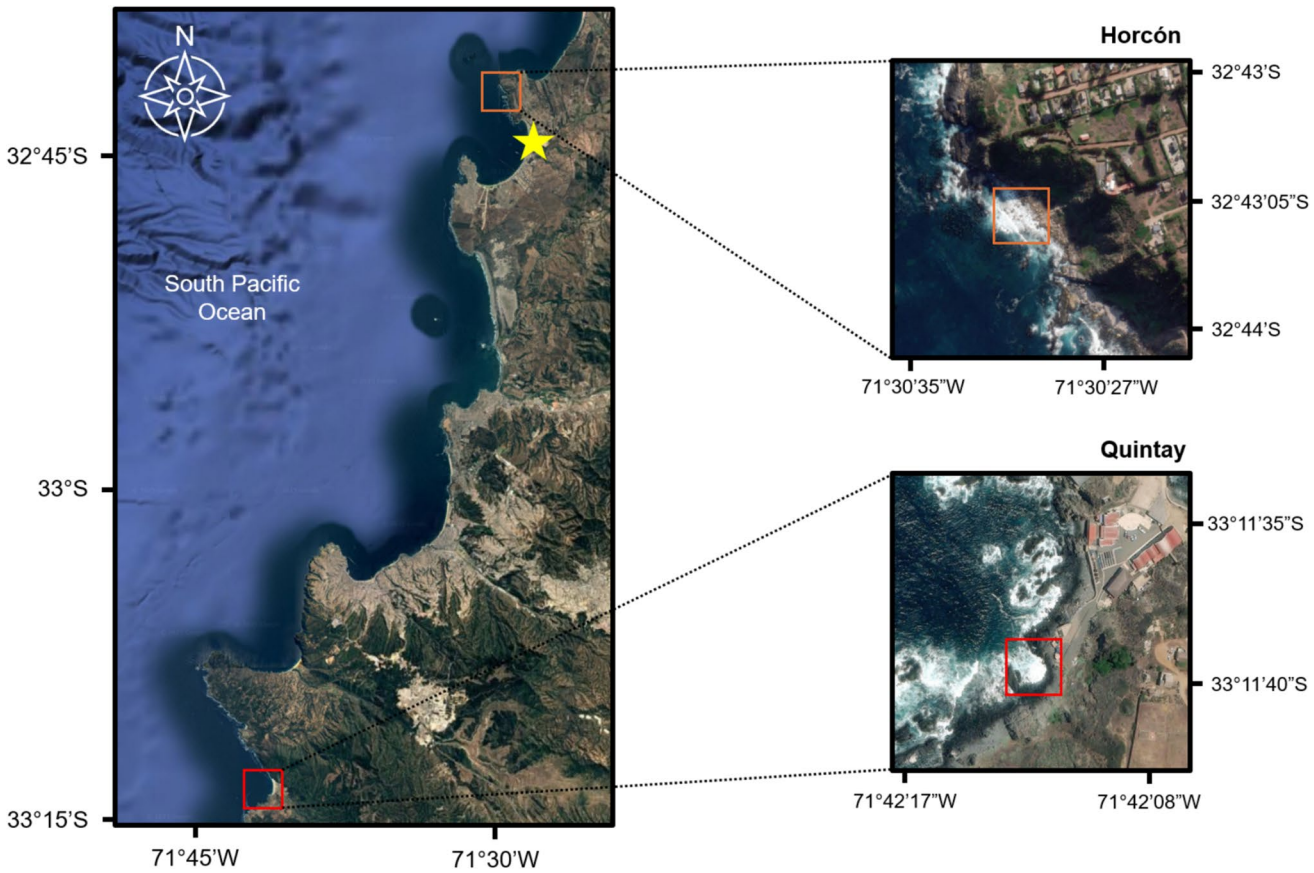

Fig. 1 Geographic locations of the sampling sites for *Lessonia spicata* at Caleta Horcón and Quintay, Valparaíso Region, Chile. The maps on the right detail the specific coastal areas surveyed, with a star indicating the location of the Quintero-Puchuncaví industrial park

et al. 2016; Oyarzo-Miranda et al. 2020; Gayó et al. 2022). Hydrodynamic conditions in the southern sector of Quintero Bay are characterized by persistent northwesterly currents throughout the water column, with greater intensity near the surface (Contreras-Porcia et al. 2023). These currents facilitate vertical export from deeper layers and promote offshore advection in the upper water column. As a result, floating debris and pollutants are transported away from the bay and directed northward, influenced by prevailing winds and surface wind-driven circulation (Contreras-Porcia et al. 2023).

Severe ecological and social impacts have been documented in the vicinity of the Quintero-Puchuncaví industrial park. For instance, Latorre-Padilla et al. (2021) assessed heavy metal concentrations in the biomass of the kelp *Macrocystis pyrifera* and in the gonads of the black sea urchin *Tetrapygus niger* collected from Horcón, a highly impacted site (Fig. 1). Their results revealed significantly elevated concentrations of copper (Cu: 0.75 mg kg^{-1}), arsenic (As: 1.39 mg kg^{-1}), and cadmium (Cd: 0.04 mg kg^{-1}) in tissues of *M. pyrifera* from Horcón compared to specimens of a more southern non-impacted site such as Algarrobo (33°21′51.67″ S, 71°40′29.67″ W). Moreover, the high bioconcentration factors (BCFs), ranging from 3.4 to 4214, particularly for cadmium, indicate that *M. pyrifera* acts as a hyperaccumulator of metals. In parallel, *T. niger* from the impacted area exhibited higher concentrations of Cu (3.07 mg kg^{-1}) and As (7.98 mg kg^{-1}) in their gonads, suggesting trophic transfer of contaminants from seaweeds to higher trophic levels (Latorre-Padilla et al. 2021).

Oyarzo-Miranda et al. (2020) investigated the effects of pollution on populations of the intertidal kelp *Lessonia spicata* at three sites near the Quintero-Puchuncaví industrial park: Cachagua, Horcón, and Ventanas. In general, coastal waters at these locations exhibited elevated concentrations of copper (Cu: 19–859 µg L^{-1}) and arsenic (As: 6–1484 µg L^{-1}), exceeding international water quality criteria for the protection of aquatic life (U.S. EPA 1999). Morphological differences among *L. spicata* populations were observed, with individuals from Ventanas displaying significantly smaller holdfasts and shorter blades compared to those from Horcón and Cachagua. The study also emphasized that early developmental stages of *L. spicata* are particularly vulnerable to contamination, as evidenced by a reduced percentage of male gametophytes and increased sensitivity to pollutants. Complementarily, Espinoza-González et al. (2021) assessed the ecotoxicological effects of copper and polycyclic aromatic hydrocarbons (PAHs) on *L. spicata*. They found that the combined exposure to copper and PAHs caused the highest inhibition of gametophyte development after 21 days. While the formation and growth of early sporophytes were most inhibited by the combined contaminants, juvenile sporophytes were more strongly affected by copper alone. Together, these studies provide compelling evidence that both metallic and organic pollutants disrupt key stages of the *L. spicata* life cycle. Such disruptions can ultimately alter population dynamics, affecting growth and reproduction, and compromise the ecological functions and ecosystem services provided by these foundational kelp species along Quintero Bay.

Although substantial research has addressed the effects of pollution on seaweed (e.g., Coelho et al. 2000; Contreras-Porcia et al. 2023; Veluchamy et al. 2023), most studies have predominantly focused on adult stages, leaving a notable gap in our understanding of the phenological responses of seaweeds in environments subjected to intense anthropogenic pressures. For example, Reed et al. (1994) assessed the impact of a nearshore oil-production outfall on *M. pyrifera* recruitment. Field and lab experiments showed that negative effects mainly reduced gametophyte survival and sporophyte formation were limited to within ~ 50 m of the diffuser. The primary cause of impairment appeared to be microbial competition, rather than direct toxicity. Laboratory assays confirmed reduced reproductive performance at contaminant concentrations expected near the outfall. Nevertheless, the potential transference of environmental stress from the macroscopic stage to the early microscopic stages of development remains poorly explored, despite its critical implications for population dynamics and the provision of ecosystem services.

Phenology is defined as"the study of the timing of recurrent biological events and the causes of their temporal patterns in relation to biotic and abiotic factors"(Espinoza-Avalos 2005). Phenological studies have proven instrumental in elucidating how seasonal variation influences organismal fitness, revealing phenology as a key factor shaping species distribution, population dynamics, and even life history evolution (Chuine and Regniere 2017; De Bettignies et al. 2018; Chefaoui et al. 2019; Ponti and Sannolo 2023; Biancacci et al. 2024). Particularly, phenological studies have demonstrated that intertidal and subtidal seaweeds regulate the timing of growth and reproductive events in response to seasonal environmental factors such as photoperiod, temperature, and nutrient availability (Kain 1989; Espinoza-Avalos 2005; Bellorín et al. 2022).

Although many seaweed species exhibit year-round growth and reproductive activity, these processes tend to peak under optimal environmental conditions (Bellorín et al. 2022). Importantly, resource allocation trade-offs have been observed, where investment in reproduction can reduce vegetative growth due to the diversion of nutrients to reproductive meristems. For example, Tala et al. (2004) investigated the subtidal kelp *Lessonia trabeculata* and reported that growth peaked during spring–summer, while reproductive effort increased markedly in autumn, as evidenced by a significant rise in blade area and reproductive biomass. Conversely, studies on *Ascophyllum nodosum*, a

knotted wrack kelp, revealed that the reproductive cost is relatively low for large individuals, which can allocate up to 70% of net productivity to reproduction without compromising growth (Aberg 1996). In the case of *Lessonia corrugata*, its reproductive dynamics were studied over five consecutive seasons at three sites differing in wave exposure (Nardelli et al. 2025). *Lessonia corrugata* reproduced in all seasons except austral spring, with maximal zoospore release during winter. Zoospores from high-wave exposure sites exhibited longer swimming durations, up to 52 h compared to those from sheltered sites. These patterns suggest reproductive timing and propagule performance are influenced by wave environment. These contrasting strategies suggest that seasonal reproductive patterns in seaweed exhibit considerable phenotypic plasticity, influenced by species-specific life history traits and local environmental conditions. In this context, pollutants such as heavy metals may act as chronic environmental stressors at local or regional scales. These contaminants can interfere with critical phases of the algal life cycle, potentially reducing reproductive effort, compromising gamete quality, impairing fertilization, and inhibiting germination and early development (Coelho et al. 2000). Such disruptions could have cascading effects on population dynamics and ecosystem functioning, particularly in highly impacted coastal zones.

The kelp *Lessonia spicata*, the biological model of this study, is a key habitat-forming species in the exposed rocky intertidal zones of south-central Chile and inhabits from 30° to 43°S and has been reported as far as 49°S, a thermal range of almost 20 °C (Lara et al. 2019; Rosenfeld et al. 2019). It delivers crucial ecological functions and supports economically valuable resources (Vásquez et al. 2013; Cotas et al. 2023; Eger et al. 2023; Oyarzo-Miranda et al. 2023; Contreras-Porcia et al. 2025). This species exhibits a complex heteromorphic haplodiplontic life cycle, consisting of a macroscopic diploid sporophyte (2n) and microscopic haploid gametophytes (n), which are sexually dimorphic (Contreras-Porcia et al. 2017; Contreras-Porcia et al. 2025). These life stages may respond differently to environmental variation, including seasonal changes in temperature, nutrient availability, and ultraviolet radiation (Ávila et al. 1985; Tala et al. 2007; Oppliger et al. 2012; Nardelli et al. 2023), as well as anthropogenic stressors such as heavy metal contamination (Espinoza-González et al. 2021).

In this study, we evaluated the phenological responses of *L. spicata* through in vitro cultures established from reproductive sori collected in two contrasting seasons, early spring 2023 and early autumn 2024, from two sites in central Chile: Horcón, a heavily polluted area, and Quintay, a less-impacted reference site. Reproductive effort in the macroscopic phase was estimated using the reproductive blade area as a proxy for reproductive output. In the microscopic stages, we quantified the abundance, proportion, and developmental status of spores, female and male gametophytes, and juvenile sporophytes, along with fecundity and reproductive success. We hypothesized that phenological traits would differ between seasons and pollution levels, with microscopic stages from Horcón showing reduced performance due to prior in situ contaminant exposure affecting the reproductive tissues. Consistent with previous observations for *L. spicata* in central Chile (Santelices and Ojeda 1984), we also expected reproductive traits to peak in autumn and be comparatively lower in spring.

Materials and methods

Sample collection

Seasonal sampling of reproductive biomass was conducted at Horcón (Playa El Tebo; 32°43′34.52″S, 71°30′11.58″W; Fig. 1) during early spring 2023 and early autumn 2024. This site, located near the industrial zone of Quintero Bay in central Chile, was selected due to its documented history of contamination, with copper (Cu) and arsenic (As) concentrations in seaweed, sea urchins, seawater, and sediments exceeding international marine water quality standards (Oyarzo-Miranda et al. 2020; Latorre-Padilla et al. 2021). A second site, Quintay (CIMARQ; 33°11′39.71″S, 71°40′29.67″W; Fig. 1), characterized by low pollution levels, was also sampled during the same seasons. Quintay, located south of Horcón and outside the influence of the Quintero-Puchuncaví industrial complex, served as a control site (Contreras-Porcia et al. 2023). Seawater temperatures at the two sites are different, with Quintay having lower temperatures (Fig. S1, Supplementary Materials). The selected seasons were based on previous research on another species of *Lessonia* (*L. trabeculata*), which identified summer-spring as the period of maximum individual growth and autumn as the season of peak reproductive output (Tala et al. 2004). It is important to note that the experimental area at the polluted site is currently devoid of the characteristic *Lessonia* belt that typically dominates the low intertidal zone along the central-southern coast of Chile (Santelices et al. 1980; Santelices and Ojeda 1984, and references therein; Oyarzo-Miranda et al. 2020).

Blades bearing reproductive sori of *L. spicata* were randomly collected from a minimum of 10–15 individuals at each site and season to obtain a representative sample of the population. Collected blades were cleaned to reduce contamination by epiphytes, bacteria, protozoa, diatoms, and other microorganisms according to Contreras-Porcia et al. (2025). The cleaning procedure involved brief sequential rinses in 4% ethanol, distilled water, and 1 µm filtered seawater, followed by gentle drying with absorbent paper. Blades were

then transported in darkness and maintained at 10–14 °C in coolers containing ice packs to the LEBMA laboratory (www.lebma.cl).

In the laboratory, blades and sori were photographed and analyzed using ImageJ software (version 1.54 k; Schneider et al. 2012) to estimate sori area (area × 2, because a similar reproductive area is developed on both sides of the blade) relative to total blade area as following Tala et al. (2004). The reproductive effort was expressed as percentage relating the area of reproductive to non-reproductive tissue (De Wreede and Klinger 1988).

Release of spores

The selection of sori areas was performed by trimming the blades and discarding sections with epiphytic growth. The selected sections were initially desiccated in a laminar flow hood under white light for 1 h. Subsequently, sori were placed in 2-L Schott bottles containing 0.22-µm filtered seawater and agitated for 12 h at 15–17 °C to stimulate spore release. During this process, the bottles were wrapped in aluminum foil to maintain complete darkness and protect the reproductive tissue.

Culture and maintenance

Spore density was determined in triplicate using a Neubauer chamber by counting the number of spores per milliliter. The spore suspension was subsequently diluted to a final concentration of 10,000 spores mL^{-1}, and 20 mL of this solution was inoculated into six sterile 100 mm plastic Petri dishes for each sampling site and season.

Cultures were maintained at 15–17 °C under a light intensity of 30–50 µmol photons m^{-2} s^{-1} and a 12:12 h light–dark photoperiod for 28 days. The culture medium consisted of 1-µm filtered seawater enriched with von Stosch medium (8 mL L^{-1}) and was replaced weekly. The first medium change and enrichment were performed 48 h after inoculation. To prevent contamination, either an antibiotic mixture (ampicillin, penicillin, and streptomycin at 0.25 g L^{-1}) or germanium dioxide (GeO_2 at 1 g mL^{-1}) was added to the medium to control bacteria and diatoms, respectively.

Microscopic developmental stages were monitored 48 h after culture initiation and subsequently at 7, 14, 21, and 28 days. Counts of *L. spicata* life stages were performed using an inverted microscope (Eclipse Ts2, Nikon, Japan). For spore settlement and germination, observations were conducted in twelve 0.5 mm^2 fields per Petri dish. For the quantification of undifferentiated gametophytes, male and female gametophytes, and juvenile sporophytes, twelve 1 mm^2 fields per Petri dish were examined. Each stage was expressed as a percentage of the total stages observed at each time point. Final sporophyte density was calculated as the number of individuals per cm^2. The sex ratio was determined based on the proportion of male gametophytes following the formula described by Oppliger et al. (2011):

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

where *MG* represents male gametophytes and *FG* represents female gametophytes. In addition, fecundity and reproductive success were calculated following the formulas described by Lee and Brinkhuis (1986):

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

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

where *TS* represents total sporophytes, *FGO* represents female gametophytes with oogonia, and *FGwO* represents female gametophytes without oogonia. This approach allowed us to determine the timing (in days) of each developmental stage and its quantitative representation.

Statistical analysis

All data, except for final sporophyte density, were expressed as percentages. Normality and homogeneity of variances across seasons and sites were assessed using Shapiro–Wilk and Bartlett's tests, respectively. When assumptions were met, a two-way analysis of variance (ANOVA) was conducted to evaluate the effects of season, site and their interaction on the response variables, specifically the percentage of reproductive effort with arcsine transformation and the final density of *L. spicata* sporophytes. Post hoc comparisons were performed using Tukey's HSD test. For datasets that violated the assumption of homogeneity of variance, generalized linear mixed models (GLMMs) with a beta distribution were applied. Percentages were transformed into proportions to avoid extreme values (0 or 1) following the method proposed by Smithson and Verkuilen (2006). The effects of site and season were included as fixed factors, while time (in days) was treated as a random factor to account for repeated measures on additional response variables, including the percentage of each life stage, sex ratio, fecundity, and reproductive success, were analyzed using GLMMs, with significance assessed via χ^2 statistics. Post hoc analyses were performed using estimated marginal means (EMMs) with the 'emmeans' package (Version 1.11.2; Lenth et al. 2025), applying a Tukey adjustment for multiple comparisons. All statistical analyses were performed in R software (version 4.3.0; R Development Core Team 2024).

Results

Reproductive effort

The maximum reproductive effort of *L. spicata* was recorded during autumn at both locations, with values exceeding 50% (Fig. 2). The statistical analysis revealed no significant differences between sites ($F_{1,24} = 1.16$, $p = 0.29$), while a significant independent effect of season on reproductive effort was detected ($F_{1,24} = 12.88$, $p < 0.001$). Additionally, a significant interaction between site and season was observed ($F_{1,24} = 6.92$, $p < 0.01$) (Table S1, Supplementary Materials). Post hoc comparisons indicated that reproductive effort was significantly lower in Quintay samples during spring (24.6 ± 9.5%, mean ± SD) compared to Quintay in autumn (60.9 ± 18.2%, mean ± SD) and to Horcón samples in both seasons (Fig. 2).

Life cycle development

Observations revealed no significant differences in the percentage of settled spores between sites ($\chi^2(1) = 2.04$, $p = 0.153$) or between seasons ($\chi^2(1) = 2.28$, $p = 0.131$) (Fig. 3), and no significant interaction between these factors was detected. Although the overall model did not show statistically significant effects, post hoc comparisons revealed significant differences ($p < 0.05$) involving Quintay in autumn. Specifically, Quintay in autumn differed significantly from Horcón in both autumn and spring, as well as from Quintay in spring (Table S2, Supplementary Materials).

For germinated spores, no significant differences were observed between sites ($\chi^2(1) = 0.29$, $p = 0.588$), with values exceeding 80% on day 2 across all cases (Fig. 3). In contrast, a significant seasonal effect was detected ($\chi^2(1) = 6.87$, $p = 0.008$), although no significant interaction between site and season was found. Post hoc analysis revealed significant differences ($p < 0.05$) between seasons at both sites. Additionally, significant differences were observed between Horcón in autumn and Quintay in spring, as well as between Quintay in autumn and Horcón in spring. Spring cultures from Horcón exhibited the highest percentage of germinated spores (59 ± 20%), while in autumn, germinated spores at both sites were nearly absent after day 7 (Fig. 3). This seasonal pattern suggests a faster but shorter differentiation process from germinated spores to gametophytes during autumn, compared to a slower but more sustained development during spring at both sites.

Significant differences between sites were found for both female ($\chi^2(1) = 18.67$, $p < 0.001$) and male gametophytes ($\chi^2(1) = 32.72$, $p < 0.001$), whereas no significant seasonal effect was detected ($p > 0.05$) (Fig. 3). However, a significant interaction between site and season was observed for both female ($\chi^2(1) = 10.21$, $p < 0.001$) and male gametophytes ($\chi^2(1) = 11.42$, $p < 0.001$). Post hoc analysis revealed significant differences ($p < 0.05$) across all site and season combinations for both female and male gametophytes, except for comparisons between sites in spring (Table S2, Supplementary Materials).

On day 7, seasonal differences became evident, with higher percentages of female than male gametophytes in autumn cultures (female: Quintay = 47 ± 11%, Horcón = 32 ± 17%; male: Quintay = 36 ± 7%, Horcón = 23 ± 10%), showing a clear predominance of female gametophytes. In contrast, no gametophyte formation was observed on day 7 in spring cultures at either site. In these spring cultures, both spore germination and the transition to gametophytes occurred more gradually over time (Fig. 3).

By day 14, differences in gametophyte development were evident, with notably low percentages of both female and male gametophytes in the autumn cultures from Horcón. Overall, lower gametophyte percentages were recorded in autumn compared to spring at both sites. The highest percentage of female

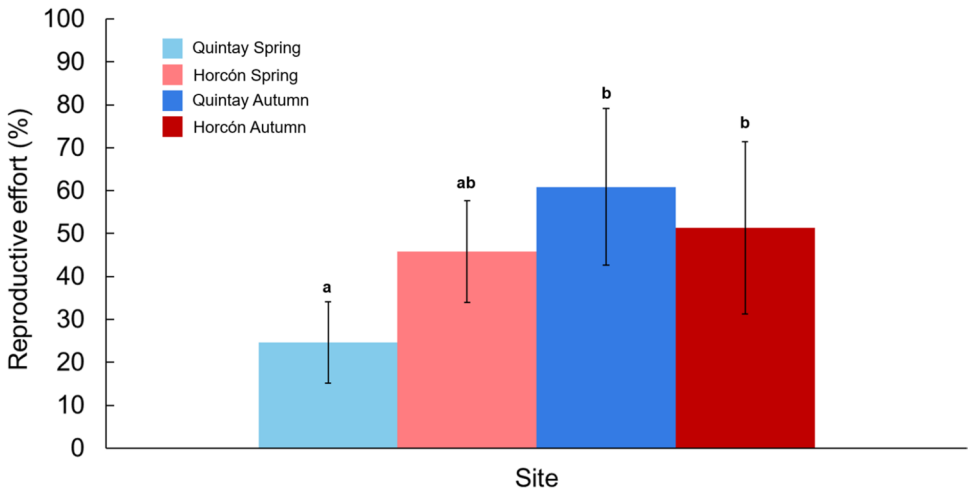

Fig. 2 Reproductive effort (%) of *Lessonia spicata* populations from Quintay and Horcón during spring 2023 and autumn 2024. Different letters indicate significant differences among seasons and sites (two-way ANOVA, $p < 0.05$, followed by Tukey's post hoc test). Bars represent mean ± SD ($n = 7$)

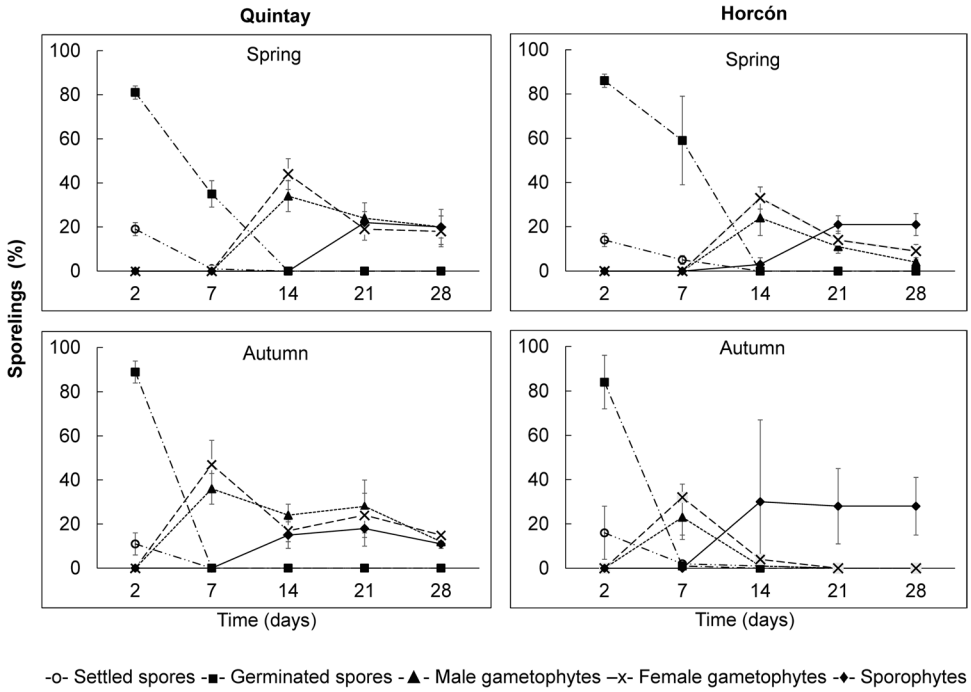

Fig. 3 Life cycle stages (%) of *Lessonia spicata* determined at Quintay and Horcón during spring 2023 and autumn 2024. The percentages of settled spores, germinated spores, male and female gametophytes, and sporophyte stages were recorded at 2, 7, 14, 21, and 28 days of culture. Data are shown as mean ± SD ($n = 6$)

gametophytes was observed in the spring cultures from Quintay (44 ± 7%), while male gametophyte development followed a similar pattern, with the highest values also recorded in the spring cultures from Quintay (34 ± 7%; Fig. 3).

On day 21, the absence of both female and male gametophytes in the autumn cultures from Horcón emerged as the most pronounced pattern. This observation is consistent with the previously detected significant site-specific differences, highlighting that the spring cultures from Quintay exhibited the highest gametophyte percentages across all site-season combinations. By day 28, these trends persisted, with no substantial changes in gametophyte presence (Fig. 3).

Significant differences in the timing of sporophyte formation were observed between sites and seasons. A significant site effect was detected ($\chi^2(1) = 3.89$, $p = 0.049$), with the highest sporophyte percentage recorded in the Horcón autumn cultures (28 ± 13%) at 28 days. A significant seasonal effect was also identified ($\chi^2(1) = 7.95$, $p = 0.005$), although no significant interaction between site and season was found ($p = 0.627$). Post hoc analysis revealed significant differences ($p < 0.05$) between sites during the spring season, as well as between seasons at both sites. Additionally, a significant difference was observed between Horcón in autumn and Quintay in spring.

Sex ratio

A significant difference in the sex ratio between sites was detected ($\chi^2(1) = 25.55$, $p < 0.001$), while no significant seasonal effect was observed ($\chi^2(1) = 0.06$, $p = 0.811$). However, a significant site–season interaction was identified ($\chi^2(1) = 18.65$, $p < 0.001$) (Fig. 4). Consistent with the post hoc results obtained for the gametophyte phase, significant differences ($p < 0.05$) were found across all site and season comparisons, except between sites during the spring season (Table S2, Supplementary Materials).

Sex ratio data were available on day 7 only for the autumn cultures, with identical values recorded at both sites (Quintay = 43 ± 3%; Horcón = 43 ± 4%). In contrast, no gametophytes were observed in the spring cultures at this time point (Fig. 4), consistent with the delayed transition from germinated spores to gametophytes during spring compared to autumn (Fig. 3).

On day 14, gametophytes were observed at both sites and during both seasons. The autumn culture from Quintay exhibited the highest sex ratio (59 ± 7%), whereas the lowest was recorded at Horcón during the same season (16 ± 4%; Fig. 4). By day 21, no male or female gametophytes were present in the Horcón autumn cultures, consistent with the life cycle disruption observed at this site compared to the spring culture at Horcón and both seasonal cultures at Quintay (Fig. 3). At this time, a balanced sex ratio (~ 50%) was maintained in Quintay across both seasons. This trend persisted through day 28, with Quintay cultures maintaining a sex ratio close to 50%, while no gametophytes were detected in Horcón autumn cultures (Fig. 4).

Fecundity

Fecundity exhibited temporal variation associated with the rate of gametophyte development and gamete maturation,

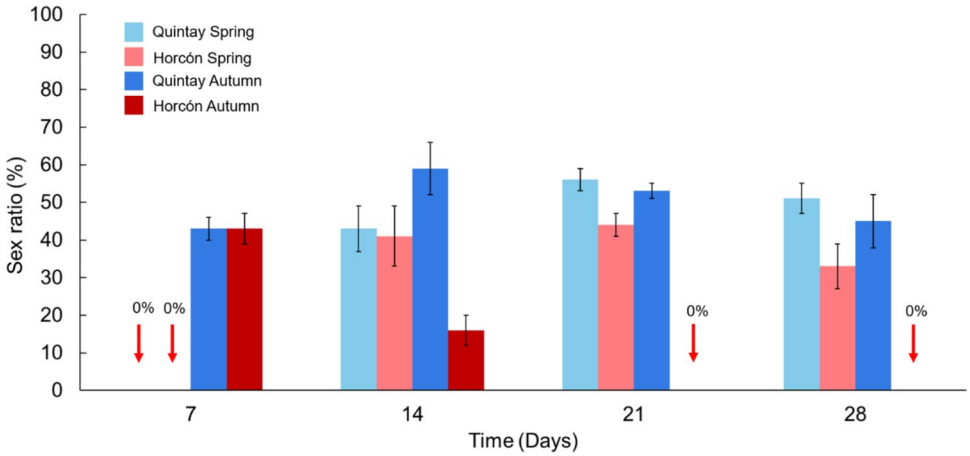

Fig. 4 Sex ratio (%) based on male gametophytes determined at both sites (Quintay and Horcón) during spring of 2023 and autumn of 2024. Zero values represent non-differentiation in gametophyte stages. The sex ratio, expressed as the percentage of male gametophytes, was measured at 7, 14, 21, and 28 days of culture. Bars are mean ± SD ($n = 6$)

which in turn influenced the timing of sporophyte formation and the persistence of gametophytes (Figs. 3, 5).

On day 14, no development of sporophytes or female gametophytes with oogonia was observed in the spring cultures from Quintay, indicating a delay in fecundity-related processes at this site and season (Fig. 5). In the Horcón autumn cultures, female gametophytes were absent on both days 21 and 28. Consequently, fecundity was estimated based solely on the non-necrotic sporophytes present at these time points. No significant differences in fecundity were found between sites ($\chi^2(1) = 0.65$, $p = 0.419$) or between seasons ($\chi^2(1) = 0.55$, $p = 0.458$). However, a significant site–season interaction was detected ($\chi^2(1) = 9.52$, $p = 0.002$), suggesting context-dependent variations in fecundity. Post hoc analysis revealed significant differences ($p < 0.05$) between sites in both seasons, as well as between seasons at both sites. By day 28, fecundity patterns remained consistent with those observed on day 21, with the highest values recorded in the Horcón autumn cultures (Fig. 5).

Reproductive success

No significant differences were detected between sites ($\chi^2(1) = 0.82$, $p = 0.364$) or between seasons ($\chi^2(1) = 0.25$, $p = 0.620$). However, a significant interaction between site and season was observed ($\chi^2(1) = 8.39$, $p = 0.004$) (Fig. 6). Similar to the fecundity post hoc analysis, significant differences ($p < 0.05$) were observed between sites across both seasons, and between seasons within each site.

On day 14, the most pronounced seasonal differences occurred at Horcón, where sporophyte formation reached 88 ± 11% in autumn compared to only 9% ± 8 in spring (Fig. 6). By day 21, site differences were minimal in spring (Quintay = 54 ± 6%; Horcón = 60 ± 9%), and seasonal differences at Quintay were also reduced (spring = 54 ± 6%; autumn = 43 ± 8%).

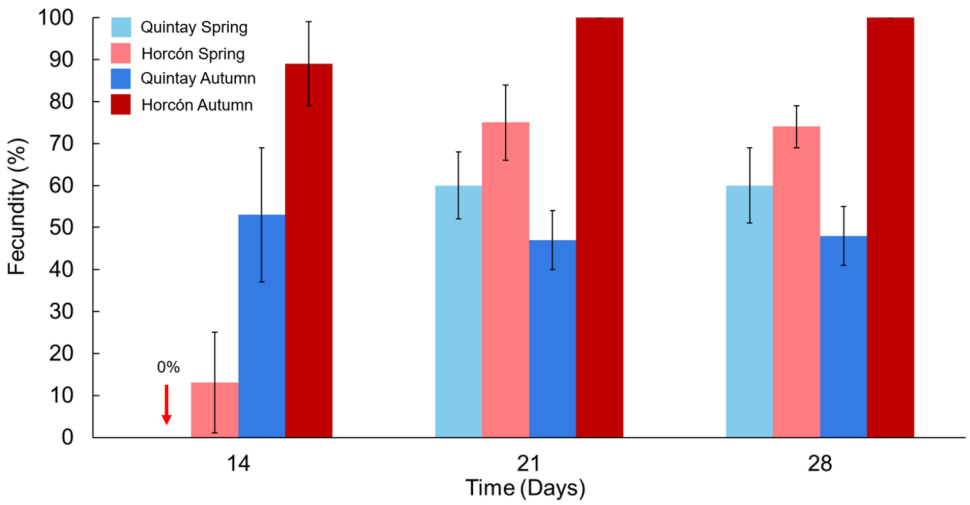

Fig. 5 Fecundity (%) at Quintay and Horcón during spring 2023 and autumn 2024. The percentage of fecundity was measured at 14, 21, and 28 days of cultivation. Bars represent mean ± SD ($n = 6$)

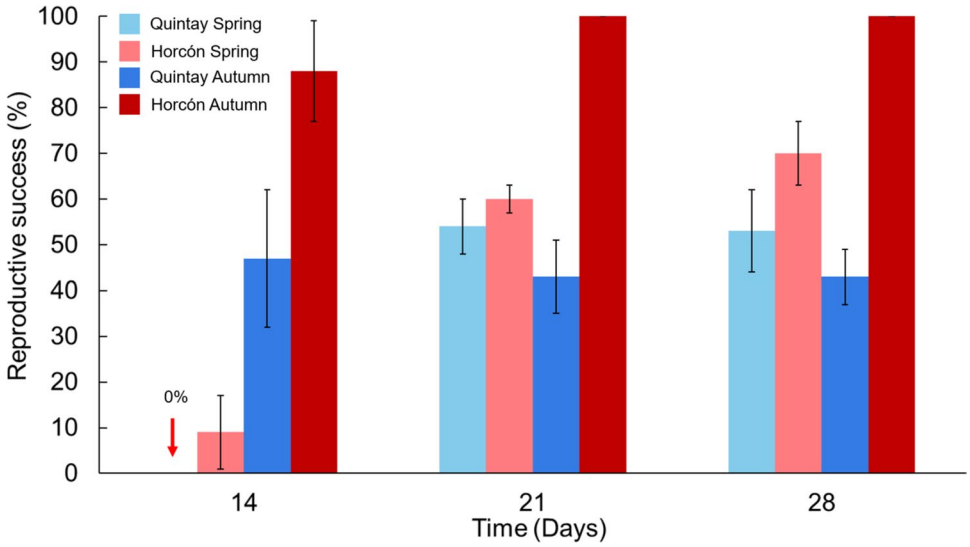

Fig. 6 Reproductive success (%) at Quintay and Horcón during spring 2023 and autumn 2024. The percentage of reproductive success was measured at 14, 21, and 28 days of cultivation. Bars represent mean ± SD ($n = 6$)

By day 28, sporophyte formation percentages between sites in spring were relatively similar (Quintay = 53 ± 9%; Horcón = 70 ± 7%) (Fig. 6). In contrast, Horcón maintained a 100% sporophyte formation rate in autumn, representing the highest values recorded in the study (Fig. 6). These patterns align with the fecundity trends previously described, particularly the consistent 100% sporophyte formation recorded in Horcón during autumn at both 21 and 28 days (Fig. 5).

Juvenile sporophyte density

Sporophyte density varied according to site- and season-dependent delays in formation. After 28 days, final densities were lower in autumn at both sites, particularly at Horcón (102.97 ± 48.50 individuals per cm^2; Table 1). Significant differences were detected between sites and seasons ($p < 0.01$), with post hoc analysis revealing divergences between sites in autumn and between seasons at both sites, with peak densities recorded in spring.

Across the monitoring period (14, 21, and 28 days), sporophyte density was consistently higher at Quintay than at Horcón. However, at 14 days, this pattern reversed seasonally, with higher densities in autumn (Quintay = 1002 ± 319 individuals cm^{-2}; Horcón = 2417 ± 897 individuals cm^{-2}) and lower densities in spring (Quintay = 0; Horcón = 615 ± 497 individuals cm^{-2}). At 21 days, maximum densities were recorded in spring, although autumn values remained markedly higher at Quintay (1003 ± 224 individuals cm^{-2}) than at Horcón (365 ± 149 individuals cm^{-2}). In Horcón during autumn, necrosis of sporophyte tissue emerged at 21 days and intensified by 28 days, resulting in discolored, diffuse morphologies (Figs. 7).

Table 1 Sporophyte density (individuals cm^{-2}) after 28 days of cultivation at the two study sites (Quintay and Horcón) during spring 2023 and autumn 2024 (mean ± SD)

Site/Season	Density (N° ind. cm^{-2})
Quintay/Spring	1378 ± 243.62
Horcón/Spring	1120 ± 193.45
Quintay/Autumn	427 ± 65.51
Horcón/Autumn	102 ± 48.50

Discussion

The early development of *L. spicata* exhibited clear seasonal and site-specific patterns, with cultures initiated in autumn displaying rapid but short-lived germination, while those from spring showed slower yet more sustained growth. Gametophyte abundance was significantly higher in spring, particularly at Quintay, indicating more favorable environmental conditions. In contrast, Horcón cultures, especially in autumn, showed reduced gametophyte formation, early loss, and markedly lower cumulative densities of both gametophytes and sporophytes. Despite this, sporophyte production peaked in Horcón autumn cultures, accompanied by a higher reproductive effort, as evidenced by increased sori development and earlier gametophyte maturation. However, the phenological advantages observed in autumn were offset by signs of physiological stress, including tissue bleaching and necrosis by days 21 and 28. This high reproductive success is attributed to early bleaching events that eliminated most gametophytes, leaving only viable individuals that were successfully fertilized and developed into sporophytes, thus leading to an overestimation of the calculated success rates. Finally, both variables, fecundity and reproductive success,

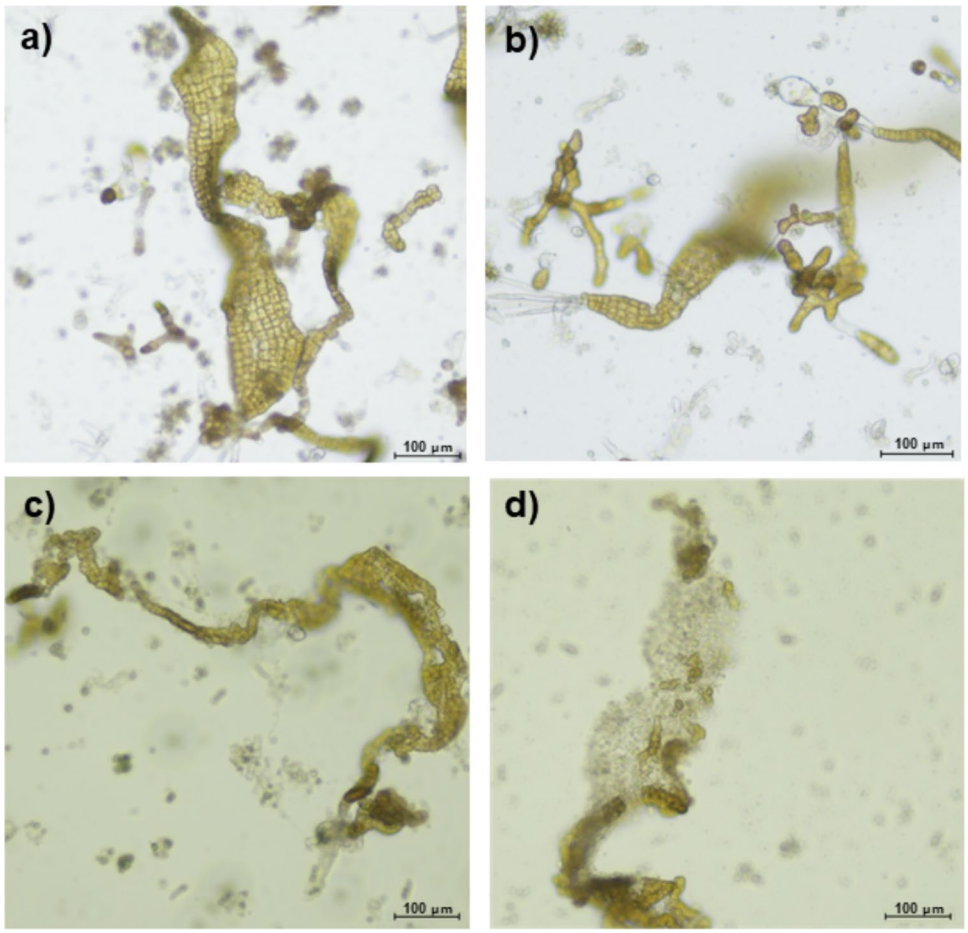

Fig. 7 Photographs obtained after 28 days of cultivation of sporophytes at Quintay (**a, b**) and Horcón (**c, d**) during autumn. Horcón images exhibit sporophyte necrosis and a bleached background associated with gametophyte mortality (scale bar = 100 µm)

did not show significant differences with respect to site or season individually but did exhibit a significant interaction between site and season. These findings underscore the strong influence of seasonality on reproductive dynamics and highlight the detrimental impact of environmental effects, particularly during early stages in polluted coastal areas (Fig. 8).

Previous studies in Laminariales have demonstrated that phenological shifts, seasonally driven variations in life cycle events, exhibit a degree of plasticity yet are predominantly regulated by environmental factors such as photoperiod and sea surface temperature (SST) (Kain 1989; De Bettignies et al. 2018). Less commonly reported, but ecologically relevant, are additional drivers such as blue-light-mediated gametogenesis in *Laminaria* spp. and episodic swell and rainfall events that can trigger spore release in edge populations of *Ecklonia radiata* (Veenhof et al. 2023). In the case of the intertidal kelp *L. spicata* of central Chile, previous surveys by Santelices and Ojeda (1984) have indicated that reproduction and development of microscopic life stages occur all year round but exhibit maximum values during the autumn and winter seasons, with the recruitment of juvenile sporophytes taking place more frequently at the end of winter through to spring and maximum growth of the macroscopic phase during spring and summer. As these authors pointed out, maximum fertility in this species and in the subtidal *L. trabeculata* (Tala et al. 2004) is usually observed in autumn–winter. In fact, recruitment mostly takes place after the occurrence of autumn and winter storms, which are strong enough to remove whole *L. spicata* adult plants, thus opening patches and enabling the settlement of juvenile kelp individuals (Ojeda and Santelices 1984). Our laboratory results reflect the potential for early stages of development depending on their origin (site) and seasonality. In the natural environment, both gametophytes and early sporophytes can undergo delayed development during unfavorable conditions, forming a bank of microscopic stages that can be maintained on the substratum (Hoffmann and Santelices 1991; Edwards 2022). Under favorable environmental conditions, which vary depending on the site, different recruitment patterns may occur that are not directly correlated with the species'maximum fertility.

Lessonia spicata from Horcón and Quintay showed both a higher reproductive effort in adult sporophytes and an earlier development of gametophytes and sporophytes from the autumn than the spring cultures. This trend for both

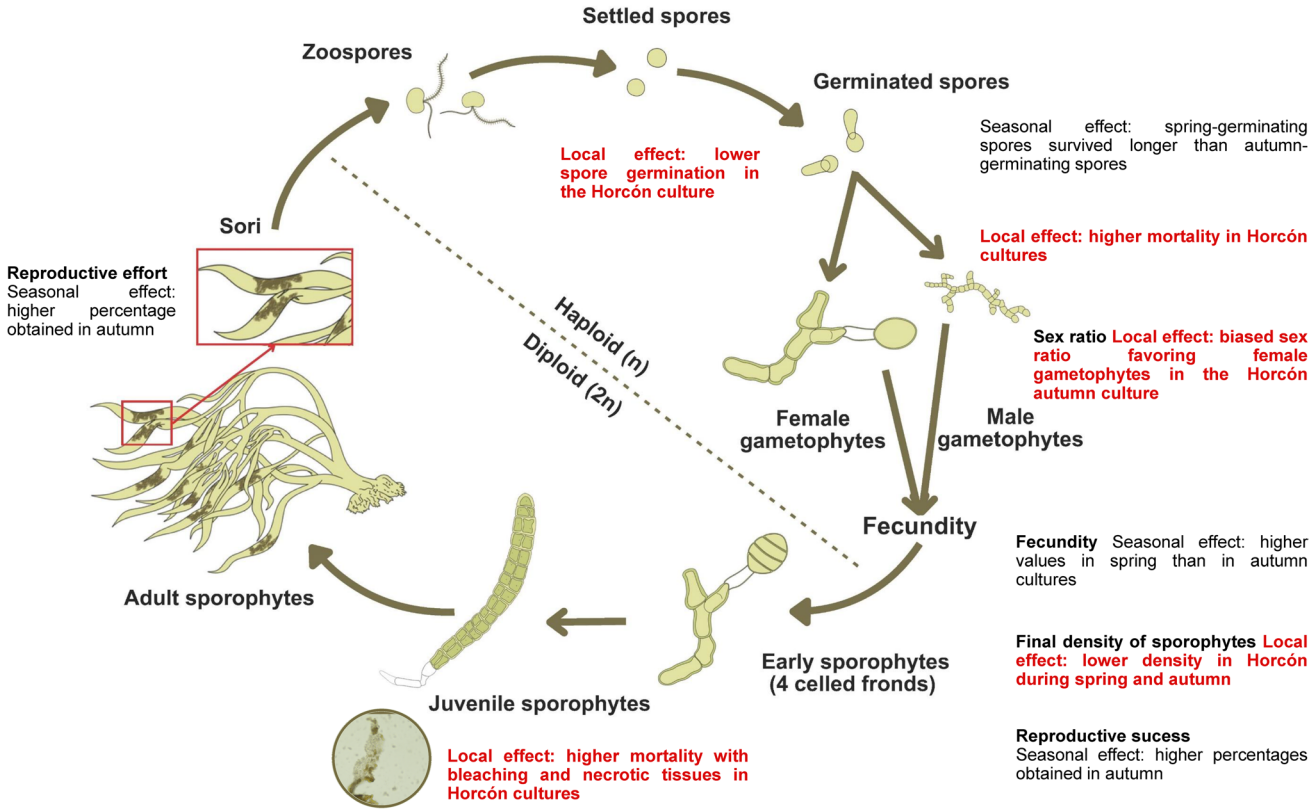

Fig. 8 Schematic overview of the phenological effects of marine contamination and seasonal variability on the life cycle of *Lessonia spicata*. Negative impacts recorded at Horcón, a contaminated site on the central coast of Chile, are indicated in red

sites is coincident with reproductive seasonality typical of "short-length" temperate seaweed species, where reproductive maturation is triggered as day length shortens at lower temperatures (Cunningham et al. 1993). Nonetheless, results of statistical analyses assessing the effects of site, season, and their interaction on the different phenological traits suggested the following more specific patterns. In the first place, the reproductive effort was significantly influenced by both season and the interaction between site and season. This pattern is reflected in the higher values observed in autumn compared to spring at both sites. The interaction effect was evident in the seasonal shift of the site exhibiting the highest reproductive effort, that is, either Horcón or Quintay, depending on the season (Fig. 2). Furthermore, most composite indices (i.e., sex ratio, fecundity, and reproductive success) were mainly influenced by the interaction of site and season, revealing more generally the influence of seasonal environmental variation (higher values in autumn than spring), as well as an additional environmental determination, such as pollution level, that could also play a role in phenological shifts and their magnitudes.

Despite the earlier development of microscopic stages in autumn, the cumulative number of gametophytes and sporophytes over 28 days was higher in spring. This suggests lower overall developmental success in autumn, probably because autumn cultures showed rapid but short-lived germination, while spring cultures displayed slower, sustained development. However, as Schiel and Foster (2006) noted, seasonal viability of spores and early stages remains uncertain. Santelices et al. (1980) also reported a seasonal lag between peak fertility in summer and juvenile sporophyte appearance in late autumn–winter, suggesting delayed recruitment. Since fertile sporophytes typically reach 150 cm, fertility likely correlates with the proportion of large individuals in the population.

The earlier and faster development observed in autumn cultures could reflect inherited traits and environmental triggers, including photoperiod, temperature (De Bettignies et al. 2018), and light quality (e.g., blue light or low irradiance in winter; Lüning 1980; Reed et al. 1997). Similar autumnal fertility patterns and wave-stimulated spore release were reported for *Alaria marginata* in California (McConnico and Foster 2005), consistent with increased kelp strandings in Horcón during autumn–winter (Santelices et al. 1980).

Thermal tolerance varies among kelps depending on their distribution. For instance, *Lessonia corrugata* (Tasmania) has a narrow optimal range (15.7–17.9 °C) (Paine

et al. 2021), while *Ecklonia radiata* shows broader tolerance (~ 18–23 °C) (Mohring et al. 2014). *Lessonia spicata* gametophytes can survive at 20 °C but remain small and infertile, unlike the more tolerant *L. berteroana* (Oppliger et al. 2012). Oceanographic conditions in Horcón due to weaker upwelling may explain the lower densities observed there compared to the more intense upwelling in Quintay (Aravena et al. 2014 and Fig. S1, Supplementary Materials), particularly in autumn. Indeed, gametophyte abundance was significantly higher in spring, particularly at Quintay, suggesting more favorable conditions. In contrast, Horcón cultures, especially in autumn, showed reduced gametophyte formation and early loss. We do not attribute the differences in gametophyte abundance to temperature alone. Within the thermal tolerance range of *L. spicata* across its biogeographic distribution, the temperature difference between Horcón and Quintay is relatively minor (Lara et al. 2019). In contrast, the presence of recently upwelled waters near Quintay suggests substantial differences in nutrient availability for sporophytes, potentially resulting in a mild maternal effect that may contribute to the observed differences in sporophyte performance between the two populations.

In summary, the early development of *L. spicata* exhibited strong seasonal and site-specific patterns. Faster gametophyte maturation was observed in both autumn cultures, especially in Horcón, where higher fecundity by day 14 suggests stimulation by seasonal signals. Sporophyte production also peaked in Horcón autumn cultures, despite overall developmental instability. However, necrosis and bleaching in some sporophytes on days 21 and 28, along with the absence of gametophytes from day 21 onwards, indicate a likely increase in mortality. In contrast, sex ratios in Quintay remained stable at ~ 50% from day 14 in both seasons, while in Horcón, autumn cultures showed a drastic decline, suggesting an unstable sex ratio likely due to environmental stress. Although mild shifts in sex ratios have been linked to thermal stress in *L. spicata* and *L. berteroana* (Oppliger et al. 2011), the sharp imbalance observed in Horcón would be indicating an additional stressor influencing reproductive dynamics beyond temperature alone. These results highlight the influence of environmental quality and seasonality on *L. spicata* recruitment, with populations in impacted areas facing greater challenges in maintaining early life stage success.

These findings align with previous studies in the impacted Quintero-Puchuncaví area, near the industrial park, where *L. spicata* from the most polluted site, Ventanas, exhibited the shortest blades, smallest holdfasts, and the lowest spore release and settlement rates after 120 h when exposed to local seawater (Oyarzo-Miranda et al. 2020). The same study reported increased male gametophyte mortality under pollutant-induced stress, causing a sex ratio bias toward females. Elevated levels of contaminants, such as copper (Cu), arsenic (As), and PAHs, have been consistently recorded in the seawater and sediments of the area (Oyarzo-Miranda et al. 2020). In vitro studies further confirmed that spore development in *L. spicata* ceases upon exposure to high Cu concentrations (7.87 µg L^{-1}), with toxic effects impairing gametophyte formation and disrupting the life cycle (Contreras et al. 2007; Contreras-Porcia et al. 2017). Similar sensitivity has been observed in other kelps like *Macrocystis pyrifera* and *Undaria pinnatifida* (Leal et al. 2016; Meynard et al. 2021). Moreover, metal and naphthalene accumulation in *M. pyrifera* and its trophic transfer to *Tetrapygus niger* have been documented, exceeding Codex Alimentarius Safety Limits (Contreras-Porcia et al. 2017; Latorre-Padilla et al. 2021). Thus, the comprehensive phenological analysis conducted in this study suggests detrimental effects of marine pollution, as well as the combined influence of environmental variables such as temperature and nutrient availability, on *L. spicata* populations. Furthermore, the results provide clear evidence of negative impacts throughout the marine area of the Quintero-Puchuncaví coastal zone, highlighting the urgent need for environmental management measures.

Conclusions

This study demonstrates that both seasonal environmental factors and local anthropogenic pollution significantly influence the reproductive phenology of *L. spicata*. Cultures developed from reproductive material collected in autumn showed enhanced reproductive performance compared to those from spring, suggesting a seasonal induction for reproductive shifts. On the other hand, the generally lower sea surface temperatures (SSTs) associated with stronger upwelling conditions could potentially contribute to the higher densities of microscopic life stages observed in Quintay compared to Horcón. This pattern might be linked to enhanced survival at relatively lower temperatures; however, further analyses are needed to confirm this hypothesis. However, in the polluted site of Horcón, signs of reproductive impairment, including rapid but short-lived germination, skewed sex ratios, gametophyte absence, and sporophyte necrosis, highlight the combined impact of contamination. These findings suggest that in highly impacted coastal environments, pollution may act synergistically with seasonal stressors to alter the timing, success, and viability of key life cycle stages in kelp populations. This underscores the need for targeted environmental management strategies in degraded marine areas to support the resilience and persistence of foundational algal species.

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Authors' contribution All authors contributed to the research design and the development of field and laboratory methodologies. The first draft of the manuscript was prepared by A.M., B.P., G.V., and L.C.-P. All authors participated in the editing of draft versions and approved the final manuscript. This work formed part of G.V.'s marine biology thesis at Universidad Andrés Bello, supervised by L.C.-P. and F.T.

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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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