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RESEARCH ARTICLE

Spore priming by coastal upwelling in the intertidal kelp *Lessonia spicata*

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Abstract

The kelp populations of two cryptic species of *Lessonia* inhabiting the intertidal zone of the southeastern Pacific are vulnerable to local extinction and range contraction by being exposed to large-scale thermal extremes and strong harvesting by artisanal fisheries. Our study explored the effect of variable ocean temperature conditions on the germination of spores, a critical stage for post-disturbance persistence of local populations, including harvesting. Over a 15-month experimental period, we collected reproductive tissues from 10 tagged sporophytes of a wild local population of *L. spicata* in Central Chile (~33.5° S) and measured germination success. Reproductive activity closely tracked the presence of low (<14°C) ocean temperatures at the study site. Mean spore germination was over 80% from late Austral fall to late spring and sharply declined and became more variable under the warmer ocean conditions of summer and early fall. Unexpectedly, a mid-summer mesoscale upwelling event cooled seawater below 14°C, and spore germination success increased from <50% to up to 90%. Across the study period, germination showed a significant negative correlation with seawater temperature, down to a lag of 4 days prior to the collection of reproductive tissue. These results suggest both a temperature threshold and a temporal scale for spore priming in *L. spicata*, providing support to earlier hypotheses positing spatial heterogeneity in the upwelling regime as the leading driver of speciation in the *Lessonia* complex. Together, our results provide an important evolutionary insight for the conservation, restocking, and management of the *Lessonia* complex.

KEYWORDS
conservation, ENSO, kelp reproduction, La Niña, Laminariales, *Lessonia berteroana*, speciation, spore germination

INTRODUCTION

Many kelps are foundation species in temperate coastal environments where they provide vital ecosystem services (Graham et al., 2007; Eger et al., 2023; Edwards, 2025). Worldwide, warm-edge populations of different kelp species are experiencing local extinction following increasing global temperature and recurrent marine heatwaves (MHWs), thus threatening the coastal social-ecological systems that rely on them (Cavanaugh et al., 2019; Krumhansl et al., 2016; Starko et al., 2024; Wernberg et al., 2025). The loss of macroscopic sporophytes may be due to local processes—such as dislodgement caused by harvesting or seasonal storms—or

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Abbreviations: AVHRR, Advanced Very High Resolution Radiometer; ECIM, Estación Costera de Investigaciones Marinas; ENSO, El Niño–Southern Oscillation; KW, Kruskal-Wallis test; L3C, level 3 collated; MHW, marine heatwave; SST, superficial seawater temperature.

they may occur following regional disturbances driven by large-scale climatic processes, including warm El Niño-Southern Oscillation (ENSO) events or MHWs (Barradas et al., 2011; Cavanaugh et al., 2019; Dayton et al., 1999; Eggert, 2012; Ladah et al., 2002; McConnico & Foster, 2005; Schimpf et al., 2022). Given the limited propagule dispersal capacity in kelp species, population recovery after local extinction relies on the persistence of microscopic phases (Edwards, 2022; Parada et al., 2016; Schiel & Foster, 2006). Spores settle onto the benthic environment, where they produce gametophytes and sporophytes that can persist for extended periods as microscopic haploid or diploid individuals (Edwards, 2022; Hoffmann & Santelices, 1982, 1997). On the low intertidal zone of central-northern Chile, dense stands of *Lessonia* spp. (Laminariales) dominate the community (Castilla & Camus, 1992; Duarte et al., 2025). Two cryptic species of *Lessonia* (*L. beteroana* and *L. spicata* ex *L. nigrescens*) coexist in a parapatric mosaic inside a limited geographic area between 29 and 30° S (González et al., 2012; Tellier et al., 2009; Tellier, Vega, et al., 2011; Tellier, Tapia, et al., 2011). It is well established that sporophytes of the two species have different thermal affinities, and it has been posited that limited dispersal and an environmental mosaic may have acted as the drivers of the speciation process (Oppliger et al., 2012; Tellier, Tapia, et al., 2011). Therefore, a dynamical relation between environmental variability and temperature-dependent reproductive success of the microscopic stages may be a key driver of the speciation process and local population persistence (Martínez, 1999; Oppliger et al., 2012; Tellier et al., 2009).

Along central-northern Chile, *Lessonia* populations are harvested by artisanal fishermen through the detachment of entire sporophytes over extensive tracts of low intertidal zones and constitute a major fishery (Tellier, Vega, et al., 2011; Vásquez et al., 2012; Westermeier et al., 2019). The recovery of local populations and the sustainability of the fishery hinges on successful post-harvest recruitment (Ojeda & Santelices, 1984; Vásquez et al., 2014). Spore priming is the physiological preparation of spores within sori or sporophylls, which can determine spore recruitment after release from the sporophyte (Bewley et al., 2013; Johansson et al., 2013; Lüning, 1980). Different environmental factors can influence spore priming, particularly light levels, nutrient levels, and superficial seawater temperature (SST), as shown by Lüning (1980), Gauci et al. (2022), and Véliz et al. (2025). Studying reproductive structures and the microscopic stages in situ remains challenging due to their small sizes and the dynamic conditions (wave impact) of the intertidal and shallow subtidal zone (Edwards, 2022; Johansson et al., 2013). Our work was part of a set of field and laboratory studies on ecological interactions and local population persistence of *L. spicata*, including on the dispersion and recruitment challenges (Parada et al., 2016, 2017). The study's intensive observational component, at a single location at 33.5° S (see below), allowed us to continuously monitor reproductive responses and demographic outcomes under changing environmental conditions in the wild. To this end, we used a natural experiment—changes in SST over the scale of days—to examine the consequences of environmental variability on sporophytes through spore priming and its impact on spore germination after release. Local environmental conditions are key to reproductive dynamics, particularly regarding sporogenesis. As such, we hypothesized that the presence of cold, recently upwelled waters, even outside the normal phenological cycle, contribute to spore priming in *Lessonia spicata*. Using the insights from these results we examined the consistency of the results with local seawater temperature patterns from sites within the transitional mosaic of the two cryptic *Lessonia* species, to indirectly test the hypothesis of temperature-dependent reproductive success as a driver of speciation in the group.

MATERIALS AND METHODS

To evaluate spore numbers and their germination, during April 1999 (Austral fall) we tagged 10 adult *Lessonia spicata* sporophytes on the rocky intertidal zone of the University Coastal Field Station (Estación Costera de Investigaciones Marinas, ECIM, 33.5° S). For 15 months, we collected 2 g (fresh weight) of sori tissue from mature sporophytic fronds of the same tagged individuals. Samples were immediately transported to the laboratory at ECIM and kept at 4°C until spores were released and processed following the protocol of Martínez and Santelices (1998). Spores were incubated for 24 h on slides in filtered seawater (0.45 μm) at 15°C under a 12:12 h light: dark photoperiod and a light intensity of 15 μmol photons · $m^{-2} \cdot s^{-1}$. Using a Nikon TMS-(400×) inverted microscope, we counted the number of spores that settled on the slides by focusing on a field and repeating in as many fields as necessary to count 100 or more spores (triplicates per plant). Germination was evaluated after the incubation (presence of a germ tube) and expressed as a percentage of the total number of spores. During late March of 2000, strong swells precluded the access of the 10 tagged sporophytes; hence, we collected reproductive tissue from eight different individuals at the ECIM site. We assessed ocean temperature variability using two complementary approaches. Firstly, we utilized SSTs collected on the shore of ECIM for the entire study period. Temperature data were recorded automatically every 20 min using an Onset®Hobo temperature logger encased in a PVC pipe that had been drilled to freely exchange water with the surrounding water. Temperature loggers were either anchored to the low intertidal zone or housed inside a concrete block submerged in the shallow subtidal and attached to the shore with a chain bolted to the rock. Central-southern Chile (i.e., poleward of 30° S) experiences intense wave action year round (Beyá

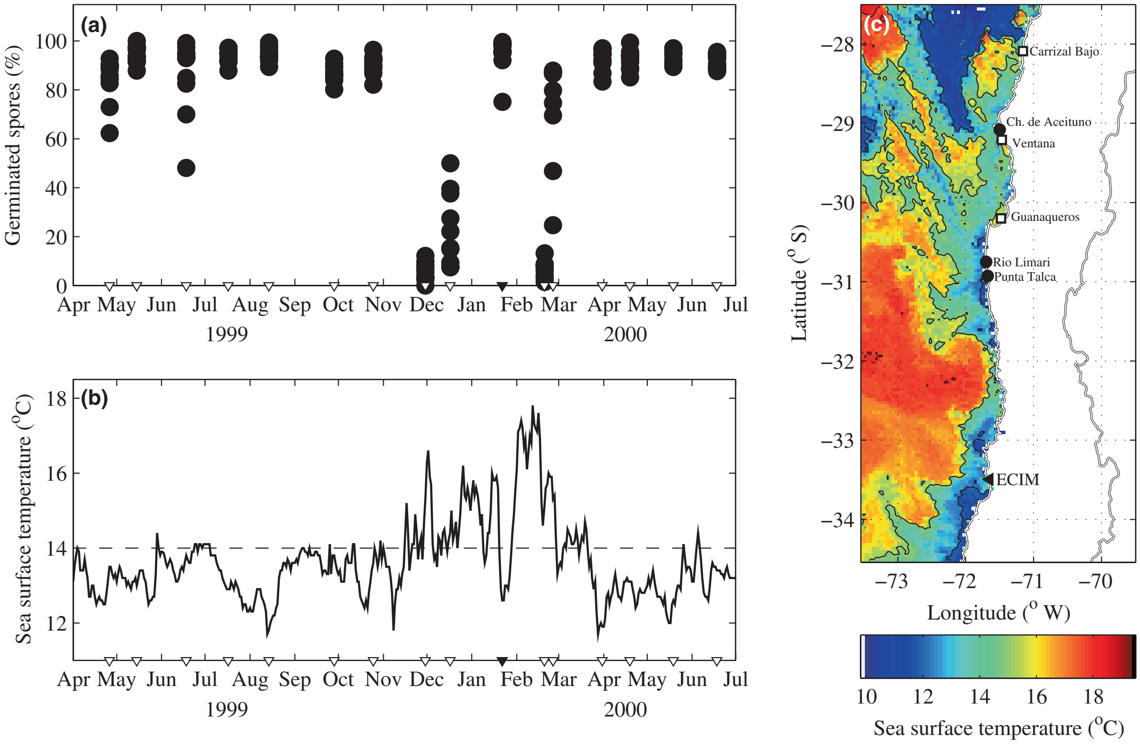

FIGURE 1 (a) Percentage of germinated spores released from reproductive tissue collected from adult sporophytes in the field on the dates indicated by inverted open triangles on the time axis; the bold triangle indicates the mid-summer upwelling event. Note the seasonal changes in germination with variable or reduced success during Austral summer–fall (late December to late June), excepting the peak in January. (b) Daily SSTs between April 1, 1999, and July 1, 2000, recorded at the low intertidal zone of the Estación Costera de Investigaciones Marinas (ECIM). Open inverted triangles on the time axis as in (a), the dotted horizontal line at 14°C is plotted for reference. (c) Nighttime L3C sea surface temperature from AVHRR for January 21, 2000 (Austral summer); black contours are 12, 16 and 18°C and highlight the separation of the cold recently upwelled waters inshore around our ECIM study site, indicated by a black triangle. The six sites along the equatorward part of the image correspond to locations where we used long-term daily in situ SST records to calculate the water temperature probability density as shown in Figure 2b. Open squares indicate populations of *Lessonia berteroana* while close dots are populations of *L. spicata*.

et al., 2016). Thus, our temperature records reflected conditions in seawater approximately within the first meter below the surface and along the lower part of the intertidal zone. Daily means were calculated excluding temperature values during low-tide periods when the loggers may not have been underwater. (Full methods are detailed in Tapia et al., 2014 and Aravena et al., 2014.) To establish between-site conditions along the transitional zone of the two *Lessonia* species, we used the long-term temperature records to examine local thermal conditions at six sites between 28 and 31° S, three sites for each species (Aravena et al., 2014). To visualize differences between sites, we pooled the data for the sites harboring populations of either *L. spicata* or *L. berteroana* using a normal kernel probability density function. To avoid serial correlation, we bootstrapped 10,000 times the pooled daily seawater temperatures and tested for differences in the distribution between groups of sites using a Kolmogorov-Smirnov test (Manly, 1997). Secondly, to bolster our interpretation of mesoscale SST patterns during the field experiment and provide a visualization of SST conditions along the study region, we obtained nighttime satellite SST imagery from the Advanced Very High Resolution Radiometer (AVHRR) for the version 5.3 level 3 collated (L3C) dataset (Casey et al., 2010; Saha et al., 2016). To assess the effect of seawater temperature in the field on germination, we used lagged rank correlations between the mean percentage of spores germinated on each sample date and in situ daily SST during each of the 4 days prior to the sampling of reproductive material at ECIM (Broitman et al., 2009). Seasonal differences in germination were analyzed using a Kruskal-Wallis test (KW) with post hoc multiple comparisons (Siegel & Castellan Jr., 1988). Extraction and manipulation of satellite images, cross-correlations, kernel probability density estimates, and KS tests were carried out using MatLab R2014a.

RESULTS

The annual cycle of spore germination of *Lessonia spicata* at ECIM over the study period is shown in Figure 1a. A seasonal analysis revealed that as expected for kelps, the highest average germination rates were observed during the colder seasons, with 89%

germination in Austral fall 1999 (late March to late June), 91% in Austral winter 1999 (late June to late September), and 92% in fall 2000, showing no significant differences among these periods. As expected, germination rates were lower during warmer seasons, reaching 52% in Austral spring (late September to late December) 1999 and 56% in summer (late December to late March) 1999–2000, with no significant differences between these two seasons. Statistical analysis confirmed significant differences between cold and warm seasons: KW (4,149) = 47.123; $p < 0.001$. Specifically, winter 1999 and fall 2000 germination rates were significantly higher than those in Austral spring 1999 and summer 1999–2000, although fall 1999 germination was statistically similar to summer 1999–2000 but distinct from spring 1999. The 10 tagged plants exhibited relatively uniform contributions, each accounting for approximately 10% of the total germination, yet the absence of sori in some plants during summer–fall diminished the populational reproductive output. A more detailed analysis of monthly germination percentages revealed higher variability from November 1999 to January 2000, ranging from 6% in November to 93% in January 2000, the warmer season of the southern hemisphere (Figure 1a). A mid-summer cooling of seawater (named here a natural experiment) extended from mid to late January 2000, lasting approximately 12 days (Figure 1b). Inspection of L3C AVHRR images for the period effectively indicated a coastal upwelling event. In an image from January 21, 2000 (Figure 1c), the day before we collected reproductive tissue in the field, upwelling plumes of cold water (<14°C) were evident against the warm offshore waters (>16°C). Cold water plumes could be seen around Punta Curaumilla and Punta Toro, two known upwelling centers located immediately north and south of ECIM, respectively (Figure 1c, Johnson et al., 1980, Tapia et al., 2014). The persistence of upwelling conditions around our study site appeared to have primed spores in the reproductive tissues of the sporophytes, abruptly increasing spore germination from the sori collected during that period. Spore germination percentages exceeded 80% only when SSTs were below 14°C and defined a sharp temperature threshold for germination (Figure 2a). Moreover, across the study period, there was a strong and highly significant negative correlation between SST the day before we collected reproductive tissue and the percentage of germinated spores (Spearman's $R = -0.87712$; $p < 0.0001$); the relationship remained significant down to a lag of 4 days (Spearman's $R = -0.69904$; $p = 0.0026$). The persistence of the statistical association and the successful germination for the January samples (Figure 2a, open dot) showed that the annual cycle of spore germination in *L. spicata* is largely temperature-dependent (Santelices, 1990). Our analysis of long-term seawater temperature patterns pooled among sites harboring populations of either *L. spicata* or *L. berteroana* rejected the null hypothesis that the two distributions were drawn from the same population (two-sample KS, $p < 0.0001$, Figure 2a). It is worth noting that the comparison is drawn from a rather large number of daily seawater temperature observations (*L. berteroana*, $n = 15{,}066$; *L. spicata*, $n = 14{,}090$). The global bootstrapped mean SST for all the field data across all six sites was 14.035°C (Figure 2b).

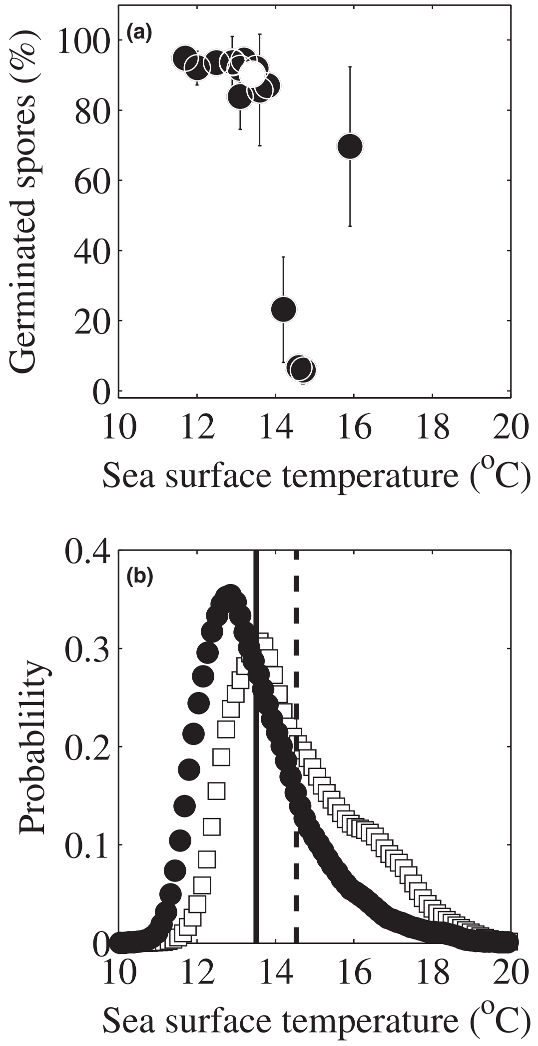

FIGURE 2 (a) Percentage of germinated spores (∓1 *SD*) and SST the day before collection of reproductive tissue for germination. The negative rank correlation is strong and highly significant ($R = -0.87712$, $p < 0.0001$). Results from the open circle correspond to spores obtained from reproductive tissue samples collected during January 2000, the mid-summer upwelling event. Note the large populational heterogeneity over 14°C. (b) Probability distribution of daily SSTs and arithmetic mean for six locations along the allopatric mosaic between *Lessonia spicata* (open circles and solid line) and *L. berteroana* (open squares, dotted line) at sites reported by Tellier et al. (2009) and shown in Figure 1c using the same symbols. We used a normal kernel function to compute the probability density estimate of seawater temperature using all daily temperature records available at each of the locations occupied by populations of either *L. spicata* or *L. berteroana*. The alternating geographic distribution of sites occupied by either *Lessonia* species across the transitional region supports the persistence of small-scale spatial patchiness in temperature regime.

DISCUSSION

Understanding the processes impacting their microscopic life stages is critical for guiding future conservation efforts and informing management and restoration strategies (Ebbing et al., 2025). Studying germination in isolation of further developmental stages limits our conclusions about the effects of spore priming, yet it provides a useful starting point for further studies. Successful spore germination for *Lessonia spicata* took place largely during low (<14°C) SST periods; curtailed germination with warmer SSTs is consistent with studies indicating that warming reduces spore viability in kelps (de Bettignies et al., 2018). We interpret the abnormal mid-summer sudden increase in germination to a rare coastal upwelling event, rather characteristic of Austral spring in our study region (Aravena et al., 2014; Johnson et al., 1980; Poulin et al., 2002). The presence of low seawater temperature along north-central Chile is associated with events of wind-driven upwelling of subsurface water, which also deliver nutrients to the photic zone, particularly nitrates (Nielsen & Navarrete, 2004; Palacios et al., 2013; Reyes-Macaya et al., 2022; Silva et al., 2009). Beyond low temperature, surplus nutrients could have further boosted the reproductive response of our *L. spicata* population. Similar responses to nutrients have been observed in *Macrocystis pyrifera*, for which nitrogen sufficiency mitigates thermal stress (Fernández et al., 2020). Conversely, it is worth noting that our study took place during a multiyear cold La Niña event (Wang, Sun, et al., 2023), and our study area was dominated by cold temperature anomalies over the period (Navarrete et al., 2002). In this way, the short-lived summer reproductive peak shows the tight linkage between reproduction and temperature variability for *L. spicata*: Rapid and successful spore priming took place despite the phenological mismatch (Oppliger et al., 2012; Santelices, 1982; Santelices & Ojeda, 1984; Véliz et al., 2025).

Chile is the world's leading exporter of wild-harvested kelp (Food and Agiculture Organization of the United Nations, 2022), and our results provide an actionable benchmark for the management of natural populations of *Lessonia spicata* in central Chile based on SSTs. To this end, the use of satellite-SST products is useful for approximating local conditions, but these products can underestimate the strength of upwelling in the nearshore (Meneghesso et al., 2020). Also, remote sensing or reanalysis products failed to capture small-scale and between-site variability along the shoreline that is important for recruitment success (Foulk et al., 2024; Lagos et al., 2008; Martínez & Santelices, 1998; Parada et al., 2017). Moreover, our field measurements of temperature did not capture the small-scale patterns within the kelp belt during low-tide periods. Hence, field observations should remain a cornerstone in the deployment of improved management initiatives, since future extreme events may elevate seawater temperatures over periods and magnitudes highly detrimental to Laminariales (de Bettignies et al., 2018; van den Hoek, 1982). Recurrent MHWs have decimated local kelp forests and driven permanent or persistent range contractions around the world over the past decades (Smith et al., 2024; Wernberg et al., 2025). The southeastern Pacific has so far experienced very limited MHWs of the magnitude recorded elsewhere. Nonetheless, its biota is vulnerable to exposure to extreme thermal stress driven by El ENSO events, MHWs (Cai et al., 2021; Wang, Jing, et al., 2023), and artisanal fisheries pressure (Vásquez et al., 2014). After the strong 1982–1983 El Niño event, the equatorward edge of the range of *L. berteroana* (ex *L. nigrescens*) fragmented and contracted after local populations went extinct over approximately 600 km of coastline. Recolonization was dispersal-limited as the populations that were able to persist, located around areas exposed to coastal upwelling, were distant among themselves and still subject to fisheries harvest. After 2 decades, newly established populations exhibited markedly reduced genetic diversity and a subdued fisheries potential (Castilla & Camus, 1992; Martínez et al., 2003). Although our focus was on the germination phase, it is worth stressing that the recruitment process into adult sporophytes is not guaranteed by high germination rates; post-release bottlenecks—including limited spore dispersal distances, substrate quality and availability, and intense herbivore pressure—strongly constrain full recruitment success (Johansson et al., 2013; Oróstica et al., 2014; Parada et al., 2016, 2017).

The 14°C thermal threshold serendipitously identified in our study carries an important insight into the selective processes underpinning the speciation for the *Lessonia* species complex. We identified this particular temperature using the data for spore priming and germination strength in *L. spicata*, a model of reproductive fitness. The atypical summer germination peak observed in *L. spicata* mirrors reproductive responses of brown macroalgae in cold temperate regions, where low temperatures and nutrient availability can induce off-season fertility peaks (Gauci et al., 2022; Liu et al., 2017). The geographic range edge between the two cryptic species, *L. spicata* and *L. berteroana*, is a parapatric mosaic organized as distinct populations between 29 and 30°S (Figure 1c, Tellier et al., 2009; Tellier, Tapia, et al., 2011; Oppliger et al., 2012). Populations of the two species occur inside a broad bay along a section of the coastline where the upwelling regime changes from strongly seasonal poleward to semipermanent and intermittent equatorward (Aravena et al., 2014; Lara et al., 2019; Reyes-Macaya et al., 2022; Tapia et al., 2014). As the probability distribution of SSTs showed, the two species coexist in a thermal landscape of neighboring sites in which mean conditions diverge around a 14°C threshold SST (Figure 2b, vertical lines). Our analysis showed that six closely located sites, in which earlier genetic studies located the transitional mosaic between species, were indeed thermally distinct, despite the short spatial scales separating them and consistent with their geographic affinity of their distributions toward the warmer north (*L. berteroana*) and the colder south (*L. spicata*). Thus, the alternating geographic distribution of sites occupied by either *Lessonia* species across the transitional region supports the persistence of striking small-scale spatial patchiness in long-term temperature regime. A higher tolerance to aerial exposure—which increases toward lower latitudes—by the microscopic stages of *L. berteroana* compared to *L. spicata* is consistent with between-site scale environmental heterogeneity as the determinant to the isolation between species (Beyá et al., 2016; López-Cristoffanini et al., 2013). The change in upwelling regime around the transitional region coupled with the limited dispersal capacity of both species likely reinforced genetic divergence and speciation by favoring distinct environmental tolerances (Duarte et al., 2025; González et al., 2012; Oppliger et al., 2012; Parada et al., 2016). The deep evolutionary basis of the divergence suggests that responses to novel patterns of environmental variability may vary between species or even within the ranges of the species, influencing species distribution, genetic diversity, and associated biodiversity, after MHW or ENSO events, for example (Duarte et al., 2025; Graham et al., 2007; Martínez et al., 2003; Starko et al., 2024; Teagle et al., 2017). To date, all studies in central Chile on the microscopic stages of *L. spicata* have been conducted under controlled laboratory conditions (e.g., Hoffmann & Santelices, 1982; Hoffmann et al., 1984; Avila et al., 1985; Martínez, 1999; Oppliger et al., 2012; for a review see Alsuwaiyan et al., 2019). Moreover, the seasonal collection of reproductive material has been limited to a single date per season and has often relied on satellite imagery to approximate the thermal environment of the sporophytes (Foulk et al., 2024). The coarse temporal and environmental context of earlier studies has left a critical gap in our understanding of reproductive dynamics in the wild that is key to linking basic biological insights with the design of management strategies for the future, which will have lasting socioecological impacts (Duarte et al., 2025; Gauci et al., 2024; Vásquez et al., 2012).

CONCLUSION

Our results, based on intensive and detailed in situ observations, stress the importance of understanding how environmental variability and complex life cycles have interacted over evolutionary scales in shaping the biology and ecology of Laminarians and explain the strong spatial genetic structure and surprising parapatric speciation of the *Lessonia* species complex over very short spatial scales. These results also provide important underpinnings for management decisions at short time scales through the use of in situ observations of the seawater temperature.

AUTHOR CONTRIBUTIONS

Gloria M. Parada: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal). **Enrique A. Martinez Mosqueira:** Conceptualization (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); writing – original draft (equal); writing – review and editing (equal). **Bernardo R. Broitman:** Investigation (equal); methodology (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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DISCLOSURE

Large language models (LLMs) did not exist when we collected the data for this study and were not used in the analysis of the data, only for manuscript formatting, language, and word count analysis, hence ensuring compliance with journal guidelines.

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