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Coalescence and chimerism in *Codium* (Chlorophyta) from central Chile

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This study evaluates the natural occurrence of inter- and intracrust fusions of patches of a common species of *Codium* in central Chile. Field experiments suggested a high capacity for vegetative growth in the species followed by fast colonization of new areas. When two crusts encounter each other on a new substratum, their respective rhizoidal filaments and utricles grow intermixed, forming a continuous crust. Growth is initiated by the production of colourless cytoplasmic projections from the borders of the utricles. Protoplasm and plastids then invade these syncytial outgrowths, which then elongate, growing as creeping filaments on the new substratum. Creeping filaments later differentiate into utricles and rhizoidal filaments. Inter- and intracrust contact areas then become covered with the intertwining utricles and rhizoidal filaments of the two neighbouring crusts. Measurements of intracrust genetic variability, screened with three organellar markers (chloroplast partial *rbc*L, mitochondrial rLSU and chloroplast Trn-Gly gene), revealed widespread occurrence of intracrust genetic heterogeneity and chimerism at four localities of northern and central Chile. This is the first report of coalescence and chimerism in a green alga.

INTRODUCTION

Coalescence involves fusion between two or more organisms, often generating genetically heterogeneous entities (Santelices *et al.* 1999; Pineda-Krch & Lehtila 2004). Ecologically, interindividual fusions have been associated with cooperation, reducing competition or maintaining a trade-off between cooperation and competition (Buss 1982, 1999). Interorganism fusions and chimera formation occur in several major groups in various kingdoms, including slime moulds, protists, fungi, plants, invertebrate and vertebrate animals (see reviews by Buss 1982; Pineda-Krch & Lehtila 2004). Among seaweeds, the process has been described only for members of the red algae (see data in Santelices *et al.* 1999), occurring among conspecific partners of similar or different karyological phases, sizes or ages (Santelices *et al.* 2003a, 2004). Benefits derived from coalescence include increased size of the organisms, reduction of mortality risks associated with herbivory and competition, increased rates of recruitment, fecundity, productivity and greater intraorganismal genetic variability (Santelices *et al.* 1999, 2003a, b, 2004; Morley *et al.* 2003; Shaughnessy 2004).

Many mid- and low-intertidal levels of wave-exposed rocky habitats along the Chilean coastline (*c.* 17°S–40°S) are dominated by dark green, crustose cushions of *Codium* to 6–15 mm thick and up to 1.5 m in diameter. Traditionally the species has been recognized as *Codium dimorphum* Svedelius (e.g. Levring 1960; Santelices *et al.* 1981; Ramírez & Santelices 1991). However, recent morphological and molecular studies (González 2007; González *et al.*, in prep.) suggest that *C. dimorphum* is so far known from Melinka Island only (43°03′S–73°44′W), while the crustose species of *Codium* occurring along most of the Chilean coastline corresponds to a different, seemingly undescribed species. Pending the final identity of this taxon, in this manuscript this species is referred as *Codium* sp.

Experimental field studies have shown *Codium* sp. in central Chile influences community organization and successional events in middle intertidal habitats because of its ability to overgrow and exclude other intertidal organisms (Santelices *et al.* 1981; Santelices 1990). The large size and exclusion capacity of this species might be due to coalescence, as suggested by Maggs and Cheney (1990), but the occurrence of coalescence in green seaweeds has remained untested. Since field observation with *Codium* sp. in central Chile (e.g. Santelices *et al.* 1981; González 2007) and with *Codium setchellii* Taylor in the central Oregon coast of the Pacific USA (Trowbridge 1996) have suggested the probability of intercrust fusions, a more detailed study on the nature of the fusion process in *Codium* sp. in central Chile was undertaken. Evaluation of inter- and intracrust coalescence involved field experiments, histological analysis and genetic studies of haplotype variability in natural crusts of *Codium* sp. at various geographic localities.

MATERIAL AND METHODS

Study organisms

Similar to other species in the genus, *Codium* sp. is composed of a siphonous syncytium. In a prostatre thallus, there is a basal layer of nearly colourless siphons, traditionally called rhizoidal filaments, which provide substratum adherence (Silva 1957). The upper layer of a prostate thallus is made up of filaments that branch sympodially, with the apices pushed upward and enlarging into nuclei and chloroplast-rich utricle, which form a palisade on the surface. In the field, these prostate thalli appear as dark green, crustose cushions of variable

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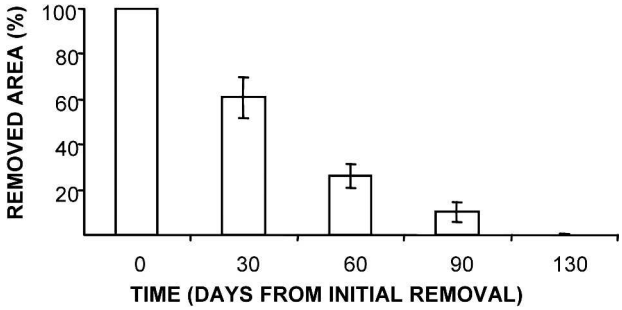


Fig. 1. Recolonization of experimentally removed intracrust areas in *Codium* sp. from Horcón. Bars are standard errors; $n = 40$.

diameter. In rocky intertidal habitats of central Chile, these crusts form a permanent belt, with maximum cover during autumn and winter (April–August; Santelices *et al.* 1981).

Study sites

The field study was conducted from May 2004 to December 2005. Four localities within the distributional limits of the species in Chile were used. Two localities in central Chile, Horcón (32°42′S, 71°30′W) and Maitencillo (32°39′S, 71°29′W), were selected for field experiments because of the presence of abundant *Codium* sp. crusts of different sizes. Paposo (25°07′S, 70°20′W) and Loncoyén (38°43′S, 73°24′W) are localities situated about 1000 km to the north and south of central Chile, respectively, and were used to increase the representation of geographically distant samples in the genetic studies.

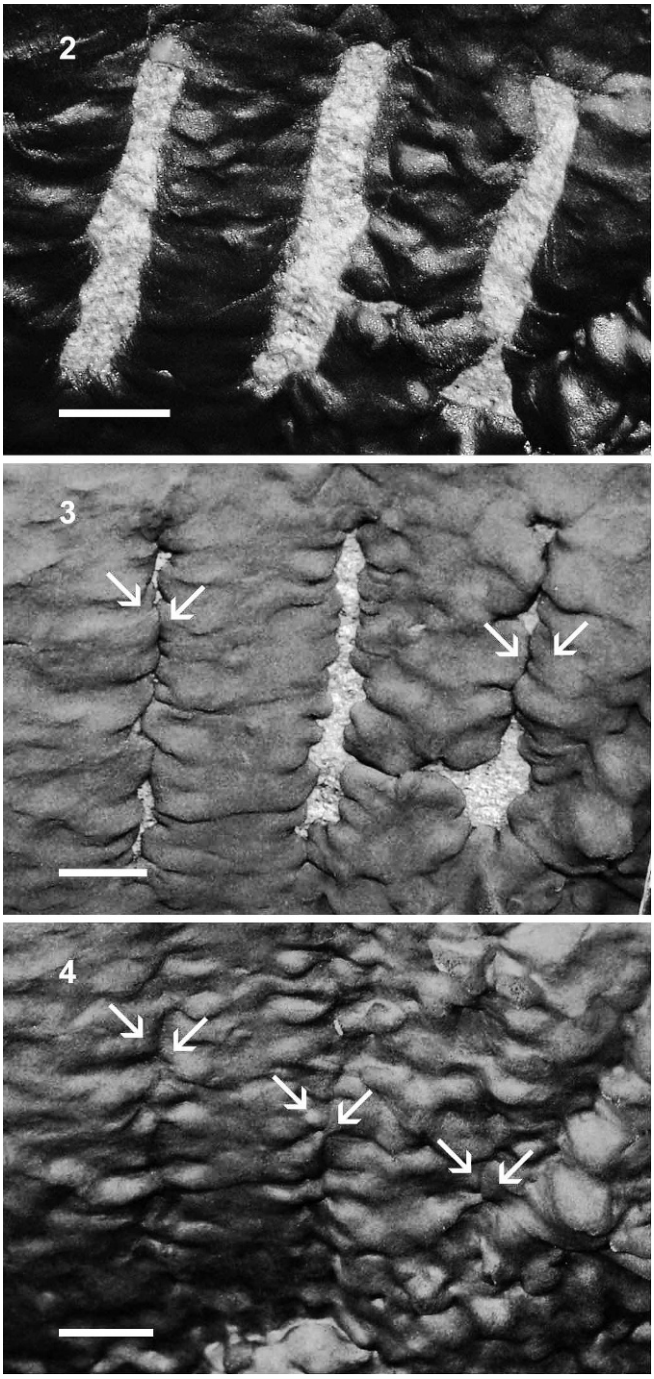
Field experiments and observations

INTRACRUST FUSIONS: The ability of this species to fuse at the intracrust level was tested by disrupting the continuity of the crust, that is, excavating a 1 × 10-cm groove within the crust. To prevent the entrance of grazers into the groove, care was taken not to extend the groove to within less than 2 cm from the border of the crust. Experiments were conducted in Horcón, starting in May 2004 and monitored every 15 days for a total of 120 days. We followed 40 replicate experimental crusts with three grooves within each crust and 15 untreated (control) crusts.

INTERCRUST FUSIONS: The ability of *Codium* sp. to fuse with neighbouring crusts was measured between June and December 2004 in Maitencillo. A total of 15 pairs of crusts of *Codium* sp. of approximately similar dimensions and occurring naturally 1.5–2 cm apart were tagged and monitored up to the point of full contact. Another 15 untreated crusts occurring at larger distances were used as controls mainly for morphological observations.

MORPHOLOGICAL OBSERVATIONS: Comparisons of the growth borders were conducted in experimental and untreated (control) crusts in Horcón and Maitencillo during monitoring periods. Tissue samples were extracted from the crust border, observed fresh in the laboratory or fixed for histological analysis as explained below.

Experimental and untreated thalli were followed by photographic monitoring, using a digital camera (Fuji FinePix 5000), with a 10-cm ruler used as a reference scale. The digital photographs were analysed using the software Sigma Scan Pro Version XX (Demo), measuring area and neighbour distance. Once thallus fusion occurred, we extracted tissue samples from the contact zones and crust borders, which were first observed and photographed under a stereoscope (Nikon SMZ-10A) and then subjected to histological studies to identify potential branch fusions.



Figs 2–4. Recolonization patterns in experimentally removed intracrust areas in *Codium* sp. from central Chile. Arrows indicate the experimental border at 15 days (Fig. 2), 60 days (Fig. 3) and 90 days (Fig. 4) after removal. Scale bar = 3 cm.

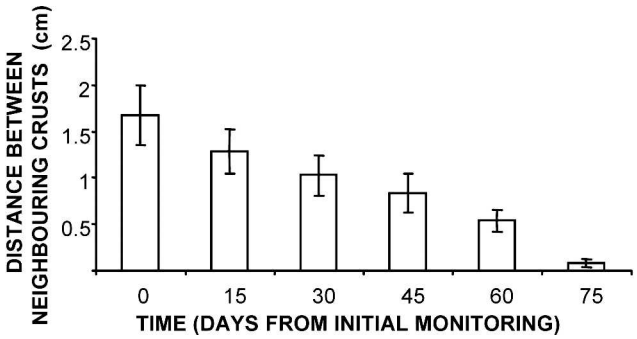
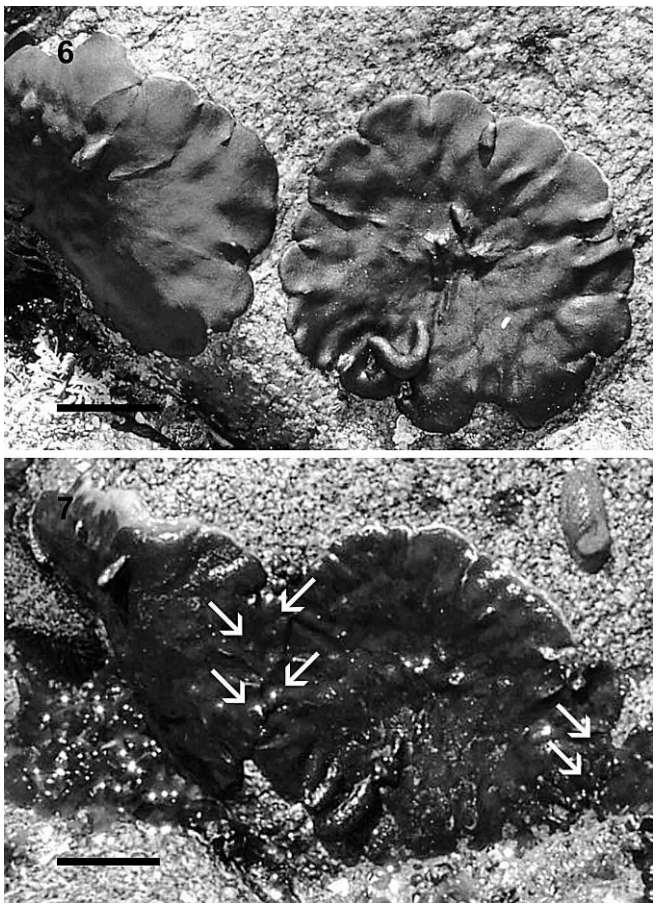


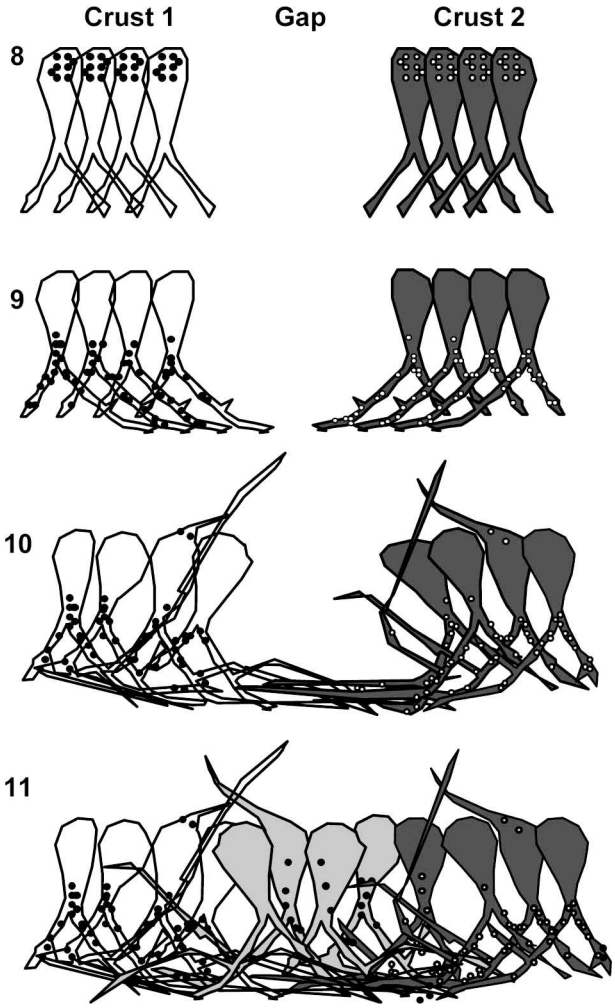
Fig. 5. Distance reduction between tagged independent neighbouring thalli of *Codium* sp. in Maitencillo. Bar are standard errors; $n = 15$.

Histological studies

All the tissue samples collected in the field were fixed for ultrastructural analysis. Tissue fixation employed a mixture composed of glutaraldehyde (3%), paraformaldehyde (1%) and SFC culture medium at 5°C, followed by postfixation in osmium (2%), with ascendant dehydration in ethanol and SPURR inclusion (Spurr 1969; Santelices *et al.* 1999). The samples were sectioned in an ultramicrotome (Leica, Ultracut R). Thicker sections (800 nm) were stained with 0.25% toluidine blue, observed and photographed with a microscope (Nikon, Optiphot-2) equipped with a CoolSNAP-Pro*cf* digital camera (Media Cybernetics). Image acquisition used Image Pro® Plus 4.5 software (The Proven Solution™, Version 4.1.0.0, 1993–1995 Media Cybernetics). Fine sections (90 nm) were made in a ultramicrotome, stained with uranyl acetate and lead citrate and analysed using a Philips Tecnai 12 Electron Microscope operated at 60 kV.



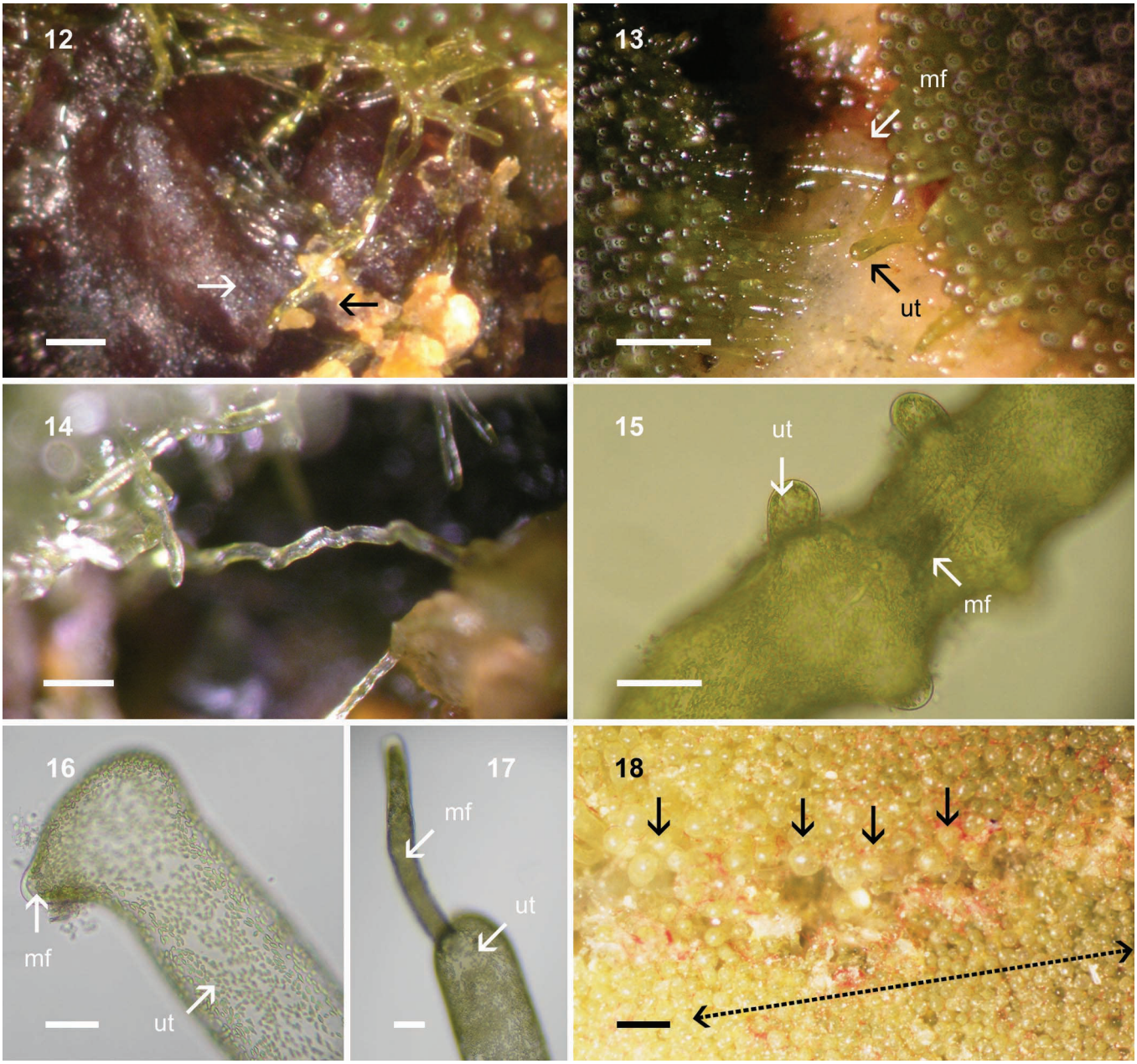
Figs 6, 7. Intercrust thallus fusions in *Codium* sp. monitored at Maitencillo, central Chile (Fig. 6) 45 days and (Fig. 7) 75 days from initial monitoring. Scale bar = 3 cm.



Figs 8–11. Thallus crust fusion in *Codium* sp.
Fig. 8. Two neighbouring crusts with numerous chloroplasts in the distal utricle region.
Fig. 9. Proximal chloroplast migration to rhizoidal filaments which develop elongated projections.
Fig. 10. Modified marginal utricles, with apical and basal outgrowths in which make contact with extensions from a neighbouring crust.
Fig. 11. Production of new utricles (grey) from the filamentous extensions of both partners in the newly colonized gap.

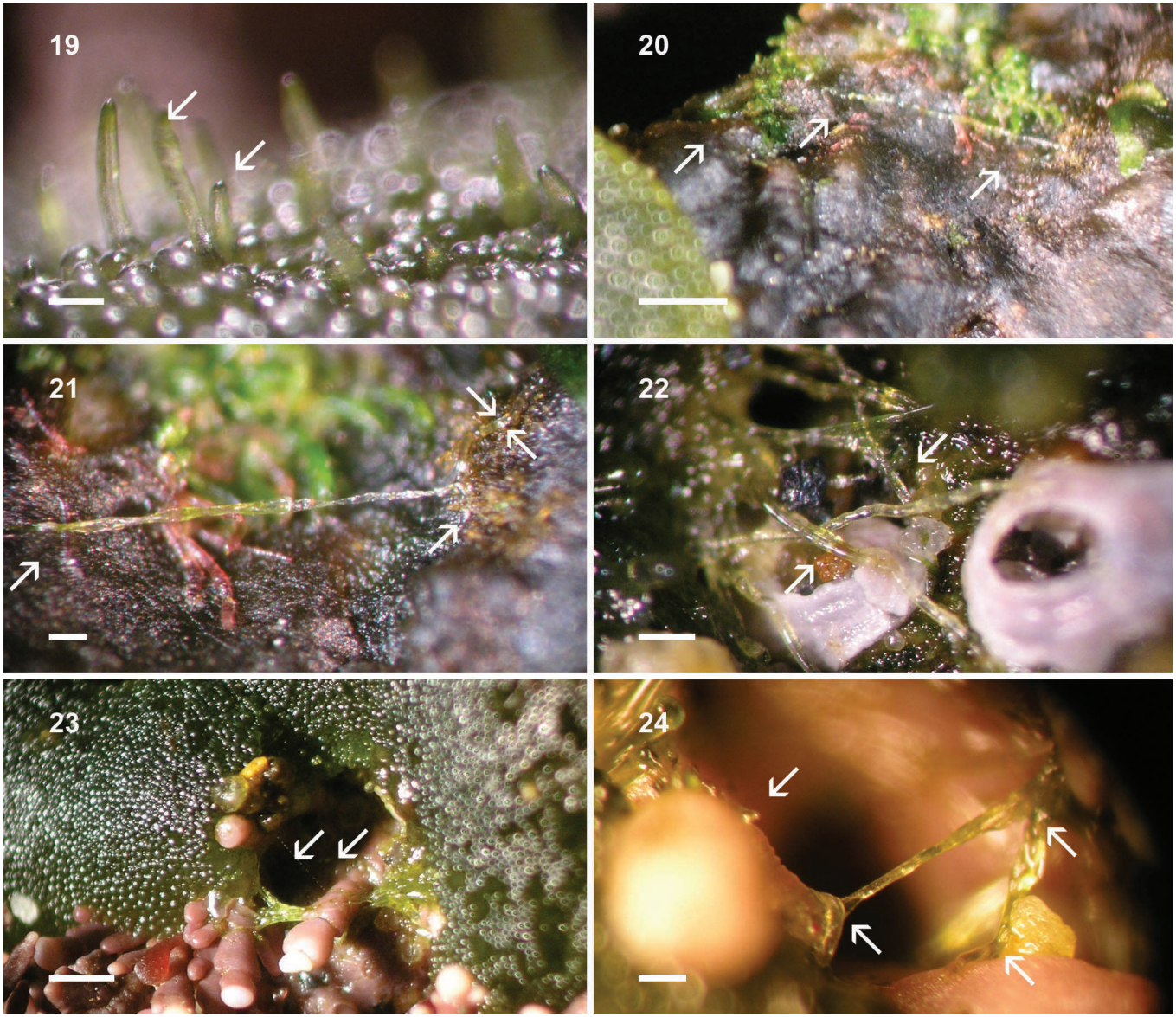
Genetic analysis

Intracrust genetic variability was measured to identify the occurrence of monomorphic or polymorphic haplotype patterns inside 10 replicate crusts collected at four localities along the central Chilean coastline between 25° and 38°SL. The four localities were Paposo, Horcón, Maitencillo and Loncoyén. Sampling was performed between July and November 2005. A horizontal transect running from one



Figs 12–18. Coalescence at microscopical level in manipulated crusts of *Codium* sp.
Fig. 12. Highly pigmented rhizoidal filaments, extending across the discontinuity between two crusts. Scale bar = 200 μm.
Fig. 13. Rhizoidal filaments (white arrows) and modified utricles (black arrows) extending from the thallus border, invading the new substratum. Scale bar = 200 μm.
Fig. 14. Close-up of a rhizoidal and/or modified utricles extending across a crust discontinuity. Scale bar = 200 μm.
Fig. 15. Rhizoidal filaments producing new utricles in contact zone. Scale bar = 100 μm.
Figs 16, 17. Utricles producing new elongated filaments in the contact zone. Scale bar = 50 μm and 100 μm, respectively.
Fig. 18. Contact zone between the two thalli that appears as a scar (dotted arrow). Several new utricles (black arrows) are seen broader and dispersed irregularly in the contact zone. Scale bar = 200 μm.

margin to the other of each crust was traced. Three replicate tissue samples were taken along the transect at equidistant distances from the crust borders. Total genomic DNA was extracted from 120 silica gel-dried tissue samples, as described in Wattier *et al.* (2000) with modifications to DNA centrifugation and precipitation times. The genetic variability within a thallus of *Codium* sp. was screened with three organellar markers: chloroplast partial *rbc*L (~ 700 base pairs [bp]; Shimada *et al.* 2004), mitochondrial rLSU (~ 800 bp; Pedroche 2001) and chloroplast Trn-Gly gene (~ 300 bp; Provan *et al.* 2005). The PCR product was quantified visually in 1.5% agarose gels stained with ethidium bromide and purified by the QIAquick PCR Purification Kit (Qiagen). The products were automatically sequenced on an ABI-3100 (Applied Biosystems), in the DNA sequence service of Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile. In order to estimate and describe the



Figs 19–24. Growth and colonization pattern in natural crust of *Codium* sp.
Fig. 19. Border of a crust, with numerous elongated, highly pigmented utricles. Scale bar = 100 μm.
Figs 20, 21. Utricle and/or rhizoidal filament, extending up to 1 cm beyond the crust border, attaching to the substratum by numerous points of adhesion (white arrows). Scale bar = 500 μm and 200 μm, respectively.
Fig. 22. Rhizoidal filaments adhered to and overgrowing sessile marine invertebrates (*Balanus*). Scale bar = 100 μm.
Fig. 23. Rhizoidal filaments adhered to and overgrowing some a calcareous some algae (*Corallina* sp.). Scale bar = 500 μm.
Fig. 24. Close-up of a pigmented and intertwined rhizoidal filament attached to two erect branches of *Corallina* sp. showing pigmented and intertwined rhizoidal filament. Scale bar = 100 μm.

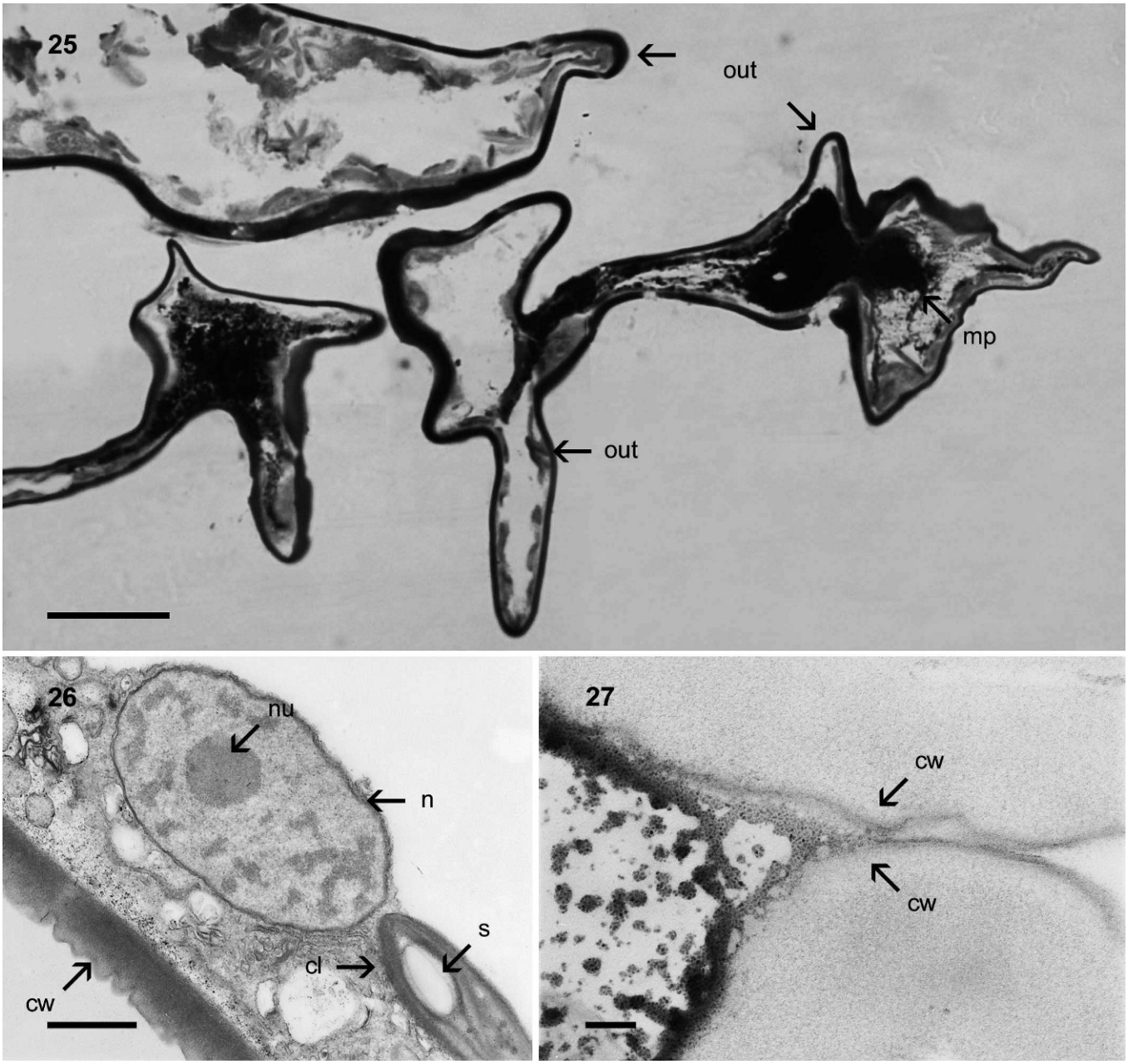
number of haplotypes, sequences were manually aligned in ProSeq v. 2.91 software (Filatov 2002) and then compared in DnaSP 4.10 software (Rosas *et al.* 2003).

RESULTS

Field experiments and observations

INTRACRUST FUSIONS: At the intracrust level, *Codium* sp. colonized and covered the experimentally cleared rocky surface in a maximum of 120 days (Fig. 1). Initial intracrust growths were observed at day 15 (Fig. 2). By day 30, an average of 60 ± 11% of the experimentally cleared surface had been recovered. By day 60, the experimentally removed area had recovered an average of 75 ± 5% (Fig. 3). By this time, the excavated grooves in 11 of the 40 experimental crusts appeared as closed scars, which disappeared completely by day 90 (Fig. 4). Between days 75 and 90, all but one crust had completely covered the cleared area. By day 90, scars were visible in only three of the experimental crusts, while all others exhibited a smooth, continuous surface (Fig. 4).

INTERCRUST FUSION: At the intercrust level, field measurements (Fig. 5) indicated gradual increases in crust diameter



Figs 25–27. Contact zone between filaments of *Codium* sp.
Fig. 25. Three rhizoidal filaments and or modified utricles in contact or close proximity. All filaments exhibit numerous outgrowths (out) and mucopolysaccharides accumulations (mp) in central zones. Scale bar = 10 μm.
Fig. 26. Elongate filaments in a contact zone. The filaments shows cell wall (cw), nucleus (n), nucleolus (nu), chloroplast (cl) and starch grains (s). Scale bar = 1 nm.
Fig. 27. Contact between two filaments. Each filaments maintains its own cell wall (cw) (absence of cell wall fusion). Scale bar = 100 nm.

and consequently a gradual reduction of the intercrust distances until neighbouring crusts encountered each other (Figs 6, 7). For crusts separated by an average distance of 1.75 ± 0.25 cm, it takes 75–100 days to completely cover the intercrust distance and to achieve full contact between independent crusts (Fig. 7). Similar to intracrust fusions, a scar is first formed at the site of contact, which then disappears completely. By day 135, a smooth continuous surface was observed extending from one crust to another in all the pairs of crusts monitored during this study.

MORPHOLOGICAL OBSERVATIONS: Similar syncytial changes were found within the contact area of intra- and intercrust fusions. A diagrammatic representation of these changes is shown in Figs 8–11 and pertinent illustrations shown in Figs 12–18. Initially, from the utricles on the edge of each crust (Fig. 8), the rhizoidal filaments produce several projections (Fig. 9). Protoplasm and plastids then invade these projections, which later elongate, growing as creeping filaments on the new substrate (Fig. 12). Additionally, some border utricles become narrower and more prostrate,

Table 1. Polymorphic nucleotide positions in sequences of *Codium* sp., originating 11 different haplotypes with variable frequency in 120 samples of 40 crusts from four different localities along central Chile.

		Sequence position															
Haplotype	No. of thalli	11	12	13	14	15	18	23	30	36	38	42	43	65	70	88	115
HAP 1	8	A	A	A	T	C	A	A	T	T	T	T	T	A	A	A	T
HAP 2	6	A	A	T	C	A	A	A	T	T	T	T	T	A	A	A	T
HAP 3	1	A	A	A	T	C	A	A	T	T	T	T	T	A	A	G	T
HAP 4	82	A	A	A	A	A	A	A	T	T	T	T	T	A	A	A	T
HAP 5	6	A	A	A	T	C	A	A	T	T	T	T	T	A	T	A	T
HAP 6	4	A	A	A	A	A	A	A	T	T	C	T	T	A	A	A	T
HAP 7	1	A	A	A	A	A	A	T	T	T	T	T	T	T	A	A	T
HAP 8	3	A	A	A	A	A	A	A	T	T	T	T	C	A	A	A	T
HAP 9	1	A	A	A	A	A	A	T	T	T	T	T	T	A	A	A	T
HAP 10	7	A	A	A	A	A	T	A	T	C	T	T	T	A	A	A	T
HAP 11	1	A	A	A	A	A	A	A	T	T	T	T	T	A	A	A	G

approaching the morphology of the rhizoidal filaments (Figs 10, 13). The creeping filaments arising from the utricles and the utricles modified into elongated filaments attach to the substratum (Fig. 14), eventually giving rise to new utricles (Fig. 15) and rhizoidal filaments (Figs 16, 17) that continue expanding in the colonizing area. The substratum in the contact area gradually becomes covered with intertwining and firmly attached utricles and rhizoidal filaments of the two neighbouring crusts, which soon become entangled (Fig. 11). The first utricles produced by the creeping filaments in the contact area are broader than the rest of the utricles and dispersed irregularly (Fig. 18). Later, the utricles density increases, reducing gradually their width and covering the discontinuity between the two crusts. Elongation and growth of additional rhizoidal syncytia from both partners eventually generates new utricles, filling in the scar area.

Table 2. Haplotype composition in crusts of *Codium* sp. from localities along the Chilean coast. Chimeric thalli are composed by more than one haplotype.

Locality	Thallus no.	Haplotype combination	No. of haplotypes
Paposo	1	Hap 4 – Hap 4 – Hap 9	2
Paposo	2	Hap 4 – Hap 4 – Hap 8	2
Paposo	3	Hap 4 – Hap 4 – Hap 8	2
Paposo	4	Hap 8 – Hap 10 – Hap 10	2
Paposo	5	Hap 4 – Hap 4 – Hap 4	1
Paposo	6	Hap 6 – Hap 6 – Hap 7	3
Paposo	7	Hap 4 – Hap 10 – Hap 10	2
Paposo	8	Hap 4 – Hap 10 – Hap 11	3
Paposo	9	Hap 4 – Hap 10 – Hap 10	2
Paposo	10	Hap 4 – Hap 6 – Hap 6	2
Maitencillo	1	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	2	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	3	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	4	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	5	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	6	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	7	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	8	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	9	Hap 4 – Hap 4 – Hap 4	1
Maitencillo	10	Hap 4 – Hap 4 – Hap 4	1
Horcón	1	Hap 4 – Hap 4 – Hap 4	1
Horcón	2	Hap 4 – Hap 4 – Hap 4	1
Horcón	3	Hap 4 – Hap 4 – Hap 4	1
Horcón	4	Hap 4 – Hap 4 – Hap 4	1
Horcón	5	Hap 4 – Hap 4 – Hap 4	1
Horcón	6	Hap 4 – Hap 4 – Hap 4	1
Horcón	7	Hap 4 – Hap 4 – Hap 4	1
Horcón	8	Hap 4 – Hap 4 – Hap 4	1
Horcón	9	Hap 4 – Hap 4 – Hap 4	1
Horcón	10	Hap 4 – Hap 4 – Hap 4	1
Loncoyén	1	Hap 1 – Hap 5 – Hap 4	2
Loncoyén	2	Hap 2 – Hap 4 – Hap 4	2
Loncoyén	3	Hap 1 – Hap 1 – Hap 4	2
Loncoyén	4	Hap 1 – Hap 2 – Hap 3	3
Loncoyén	5	Hap 4 – Hap 4 – Hap 4	1
Loncoyén	6	Hap 2 – Hap 2 – Hap 2	1
Loncoyén	7	Hap 1 – Hap 1 – Hap 1	1
Loncoyén	8	Hap 4 – Hap 5 – Hap 5	2
Loncoyén	9	Hap 2 – Hap 4 – Hap 4	2
Loncoyén	10	Hap 1 – Hap 5 – Hap 5	2

Examination of the border of naturally growing crusts of *Codium* sp. in the field indicate the existence of numerous elongated, pigmented filaments originating either from the utricles or from the rhizoidal filaments (Fig. 19). These elongated and pigmented filaments extend for up to 1 cm beyond the crust border, maintaining numerous adhesion points to the substratum (Fig. 20). These filaments tolerate full air exposure during low tide (Fig. 21) and often are seen adhering and overgrowing sessile marine invertebrates (Fig. 22) and calcareous articulated and nonarticulated macroalgae (Figs 23, 24).

Histological studies

Examination of the elongated filaments in the contact area in thin and semithin sections shows an abundance of syncytial outgrowths (Fig. 25) with numerous circular plastids and nuclei (Fig. 26). Even though the surface of the filaments from different partners was in close contact, no cell wall fusion or interfilaments connections were observed in any of the 55 contact areas studied (Fig. 27).

Genetic analysis

The two longer organellar markers used (chloroplast partial *rbc*L and mitochondrial rLSU) gave monomorphic genetic patterns only. In contrast, the chloroplast Trn-Gly gene and spacer region (231-bp length) exhibited 11 different haplotypes, with 11 variable sites (14.7%) and variable frequency (Table 1). Haplotype 4 was the most frequent (68%) and was found in all populations studied. In several

cases, a single crust included different haplotypes (40%) in variable combinations (Table 2).

The crust populations from Horcón and Maitencillo were monomorphic, exhibiting only one haplotype (HAP4). In contrast, the Paposo and Loncoyén populations showed higher haplotype diversity. The crust from Paposo was characterized by six different haplotypes (HAP 6 to HAP 11), and 83% of them were haplotypes private to their locality. Genetic variability within the thallus indicated high intracrust genet heterogeneity (90%), composed by two or three different haplotypes in variable combinations (Table 2).

The crust from Loncoyén also showed high haplotype diversity ($N = 5$, HAP1-HAP5) (70%) with four haplotypes exclusive to the locality. As for Paposo, the within-thallus haplotype combination in Loncoyén showed high intracrust genetic heterogeneity (70% of the crusts).

DISCUSSION

The results provided here demonstrate a substantial fusion capacity in *Codium* sp. from central Chile, both at the intra- and at the intercrust level. The latter fusion type may result in genetically heterogeneous (chimeric) crusts that, within the size range of crusts included in this study, may be formed by up to three different haplotypes. This is the first report of coalescence and chimerism in green algae, which up to now, had been described only for red algae (for a review, see Santelices 2004).

Microscopically, thallus fusion is characterized by morphofunctional syncytial changes somewhat similar to those described during morphogenesis and growth of the siphonous seaweed *Acetabularia* (Mandoli 1996; Serikawa & Mandoli 1988; Kratz & Mandoli 1999). New utricles and rhizoidal filaments are produced from numerous syncytia outgrowths followed by migration of protoplasm and organelles. Later, the new filaments produced from the outgrowths may elongate extending into and attaching to new substrata. Growing fronts from neighbouring crusts may grow with their filaments intermixed, which later will differentiate new utricles and rhizoidal filaments.

In contrast to the coalescence processes described for red algae (e.g. Santelices *et al.* 1999), the coalescing partners of *Codium* sp. do not exhibit filament fusions, do not form a common cell wall around the contacting filaments and do not establish intercellular connections among the syncytia of the coalescing partners. Thus, coalescence in *Codium* sp. is restricted to the intertwining and mixing of growth filaments from two different partners whenever they are jointly invading a new substratum. The high frequency of chimeric thalli (70–90%) found in the natural populations of Paposo and Loncoyén suggest fusion of different genetic individuals that come into contact during the spreading of thallus growth, similar to the process just described in our experimental work. The existence of up to three haplotypes within a crust suggests the occurrence of more than one of these encounters during the life of a crust and alert to the possibility of intracrust competition among syncytial lineages from different partners, a process widely documented for colonial invertebrates (Buss 1982) but not yet studied in coalescing macroalgae.

Previous studies (e.g. Maggs & Cheney 1990) have suggested that the large size and exclusion capacity of *Codium* sp. with respect to other intertidal species in central Chile might be due to coalescence. Our studies suggest that both coalescence and exclusion of other organisms result from the high capacity for vegetative growth shown by all the *Codium* sp. crusts examined in this study. The morphophysiological changes of the filaments at the borders of the crusts allow them to generate new, invasive filaments, to extend onto new substratum, to restore the thallus after some kind of disturbance (e.g. grazers), to coalesce with neighbouring crusts and to overgrow and eventually out compete other rocky intertidal organisms.

Even though we have not experimentally evaluated the benefits for *Codium* sp. arising from coalescence, a few may be anticipated. Fusion followed by the intermingling of siphonous filaments of different origins, as seen in *Codium* sp., will spread the modules of each genotype throughout a large total thallus size and may, accordingly, reduce the risk of genotypic extinction. In addition, the rapid increase in size produced by crust fusion may increase competitive capacity for space, reduce sensitivity to herbivores and perhaps speed the onset of sexual maturity, similar to the size-dependent reproduction observed in *C. bursa* (Olivi) C. Agardh (Vidondo & Duarte 1998). Equivalent fitness benefits, along with enhanced genetic variability and possible developmental synergism within the chimera, have been documented both in sessile colonial invertebrates (Buss 1982; Rinkevich & Weissman 1992; Grosberg & Strathmann 1998) and in red seaweeds (Santelices *et al.* 1999, 2003a, b, 2004; Morley *et al.* 2003; Shaughnessy 2004).

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