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Short communication

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Interactions between kelp spores and encrusting and articulated corallines: recruitment challenges for *Lessonia spicata*

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Abstract: Intertidal kelps like *Lessonia spicata* (Laminariales) dominate low intertidal habitats, where they coexist with morphologically diverse coralline seaweeds. We show that crustose and articulated coralline algae have contrasting effects on the settlement and recruitment of this kelp species. Crustose coralline algae significantly inhibited the settlement of kelp spores, while they readily settled on the genicula of articulated coralline algae. This pattern was observed both in laboratory experiments and in field experiments conducted in the low intertidal zone at three locations. Field surveys confirmed that *L. spicata* juveniles were significantly more likely to be found on articulated corallines than on crustose corallines. This pattern held in field surveys at 10 sites, where primary space occupancy of *L. spicata* showed a significant negative correlation with the cover of crustose coralline algae in 3 out of 4 years, across all sites. Our results provide an important ecological clue to the processes determining recruitment limitation for ecologically and economically important seaweeds, and support conservation and management actions.

Keywords: facilitation; intertidal kelps; seaweed interactions; spore settlement.

Intertidal kelps like *Lessonia spicata* (Suhr) Santelices (Laminariales) inhabit rocky shores in the Southeastern Pacific where they coexist with morphologically diverse coralline seaweeds. Together, they dominate primary space in the low intertidal zone (Santelices and Ojeda 1984) and provide substrate for the settlement of a diverse suite of invertebrates and other seaweeds (Camus 1994), and refuges from predation (Coull and Wells 1983, Hicks 1986, Akioka et al. 1999). Regional kelp mortality events take place periodically following ENSO events (Martínez et al. 2003), and local biomass removal occurs through ecological interactions (e.g. grazing; Aguilera et al. 2015), human harvesting (Vega et al. 2014) and other abiotic factors, such as desiccation (Buschmann 1990, Santelices 1990). Biomass removal processes modify benthic community composition, which in turn reduces recruitment opportunities for kelp spores. The presence of suitable substrates for spore settlement is key for kelp recolonization, and coralline algae have been shown to have a negative interaction with kelp spores (Masaki et al. 1981, 1984, Kim et al. 2004). Following previous observations and studies in Chile (e.g. Camus 1994, 2008, Parada 2001, Oróstica et al. 2014), we hypothesized that different morphologies of coralline algae have differential effects on kelp population dynamics through kelp recruitment. *Lessonia* spp. and calcified coralline seaweeds overlap in their vertical distribution, but a spatially explicit positive or negative interaction between them has not yet been established (see Oróstica et al. 2014 for discussion). Here, we examine the results of interactions between coralline algae of different morphologies and the recruitment dynamics of *L. spicata* using *in situ* measurements and field and laboratory experiments. Specifically, we evaluated: (1) the effect of crustose coralline algae on *L. spicata* spore settlement (laboratory and field experiments) and

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(2) the abundance of the substratum type used by *L. spicata* relative to the establishment sites of small-sized, juvenile kelps (<5 cm; field observations). In particular, we examined the relationship between the presence of articulated *Corallina officinalis* Linnaeus and a complex of encrusting coralline species (*Spongites* Kützing-*Mesophyllum* Me. Lemoine-*Lithothamnion* Heydrich species complex) in relation to the presence of juvenile *L. spicata* (sampling sites in Figure 1). To evaluate the effect of crustose coralline algae on *L. spicata* spore settlement in the laboratory, we sowed fresh *L. spicata* spore suspensions on living and dead coralline crusts (LCC and DCC, respectively), which were also subject to treatments with and without water movement. Kelp spores were obtained from fresh and mature *L. spicata* fronds (protocols described in Martínez and Santelices 1998, Martínez 1999 and Parada et al. 2016). We used scanning electron microscopy to estimate *L. spicata* germling density and compared densities among treatments using the Kruskal-Wallis test and an *a posteriori* test. To evaluate the effect of crustose corallines on *L. spicata* spore settlement in the field, rock chips with LCC and DCC were collected and fixed on stainless steel nets (to avoid herbivore consumption) using epoxy putty (see Figure 2A,B). Rock-net pieces were fixed to hard substrata at the tidal height of the *L. spicata* belt with stainless steel screws (Figure 2A). These experimental units were installed at three sites (black square symbols in Figure 1): Pichicuy (32°20′44.1″S, 71°27′36.4″W, n = 23 units), Montemar (32°57′S, 71°33′W, n = 21 units) and Las Cruces (33°30′S, 72°30′W, n = 37 units). Experiments were conducted during austral autumn and early winter when *L. spicata* sori reach sexual maturity (April–July 1999). The presence of *L. spicata* recruits and of other algae on LCC and DCC in the experimental units was monitored monthly from May to August 1999. In addition, we estimated natural settlements of juvenile *L. spicata* on encrusting and articulated coralline algae at Los Molles (32°14′S, 71°39′W), which is located 12 km north of Pichicuy, in December 1999. We compared the establishment of juvenile sporophytes by counting *Lessonia* sporophytes smaller than 5 cm in length along a 500-m horizontal transect, within the settling limits of intertidal *Lessonia* spp. (no wider than 1 m in height and normally close to adult individuals and clumps of small plants, as in Figure 2D). For each sporophyte, we recorded the specific substratum type on which it had settled, and the relative cover of all available substrata along the shoreline at the tidal height of the *L. spicata* belt was estimated using the point intercept method (100 points in 0.0625-m^2 quadrats). Using a χ^2-test, the quantity of sporophytes observed per substratum type was compared with the quantity expected by assuming a direct and positive relationship between the number of *Lessonia* sporophytes counted in the quadrats and the space available of each substratum type for spore colonization. The null hypothesis was that sporophytes will be distributed over the available substrata in direct proportion to its available surface (estimated by the point intercept method). Thus, to estimate the expected number of recruits, we multiplied the proportion of each type of substratum by the total number of *L. spicata* recruits. We also recorded the relative abundances of adult *L. spicata* (primary cover: holdfast) and different calcified algae using 0.25-m^2 quadrats along a horizontal transect at the tidal height of the *L. spicata* belts at 10 rocky intertidal sites, located between 32°14′S and 35°49′S (see open circles in Figure 1 and Broitman et al. 2001, 2011 for further

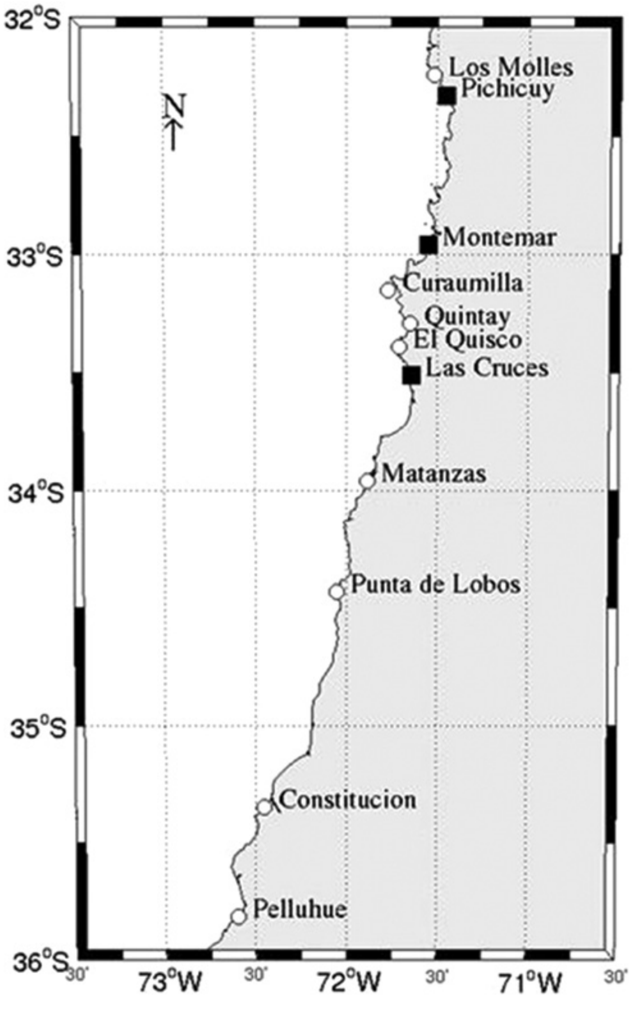

Figure 1: Map of coastline of central Chile showing locations of field surveys (open circles) and experiments (filled squares) from 1998 to 2003.
Experimental field sites and surveys overlapped at two locations (Montemar and Las Cruces).

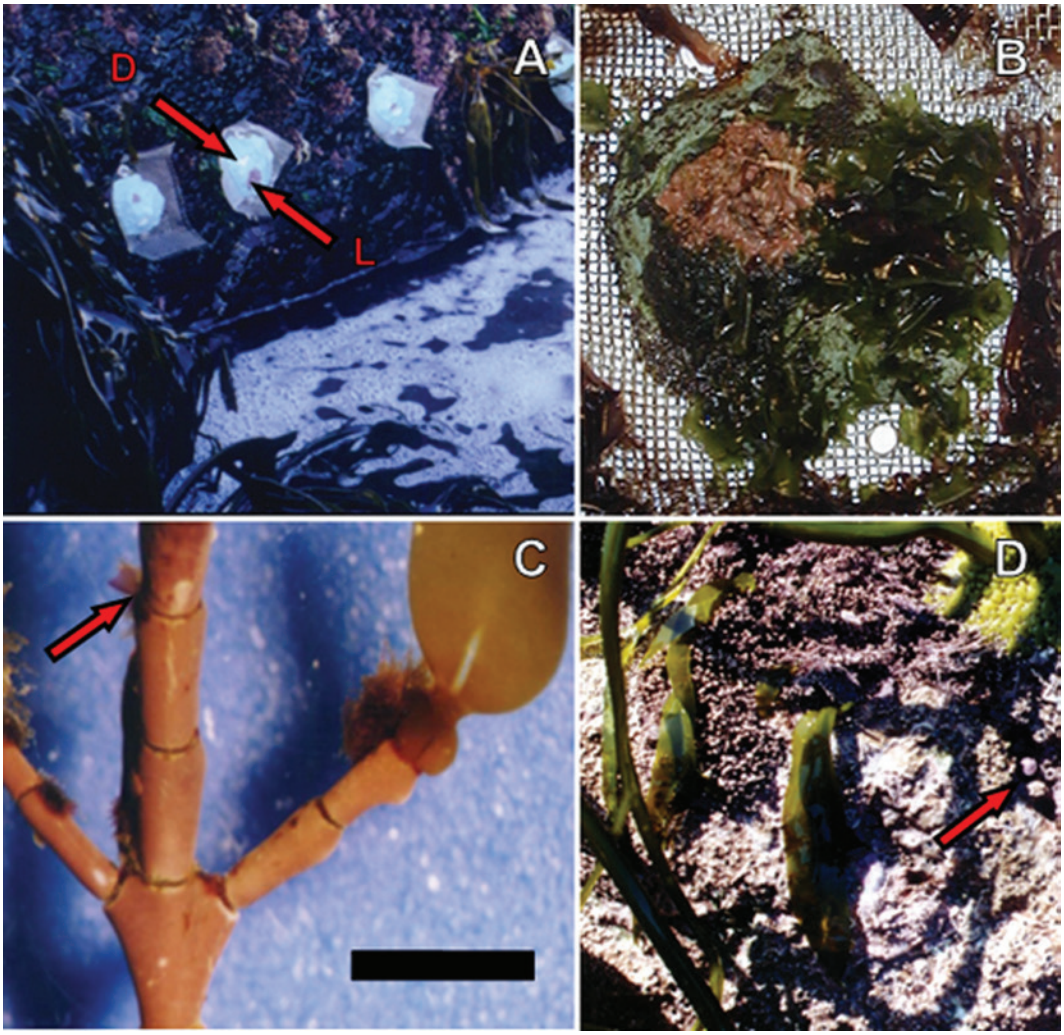

Figure 2: Field experimental units with coralline crusts and Lessonia recruits on *Corallina officinalis*.
(A) Field view of three experimental units used to monitor algal settlement on red, living (L) and white, dead (D) coralline crusts (red arrows). The rock pieces covered with coralline crusts were attached between two adult individuals of *Lessonia spicata* using epoxy putty and stainless steel nets to exclude herbivores and were screwed to the rock. (B) One experimental unit (5 cm in diameter) with recruitment of seaweeds on a dead coralline crust (fully recruited) and no recruitment on the living (reddish) crustose coralline. (C) One recruited juvenile *L. spicata* on the branch (intergenicula) of *Corallina officinalis* (scale bar = 3 mm). Note the presence of other algae on the intergenicula (red arrow). (D) *Lessonia spicata* juveniles established within understorey turf of *C. officinalis* from which *Tegula atra* snails (red arrow) were excluded.

method and site descriptions). Using the relative abundance data at these sites, we estimated Spearman rank correlations between the cover of different algal species for the years 1998, 1999, 2000 and 2003.

In the laboratory, water movement significantly reduced spore attachment, but it did not suppress it. Regardless of water movement, the density of settled spores of *L. spicata* was significantly lower on LCC compared with the other treatments and, by the end of the experiment, spore density was significantly higher on inert substrata such as glass pieces or DCC (Figure 3). In the field experiments, no algal settlement was observed on LCC at any time, including the 2-year period after the experiment installation. Surfaces of LCC were always clean of epiphytes (see Figure 2A and B). Instead, different species of algae settled on DCC or on the stainless steel exclusion nets (Figure 2B). The most common algal groups were ulvoids and *Pyropia* J. Agardh (ex *Porphyra*). *Lessonia spicata* individuals also settled on some of the exclusion nets, but only rarely. However, *L. spicata* recruits were never observed on crustose corallines, either living or dead. Field surveys supported the experimental results. Thus, for *L. spicata* populations at Los Molles, out of 123 juvenile sporophyte individuals detected, 95 had settled

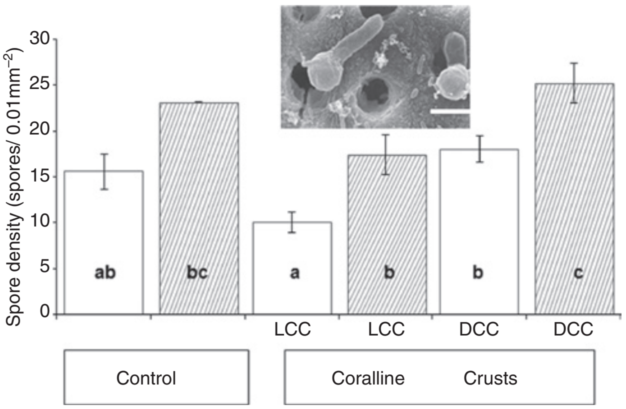

Figure 3: Effect of water motion and living crustose coralline (LCC) or dead crustose coralline (DCC) algae on the settlement of sporelings of *Lessonia spicata*.
LCC and DCC white crusts were obtained from shells of the common trochid gastropod, *Tegula atra* (Figure 2D). Snail shells were broken to obtain pieces of about 0.25 cm^2 completely covered by LCC or DCC; crusts were brushed and cleaned under filtered seawater to dislodge any algal spores. A spore suspension (270×10^3 spores ml^{-1}) was poured over shell pieces and left for 12 h for attachment, before rinsing in filtered seawater. In the control, glass pieces were seeded with the same spore suspension to observe gametophyte development under the microscope. Half of the pieces with LCC, DCC and glass (open bars) were previously fixed to polystyrene bases and subjected to water movement for 48 h (140 rpm in an orbital shaker; at 13°C, 12:12). The filtered seawater was changed four times. The other half (hatched bars) were kept in still-filtered water for the same time. After 48 h, the control and treatment samples were removed and treated as explained in Martínez and Correa (1993) for scanning electron microscopy observations and sporeling counts (inset photo, bar = 5 μm). Twelve photographs were taken of each treatment for statistical analysis. Different letters indicate significant differences after an *a posteriori* non-parametric test for paired comparisons (Kruskal-Wallis = 38.308, $p < 0.001$).

on *Corallina officinalis*, while the remaining 28 were found on the borders of a matrix of crustose corallines ($\chi^2 = 64.8$; $p < 0.0001$). The juvenile sporophytes found growing on *C. officinalis* (77%) were settled on the branches or the basal portions of these algal turfs, which occupied only 31.7% of the available substratum (Table 1). Conversely, the sporophytes observed on the encrusting corallines (23%) had established themselves only on the corallines' edges, and not directly on them. Living coralline crusts usually have clean surfaces, as seen in Figure 2A, B and D. These crusts, on average, occupied 44.5% of available space (Table 1). The remaining available space consisted of bare rock (3.2% cover) and other erect algal species of different genera (*Gelidium* Lamouroux, *Glossophora* Agardh, *Lessonia* Bory), which together occupied 20.3% of the total surveyed area and were not colonized by *Lessonia* recruits (Table 1).

Table 1: Mean substratum cover (%, n = 21 quadrats of 0.25 m^2 each) at the *Lessonia spicata* adult kelp beds in Los Molles, a managed area in central Chile (SD, standard deviation).

Substratum type	% Cover (SD)
Crustose corallines (mainly *Spongites* sp.)	44.5 (16.7)
Corallina officinalis	31.7 (17.6)
Gelidium chilense (Montagne) Santelices & Montalva	8.8 (22.9)
Glossophora kunthii (C. Agradh) J. Agardh	6.0 (9.3)
Ulvoids	3.3 (4.7)
Juvenile *Lessonia spicata*	2.2 (2.1)
Non-calcareous crustose algae	0.3 (1.5)
Bare rock	3.2 (3.7)

Additionally, our field surveys of 10 sites in the central region of Chile indicate that there are negative correlations between the presence of LCC (mostly *Lithothamnion*) and the cover of *L. spicata* across all sites. This relationship was significant for 3 of the 4 sampling years (1998 $r_S = -0.15$, $p = 0.0261$; 1999 $r_S = -0.4$, $p = 0.0005$; 2000 $r_S = -0.07$, $p = 0.6033$; 2003 $r_S = -0.38$, $p < 0.0001$, using a Bonferroni correction of $p < 0.05/4 = 0.0125$). The low correlation coefficients were probably due to the fact that high and low kelp densities are grouped together across sites, and this could make abundance patterns harder to discriminate, or reduce the statistical significance of any relationships detected, as noted by Melville and Connell (2001).

Our laboratory and field experiments together with field surveys indicate that crustose corallines inhibit the establishment of *L. spicata* spores. Other studies show that these propagules seem to compensate for this inhibition by attaching themselves to the substrate over short time scales, even under constant water movement, and that spores experiencing high dilution rates from the source have evolved efficient attachment strategies over small spatial scales (Gaylord et al. 2004, 2006). These mechanisms, although efficient, last for short time scales (only a few hours; Parada et al. 2016). The low abundance of adult sporophytes, high spore dilution and the fast decay of the initial attachment competency likely contributed to the slow rate of recovery of *Lessonia berteroana* Montagne after the massive mortality observed during the 1982/83 ENSO event in northern Chile (Martínez et al. 2003, Parada et al. 2016). Once *L. spicata* spores settle, extrinsic factors like grazing by herbivores (Aguilera et al. 2015) and the absence/presence of coralline algae (this study) can further delay population recovery. The crustose coralline algae shed their outer cell walls and/or cell layers (Masaki et al. 1981, Masaki et al. 1984, Keats et al. 1993) and some of them produce allelopathic substances (Suzuki et al.

1998, Kim et al. 2004) that inhibit kelp recruitment or growth. On the other hand, our study shows that sporophytes preferentially settled on articulated corallines, although such corallines were not the most abundant substratum. Similar observations highlight the importance of the patch dynamics of articulated corallines to the spatial distribution of the northern intertidal *Lessonia* species, *L. berteroana*, at small spatial scales (e.g. 10s of cm, Camus 1994, Oróstica et al. 2014). This suggests that the branched morphology of articulated corallines, when compared to crustose coralline morphology (Steneck and Dethier 1994), can provide more suitable microhabitats for sporophytes to settle and grow. This observation seems to be related not only to defense from herbivores through association with articulated corallines (*sensu* Hay 1986) as topographical refuges for kelps (*sensu* Franco et al. 2015), but also to protection from desiccation, as shown with other intertidal organisms (Martínez and Santelices 1998, Irving et al. 2004). Like *Hedophyllum sessile* (C. Agardh) Setchell, adults of *L. spicata* are heavier than articulated corallines thalli, but *L. spicata* rapidly develops a massive holdfast improving the initial attachment, and finally overgrowing the articulated corallines (Milligan and DeWreede 2000) as seen in our field observations (Figure 2D). Recent studies of intertidal kelp communities also show that kelp recruitment is facilitated by articulated corallines, and that the abundance of coralline crusts is somehow favored by the dynamics of kelp beds (Barner et al. 2016). The association with articulated corallines provides more than physical protection, as sporophyte attachment seems not to occur on the calcified parts of the thalli, but only on the genicula, a site also used by other epiphytes (Figure 2C). Some signaling or chemical cue recognition between these microscopic parts of the articulated corallines and the kelp spores could contribute to a mechanism for spore attachment. This hypothesis is based on polysaccharide-mediated interactions for spore attachment, as alginates are also present in coralline algae (Okazaki et al. 1982) and it has been reported that oligosaccharides derived from alginates are important attachment signals between epiphyte spores and kelp surfaces. One particular case was described for *Laminaria digitata* (Hudson) Lamouroux (Küpper et al. 2001). Some signals inhibit epiphyte spore settlement by an oxidative burst of reactive oxygen species (ROS). However, other ROS-induced signals create crosslinking of cell wall proteins (Brisson et al. 1994, Otte and Barz 1996), which may promote spore attachment to the proteins of genicula. More experiments are needed to evaluate physical and/or chemical mechanisms for this strong facilitation of kelp recruitment by articulated corallines (Oróstica et al. 2014). Once coralline algae are present, they bleach periodically following summer irradiation. Bleaching may inhibit kelp establishment in some seasons, but the corallines do recover afterwards (Figueiredo et al. 2000).

The low recovery potential of kelps after mass mortality events (e.g. after strong ENSO events) is expected because of dispersal limitation (Parada et al. 2016) and competition for primary space (see Figure 2 in Camus 1994). Landings for 2014 (in metric tons) of the two *Lessonia* species (*L. spicata* and *L. berteroana*) reported by The National Fisheries Service of Chile (SERNAPESCA) stood around 25,000 t, accounting for 40% of all seaweed extraction in the country. These species are mostly used in the alginate industry, but *Lessonia* spp. is also used as fresh food for introduced abalone in aquaculture facilities (Vásquez 2008). Considering the economic and ecological importance of *Lessonia* species in Chile, a precautionary approach to the single-species management strategies is currently in place (Tellier et al. 2011, Vásquez et al. 2012, Rodríguez et al. 2014, Vega et al. 2014). According to our results, considering a multi-species management approach incorporating articulated coralline algae as settlement facilitators would represent a sensible step to the management and conservation of these productive coastal habitats, thus avoiding irreversible ecological changes, as suggested by Filbee-Dexter and Scheibling (2014) and by Ling et al. (2015).

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