

Effect of grazing on distribution and recovery of harvested stands of *Lessonia berteroana* kelp in northern Chile

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ABSTRACT: Understanding the ecological factors regulating exploited natural communities is important in establishing conservation and management strategies. Since the 1960s, artisanal fishermen have harvested up to 300 000 dry tons yr⁻¹ of wild populations of *Lessonia* spp. kelps. Adult kelps form a key habitat on the rocky shores of Chile, and benthic grazers regulate kelp populations by grazing or bulldozing microscopic and juvenile stages. To establish the role of the grazer assemblage in the recovery of kelp stands following harvesting, we conducted a manipulative experiment simulating artisanal kelp extraction and then manipulating the presence of grazers. We followed community succession and spatial distribution of *L. berteroana* recruits in manipulated and control rocky shore platforms for ca. 12 mo. Inter-individual distances of recruits and spatial autocorrelation analyses showed that the presence of grazers determined a patchy distributional pattern of *L. berteroana*. The aggregated spatial pattern of kelp recruits in the presence of grazers was followed by numerous coalescence events between small holdfasts, but no coalescence events were observed between recruits in the grazer removal areas. Our results suggest that grazing and recruit coalescence play an important role in the recovery of kelp stands following artisanal harvesting. Incorporating these processes into conservation and management strategies may bolster current strategies, which are based solely on the spatial structure of kelp stands.

KEY WORDS: Algae-herbivore · Harvesting · Grazers · Kelp communities · Spatial structure

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INTRODUCTION

Marine ecosystems worldwide are intensely exploited and their spatial distribution is altered in space and time (Steneck et al. 2013, Tamburello et al. 2014). Thus, determining the key ecological mechanisms at play in exploited natural communities is relevant to understand their vulnerability and resilience potential (e.g. soft-sediments and seafloor: Thrush & Dayton 2002; corals reef: Hughes et al. 2010; kelp communities: Dayton et al. 1984, 1992, Steneck et al. 2002, 2013, Graham 2004, Wernberg et al. 2010). The patterns of spatial distribution

between individuals are an important ecological attribute that is readily altered by exploitation of benthic communities. Spatial heterogeneity is driven by ecological interactions such as consumer–resource dynamics (Tegner & Dayton 2000, Graham 2004, Steneck et al. 2013, Díaz & McQuaid 2014). On the other hand, local variation in spatial heterogeneity or the spatial structure of resources is directly related to consumption intensity and magnitude (Adler et al. 2001) or to specific responses of biotic resources at different life stages following recolonization after natural or anthropogenic disturbances (Dayton et al. 1992).

Herbivory is an important ecological process generating spatial heterogeneity in the distribution and abundance of primary producers in different ecosystems (Lubchenco & Gaines 1981, Adler et al. 2001, Poore et al. 2012). Depending on the availability of food, foraging strategies, identity and abundance of grazers, and exploitation intensity, primary producer stands can change their spatial and temporal patterns of distribution (Adler et al. 2001, Duffy 2002, Steneck et al. 2013, Poore et al. 2014). Herbivory influences both intra- and inter-specific relationships in local communities and modifies the landscape structure (Duffy 2002, Poore et al. 2012). In this way, the role of herbivores is especially relevant in human-disturbed communities where impacts on the spatial distribution and composition of primary producers can be either compensated or intensified by herbivory (Tegner & Dayton 2000, Steneck et al. 2002, 2013, Graham 2004, Tamburello et al. 2014).

Kelp communities, growing as mixed or single stands of Laminariales and/or Fucales, are among the most diverse and productive ecosystems worldwide and provide a range of important services (Schiel & Foster 2006, Graham et al. 2007, Vásquez et al. 2014). In temperate habitats, kelp species are harvested through whole-plant or vegetative tissue removal (Tegner & Dayton 2000, Steneck et al. 2002, 2013, Vásquez 2008). Along the Chilean coast, the dominant kelp species inhabiting intertidal habitats are *Lessonia* spp., which are heavily harvested by local fishermen who traditionally remove the whole plant from the substrate (see Fig. 1 in Tellier et al. 2011). *Lessonia* spp. (formerly *L. nigrescens*) were recently separated into 2 species: *L. spicata*, which is found between 42° and 30° S, and *L. berteroaana*, which is distributed between 17° and 30° S and forms single-species stands (Tellier et al. 2011, González et al. 2012). Kelp fishery in Chile lands up to 300 000 dry tons annually and has an economic value exceeding ~US\$70 million (Vásquez 2008, Vásquez et al. 2014). Harvesting of this ecologically relevant species is managed following a spatial rule that is based only on the spatial structure of mature kelp stands, but this spatial management approach does not consider the mechanisms underpinning the development of this spatial heterogeneity.

The distribution in space of recruits and adult individuals is relevant for demographic and life history dynamics of kelp populations (i.e. size structure, fecundity, and survival; Schiel & Foster 2006). Thus, understanding the main factors determining kelp spatial distribution is critical for management and to

improve conservation strategies (Steneck et al. 2002, Graham 2004, Schiel & Foster 2006). In this context, at least 2 factors have been shown to maintain the spatial structure of kelp-dominated habitats: (1) grazing and (2) topographic (e.g. crevices, pits) and/or biogenic heterogeneity (e.g. calcareous algae; Camus 1994, Sala & Graham 2002, Steneck et al. 2002, Graham 2004, Henríquez et al. 2011, Sala & Dayton 2011, Okamoto et al. 2013). The former can reduce the density of propagules and juvenile plants and the latter acts as a spatial refuge for sporophyte survival and/or settlement facilitation (Santelices 1990). Grazers impact algae at different life history stages, affecting recruitment or adult spatial distribution at scales ranging from centimeters up to 10s of meters (Lubchenco & Cubitt 1980, Coleman et al. 2006, Díaz & McQuaid 2011, 2014). As most benthic grazers are only able to feed on the early life stage of kelp species (Poore et al. 2012), they may influence post-settlement distribution of juveniles at micro-scales (i.e. a few centimeters). Also, and given that per capita effects of different grazers are dependent on species-specific traits (see Duffy 2002, Poore et al. 2012 for reviews of the importance of grazer traits), a diverse benthic grazer guild can have an unexpectedly large impact on resident species (Benedetti-Cecchi 2000, Adler et al. 2001).

Other processes indirectly associated with grazing can determine the spatial distribution of algae (Santelices 1990). Positive or negative interactions among algae (i.e. intra- or inter-specific) during early life stages can also affect recruitment success, thus determining the spatial structure of adult individuals (Santelices et al. 2003). In red algae, spore aggregations during settlement facilitate the coalescence process (or fusion) of sporelings and/or juvenile individuals, which has been suggested to reduce vulnerability of juveniles to grazing as compared to solitary individuals (Maggs & Cheney 1990). In brown algae, coalescence events are restricted, but not uncommon (Malm & Kautsky 2004, Wernberg 2005, Rodríguez et al. 2014, Segovia et al. 2014). For example, coalescence in *Fucus vesiculosus* generates fronds emerging from a single holdfast that comprise different individuals (Malm & Kautsky 2004), and the coalescence of small plants of *L. berteroaana* modified performance indicators like holdfast diameter and stipe numbers (Rodríguez et al. 2014, Segovia et al. 2014). Furthermore, coalesced plants tend to have larger holdfasts, rendering their detachment by waves less likely (Denny 1988; see also Malm & Kautsky 2004 for *F. vesiculosus*, Wernberg 2005 for *Ecklonia*

radiata, Segovia et al. 2014 for *L. berteroa*). However, the consequences of grazers on algal coalescence are unknown.

Surveys pre-dating the current intensive kelp harvesting showed that intertidal kelp cover was negatively correlated with the abundance of invertebrate grazers like mollusks and sea urchins (Broitman et al. 2001). However, large intertidal benthic grazers like keyhole limpets and snails are targeted only by 'subsistence harvesters' (Castilla 1999), thus these species are not collected by 'kelp harvesters' in northern Chile (Vásquez 2008). Therefore, beyond the effect of grazers on natural communities of the kelp understory (i.e. intact or pristine habitats; see Camus 1994 for grazing on the understory *Lessonia* spp.), the benthic grazer guild is expected to have important, yet unexplored, effects on kelp recovery and community structure after harvesting occurs.

The influence of herbivores on the abundance and distribution of *Lessonia* spp. seems particularly relevant, as grazing on small sporophytes may determine spatial distribution patterns of recruits and/or juveniles (Santelices & Ojeda 1984, Camus 1994, Martínez & Santelices 1998). Most intertidal benthic grazers present on the rocky shores of northern and central Chile have a limited foraging range (e.g. 20–50 cm; Aguilera & Navarrete 2011, M. A. Aguilera unpubl. data), and it is expected that the spatial distribution of *Lessonia* spp. recruits will be patchy at small spatial scales. In this context, Vásquez & Santelices (1990) demonstrated that the removal of *Lessonia* spp. adult individuals increased interholdfast distances (i.e. conspecific nearest-neighbor distances), facilitating herbivore access to and consumption of small *Lessonia* spp. recruits. Additionally, if grazing on spores and sporelings of *L. berteroa* is concentrated at small spatial scales (i.e. gregarious foraging), grazers could indirectly affect the probability of coalescence between recruits. Thus, it is of interest to determine the role of grazing as the main factor determining changes in abundance and spatial distribution of individual plants (e.g. nearest neighbor inter-disc distances), which can affect the recovery of harvested kelp communities (Camus 1994, Rodríguez et al. 2014, Vega et al. 2014). Since many human populations persist based exclusively on kelp harvesting (Vásquez 2008, Vásquez et al. 2014), this information is relevant to help improve management strategies and local policies.

Here, we examined the influence of intertidal grazers on the spatial distribution and abundance of *L. berteroa* recruits at small scales following arti-

sanal harvesting. We tested the following hypotheses: grazer consumption of spores and sporelings after harvesting determines (1) a spatially aggregated distribution pattern of recruits of *L. berteroa*, and as a consequence of this pattern, (2) increases the frequency of coalescence events between recruits.

MATERIALS AND METHODS

Study site, experimental layout and *Lessonia berteroa* harvesting

Our study was carried out on the rocky shore of Lagunillas in northern Chile (30° 05' S, 71° 22' W). The tidal range at Lagunillas is 2 m (Chilean Navy Hydrographic and Oceanographic Service of Chile, www.shoa.cl/). The low intertidal zone community is dominated by *L. berteroa*, the encrusting calcareous algae *Lithothamnion* spp., and the articulated coralline alga *Corallina officinalis*. Keyhole limpets (i.e. *Fisurella costata* and *F. crassa*), large chitons (i.e. *Achanthopleura echinata* and *Enoplochiton niger*), black sea urchins *Tetrapygus niger*, and black snails *Tegula atra* are common grazers across the low tide zone.

Around this location, we randomly selected 6 rocky platforms of ~5 m² (i.e. the experimental units) with similar conditions of slope, topographic heterogeneity, and wave exposure. Platforms were allocated in 2 groups separated by ~150 m of continuous rocky shore. Within each group (3 rocky platforms per group), platforms were separated by 1.5 m, usually by surge channels. Replication of experimental units (i.e. platforms) was limited by constraints from local authorities and fishermen (i.e. co-management under the Management and Exploitation Areas for Benthic Resources (MEA-BR), Fisheries and Aquaculture Law 1991, Chile). However, our replication level allowed us to explore the specific mechanisms determining spatial distribution patterns and captured well the environmental heterogeneity in the different treatments at local scales (Fortin & Dale 2005).

Harvesting of *Lessonia* spp. in Chile is carried out with large crowbars or heavy steel rods that are used to pry off the holdfast, thus removing the entire plant from the substrate. This traditional technique leaves large areas of the substrate barren (5–12 m², M. H. Oróstica pers. obs.), and understory algae such as turf-forming species bleach before *L. berteroa* recolonizes the area.

Spatial patterns of *L. berteroana* and community structure: pre-manipulation

During October 2011, on each experimental platform we placed 2 stainless-steel bolts affixed to the rock and separated by a distance of 2.5 m. We measured the distance between each bolt and all holdfasts from adults, juveniles, and recruits of *L. berteroana*, obtaining the x,y position of each individual. This straightforward 'point-pattern based' methodology (Perry et al. 2002), where each individual has a spatial coordinate, provided a sampling procedure that is more independent than direct individual-to-individual techniques (Fortin & Dale 2005). Using these spatial coordinates, we measured the nearest-neighbor (NN) linear distance by calculating the Euclidean distance between all individuals on each platform. The NN technique has been extensively used for other sessile or mobile organisms (Clark & Evans 1954) and allowed us to quantitatively characterize the spatial structure of the recovering kelp stand.

To estimate the abundance of herbivores and other species present in the intertidal community (i.e. sessile invertebrates and algae), 3 transects (2 m in length) were placed parallel to the coastline. Each transect was placed in the lower, central, or upper section of each experimental platform. We placed 4 consecutive quadrats of 0.25 m² on each transect (i.e. 12 quadrats per platform; $n = 72$ quadrats) where all herbivore species present were identified and counted. In parallel, the abundance of sessile invertebrate and algal species was estimated using the point-intercept method (Dethier et al. 1993).

Herbivory on *L. berteroana* recruits

In order to examine the impact of benthic intertidal grazers on the spatial structure of *L. berteroana* recruits after harvesting, during November 2011, we manipulated the grazer guild via 2 treatments: (1) herbivore removal (\bar{H}), where every 15 d during a period of 12 mo, we manually removed both small and large benthic grazers present in the study area, including limpets, chitons, urchins, and snails; and (2) herbivores not removed (^+H), where grazer densities were not manipulated (i.e. natural densities). The traditional harvesting technique was used for *L. berteroana* removal in both herbivore treatments (i.e. \bar{L} ; see 'Introduction' and Tellier et al. 2011). Therefore, experimental treatments were (1) herbivore removal/*Lessonia* removal (i.e. $\bar{H}\bar{L}$; $n = 2$ platforms), which resembled a scenario of both 'subsistence-

harvesting' and 'kelp-harvesting' activities (Castilla 1999, Vásquez 2008), and (2) herbivores not removed/*Lessonia* removal (i.e. $^+H\bar{L}$; $n = 2$ platforms), the scenario for only 'kelp-harvesting' activities (Vásquez 2008, Vega et al. 2014). Finally, we considered (3) a control, viz. platforms on which neither herbivore manipulation nor removal of *L. berteroana* individuals was performed (i.e. $^+H^+L$; $n = 2$ platforms).

Preliminary observations and data analyses of experimental results indicated that the spatial variation and abundance of *Corallina officinalis* were similar in all experimental platforms both at the start of the experiment and during the recruitment season of *L. berteroana* (see Fig. A1 in Appendix 1). All treatments were replicated twice and assigned randomly to the experimental platforms. Note that we did not consider a 'herbivore removal/*Lessonia* not removed' (\bar{H}^+L) treatment, which would have rendered an orthogonal design, as we were not interested in the effects of grazers on understory-kelp community species. Instead, we focused on the spatial patterns (i.e. spatial statistics) of *L. berteroana* recruitment and recolonization following human disturbance, considering that the \bar{H}^+L treatment does not provide relevant information when compared to the control (Fortin & Dale 2005; see also Moreno & Jaramillo 1983 for zonation of intertidal macroalgae, Santelices & Ojeda 1984 for *Lessonia* spp., Ling 2008 for macroalgae-dominated rocky reefs). Hence, this kind of treatment is relevant to test hypotheses concerning the role of benthic grazers on spatial heterogeneity of intact kelp communities along the Chilean coast (see Camus 1994, Vega et al. 2014).

The temporal frequency of benthic grazer removal applied in our experiment has been considered to be effective at maintaining low densities of grazers through time (mostly mollusks) in comparable natural systems (e.g. Moreno & Jaramillo 1983, Dethier et al. 2005, Bracken et al. 2011). We carried out estimations of sessile invertebrates and algal species cover and grazer species density in each experimental treatment monthly during the 12 mo experimental period (as outlined above; $n = 24$ quadrats of 0.25 m² per experimental treatment) to confirm the effectiveness of grazer removal.

Effect of grazers on spatial patterns of *L. berteroana* recruits post-harvesting

To assess the effects of grazers on the NN spatial distribution of *L. berteroana* recruits after harvesting in the $\bar{H}\bar{L}$ and $^+H\bar{L}$ treatments, we estimated the

position of each new recruit (i.e. 'point-pattern' methodology outlined above) every 30 d during 12 mo (beginning in December 2011). New sporophytes with <3 cm holdfast diameter and <5 cm length observed in each survey were considered recruits. Spatial patterns of *L. berteroana* recruits were measured every 4 mo in controls ($^+H^+L$).

In addition to the spatial distribution of individual *L. berteroana* recruits, during the 12 mo study period we recorded on a monthly basis the number of coalescence events between holdfasts, defined as the fusion between 2 holdfasts, following small recruit–recruit inter–holdfast distances during the first developmental stages (see Fig. 1 and Table 1, both in Rodríguez et al. 2014). This complementary information gave us a more comprehensive understanding of the specific mechanisms determining the spatial distribution of *L. berteroana*.

Statistical analyses

To determine the spatial distribution of *L. berteroana* before the experimental manipulation, NN distance distributions were compared against an expected Poisson distribution calculated from the empirical NN distances using a Kolmogorov–Smirnov test ($\alpha = 0.05$). To compare the monthly herbivore density between treatments after the experimental manipulation (i.e. 12 mo monitoring period), we used a non-parametric Kruskal–Wallis test ($\alpha = 0.05$) given the heteroscedasticity and lack of normality in the raw and transformed data (Shapiro–Wilk and Cochran's *C*-tests, respectively).

To characterize the spatial pattern of *L. berteroana* recruits, we used 2 methods: (1) the relative frequency distribution of all NN distances compared to an expected Poisson distribution from all observed NN distances from monthly surveys for each treatment. We used a Kruskal–Wallis test ($\alpha = 0.05$) to compare these observed vs. expected distributions; and (2) a Mantel spatial correlation analysis (r_M) for each experimental treatment, which allowed us to calculate the significance of spatial correlations at each NN distance class (i.e. significant patch scales; Legendre & Legendre 1998). According to observations in the field and the distribution of holdfast diameters of *L. berteroana* recruits (~0.5–3 cm), 8 distance classes separated by 10 cm were considered for all treatments. To test the significance of each distance class, we used 999 permutations after a Bonferroni correction for multiple comparisons (Legendre & Legendre 1998).

Finally, to compare the number of coalescence events, we used a non-parametric Kruskal–Wallis test ($\alpha = 0.05$) given the heteroscedasticity and lack of normality in the raw and transformed data (Shapiro–Wilk and Cochran's *C*-tests, respectively). Coalescence events were not observed in every month of the 12 mo period; thus, for the analysis we only considered the dates when we recorded coalescence events in at least 1 treatment. Cumulative frequency of new coalescence events in each treatment through time (monthly) was also examined.

All statistical analyses were done using CRAN R project (R Core Team 2013). For Kolmogorov–Smirnov and Kruskal–Wallis tests, we used the STATS package. The Mantel spatial correlation analysis (r_M) was carried out using the MPMCOR–RELOGRAM package.

RESULTS

Spatial patterns of *Lessonia berteroana* and community structure: pre-manipulation

The NN spatial structure of *L. berteroana* holdfasts did not differ from the expected Poisson distribution (Fig. 1A). The most abundant herbivore was *Tegula atra*, followed by *Acanthopleura echinata*, *Tonicia* sp., *Fissurella crassa*, *F. costata*, and the sea urchin *Loxechinus albus* (Fig. 1B). The most abundant alga was *L. berteroana*, with average percent cover ranging from 49 to 90% across platforms (Fig. 1C). Other algae such as red turf algae *Gelidium* spp., the red encrusting alga *Hildenbrandia lecanellieri*, *Lithothamnion* sp., and *Corallina officinalis* did not exceed 25% cover at any platform (Fig. 1C).

Effect of grazers on spatial patterns of *L. berteroana* recruits post-harvesting

Our biweekly removal of herbivores over the 12 mo period reduced the overall herbivore density in the $^-H^-L$ treatment (Kruskal–Wallis test, $K-W = 38.905$, $p < 0.001$, $df = 2$; Fig. 2). *T. atra* was the only species able to re-colonize the $^-H^-L$ treatment, but densities were $<6 \text{ ind. m}^{-2}$ (Fig. 2). The most abundant herbivore in the $^+H^-L$ treatment and controls were *T. atra* and *Tetrapygyus niger*, followed by *Scurria variabilis*, *Tonicia* sp., *F. costata*, *F. crassa*, and *A. echinata* (Fig. 2).

The main species to appear on platforms after kelp removal over the 12 mo experimental period were

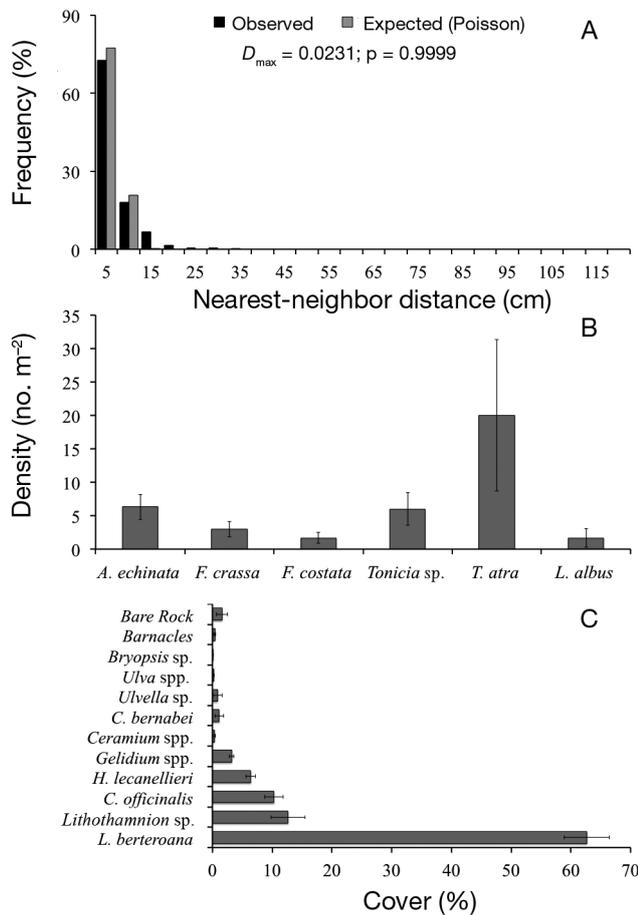


Fig. 1. (A) Frequency distribution (%) of observed (black) and expected (grey) nearest-neighbor (NN) distances (cm) following an expected distribution between all *Lessonia berteroana* individuals present on all platforms ($n = 6$) before the beginning of the experimental manipulation. NN distances observed were obtained from each x, y individual position (i.e. 'point-pattern' methodology, see 'Materials and methods') and are included in distance classes on the x-axis. Mean \pm SE NN distance was 4.00 ± 0.21 cm. D : Kolmogorov-Smirnov test. (B) Mean \pm SE density of grazer species on all rocky platforms ($n = 6$) before the beginning of the experimental manipulation. (C) Mean \pm SE percentage cover of sessile species present on all rocky platforms ($n = 6$) before the beginning of the experimental manipulation

C. officinalis, *Lithothamnion* sp., *Gelidium* spp., *H. lecanellieri*, and filamentous red algae (e.g. *Ceramium* spp.), together with *L. berteroana* recruits and juvenile individuals (Fig. 3). *L. berteroana* appeared on the experimental platforms during April 2012 (austral fall), about 6 mo after we started removing *L. berteroana* and manipulating grazers (November 2011; Fig. 3). In both herbivory treatments ($-H^{-}L$ and $+H^{-}L$), the average cover of *L. berteroana* did not exceed 25% at the end of the study (Fig. 3). In controls, the average cover of *L. berteroana* adults was around 75% throughout the study (Fig. 3).

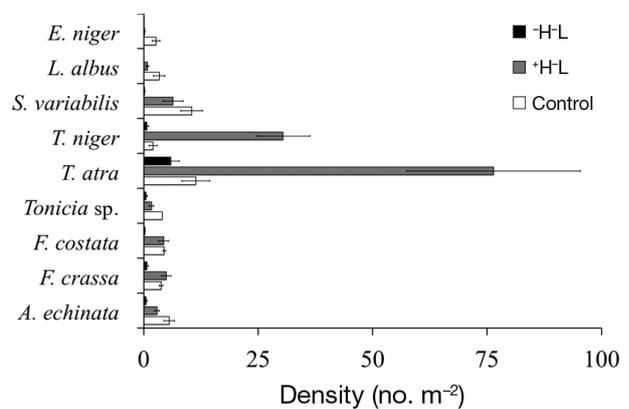


Fig. 2. Mean \pm SE density of grazer species over the 12 mo period in each experimental treatment after harvesting of *Lessonia berteroana* ($n = 24$ quadrats of 0.25 m² per month and experimental treatment). Treatments: herbivores removed, *L. berteroana* removed ($-H^{-}L$); herbivores not removed, *L. berteroana* removed ($+H^{-}L$); and herbivores not removed, *L. berteroana* not removed ($+H^{+}L$, i.e. control)

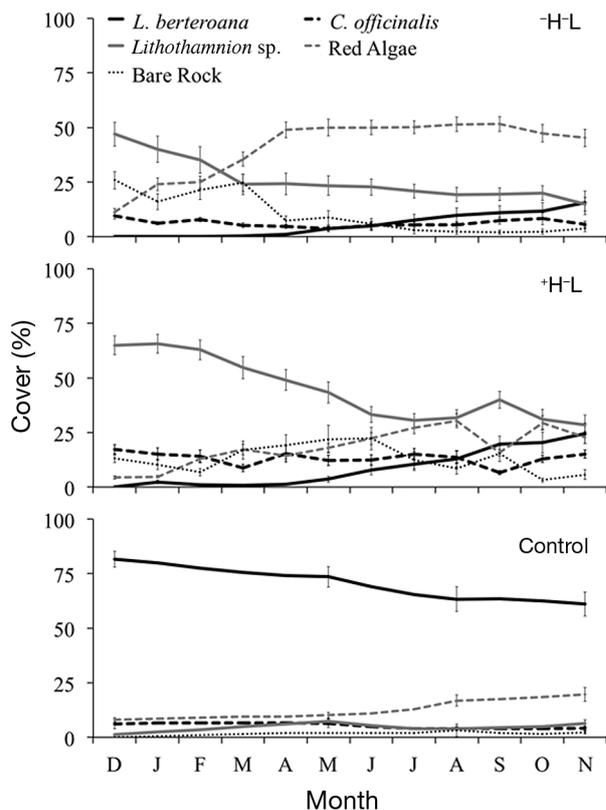


Fig. 3. Mean \pm SE percentage monthly cover of *Corallina officinalis*, *Lithothamnion* sp., red algae (*Gelidium* spp., *Hildenbrandia lecanellieri*, and *Ceramium* spp.), *Lessonia berteroana*, and bare rock per experimental treatment after harvesting of *L. berteroana* ($n = 24$ quadrats of 0.25 m² per month and experimental treatment). Treatments: herbivores removed, *L. berteroana* removed ($-H^{-}L$); herbivores not removed, *L. berteroana* removed ($+H^{-}L$); and herbivores not removed, *L. berteroana* not removed ($+H^{+}L$, i.e. control)

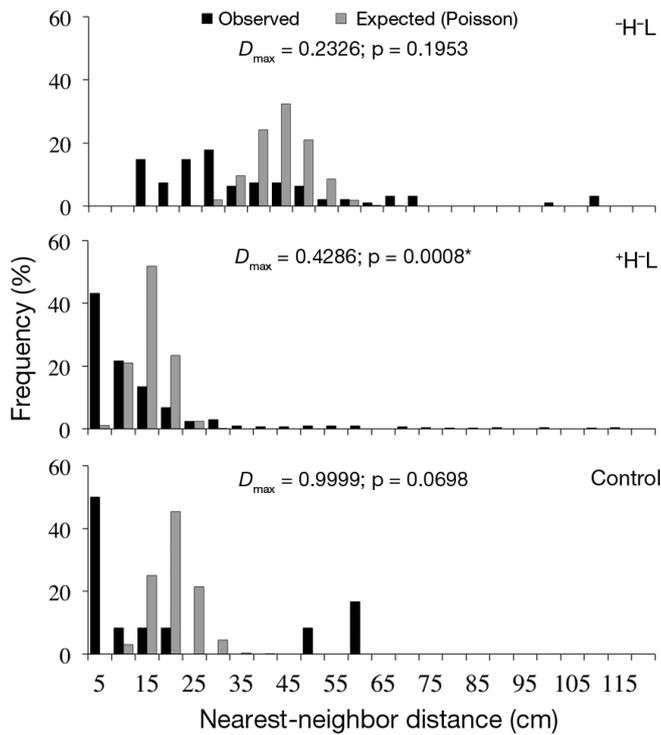


Fig. 4. Frequency distribution (%) of all observed (black) and expected (grey) nearest-neighbor (NN) distances (cm) following a random distribution between *Lessonia berteroana* recruits (over the 12 mo period) per experimental treatment after harvesting of *L. berteroana*. NN distances observed were obtained from each x,y individual position (i.e. 'point-pattern' methodology, see 'Materials and methods') and are included in distance classes on the x-axis. Mean \pm SE NN distances in the herbivores removed/*L. berteroana* removed ($-H-L$), herbivores not removed/*L. berteroana* removed ($+H-L$), and herbivores not removed/*L. berteroana* not removed (control) treatments were 37.7 ± 3.0 cm, 13.3 ± 1.1 cm, and 18.1 ± 6.3 cm, respectively. D : Kolmogorov-Smirnov test; * $p < 0.05$ ($\alpha = 0.05$)

Over the 12 mo period, the distribution of NN distances of *L. berteroana* recruits differed from an expected Poisson distribution only in the $+H-L$ treatment (Fig. 4). In this treatment, about 85% of NN distances among recruits were between 0 and 20 cm, which is in contrast to the $-H-L$ treatment, where only 22% of the NN distances were between 0 and 20 cm (Fig. 4). In the controls, about 75% of NN distances between recruits of *L. berteroana* were between 0 and 20 cm, but the distribution of NN distances was not different from a random distribution (Fig. 4). Thus, although the NN distribution found in $+H-L$ treatment and controls were similar, we only found evidence for spatial dependence in the recruit distribution in the $+H-L$ treatment.

The $+H-L$ treatment showed that the first 3 distance classes (i.e. 0–10, 10–20, and 20–30 cm) were signifi-

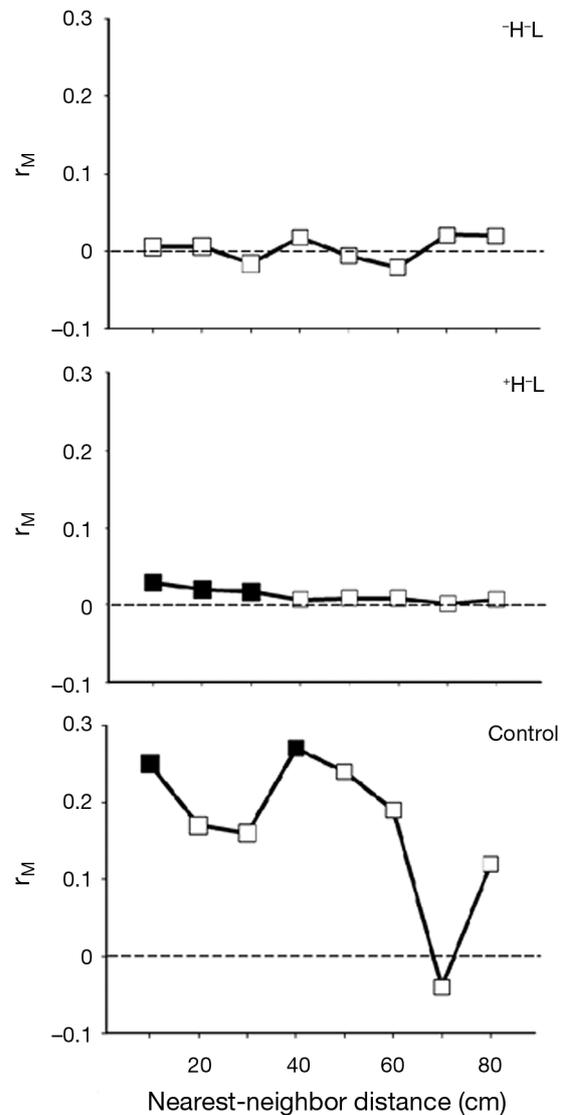


Fig. 5. Mantel (r_M) spatial autocorrelation analysis of all nearest-neighbor distances (cm) of *Lessonia berteroana* recruits (over the 12 mo period) per experimental treatment after harvesting of *L. berteroana*. Black squares show significant correlations after sequential Bonferroni correction. White squares indicate non-significant values. Treatments: herbivores removed, *L. berteroana* removed ($-H-L$); herbivores not removed, *L. berteroana* removed ($+H-L$); and herbivores not removed, *L. berteroana* not removed ($+H-L$, i.e. control)

cant and positive (Mantel spatial correlation test, $r_M = 0.028$, $p = 0.001$; $r_M = 0.019$, $p = 0.004$, and $r_M = 0.016$, $p = 0.006$, respectively; Fig. 5), indicating a patchy distribution of *L. berteroana* recruits. We observed no significant spatial autocorrelation for the $-H-L$ treatment at any distance class (i.e. random pattern; Fig. 5). For the controls, only the first (i.e. 0–10 cm) and fourth distance classes (i.e. 30–40 cm) were sig-

nificant and positive (Mantel spatial correlation test, $r_M = 0.253$, $p = 0.002$; and $r_M = 0.276$, $p = 0.048$, respectively; Fig. 5).

Although Rodríguez et al. (2014) described 5 coalescence modes in the field, over our 12 mo study period, we recorded only the first-order coalescence strategy, i.e. fusion between neighboring recruits of a same cohort (see Table 1 in Rodríguez et al. 2014). In the $^+H^-L$ treatment, coalescence events increased over time (Fig. 6A). The mean \pm SE density of *L. berteriana* recruits per month was $1.26 \pm 0.54 \text{ m}^{-2}$, with a total of 14 coalescence events. In controls, few individuals were observed to coalesce by the end of the study (Fig. 6A), and the average density of *L. berteriana* recruits per month was $0.02 \pm 0.02 \text{ m}^{-2}$, and 2 coalescence events were recorded in total. No coalescence events were observed in the $^-H^-L$ treatment (Fig. 6B), where the average density of *L. berteriana* recruits per month was $0.31 \pm 0.12 \text{ m}^{-2}$. The average number of coalescence events (i.e. recruit–recruit) differed between treatments (K-W = 7.672, $p = 0.022$; $df = 2$; Fig. 6B).

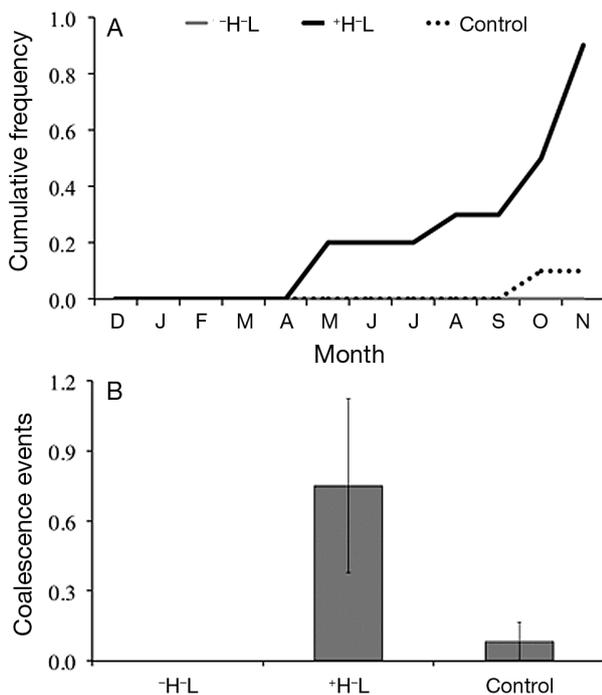


Fig. 6. Coalescence events recorded over the 12 mo period per experimental treatment after harvesting of *Lessonia berteriana*. (A) Monthly cumulative frequency of the total number of coalescence events. (B) Mean \pm SE number of coalescence events (i.e. recruit–recruit) across all sampling dates for both replicates (i.e. 2 platforms) within each experimental treatment. Treatments: herbivores removed, *L. berteriana* removed ($^-H^-L$); herbivores not removed, *L. berteriana* removed ($^+H^-L$); and herbivores not removed, *L. berteriana* not removed ($^+H^+L$, i.e. control). We did not observe any coalescence events in the $^-H^-L$ treatment

DISCUSSION

Our results show that grazing is a key mechanism determining the spatial structure of kelp communities subject to traditional harvesting techniques. The presence of benthic grazers generated an aggregated spatial pattern of *Lessonia berteriana* recruits when compared with zones where they were absent. A high number of coalescence events was recorded in grazed areas when compared to areas subject to herbivore removal. Our results suggest that after harvesting occurs, benthic grazers can directly and indirectly influence adult plant survival and persistence by promoting recruit aggregation and increasing their potential for coalescence. This information can be directly applied to improve management strategies in management zones exclusively targeted for human harvesting. Chilean local harvesting regulations are based solely on size and spatial distribution of harvested individuals (National Fishery Service of Chile, www.sernapesca.cl; Vásquez 2008), but our results provide strong ecological support for a non-intuitive measure that should protect harvested areas from benthic grazer removal.

Effect of grazers on spatial patterns of *L. berteriana* recruits post-harvesting

Grazing effects on early developmental stages of algae can generally be viewed as transient or ephemeral for the entire community. Experimental studies conducted in different systems suggest that grazing on early successional stages has strong and significant effects on successional pathways and adult community structure (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Poore et al. 2012). For example, on the southern coast of Chile, the presence of different grazers (e.g. mollusks and echinoderms) increased the abundance of early stages of kelp *Macrocystis pyrifera* in comparison to treatments with low densities and/or total exclusion of herbivores (Henríquez et al. 2011). Two reasons could explain this pattern: (1) the strong consequences of grazer abundance and identity on the intertidal landscape (see Poore et al. 2012, 2014) and (2) some biogenic habitats (e.g. calcareous algae, empty limpet shells) can provide protection from severe grazing for sporelings of macroalgae (see Camus 1994, Henríquez et al. 2011). Since impacts can scale with grazer body and population size (Sala & Graham 2002) moderate grazer densities may enhance the abundance of kelp recruits. Our study found no clear

evidence of grazing effects on cover of either recruits or juveniles of *L. berteroana* individuals (see Fig. 3). Also, our experiments lasted 12 mo, and no adult plants of *L. berteroana* developed in manipulated treatments compared to control areas. Thus, the time considered in our experiments captures well the post-settlement period where grazers can affect the spatial structure of *L. berteroana* after harvesting. Although the magnitude of the effect of grazers on the cover of early stages was low, grazers had strong effects in the spatial variance of *L. berteroana* recruit distribution, which can be a result of the diverse benthic guild present in our system (Benedetti-Cecchi 2000).

Recruit settlement was clumped at scales smaller than 30 cm in the +H-L treatment when compared to -H-L treatment and controls, suggesting a role for grazing in determining the spatial structure of intertidal kelp stands during recolonization. The aggregated spatial pattern of recruits that we found in the presence of grazers suggests a strong selective pressure on small-sized individuals of *L. berteroana*. This result is in agreement with the laboratory studies of Martínez & Santelices (1998), who focused on the microscopic stages of *Lessonia* spp., and the study of Henríquez et al. (2011), who investigated macroscopic sporophytes and microscopic stages of *Macrocystis pyrifera* in both the field and the laboratory, respectively. Martínez & Santelices (1998) reported that strong grazing pressure by the snail *Tegula atra* on *Lessonia* spp. generated mortality close to 75% and 60% of gametophytes and sporophytes, respectively. *T. atra* was the most abundant grazer species in our herbivore-present treatment, suggesting that this species can account for most of the effects on *L. berteroana* recruits. Thus, the spatial pattern of *L. berteroana* is influenced by an intense consumer-resource relationship that is focused on the first developmental stages, and individuals that settle in close proximity seem to be less likely to be consumed during their more susceptible initial stages.

Grazer density, identity, and/or food preferences (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983) together with spore and sporeling susceptibility to consumption (Santelices 1990) appear as important factors determining the spatial structure of *L. berteroana* after harvesting. Nevertheless, other processes may well contribute to determine an aggregated spatial pattern of recruits. For example, small- and medium-scale (i.e. 10s of centimeters to meters) spatial heterogeneity determined by substrate roughness, presence of refuges (Lubchenco & Cubitt 1980), wave exposure (Malm & Kautsky 2004, Wernberg 2005, Segovia et al. 2014), density of

adult plants (Santelices & Ojeda 1984), and abundance of species that facilitate escape from herbivores may play a role (Camus 1994, Henríquez et al. 2011). In this context, a high recruitment of kelp in Chile has also been attributed to the presence of species that provide refuge and facilitate the success of early stages of Laminariales, like the articulated coralline alga *Corallina officinalis* and mussel beds (Camus 1994, Henríquez et al. 2011). *C. officinalis* cover was similar in all treatments at the start of the experiment, and the presence of grazers moderately increased its abundance. Articulated coralline algae, which are resistant to grazing (Steneck & Dethier 1994, Littler et al. 1995), likely facilitated *L. berteroana* recruitment in our study by providing a refuge from grazing, thereby increasing survival potential during the first developmental stages (Camus 1994). However, we did not manipulate the abundances of articulated coralline algae given that traditional harvesting of *Lessonia* spp. by local 'kelp-harvesters' does not target them (Vásquez 2008, Tellier et al. 2011, Vásquez et al. 2014). Thus, articulated coralline/kelp interaction in this system deserves further attention to establish the relevance of biogenic structures as refuges for recruits.

Influence of grazing on coalescence of *L. berteroana* recruits

A high incidence of coalescing holdfasts between *L. berteroana* individuals was reported recently (Rodríguez et al. 2014, Segovia et al. 2014). In general, the process of coalescence joins recruits and/or juveniles into a single holdfast. The effect that grazers have on coalescence in natural populations of *L. berteroana* has been unexplored. Thus, the high frequency of coalescence events registered in the presence of grazers in our study is the first experimental evidence that an ecological mechanism may play a role in this inter-individual process. The high frequency of small inter-holdfast distances and the patchy structure of *L. berteroana* recruits found in the presence of grazers suggest a selective process favoring the survival of recruits that settle at close distances. As a consequence, it may be expected that grouped recruits have a survival advantage when faced with consumption risk (i.e. grazing) and/or physical disturbances in contrast to solitary individuals, as suggested by Malm & Kautsky (2004) for *Fucus vesiculosus*, by Wernberg (2005) for the perennial kelp *Ecklonia radiata*, and by Segovia et al. (2014) for *L. berteroana*. Furthermore, coalesced

plants tend to have larger holdfasts and could be able to better resist detachment by waves, a differential survival factor in *L. berteriana* populations (Rodríguez et al. 2014, Segovia et al. 2014). Nonetheless, we must still examine the specific direct mechanisms determining coalescence considering the spatial pattern of zoospores and susceptibility potential of grouped vs. solitary individuals.

Human harvesting and post-harvesting recovery of *Lessonia*-dominated ecosystems

Lessonia spp. holdfasts have always been considered as single individuals (i.e. Ojeda & Santelices 1984, Santelices & Ojeda 1984). However, if we consider that coalescence promotes the formation of larger holdfasts, starting from dense patches of recruits and/or juveniles, it is likely that holdfasts of 20 cm in diameter, viz. the minimal exploitable holdfast diameter (Vásquez 2008), do not belong to the harvestable population. Holdfasts that may exceed 20 cm in diameter are formed by smaller coalesced individuals who have not yet reached their maximum reproductive potential. In this way, it is necessary to evaluate the effects of coalescence on growth and reproductive potential to establish new management and conservation strategies for *L. berteriana*. The intensity and frequency of harvesting of *L. berteriana* are not homogeneous along its distributional range (Tellier et al. 2011), and kelp cover and grazer abundances are highly variable along the Chilean coast (Broitman et al. 2001). Hence, information about the temporal and spatial structure of the herbivore–kelp relationship and the role that herbivory plays on kelp coalescence appears as a highly relevant line of evidence to understand the resilience of exploited kelp stands.

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LITERATURE CITED

- Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128:465–479
- Aguilera MA, Navarrete SA (2011) Distribution and activity patterns in an intertidal grazer assemblage: influence of temporal and spatial organization on interspecific associations. *Mar Ecol Prog Ser* 431:119–136
- Benedetti-Cecchi L (2000) Variance in ecological consumer–resource interactions. *Nature* 407:370–374
- Bracken MES, Jones E, Williams SL (2011) Herbivores, tidal elevation, and species richness simultaneously mediate nitrate uptake by seaweed assemblages. *Ecology* 92:1083–1093
- Broitman BR, Navarrete SA, Smith F, Gaines SD (2001) Geographic variation of southeastern Pacific intertidal communities. *Mar Ecol Prog Ser* 224:21–34
- Camus PA (1994) Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in northern Chile: successional constraints and opportunities. *J Exp Mar Biol Ecol* 184:171–181
- Castilla JC (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends Ecol Evol* 14:280–283
- Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453
- Coleman RA, Underwood AJ, Benedetti-Cecchi L, Åberg P and others (2006) A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147:556–564
- Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R, Ven Tresca D (1984) Patch dynamics and stability of California kelp communities. *Ecol Monogr* 54:253–289
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol Monogr* 62:421–446
- Denny MW (1988) *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton, NJ
- Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover estimations: 'objective' is not always better. *Mar Ecol Prog Ser* 96:93–100
- Dethier MN, Williams SL, Freeman A (2005) Seaweeds under stress: manipulated stress and herbivory affect critical life-history functions. *Ecol Monogr* 75:403–418
- Díaz ER, McQuaid CD (2011) A spatially explicit approach to trophic interactions and landscape formation: patchiness in small-scale variability of grazing effects along an intertidal stress gradient. *J Ecol* 99:416–430
- Díaz ER, McQuaid CD (2014) Short-term spatial stability in trophic interactions. *J Ecol* 102:1138–1149
- Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–219
- Fortin MJ, Dale M (2005) *Spatial analysis: a guide for ecologists*. Cambridge University Press, Cambridge
- González A, Beltrán J, Hiriart-Bertrand L, Flores V, de Reviers B, Correa JA, Santelices B (2012) Identification of cryptic species in the *Lessonia nigrescens* complex (Pheophyceae, Laminariales). *J Phycol* 48:1153–1165
- Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357
- Graham MH, Vásquez JA, Buschmann AH (2007) Global ecology of the giant kelp *Macrocystis* from ecotypes to ecosystems. *Oceanogr Mar Biol Annu Rev* 45:39–88
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanogr Mar Biol Annu Rev* 21:195–282
- Henríquez LA, Buschmann AH, Maldonado MA, Graham MH and others (2011) Grazing on giant kelp microscopic phases and the recruitment success of annual popula-

- tions of *Macrocystis pyrifera* (Laminariales, Phaeophyta) in southern Chile. *J Phycol* 47:252–258
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends Ecol Evol* 25:633–642
- Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier Science, Amsterdam
- Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156:883–894
- Littler MM, Littler DS, Taylor PR (1995) Selective herbivore increases biomass of its prey: a chiton–coralline reef-building association. *Ecology* 76:1666–1681
- Lubchenco J, Cubitt J (1980) Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676–687
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu Rev Ecol Syst* 12:405–437
- Maggs CA, Cheney DP (1990) Competition studies of marine macroalgae in laboratory culture. *J Phycol* 26:18–24
- Malm T, Kautsky L (2004) Are bladderwrack (*Fucus vesiculosus* L.) holdfasts that support several fronds composed of one or several genetic individuals? *Aquat Bot* 80: 221–226
- Martínez EA, Santelices B (1998) Selective mortality on haploid and diploid microscopic stages of *Lessonia nigrescens* Bory (Phaeophyta, Laminariales). *J Exp Mar Biol Ecol* 229:219–239
- Moreno CA, Jaramillo E (1983) The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. *Oikos* 41:73–76
- Ojeda FP, Santelices B (1984) Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in central Chile. *Mar Ecol Prog Ser* 19:83–91
- Okamoto DK, Stekoll MS, Eckert GL (2013) Coexistence despite recruitment inhibition of kelps by subtidal algal crusts. *Mar Ecol Prog Ser* 493:103–112
- Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Miriti M, Jakomulska A, Citron-Pousty S (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25: 578–600
- Poore AGB, Campbell AH, Coleman RA, Edgar GJ and others (2012) Global patterns in the impact of marine herbivores on benthic primary producers. *Ecol Lett* 15: 912–922
- Poore AGB, Gutow L, Pantoja JF, Tala F, Jofré Madariaga D, Thiel M (2014) Major consequences of minor damage: impacts of small grazers on fast growing kelps. *Oecologia* 174:789–801
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org/>
- Rodríguez DC, Oróstica MH, Vásquez JA (2014) Coalescence in wild organisms of the intertidal population of *Lessonia berteriana* in northern Chile: management and sustainability effects. *J Appl Phycol* 26:1115–1122
- Sala E, Dayton PK (2011) Predicting strong community impacts using experimental estimates of per capita interaction strength: benthic herbivores and giant kelp recruitment. *Mar Ecol* 32:300–312
- Sala E, Graham MH (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. *Proc Natl Acad Sci USA* 99:3678–3683
- Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr Mar Biol Annu Rev* 28:177–276
- Santelices B, Ojeda FP (1984) Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. *Mar Ecol Prog Ser* 19:73–82
- Santelices B, Aedo D, Hormazábal M, Flores V (2003) Field testing of inter- and intraspecific coalescence among mid-intertidal red algae. *Mar Ecol Prog Ser* 250:91–103
- Schiel DR, Foster MS (2006) The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annu Rev Ecol Syst* 37:405–437
- Segovia NI, Vásquez JA, Faugeton S, Haye PA (2014) On the advantage of sharing a holdfast: effects of density and occurrence of kin aggregation in the kelp *Lessonia berteriana*. *Mar Ecol* (in press)
- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459
- Steneck RS, Leland A, McNaught DC, Vavrinc J (2013) Ecosystem flips, locks, and feedbacks: the lasting effects of fisheries on Maine's kelp forest ecosystem. *Bull Mar Sci* 89:31–55
- Tamburello L, Bulleri F, Balata D, Benedetti-Cechi L (2014) The role of overgrazing and anthropogenic disturbance in shaping spatial patterns of distribution of an invasive seaweed. *J Appl Ecol* 51:406–414
- Tegner MJ, Dayton PK (2000) Ecosystem effects of fishing in kelp forest communities. *ICES J Mar Sci* 57:579–589
- Tellier F, Vega JMA, Broitman BR, Vásquez JA, Valero M, Faugeton S (2011) The importance of having two species instead of one in kelp management: the *Lessonia nigrescens* species complex. *Cah Biol Mar* 52:455–465
- Thrush SF, Dayton PK (2002) Disturbance to marine benthic habitats by trawling and dredging - implications for marine biodiversity. *Annu Rev Ecol Syst* 33:449–473
- Vásquez JA (2008) Production, use and fate of Chilean brown seaweeds: resources for a sustainable fishery. *J Appl Phycol* 20:457–467
- Vásquez JA, Santelices B (1990) Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. *Hydrobiologia* 204–205:41–47
- Vásquez JA, Zuñiga S, Tala F, Piaget N, Rodríguez DC, Vega JMA (2014) Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. *J Appl Phycol* 26:1081–1088
- Vega JMA, Broitman BR, Vásquez JA (2014) Monitoring the sustainability of *Lessonia nigrescens* (Laminariales, Phaeophyceae) in northern Chile under strong harvest pressure. *J Appl Phycol* 26:791–801
- Wernberg T (2005) Holdfast aggregation in relation to morphology, age, attachment and drag for the kelp *Ecklonia radiata*. *Aquat Bot* 82:168–180
- Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecol Lett* 13:685–694

Appendix 1

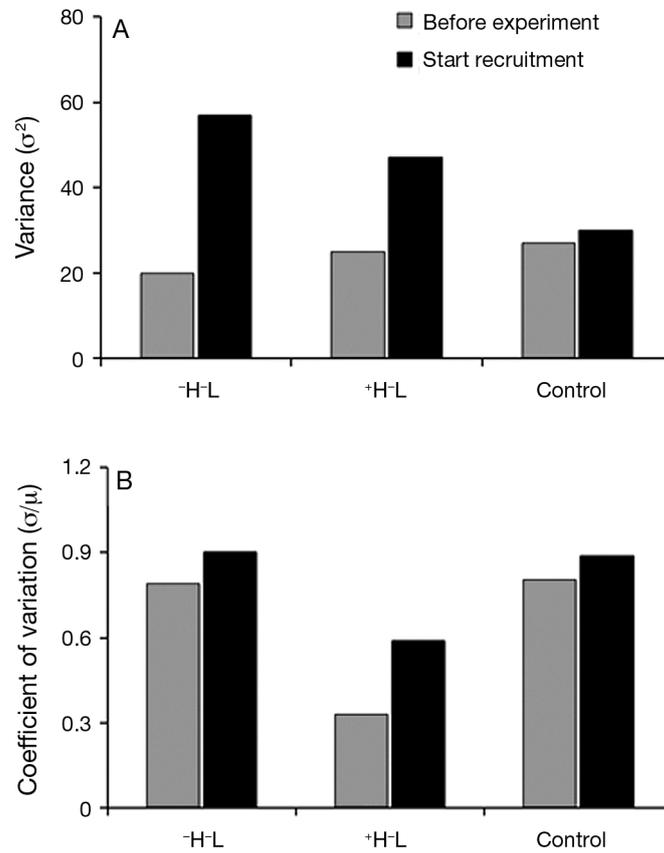


Fig. A1. (A) Variance and (B) coefficient of variation of *Corallina officinalis* in each experimental treatment (n = 24 quadrats of 0.25 m² per experimental treatment). See Fig. 2 for treatment descriptions