

# Coalescence in wild organisms of the intertidal population of *Lessonia berteroana* in northern Chile: management and sustainability effects

Dení Rodríguez · Mauricio H. Oróstica ·  
Julio A. Vásquez

Received: 24 May 2013 / Revised: 15 August 2013 / Accepted: 16 August 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** *Lessonia berteroana* is the subject of 85 % of the total harvest of Chilean brown seaweeds, representing close to 10 % of total kelp biomass worldwide harvested for alginic acid extraction. Frequent incidence of coalescent holdfasts was detected in natural populations, and this process gives rise to fused sporophytes. This study presents the coalescence events in natural populations in northern Chile. During 2011, in natural intertidal populations, 435 target sporophytes of different sizes were observed weekly and 63.90 % (278) showed physical signs of coalescent disks. We were able to distinguish five fusion modes depending on the number and size of each of the participant sporophytes and their spatial distribution. There was a progressive decrease of density and an increase in the number of stipes of each sporophyte over time. Two processes were recognized: active fusion of juvenile sporophytes and passive fusion of adult and senescent sporophytes. However, most of the coalescence processes were detected in juvenile sporophytes with a holdfast diameter of 0.5 to 2 cm. The minimum distance between pairs of coalescing sporophytes was 0.5 cm, and the maximum distance was 13 cm. For good harvesting practices, it is recommended that plants with over 20 cm holdfast diameter are

harvested from natural populations because over this size, all of the plants have reproduced. Coalescence events would produce plants with legal size requirement; however, these plant units would not be reproductive, affecting the sustainability of this important coastal resource.

**Keywords** *Lessonia berteroana* population · Coalescence process · Management and sustainability

## Introduction

Kelp harvesting in Chile has a significant social, economic, and ecological importance and provides 10 % of the biomass of brown algae worldwide (FAO 2012), with annual harvested weight of up to 300,000 dry t (Anuario SERNAPESCA 2011; Vásquez 2008; Vásquez et al. 2012); the *Lessonia nigrescens* complex contributes over 75 % of the total collected and harvested biomass. Chilean *L. nigrescens* is a cryptic species (Tellier et al. 2011) and was recently separated into two other species (González et al. 2012): *Lessonia berteroana* Montagne which is distributed in exposed rocky intertidal from southern Peru (17°S) to central Chile (30°S) and *Lessonia spicata* (Suhr) Santelices which is distributed from Coquimbo (30°S) to Puerto Montt (42°S). Population genetic studies on natural populations of *L. nigrescens* show high incidence of fused individual, where one holdfast had more than 60 % of the total stipe with different genotypes (Segovia 2009; González et al. in press).

Growth studies of *L. berteroana* (as *L. nigrescens*) in natural populations with different intensities of harvest in northern Chile showed a high incidence of holdfast fusion of juvenile plants (Vásquez et al. 2008). The fusion of juvenile sporophytes appears to be a defense mechanism against benthic herbivory pressures and is a survival strategy against mortality induced by physical events such as the dredge effect

---

D. Rodríguez  
Departamento de Biología Comparada, Facultad de Ciencias,  
Universidad Nacional Autónoma de México, Mexico City, Mexico

M. H. Oróstica  
Universidad de Atacama CRIDESAT, Atacama, Chile

M. H. Oróstica · J. A. Vásquez  
Departamento de Biología Marina, Facultad de Ciencias del Mar,  
Universidad Católica del Norte, Avda. Larrondo 1281,  
Coquimbo, Chile

J. A. Vásquez (✉)  
Center for Advanced Studies (CEAZA),  
Universidad Católica del Norte, Coquimbo, Chile  
e-mail: jvasquez@ucn.cl

caused by the impact of waves and bottom currents (Segovia 2009).

Fusion or coalescence events have been recorded for red and green algae in which a discrete entity (chimera) forms, that is genetically heterogeneous from the joint growing of two or more spores, seedlings, or basal portions of grown thalli, and in which original individuals are indistinguishable (Santelices et al. 1999; 2003; González and Santelices 2008). Coalescence is well described only for red algae where conspecific individuals of equal or different height, age, or chromosomal phase are fused with ecological consequences for the individual (such as increased growth rate) and the population (resistance to herbivory) (Maggs and Cheney 1990; Santelices et al. 1999).

In brown algae, coalescence events are restricted to certain records in Dictyotales where nonmotile spores frequently retain the mucilage cover, allowing the adhesion with other spores that develop together (Clayton 1992). The discrete entities of *Ascophyllum nodosum* (Linnaeus) Le Jolis resulting from coalescence of two or more zygotes that stay in one clamping disk (Åberg 1989) suggest polygenetic “individuals” formation. The prostrate systems of *Phaeosiphoniella cryophila* and *Haplospora globose* Kjellman are polygenetic multilayered disks formed by coalescence of monostromatic plates derived from the rhizoidal system (Kuhlenkamp and Hooper 1995). The coalescence of *Sargassum muticum* (Yendo) Fensholt holdfast structures is common, resulting in a perennial holdfast that has a unique stipe with the main branches bearing numerous lateral branches and leaves like air vesicles (Arenas and Fernández 2000).

However, the high occurrence of fused organisms (Vásquez et al. 2008; Segovia 2009; Oróstica 2013; González et al. in press) possibly forming polygenetic “individuals”, the coalescence mechanics between individuals and its ecological role in nature remain unexplored. This work evaluated the fusion process of small plants in the field, using tagged juvenile sporophytes and nearest neighbor distance relationships, as critical elements to assess the formation of fused “individuals”. With respect to the management of natural populations, we hypothesize that coalescent sporophytes of commercial size (>20 cm holdfast diameter) would not develop reproductive structures that ensure offspring, negatively affecting recruitment and the renewal of wild stocks. With respect to the persistence of natural populations, we hypothesize that coalescence events would positively affect the growth and survival of juvenile sporophytes as a strategy against or refuge from intertidal grazers.

## Materials and methods

The study was conducted in intertidal areas of Punta Lagunillas (30°06'S–70°26'W) in northern Chile. The low

intertidal community is dominated in cover and biomass by the brown algae *L. berteroa* (Hoffmann and Santelices 1997; cited as *L. nigrescens*) followed by the crustose calcareous alga *Lithothamnion* sp. and small patches of the erect crustose alga *Corallina officinalis* (see Camus 1994). The benthic grazer assemblage is formed by several species of keyhole limpets (e.g., *Fissurella limbata* and *F. crassa*), chitons (*Chiton granosus* and *Enoplochiton niger*), sea urchins (*Tetrapygus niger* and *Loxechinus albus*), and the black snail *Tegula atra*.

Field evaluation and monitoring of coalescent juvenile sporophytes of *L. berteroa* were done between March and December 2011 during low tides. Two areas of 100 m<sup>2</sup> were initially defined, where early sporophyte recruits (<1 cm holdfast diameter), juveniles (>1<10 cm holdfast diameter), and adult plants (with reproductive structures) were tagged giving a total of 435 experimental individuals.

Each plant was measured using the following morphological descriptors: holdfast diameter, number of stipes, and maximum length. The longest stipe of each experimental plant was marked with plastic ties and numbered consecutively. In order to follow each experimental plant, we affixed two stainless-steel bolts separated by 2.5 m to the rock. From these two stainless-steel points, we measured the distance of each *L. berteroa* plant. This “point-pattern based” methodology (see Perry et al. 2002) allowed us to assign spatial coordinates to all experimental individuals (i.e., adults, juveniles, and recruits). Furthermore, each plant was positioned in the field according its nearest neighbor distances to allow us to return to the same plant and measure the same holdfast and stipes in each successive sampling. Each plant or groups of plants were followed up in each low tide from March to December 2011, where fused plants would show exponential increase in holdfast diameter and number of stipes. In this context, the plant fusion process involves a decrease of plant density due to holdfast coalescence. In the experimental intertidal areas, the coalescence process was followed up for 10 months.

In addition, during June 2011, a rocky intertidal platform surface of approximately 4 m<sup>2</sup> was selected, wherein all *L. berteroa* plants were excluded, in order to evaluate new recruitment and initiate evaluation of juvenile sporophyte coalescence during the high recruitment season (autumn–late winter). The monitoring of potentially coalescing sporophytes was performed in 16 fixed 25 cm<sup>2</sup> quadrats (covering the entire experimental platform 4×4 m quadrats each) using successive and random counts of the number of plants.

## Statistical analysis

Each measured variable (i.e., holdfast diameter, distance between groups of individuals in the process of coalescence, number and length of stipes) was averaged according to sampling date. This average was compared with a one-way

ANOVA, with time as a fixed factor (Zar 2010). The time factor was categorized according to the sampling period: time 1 (May–June), time 2 (July–August), and time 3 (September–October). Shapiro–Wilk’s and Cochran’s tests were used to check and assess the normality assumptions and variances in homogeneity, in all ANOVAs (Zar 2010). If the assumptions of these tests were not met, the data were logarithm or square root transformed, as appropriate (Zar 2010). The differences found in each of the levels of the time factor (T1, T2, and T3) were explored with a Tukey HSD a posteriori test (Zar 2010). All statistical tests were performed in the R statistical environment (R Development Core Team 2012) with the “stats” package.

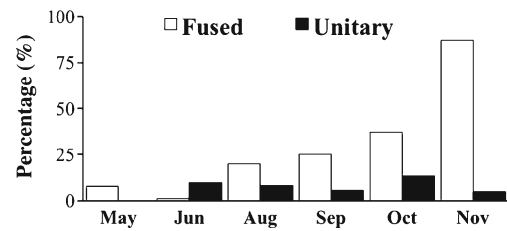
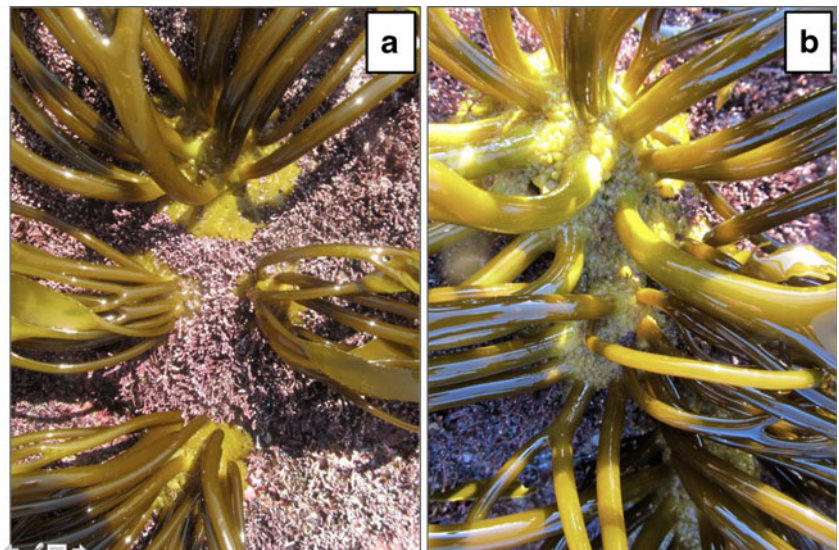
A regression analysis between holdfast diameter and the distance between sporophytes groups was performed in order to establish the relationship between the two variables (Zar 2010). This statistical test was also performed in the R statistical environment (R Development Core Team 2012) with the “stats” package.

The average density of sporophytes for each sampling date was also calculated. This average was compared with a one-way ANOVA, with “day” as a fixed factor (Zar 2010). This factor was categorized according to sampling period: 110, 125, and 153 days. Shapiro–Wilk’s and Cochran’s tests were used to check and assess the assumptions of normality and variances in homogeneity, and if the assumptions were not met, the data were log-transformed (Zar 2010). The differences detected between day factor levels (110, 125, and 153 days) were explored with Tukey’s HSD a posteriori test (Zar 2010).

## Results

In the field monitoring of 435 experimental sporophytes, the fusion mechanism was related to natural holdfast growth,

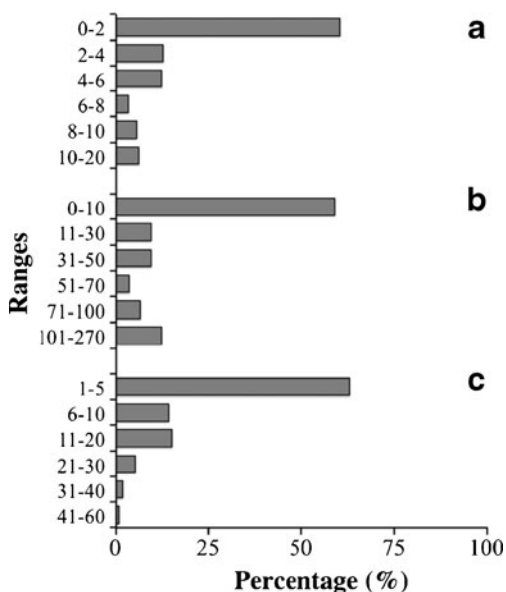
**Fig. 1** Juvenile sporophytes of *Lessonia* complex. **a** Group of “individuals” that will fuse their holdfast. **b** Same individuals after coalescence process (23 days)



**Fig. 2** Frequency of coalescent sporophytes in relation to the total experimental tagged plants during study time period

which occurred in all directions. This growth gradually decreased the distance between neighboring sporophytes until the holdfasts were touching and then progressively fused (Fig. 1). The fusion formed a single holdfast, where the original ones became indistinguishable. The resulting holdfast was always greater than each of its constituents, and its size may be linear to the sum of its holdfast diameters. The minimum distance between pairs of coalescing sporophytes in each group was 0.5 cm, and the maximum was 13 cm; this interval may be considered critical fusion distances.

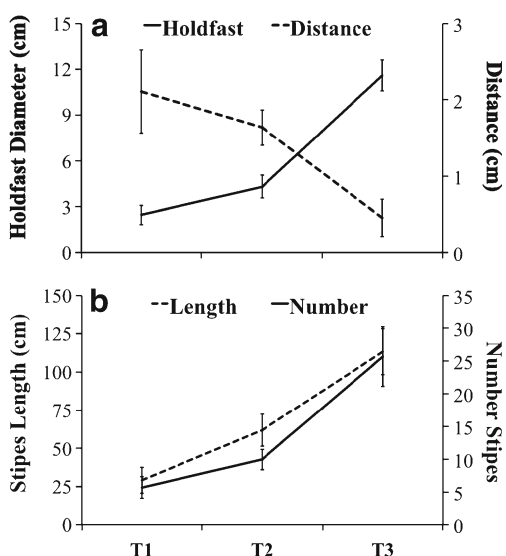
The frequency of fused individuals throughout coalescence increased significantly over time (May–November 2011) (Fig. 2). The size of most fused holdfasts was between 0.5 and 2 cm in diameter (60.43 %; Fig. 3a), with maximal length of plants of 10 cm (58.99 %, Fig. 3b), and 62.94 % of experimental sporophytes having less than five stipes per holdfast (Fig. 3c). Individual assessment of each coalescing sporophyte group (nearest neighbor distance, Fig. 4a) showed an increase in holdfast diameter (i.e., the formation of a fused plant) and a decrease of distance between tagged plants during the experimental period (ANOVA:  $F(2, 30)=28.35, P<0.05$ ,  $F(2, 30)=9.7$ , for holdfast diameter and distance between tagged plants, respectively). The relationship analysis of the coalescing holdfast diameters and the distances between the



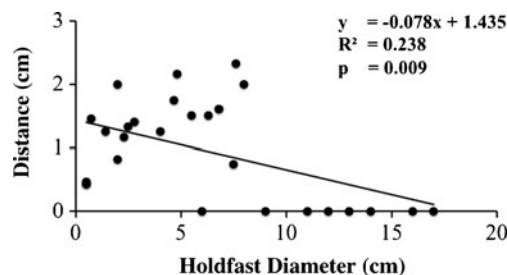
**Fig. 3** Frequency of coalescence in target experimental sporophytes of *L. berteroa*. **a** Holdfast diameter (cm), **b** maximal length (cm), and **c** no. of stipes per holdfast

groups (Fig. 5) (ANOVA:  $F(1, 25)=7.81, P<0.050$ ) suggests a logarithmic growth rate of coalescence individuals.

The cleared area of adult sporophytes had visible recruits after 110 days; from then on, this date was considered the initial time (T1) of assessment of the density per unit area ( $25\text{ cm}^2$ ). Density variation in T1 was 41–69 ( $x=55$ ) sporophytes, in T2 (15 days after), it was 6–27 ( $x=16.5$ ) sporophytes, and in T3 (28 days later), it was 6–13 ( $x=12.5$ ) sporophytes per  $25\text{ cm}^2$ , implying a progressive decrease of density over time. The average sporophyte density differed significantly according to sampling date (day ANOVA:



**Fig. 4** The *Lessonia berteroa* coalescence process (Mean±SE). **a** Trends of holdfast diameter and distance between tagged sporophytes. **b** Trends of morphological variables (length and number of stipes)

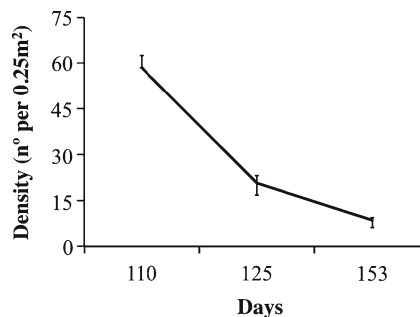


**Fig. 5** Relationship between holdfast diameter of tagged sporophytes and distances between identified experimental groups of plants

$F(2, 27)=72.66, P<0.05$ ). The a posteriori Tukey test indicated that there were differences between all levels of the factor day. With respect to the stipe number per plant, a reverse trend was observed: at the initial time (T1), the interval ranged from 1–5 stipes/sporophyte but it reached more than 20 stipes/sporophyte 170 days after the initial time (Fig. 6).


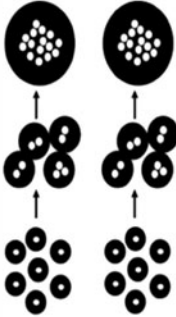
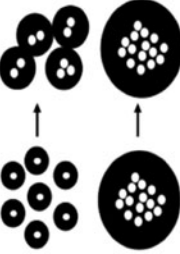
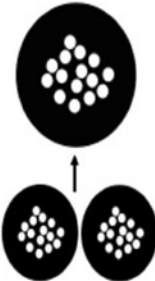
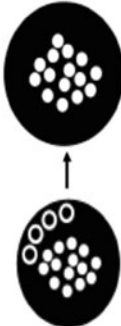
During the holdfast fusion process, two important phenomena were distinguished: (1) “active fusion”, involving simultaneous growth of several individuals or group of individuals and (2) “passive fusion”, where an adult sporophyte (>20 cm holdfast diameter) or even a senescent holdfast recruits small sporophytes or adds neighboring juvenile plants, which means that larger plants are also subjected to coalescence.

Depending on the number and size of coalescent sporophytes, the spatial distribution between them and the potential genetic variability of clumping individuals, five fusion modes occurred. In all modes, there were successive fusions of sporophytes of different sizes (based on maximum length of the stipes), which were divided into three categories: recruits (up to 20 cm), juveniles (up to 60 cm), and adults (over 60 cm). Sporophyte spatial distribution was random but always within the range of critical fusion distances. Table 1 outlines the various fusion modes, and the frequencies of occurrence of each are included. Every instance of fusion increased genetic variability, resulting in a fused sporophyte. Thus, more participants in a fusion group resulted in a greater potential for genetic variability. Consequently, it is assumed that Mode 2 has the largest genetic variability in the resulting sporophyte, followed in descending order by Mode 3, Mode 4, Mode 1, and Mode 5, but the true magnitude of increased genetic



**Fig. 6** Average density (Mean±SE) during the sporophyte coalescence process according to time sampling periods

**Table 1** Coalescence modes, characteristics, and occurrence (%) of each one

Way	Characteristics	Scheme	Occurrence (%)
First	Fusion between neighboring recruits		27
Second	Fusion between two sets of neighboring recruits		9
Third	Fusion between recruits and juvenile sporophyte		9
Fourth	Fusion of two neighboring juvenile sporophytes		55
Fifth	Fusion between recruits and another larger plant (juvenile, adult, senescent) from germination in situ		0

variability established here as a qualitative category related to the number of coalescent holdfasts. However, Mode 5 was not recorded in our experiments (adult-senescent plants were not marked and monitored) but was frequently observed at each sampling date. Senescent plants were not originally considered in our observation of the coalescence process because we considered that the coalescence process would be seen more clearly in juvenile organisms than in old organisms. However, temporal monitoring of experimental plants indicated that sporophyte recruitment over adult holdfast plant occurs quite often, as well as the fusion between adult plants and juvenile recruits

## Discussion

The social, economic, and ecological importance for Chile of *L. berteroana* gives importance to the results obtained in this study concerning the high incidence of “fused individuals” originating from coalescence processes of sporophyte basal disks in natural populations on the rocky coast of Coquimbo in Chile.

There are only three previous accounts of Chilean brown algae species coalescence. In *Durvillaea antarctica* sporophytes, which are characterized by a massive disk and fronds that emerge from a single stipe, it is common to find individuals with several stipes per disk, resulting from the coalescence of several embryos during settlement (Santelices et al. 1980), or from fusion of juvenile sporophytes forming a single holdfast (Castilla and Bustamante 1989). It is also known that *Scytosiphon tenellus* Kogame crustose sporophytes developed under culture-controlled conditions fused after physical contact (Camus et al. 2005).

Our results indicate that more than 60 % of *L. berteroana* sporophytes resulting from coalescence of holdfasts had a tendency to increase the frequency of fused sporophytes, reaching more than 80 % unitary individuals after 6 months, which probably corresponds to permanent recruitment of new individuals. Thus, our results suggest that natural populations consist almost entirely of “fused individuals”. This percentage is higher than the findings of Vásquez et al. (2008) in the same coastline, and in Segovia (2009) this percentage was 81.25 %, despite the loss of control of nearly 35 % of sporophytes during the sampling period.

A *L. berteroana* sporophytic plant is thus a chimera that starts with physical contact and continues with joint growth of two or more holdfasts, wherein the participants lose their morphological and anatomical individuality, but retain a morpho-functional unit, being genetically heterogeneous as described many times for red algae (Santelices 2001, 2004; Santelices et al. 1995, 1999, 2003, 2004, 2010, 2011). In addition, the adult sporophyte experiences several instances of coalescence throughout its development since it is a

progressive and sequential process that begins very early in development and may include some or all modes of coalescence described here which are not exclusive and continues even in adult plants although in passive form, judging by the absence of coalescing pairs of adult sporophytes (larger disks 20 cm) in this study.

The coalescence process gives rise to a single morpho-functional sporophyte that is more genetically heterogeneous because of the diverse origin of coalescent plants. The fusion processes occur in a higher proportion in small plants (0.5–2 cm), as measured by all morphological indicators of growth, showing that fusion can occur at different stages of development. The high-fusion incidence of larger holdfasts (up to 20 cm diameter) confirms that coalescence is an active process until the sporophyte reaches reproductive size. The adult sporophyte holdfasts with passive coalescence have a morphologic appearance, which suggests complete coalescence due to fading traces of other individual holdfasts, but it remains to be determined whether this process also ends with a single morpho-functional sporophyte that is genetically new. The highest incidence of fusion among sporophytes of small sizes (holdfasts between 0.5 to 2 cm diameter) suggests that coalescence is an early survival strategy. The minimum size of fusion recorded here is 0.5 cm in holdfast diameter, but in light of events that precede sporophyte recruitment in the field, this should be retested.

Recently, (Jorquera 2013) reported that in cultures where multicellular branched gametophytes produce oogonia in most apical cells after fertilization, several sporophytes were formed simultaneously, which then fuse resulting in an “individual” with several polystromatic sheets and a rhizoidal complex system, resulting in a “theoretically polygenetic” formation. This clearly suggests that the coalescence processes between the bases of the sporophytes may occur very early in development, even in microscopic stages. In this context, the above results suggest that in the field, the recruitment of zygotes in early stages of development may involve very early simultaneous coalescence processes that give rise to strict chimeras “organisms with two or more different cell lineages derived from diverse zygotes” (Pineda-Krch and Lehtilä 2004; Santelices 2004), which also have different degrees of genetic heterogeneity according to their origin, even considering that parthenogenesis has been documented for female gametophytes of *L. berteroana* (as *nigrescens* in Oppliger et al. 2007). Also, coalescence among smaller plants (<0.5 cm holdfast diameter) as we saw in this study, is perfectly possible, indicating that the minimum fusing distance (0.5 cm) could be smaller than previously thought.

Consequently, adult *L. berteroana* sporophytes that are subject to harvesting (and the entire population, for that matter) are theoretically a mosaic of chimeras, and though their genetic variability is finite, it should be very high. The results of Segovia (2009) obtained from stipes from partial samples

of 48 holdfasts from four different populations of *L. berteroa* (as *nigrescens*) indicated that in 11 of the holdfasts, at least five genotypes coexist, and in 39 of the 48 disks, at least two genotypes were found, suggesting a very high genetic heterogeneity in adult sporophytes. Monogenetic individuals reached 12.5 % (Segovia 2009), suggesting that not all sporophytes coalesced despite it being spatially possible. The causes of this are still unknown but could be related to defensive responses against herbivores or chemical compounds that damage cells in the holdfast, impeding coalescence. This seems to be the role of oligosaccharides in some red algae, serving as recognition signals for potentially coalescing individuals (Santelices et al. 2003). However, it has been proposed that genetically homogeneous organisms may rarely be faced with a very high frequency of genetically heterogeneous organisms (Pineda-Krch and Lehtilä 2004).

Initially, a direct coalescence effect was assumed, that is, a progressive reduction of the distance among holdfasts. This distance reduction resulting in natural growth of holdfasts and fusion took place when the critical distance of 13 cm was not exceeded. The critical distance of coalescence theoretically could rise to 15–20 cm or slightly more, considering that two small disks (0.5) actively growing in the right position for fusion require a holdfast radius of 10 cm, which is entirely possible.

Coalescence among sporophytes would modify the homogeneous distributions of recruits in intertidal exposed rocky shores. Thus, distance among plants (distributional patterns) would not be the result of intraspecific competition or herbivore pressures as have been discussed extensively in the literature (see Lubchenco and Gaines 1981; Johnson et al. 2008; Díaz and McQuaid 2011; Díaz et al. 2011). On the contrary, it would be an intrinsic factor in the life strategy of the plant.

Furthermore, this study also demonstrates that growth indicators like holdfast diameter or number of stipes are modified, not by classical growth but by coalescence processes. Fused sporophytes grow under a logarithmic model because they are the result of the union of several coalescent sporophytes. Coalescence is a continuous process of successive clustering corresponding to the different fusion modes described here. Apparently, the only real growth indicator seems to be the length of the stipes (apical growth).

In light of the above results, the growth indicator that has been used in the management of natural populations over the past years (holdfast diameter) might not be the most appropriate, since fusion may cause juvenile individuals of more than 20 cm basal diameter to not reach reproductive maturity and thus render them unfit for harvesting. Also, some benefits of increased tolerance to variable environmental conditions and selective advantages exceeded the fusion costs (Bus 1962; Rinkevich and Weissman 1992). This was attributed to the chimerism described and analyzed in other organisms,

including some animals. The costs have been associated with negative effects on coalescent individual fitness (Rinkevich and Weissman 1992; Pineda-Krch and Lehtilä. 2004).

The coalescence process promotes the reduction of sporophyte density; however, it increases the number of stipes per plant. This density reduction coincides with reports of *Turbinaria triquetra*, where it is assumed that the low population density could be explained by the coalescence of sporophytes (Ateweberhan et al. 2006). In this context, the decrease in plant density would not only cause by grazers as been intensively discussed over the past decades.

Coalescence processes exponentially or logarithmically increase *Lessonia* complex holdfast size, pushing juvenile plants (without reproductive structures) beyond harvestable size (>20 cm holdfast diameter). These coalescences do not ensure offspring, negatively affecting recruitment events and renewal of wild stocks. However, the coalescence process in *L. berteroa* sporophytes would be a successful survival strategy against benthic grazers. In this context, under high herbivore pressure, the probability of survival of a chimera is far greater than the survival of a plant alone and isolation. As McIntire and Fajardo (2011) suggested, “these fused superorganisms can confirm theoretical predictions that facilitation is an ecological mechanism that leads group selection.”

**Acknowledgments** The authors appreciate the field support of N. Piaget, A. Vega, G. Donoso, and V. Hevia and editorial help by I. Ruiz Boijseauneau. B. Santelices made important comments on seaweed coalescence, improving this contribution. DCR thank Universidad Nacional Autónoma de México for a sabbatical award and hospitality provided during a 2011 stay by the Universidad Católica del Norte, Chile.

## References

- Åberg P (1989) Distinguishing between genetic individuals in *Ascophyllum nodosum* populations on the Swedish West Coast. *Br Phycol J* 24:183–190
- Anuario SERNAPESCA (2011) Anuario Estadístico de Pesca. Ministerio de Economía Fomento y Reconstrucción, República de Chile. [www.sernapesca.cl](http://www.sernapesca.cl)
- Arenas F, Fernández C (2000) Size and dynamics in a population of *Sargassum muticum* (Phaeophyceae). *J Phycol* 36:1012–1020
- Ateweberhan M, Bruggemann JH, Breeman AM (2006) Seasonal module dynamics of *Turbinaria triquetra* (Fucales, Phaeophyceae) in the Southern Red Sea. *J Phycol* 42:990–1001
- Bus LW (1962) Group living, competition, and the evolution of cooperation in a sessile invertebrate. *Science* 213:1012–1014
- 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
- Camus C, Meynard AP, Faugeron S, Kogame K, Correa JA (2005) Differential life history phase expression in two coexisting species of *Scytosiphon* (Phaeophyceae) in Northern Chile. *J Phycol* 41:931–941
- Castilla JC, Bustamante RH (1989) Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Durvilleales). *Mar Ecol Prog Ser* 50:203–214

- Clayton M (1992) Propagules of marine macroalgae: structure and development. *Br Phycol J* 27:219–232
- 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, Erlandsson J, McQuaid CD (2011) Detecting spatial heterogeneity in intertidal algal functional groups, grazers and their co-variation among shore levels and sites. *J Exp Mar Biol Ecol* 409:123–135
- FAO yearbook (2012) Fishery and Aquaculture Statistics. Capture production 2010. Food and Agriculture Organization of the United Nations. Rome: 609
- González AV, Santelices B (2008) Coalescence and chimerism in *Codium* (Chlorophyta) from central Chile. *Phycologia* 47:468–476
- 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 (Phaeophyceae, Laminariales). *J Phycol* 48:1153–1165
- González AV, Borrás-Chavez R, Beltrán J, Flores V, Vásquez JA, Santelices B (2013) Morphological, ultrastructural and genetic characterization of coalescence in the intertidal and shallow subtidal kelps *Lessonia spicata* and *L. berteroa* (Laminariales, Heterokontophyta). *J Appl Phycol*. doi:10.1007/s10811-013-0112-6
- Hoffmann A, Santelices B (1997) Flora Marina de Chile Central. Ediciones Pontificia Universidad Católica de Chile, Santiago
- Johnson MP, Hanley ME, Frost NJ, Mosley MWJ, Hawkins SJ (2008) The persistent spatial patchiness of limpet grazing. *J Exp Mar Biol Ecol* 365:136–141
- Jorquera LE (2013) Efecto de la densidad de esporas asentadas sobre la fusión de esporofitos tempranos de *Lessonia nigrescens* (Laminariales, Phaeophyceae). Tesis Biólogo Marino, Departamento Biología Marina, Facultad de Ciencias del Mar. Universidad Católica del Norte, Chile
- Kuhlenkamp R, Hooper RG (1995) New observations on the Tilopteridaceae (Phaeophyceae). I. Field studies of *Haplospora* and *Phaeosiphoniella*, with implications for survival, perennation and dispersal. *Phycologia* 34:229–239
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant–herbivore interactions. I. Populations and communities. *Ann Rev Ecol Syst* 12:405–437
- Mags CA, Cheney DP (1990) Competition studies of marine macroalgae in laboratory culture. *J Phycol* 26:18–24
- McIntire EJB, Fajardo A (2011) Facilitation within species: a possible origin of group-selected superorganisms. *Am Nat* 178:88–97
- Oppliger LV, Correa JA, Peters AF (2007) Parthenogenesis in the brown alga *Lessonia nigrescens* (Laminariales, Phaeophyceae) from central Chile. *J Phycol* 43:1295–1301
- Oróstica MH (2013) Efecto de la herbivoría sobre la estructura espacial del reclutamiento de *Lessonia berteroa* (Laminariales, Phaeophyceae): consecuencias para la coalecencia. Tesis Magister en Ciencias del Mar, Departamento Biología Marina, Facultad de Ciencias del Mar. Universidad Católica del Norte, Chile
- 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
- Pineda-Krch M, Lehtilä K (2004) Costs and benefits of genetic heterogeneity within organisms. *J Evol Biol* 17:1167–1177
- R Development Core Team (2012) R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rinkevich B, Weissman IL (1992) Chimeras vs genetically homogeneous individuals: potential fitness costs and benefits. *Oikos* 63:119–124
- Santelices B (2001) Implications of clonal and chimeric-type thallus organization on seaweed farming and harvesting. *J Appl Phycol* 13:153–160
- Santelices B (2004) A comparison of ecological responses among asexual (unitary), clonal and coalescing macroalgae. *J Exp Mar Biol Ecol* 300:31–64
- Santelices B, Castilla JC, Cancino J, Schmiede P (1980) Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyceae) in central Chile. *Mar Biol* 59:179–189
- Santelices B, Aedo D, Varela D (1995) Causes and implications of intracolonial variation in *Gracilaria chilensis* (Rhodophyta). *J Appl Phycol* 7:283–290
- Santelices B, Correa JA, Aedo D, Flores V, Hormazábal M, Sánchez P (1999) Convergent biological processes in coalescing Rhodophyta. *J Phycol* 35:1127–1149
- 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
- Santelices B, Hormazábal M, Correa J, Flores V (2004) The fate of overgrown germlings in coalescing Rhodophyta. *Phycologia* 43:346–352
- Santelices B, Alvarado JL, Flores V (2010) Size increments due to interindividual fusions: how much and for how long? *J Phycol* 46:685–692
- Santelices B, Alvarado JL, Chianale C, Flores V (2011) The effects of coalescence on survival and development of *Mazzaella laminarioides* (Rhodophyta, Gigartinales). *J Appl Phycol* 23:395–400
- Segovia NI (2009). Microsatélites de *Lessonia nigrescens* revelan que existe fusión de individuos en un mismo disco de adhesión en sectores de alta y baja densidad de plantas. Tesis Biólogo Marino. Facultad de Ciencias del Mar, Universidad Católica del Norte. Chile
- Tellier F, Vega JMA, Broitman B, 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
- Vásquez J (2008) Production, use and fate of Chilean brown seaweeds: resources for a sustainable fishery. *J Appl Phycol* 20:457–467
- Vásquez J, Tala F, Vega A, Zuñiga S, Edding M, Piaget N (2008) Bases ecológicas y evaluación de usos alternativos para el manejo de praderas de algas pardas de la II y IV Regiones. Informe Final Proyecto FIP No. 2005–22, Subsecretaría de Pesca, Chile
- Vásquez JA, Piaget N, Vega JMA (2012) Chilean *Lessonia nigrescens* fishery in northern Chile: how do you harvest is more important than how much do you harvest. *J Appl Phycol* 24:417–426
- Zar JH (2010) Biostatistical analysis. Prentice Hall, Englewood Cliffs