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CONVERGENT BIOLOGICAL PROCESSES IN COALESCING RHODOPHYTA[1]

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Sporeling coalescence in *Gracilaria chilensis* Bird, McLachlan et Oliveira produces genetically polymorphic, chimeric individuals. If this is common in red algae, it may have significant biological consequences. In this study, we evaluate the hypotheses that coalescence is widespread among the Rhodophyta and that specific and convergent morphological and ecological responses characterize this as a unique growth style among marine algae. A literature survey on coalescence was undertaken to assess the distribution of this condition in the Florideophycidae. Sixty-two (54.9%) of 113 species considered germinated to form a disk. Subsequent development in 37 of these species showed crust formation and coalescence during development with other crusts in 31 species (84%). Coalescing red algae were members of the orders Ahnfeltiales, Corallinales, Gigartinales, Gracilariales, Halymeniales, Palmariales, and Rhodymeniales. Ultrastructural studies in species of *Ahnfeltiopsis*, *Chondrus*, *Gracilaria*, *Mazzaella*, and *Sarcothalia* suggested a common pattern of early development. Newly released, naked spores may fuse into a single cell, as they do in *Chondrus canaliculatus*, or they may develop individual cell walls that later are surrounded by a thickened common wall. Ultrastructural studies demonstrated two kinds of immediate development after the first mitotic division: direct development by symmetric divisions resulting in discoid sporelings or an indirect asymmetric arrangement of divisions before a diskoid sporeling was formed. Germination in coalescing species is a linear function of the initial spore density, whereas in noncoalescing species maximum germination occurs at intermediate densities. In the field, coalescing species may recruit either from solitary or aggregated spores. However, survival is significantly higher for plantlets grown from a larger number of coalescing spores. Total number of erect axes formed by the coalesced mass is a logarithmic function of the initial number of spores. Thus, germlings grown from a larger number of coalescing spores exhibited a larger photosynthetic canopy than do plantlets grown from a few spores. Juveniles and mature clumps grown from a coalescing mass may exhibit size inequalities among erect axes, with the larger axes located toward the center of the clump. These larger axes mature first or, in some cases, are the only to produce spores. The widespread occurrence of coalescence in roughly half the number of orders of the Florideophycidae, the similarity of the coalescence process, and the finding of various adaptive traits associated with coalescence characterizes this as a unique growth style, splitting the diversity of species now included in the Florideophycidae into two major groups: coalescing and noncoalescing Rhodophyta.

Key index words: ***Ahnfeltiopsis*; chimeric individuals; *Chondrus*; coalescing Rhodophyta; *Gracilaria*; *Mazzaella*; *Sarcothalia*; sporeling coalescence**

The capacity of some red algal sporelings to grow together to form a completely coalesced mass has been known since Rosenvinge's (1931) and Jones's (1956) pioneering observations on *Gigartina* and *Gracilaria*. Despite its potential importance, most of the few studies examining the process are low-resolution descriptions of coalescence among grown crusts. Only in recent years (e.g. Maggs and Cheney 1990, Muñoz and Santelices 1994) has coalescence been examined experimentally and with techniques of greater resolution.

Using *Gracilaria chilensis* as a biological model, Santelices et al. (1996) described a unique and distinctive growth pattern associated with coalescence. Settling carpospores first germinated and divided to form a disklike crust. When neighboring germlings grew close enough to one another, contacting cells from adjacent sporelings fused, establishing secondary pit connections between adjacent cells. Despite these fusions and connections, most of the original crusts maintained an independent capacity to produce upright axes within the coalesced mass. Thus, when the fusion process between compatible partners occurred, there was no evidence at the light microscopic level that the new thallus was, in fact, the product of two or more different spores and thus a genetically polymorphic, chimeric organism.

If the previously described growth pattern was to be representative of the red algae, it would have profound biological implications. Most predictions about the ecological and evolutionary responses of seaweeds are based on models of unitary organisms, predictions that would not necessarily apply to a chimeric-type organization (for a review, see Santelices 1999). For example, selection processes and evolutionary rates are expected to differ among unitary, clonal, and chimeric organisms (Tuomi and Vuorisalo 1989, Gill et al. 1995, Fagerström et al. 1998) because their respective units of selection differ.

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Further, if individuality cannot be defined, various concepts on demography, population genetics, and competition cannot be properly applied to these seaweeds. On the other hand, other nonconventional traits associated to coalescence can be expected. In the case of *Gracilaria chilensis,* sporeling coalescence increased genetic polymorphism, morphological variation, and phenotypic plasticity (Santelices et al. 1996), all traits considered to increase survival in heterogeneous environments.

Coalescence has been described in species of several red algal orders (Maggs and Cheney 1990, Santelices et al. 1996), but existing information is too fragmentary to assume that coalescence is widespread among all kinds of red algae. Similarly, even though several adaptive traits have been suggested for coalescing crusts (Jones 1956, Maggs and Cheney 1990), few have been quantified, and none has been compared with equivalent responses in noncoalescing Rhodophyta to evaluate the adaptive value of those responses. In this study, we evaluate the hypothesis that coalescence is widespread among the Rhodophyta and that specific and convergent morphological and ecological responses characterize this as a unique growth style among the seaweeds.

MATERIALS AND METHODS

Coalescence among Rhodophyta. Coalescence is here understood as the fusion and growth of two or more spores or their derivatives in such a way that the resulting individual responds as a discrete entity and some of the original cell lines no longer retain their morphological or anatomical individuality. To evaluate whether this is a widespread process among red algal species, a literature survey on their germination and growth patterns was undertaken, reviewing about 100 studies published in leading phycological journals over the last 25 years. Most of these studies did not address the question of coalescence in particular. Thus, this literature survey is an unbiased sample of what researchers found without any previous hypothesis (presence or absence of coalescence). Species within the subclass Bangiophycidae were not considered in the survey because of their different morphological organization and life histories. Descriptions and illustrations of germination, early sporeling growth, coalescence, and further analysis of tissue or cellular interactions among growing sporelings were used to separate species within the Florideophycidae. Species were then arranged in orders following the classification scheme proposed by Saunders and Kraft (1997).

Ultrastructure of spores and coalescing germlings. Ultrastructural studies were undertaken to evaluate whether the cytological and morphological processes involved in sporeling coalescence are similar among different red algal taxa. The species considered were *Ahnfeltiopsis durvillaei* (Bory) Silva et DeCew, *A. furcellata* (C. Agardh) Silva et DeCew, *Chondrus canaliculatus* (C. Agardh) Greville, *Mazzaella laminarioides* (Bory) Fredericq, and *Sarcothalia crispata* (Bory) Leister, all in the order Gigartinales.

Characterization of the process of coalescence at the cellular level followed the methods already described for *Gracilaria chilensis* (Santelices et al. 1996). Fertile cystocarpic thalli of the previously mentioned five species were collected at various places in central Chile (Table 1) and transported within 3 to 6 h to the laboratory in coolers maintained at 4° C. Spore release was stimulated by air drying of fragments of cystocarpic tissues, previously rinsed in a series of tap water and autoclaved seawater. During spore release, fragments were transferred to 60 × 10-mm glass petri dishes with SFC culture medium (Correa et al. 1988) and incubated at 15° C at 40 μmol photons·m^{-2}·$^{-1}$ and a 12:12 h LD (light:dark) photoperiod. To study carpospores and sporelings (tetrasporophytes) consisting of up to about 10 cells, spores from the release dishes were pipetted into 0.8-mL plastic BEEMs capsules containing fresh SFC culture medium. For studying older sporelings, fragments of mature tissue used for spore release were removed from the glass petri dishes, leaving the spores to settle and complete development and coalescence. Growth conditions for sporelings in the petri dishes were the same as for those in the BEEMs, although in the former, culture medium was changed twice a week. All tissue and culture manipulations were done in a laminar flow hood, and material used was autoclaved. The various stages of sporeling development included in this study are the result of incubations lasting no longer than 30 days.

Freshly released spores and the subsequent stages of development were fixed for ultrastructural analysis. Spore fixation in the glutaraldehyde–acrolein mixture in SFC culture medium, followed by postfixation in an osmium–potassium ferricyanide mixture, followed the protocol described elsewhere (Santelices et al. 1996). Sporelings were fixed at room temperature in 5% glutaraldehyde and 3% acrolein in SFC culture medium for 3 h under vacuum. A longer fixation protocol was tried for older sporelings, consisting of 3 days at 5° C, with daily changes of the fixative solution. Dehydration, embedding, and infiltration were standard (see Santelices et al. 1996). Thin sections were stained with 4% uranyl acetate and lead citrate according to Reynolds (1963) and were observed with a JEOL 100SX electron microscope operated at 60 kV.

Ecological studies. Ecological studies included comparing solitary versus aggregated recruitment in coalescing and noncoalescing red algal species, assessment of germination in the laboratory, evaluation of field and laboratory survival, laboratory growth as a function of the initial number of spores, and measurement of the spatial distribution of reproductive fronds within individual clumps. Methodological details of each one of these studies are given in the following.

Germination as a function of initial number of spores. These experiments were done using the coalescing species *Chondrus canaliculatus, Gracilaria chilensis, Mazzaella laminarioides,* and *Sarcothalia crispata.* Noncoalescing, control species were *Ceramium rubrum, Gelidium lingulatum, Laurencia chilensis,* and *Polysiphonia scopulorum.* Experimental thalli were generally collected at the same study sites used in the field recruitment experiments (Table 1) and transported to the laboratory as described previously. Once in the laboratory, thalli were washed with running tap water and maintained for 24 h in filtered seawater under constant temperature (14° ± 2° C), irradiance (20 ± 10 μmol photons·m^{-2}·s^{-1}), and photoperiod (12:12 LD). Sporulation was induced by immersing mature cystocarps in microfiltered seawater (0.45 μm). These cystocarps were dehydrated for 24 h at room temperature prior to inducing sporulation.

Carpospores released by the experimental cystocarps were incubated in holes (1.8-mm diameter, 250–300 μm deep) drilled in glass microscope slides. The number of carpospores in each hole varied from 1 to 45. Treatments with fewer than 20 carpospores sown together had four replicas. The number of spores shed from the same cystocarp was limiting for treatments with a larger number of spores; thus, they included only one or two replicates. Because germination was to be measured as a function of initial number of spores (e.g. regression analysis), this lack of replicability did not affect the statistical analysis of the experiment.

All slides were incubated in individual petri dishes (50 × 10 mm), filled with SWM-3 culture medium (McLachlan 1973), and maintained under standard culture conditions. Germination was measured after 72 h of incubation.

Aggregated versus solitary recruitment. The relative importance of aggregated and solitary recruitment was measured in circular, 6.0-cm-diameter, 0.2-cm-thick, previously detoxified (Brawley and Johnson 1991) epoxy resin (Sea Goin Poxy Putty). Three coalescing species—(*Gracilaria chilensis, Mazzaella laminarioides,* and *Sarcothalia crispata*)—were investigated. The latter two species form permanent intertidal belts in wave-exposed habitats in central Chile (Santelices 1990b), whereas *G. chilensis* forms extensive

TABLE 1. Sampling and experimental sites and dates, laboratory cultivation, and experimental time used in the various studies with coalescing and noncoalescing seaweeds.

1. Electron microscopy studies on germination and coalescence. Algae were obtained in the field and cultivated under constant laboratory conditions (40–50 μmol·m^{-2}·s^{-1}; 12:12 L:D; 14° ± 1°C).

Species	Locality	Collection date	Germination time (h)	Cultivation time for transmission electron microscopy studies (d)
Ahnfeltiopsis furcellata	Matanza (33°58′ S; 71°54′ W)	July 1997	0–72	30
Ahnfeltiopsis durvillaei	Matanza	July 1997	0–24	30
Chondrus canaliculatus	Coquimbo (29°57′ S; 71°22′ W)	January 1997	0–48	15
Mazzaella laminarioides	Matanza	May 1996	0–72	40
Sarcothalia crispata	Matanza	July 1996	0–24	30

2. Field experiments on aggregated versus solitary recruitment and survival.

Species	Locality	Date of incubation	Field incubation (d)	Date of second incubation	Extent of second incubation (d)
Gracilaria chilensis	Maullín (41°36′ S; 73°36′ W)	January 1996	10	March 1996	30
Mazzaella laminarioides	Matanza	June 1996	32	July 1996	20
Sarcothalia crispata	Montemar (32°59′ S; 71°34′ W)	February 1997	19	March 1997	22
Ceramium rubrum	Pelancura (33°34′ S; 71°37′ W)	July 1998	12		
Gelidium lingulatum	Pelancura	July 1998	12		
Laurencia chilensis	Pelancura	August 1998	14		
Polysiphonia scopulorum	Pelancura	August 1998	14		

3. Laboratory experiments on germination, survival, and growth (culture conditions as in part 1).

Species	Collecting site	Collecting date	Germination time (d)	Duration of laboratory growth (w)
Chondrus canaliculatus	Coquimbo	April 1998	7	30
Gracilaria chilensis	Maullín	July 1995	7	72
Mazzaella laminarioides	Matanza	September 1995	7	40
Sarcothalia crispata	Pelancura	June 1998	7	30
Ceramium rubrum	Pelancura	March 1998	7	
Gelidium lingulatum	Pelancura	February 1998	7	
Laurencia chilensis	Pelancura	June 1998	20	
Polysiphonia scopulorum	Pelancura	March 1997	7	

4. Spatial distribution of reproductive fronds.

A. Field samples.

Species	Karyological phase	Collecting place	Collection date	Samples (*n*)
Chondrus canaliculatus	Fertile cystocarpic	Coquimbo	October 1998	10
Chondrus canaliculatus	Fertile tetrasporic	Coquimbo	October 1998	10
Gracilaria chilensis	Fertile tetrasporic	Maullín	July 1996	10
Mazzaella laminarioides	Fertile cystocarpic	Maullín	September 1998	10
Sarcothalia crispata	Fertile cystocarpic	Maullín	October 1998	10
Sarcothalia crispata	Fertile tetrasporic	Maullín	October 1998	10

B. Cultures (laboratory conditions as in part 1).

Species	Karyological phase	Incubation time (w)	Samples
Chondrus canaliculatus	Tetrasporic	27	18
Gracilaria chilensis	Tetrasporic	72	7
Mazzaella laminarioides	Gametophytic	27	9
Sarcothalia crispata	Tetrasporic	19	18

monocrops in sheltered sandy bottoms of southern Chile (Santelices and Doty 1989). Three noncoalescing species—*Gelidium lingulatum, Ceramium rubrum,* and *Polysiphonia scopulorum*—were used as controls. These species also form distinctive permanent *(G. lingulatum)* or temporal (*C. rubrum, P. scopulorum*) belts in wave-exposed rocky intertidal habitats in central Chile.

A total of 42 plates were used to determine recruitment in each vegetational belt. Dates and locations where these experiments were undertaken are given in Table 1. At each site, six replicate plates were placed at each of three vertical levels (upper, medium, and lower) of the belt and at two vertical distances (25 and 50 cm) from above and below the belt. After 15 days in the field, plates were removed and transported to the laboratory (2–4 h) within individual petri dishes with filtered seawater maintained at 15° C in refrigerated coolers.

In the laboratory, plates were kept in a marine aquarium with circulating water set at 14° ± 2° C at 60 μmol photons·m^{-2}·s^{-1} and 12:12 h LD of daily light. Within 48 h, all plates were examined; those with recruits were sampled and photographed.

Experiments on *Gracilaria chilensis* recruitment were done at Maullín River, close to the city of Puerto Montt in southern Chile. At this site, *Gracilaria* beds extend over sandy and muddy bottoms,

TABLE 2. Taxa in the Rhodophyta with discoid germination, post-germination formation of crusts, and coalescence of neighboring crusts. Secondary pit connections have been reported for coalescing germlings of *Ahnfeltiopsis devoniensis, Chondrus crispus, Mastocarpus stellatus, Gloiosiphonia capillaris,* and *Pikea californica* (Gigartinales); *Gracilaria chilensis* (Gracilariales); and *Rhodophysema elegans* (Palmariales).

Order	Discoidal germling	Crust formation	Coalescence described or illustrated	References
Ahnfeltiales	*Ahnfeltia plicata*	*A. plicata*	*A. plicata*	16, 39
Corallinales		*Corallina officinalis*	*C. officinalis*	11
	Fosliella paschalis			36
	Hydrolithon cymodoceae			51
	Hydrolithon pellire			55
	Jania rubens	*J. rubens*		11
		Pneophyllum confervicola (as *Melobesia minulata*)		11
	Titanoderma pustulatum (as *Dermatolithon litorale*)	*T. pustulatum*	*T. pustulatum*	28
Gigartinales	*Agardhiella subulata*			57
		Ahnfeltiopsis sp.		52
	Ahnfeltiopsis devoniensis (as *Gymnogongrus devoniensis*)	*A. devoniensis*	*A. devoniensis*	42, 50
	Ahnfeltiopsis leptophyllus (as *Gymnogongrus leptophyllus*)	*A. leptophyllus*	*A. leptophyllus*	26
	Ahnfeltiopsis linearis (as *Gymnogongrus linearis*)	*A. linearis*	*A. linearis*	26
	Ahneltiopsis triquetrifolia			66
	Callophyllis firma		*C. firma*	7
	Callophyllis sp.			13
	Chondracanthus teedii (as *Gigartina teedii*)			30
	Chondrus crispus		*C. crispus*	15, 24, 44
	Chondrus nipponicus		*C. nipponicus*	45
	Chondrus ocellatus			53
	Dudresnaya sp.			7
	Dumontia contorta	*D. contorta*		31, 42
	Erithrodermis traillii (as *E. allenii*)		*E. traillii*	38
		Gloiosiphonia capillaris	*G. capillaris*	3, 44
	Gloiosiphonia verticillaris	*G. verticillaris*	*G. verticillaris*	25
		Gymnogongrus? patens	*G.? patens*	44
		Gymnogongrus crenulatus		42
	Gymnogongrus dilatatus		*G. dilatatus*	41
	Gymnogongrus griffithsiae	*G. griffithsiae*		61
	Gymnogongrus linearis	*G. linearis*	*G. linearis*	26
	Haematocelis sp.	*Haematocelis* sp.	*Haematocelis* sp.	47
	Itonoa marginifera			58
	Meredithia microphylla			42
	Mastocarpus jardinii (as *Gigartina agardhii* or *Petrocelis franciscana*)	*M. jardinii*	*M. jardinii*	9, 20, 21
	Mastocarpus papillatus (as *Gigartina* or *Mastocarpus*)	*M. papillatus*	*M. papillatus*	18, 35
		Mastocarpus sp.		42
	Mastocarpus stellatus (as *Gigartina* or *Mastocarpus*)	*M. stellatus*	*M. stellatus*	12, 15, 29, 44
	Neurocaulon grandifolium			10
	Opuntiella californica	*O. californica*	*O. californica*	48
	Petrocelis cruenta	*P. cruenta*		19, 29
	Phyllophora traillii		*P. traillii*	44
	Pikea californica	*P. californica*	*P. californica*	5, 6, 60
	Platoma abbottiana			17
	Predaea kraftiana	*P. kraftiana*	*P. kraftiana*	40
	Schizymenia pacifica	*S. pacifica*	*S. pacifica*	47
		Schizymenia sp.		42
	Schmitzia hiscockiana	*S. hiscockiana*		33, 43
	Thuretellopsis peggiana			4, 6
	Turnerella pennyi	*T. pennyi*		8
Gracilariales	*Gracilaria chilensis*		*G. chilensis*	56, 63
	Gracilaria dendroides			32
			Gracilaria verrucosa	1

TABLE 2. Continued.

Order	Discoidal germling	Crust formation	Coalescence described or illustrated	References
Halymeniales	*Dermocorynus montagnei*	*D. montagnei*	*D. montagnei*	27
	Grateloupia doryphora			49, 65
		Sebdenia dichotoma		7
	Sinkoraena okamurae			64
				64
		Sinkoraena tasmaniae		
Palmariales	*Meiodiscus spetsbergensis*			46
	Palmaria palmata			20
	Rhodophysema elegans	*R. elegans*	*R. elegans*	14, 44
Rhodymeniales	*Asteronemia peltata*			59
	Botryocladia wynnei	*B. wynnei*		37
	Cenacrum subsutum			23
		Cephalocystis furcellata	*C. furcellata*	62
	Cordylecladia erecta		*C. erecta*	34
	Champia parvula			2
	Chylocladia verticillata			2
	Gastroclonium ovatum			2
	Lomentaria articulata			2
	Lomentaria clavellosa			2
	Lomentaria orcadensis			2
	Minium parvum	*M. parvum*	*M. parvum*	22
	Semnocarpa minuta	*S. minuta*		54

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ranging from 2 to 8 m in depth (Westermeier et al. 1991). Plates were placed on previously anchored wooden sticks at 20 and 60 cm above the soft bottom. Groups of six replicate plates were placed at the center of the bed (3.5 m deep), in the shallower border (2 m deep), and at distances 0.5, 1, and 2 m away from the shallower border (1.8, 1.5, and 1.2 m deep, respectively). After 15 days of exposure, the 60 plates were collected and flown to the laboratory in Santiago.

Spores were counted on each plate under 40× magnification in 16 randomly selected fields. Recording included spore abundance per unit surface area and number of spores composing each recruitment mass. Because the total surface area of the 16 ocular fields was 1 cm^2, results were expressed as total number of spores·cm^{-2}.

Once spores had been counted, 10 plates with good recruitment were selected to measure field survival of aggregated and nonaggregated recruits (see the following discussion). All the other plates were incubated for up to 3 months under the previously described laboratory conditions to confirm the taxonomic identity of the recruits. Results from plates with taxonomic misidentifications were eliminated from the final analysis.

Aggregated versus solitary survival. The laboratory cultures used to measure germination as a function of initial number of spores were maintained to compare aggregated versus solitary survival in the laboratory. Plates were incubated under the previously described controlled conditions and cultures monitored at 3-day intervals during the first 2 weeks. Thereafter, monitoring of growth and changes of culture medium (SWM-3 + 6 μg L^{-1} GeO_2) was performed weekly. Survival was measured after 4 weeks in culture.

Field survival was measured using 10 poxy–putty plates with good recruitment, and a system was designed to ensure that the same recruit was measured at two different times under 40× magnification. First, a 0.5-mm-thick Paraplast (Merck) layer was prepared at the bottom of a 15-cm-wide, 1.7-cm-deep petri dish. In the center of the Paraplast layer, a 6-cm-diameter circular cavity was excavated to fix the recruitment plate. Both the Paraplast layer and the plates were marked with four points (one per quarter) to ensure being able to locate the plate again in the same position. A quadrat with a 1-cm^2 grid was drawn in a 6-cm-diameter circular transparent acetate, also marked at the corresponding four points. A random subsample of six 1-cm^2 cells were chosen from each plate. Under a stereomicroscope, the entire 1-cm^2 cell was examined and photographed under 40× magnification (16 ocular fields). Photographic recording followed an orderly pattern (left to right, top to bottom), and the photograph of each ocular field was numbered. Recorded information of each microscopic field included the number of propagules, the area covered, and the number of spores composing each sporeling.

Plates were returned to the field after being photographed and maintained there for 30 to 45 days. They were then recovered, measured, and photographed again. Almost half the plates used for each species were lost in the field, yielding a final number of replicates of four to five. Survival (for unisporic vs. aggregated recruits) was calculated from the differences in number of recruits found in each ocular field after field exposure. Relative survival and growth rates between aggregated and nonaggregated recruits for each species were compared using Student's *t*-test after data transformation (arcsine transformation). After data re-

cording, plates were incubated under the previously described laboratory conditions to confirm the taxonomic identity of the recruits.

Growth as function of initial number of spores. The laboratory cultures used to measure germination and survival as a function of initial number of spore were maintained to measure growth. The total duration of the experiment ranged from 15 to 72 weeks, depending on when the plantlets became reproductive or when the fronds of most of the clumps became clearly heterogeneous in size.

Depending on the size reached by the plantlets, between the 10th and the 14th week of growth, coverslips with their thalli were transferred to aerated 250-mL flasks, each containing 200 mL of SWM-3 culture medium. Other abiotic conditions were maintained as previously described, including weekly changes of culture medium.

Between weeks 3 and 7, sporeling masses were large enough to be distinguished, and the emerging erect shoots could be counted. Elongation rates and the number of lateral branches produced by the erect shoots were measured every week between weeks 3 and 10 as described by Muñoz and Santelices (1994). Data on growth patterns as functions of the original number of spores were analyzed using regression and covariance analyses.

Spatial distribution of reproductive fronds. Spatial distribution of size inequalities was measured, following Martínez and Santelices (1992), in laboratory-cultivated and wild populations of *Chondrus canaliculatus, Gracilaria chilensis, Mazzaella laminarioides,* and *Sarcothalia crispata.* The laboratory-cultivated populations were tetrasporophytes surviving from the germination and growth experiments explained previously. Some of these sporophytes became fertile under laboratory conditions.

Wild clumps were collected at the same sites as those used for the field recruitment studies (Table 1). Each clump, including its holdfast, was carefully removed with the help of steel spatulas, placed in an individual plastic bag, and transported to the laboratory.

To measure the size distribution of fronds within the plant, a transect along the basal disk of each clump was established. With the exception of *Gracilaria chilensis,* the frond height and the position of each frond along the transect were recorded. In *G. chilensis,* stipe diameter was used rather than frond height because mature plants had suffered wave-induced tip losses. Position was defined as the distance of any individual frond to one end of the disk. To undertake a standardized analysis of all transects, frond or stipe diameter or height (± 0.01 cm) was expressed as the relative height (%) with respect to the longest frond or widest stipe (100%) of each transect. Their relative position and distance (± 0.01 cm) were also expressed as a percentage from one end of the transect (0%) to the other. The ordering of frond size distribution within clumps was tested using the nonparametric Jonckheere test (Siegel and Castellan 1988). This test contrasts the trend of an increase in values toward a certain direction of sampling (frond heights toward the center of basal coalescing disks in this case) with a null hypothesis of no trend at all.

RESULTS

Coalescence among Rhodophyta

Sixty-one of the 113 species included in the survey (54.9%), germinate by forming a disk (Table 2). Subsequent developmental stages have been studied in 37 of these 61 species. In all of them, the germinating disk grew into a crust, and in 31 of these species (83.8%) coalescence with conspecific crusts has been described or illustrated. These coalescing red algal species belong to the orders Ahnfeltiales, Corallinales, Gigartinales, Gracilariales, Halymeniales, Palmariales, and Rhodymeniales (Table 2). Higher-resolution studies on seven of these species (Table 2) have documented the establishment of secondary pit connections among coalescing crusts. Formation of erect axes, when found, occurs in both coalescing and noncoalescing crusts.

Fifty-one (45.1%) of the 113 species considered in the survey do not coalesce during or after germination (Table 3). Different species among these noncoalescing taxa may exhibit different types of germination and development, which appear in the literature with specific names (e.g. as *Nemalion* type, *Gelidium* type, and bipolar type). However, the differentiation of one or several apical cells early in development is common to all these species. No description or illustration of coalescence was found among these species, even when algae were cultivated at high spore densities.

Noncoalescing species of Rhodophyta (Table 3) have been reported from eight orders within the Florideophycidae. Members within the Acrochaetiales, Nemaliales, Batrochospermales, and Rhodogorgonales all exhibit *Nemalion*-type germination. Members of Bonnemaisoniales and Gelidiales exhibit the *Naccaria*-type and the *Gelidium*-type germination, whereas all members of the Ceramiales included in Table 3 show bipolar-type germination.

With the exception of the Gigartinales, all other orders of the Florideophycidae included in Tables 2 and 3 contain only coalescing or noncoalescing species. In the case of the Gigartinales, a vast majority of the taxa studied so far (33 species; Table 2) are coalescing species. The exceptions are a parasitic taxon (*Dawsionocolax bostrychiae*) and a species of uncertain familial position (*Hummbrella hydra;* Hawkes and Johnson 1981).

Ultrastructure of Spores and Coalescing Germlings

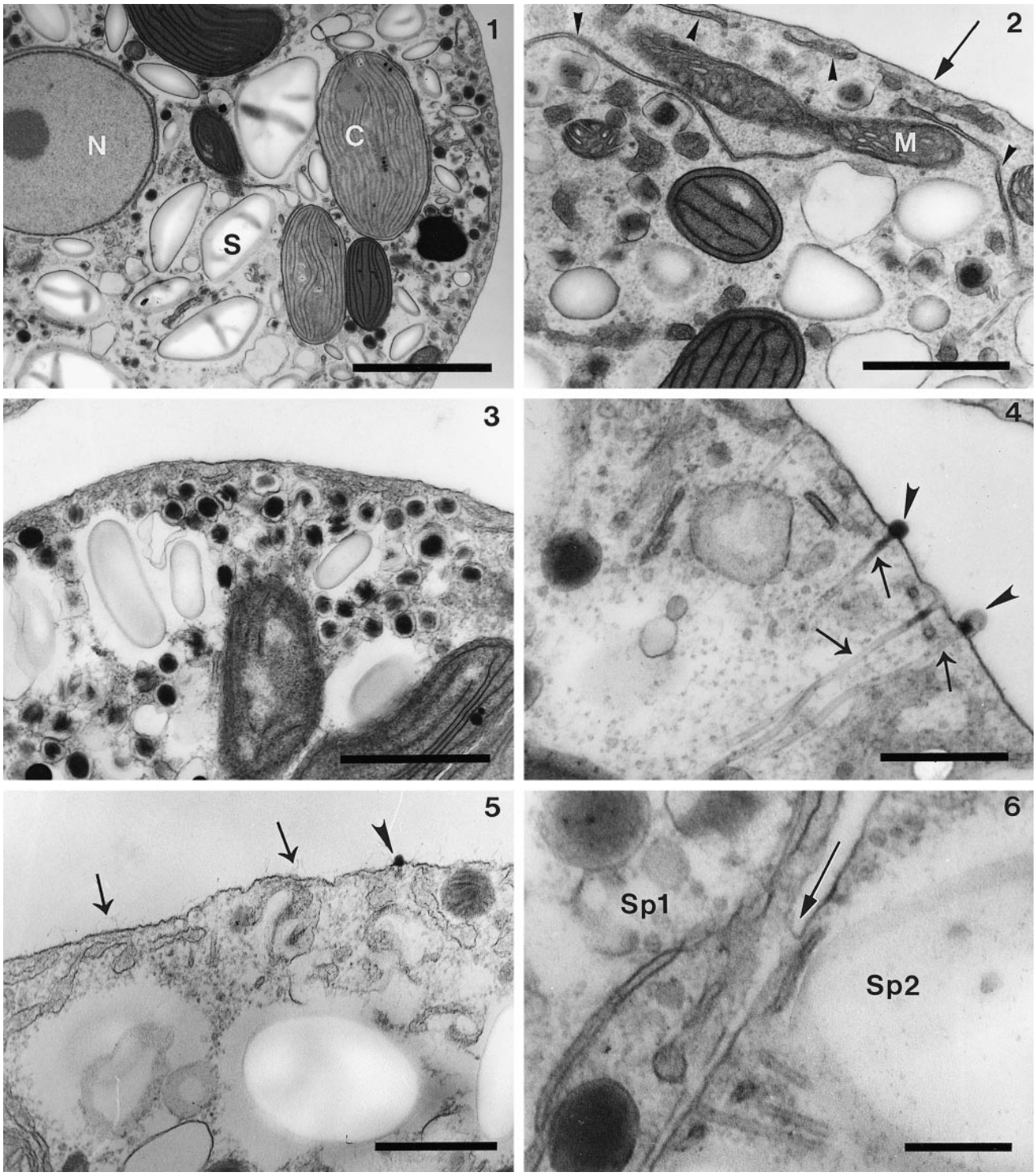
Observations of spores fixed 1 to 2 h after release indicate a similar developmental pattern for all five species studied. Thus, a general description applying to these five species follows. Recently released spores were naked, and the single nucleus was centrally located and surrounded by several lobes of the plastid (Fig. 1). Starch granules of various sizes and shapes were found, especially in a perinuclear position, where they caused irregularities in the nuclear envelope. No vacuole was found at this stage. Numerous vesicles with electron-opaque, compacted to fibrillar material appeared in close association with the plasma membrane (Figs. 2, 3). In spores of *Chondrus canaliculatus* (Fig. 4) and *Ahnfeltiopsis durvillaei* (Fig. 5), small amounts of fibrillar material were associated with the external side of the plasmalemma, from a few hours to 24 to 48 h after release from the cystocarps. Spore fusion, although of rare occurrence, was documented in *C. canaliculatus.* Spores that established physical contact immediately after release underwent plasmogamy (Fig. 6).

At the first mitosis (Fig. 7), the spore cell wall had two well-defined components: a thin inner layer surrounding each of the daughter cells and a less well defined outer layer surrounding the entire spore-

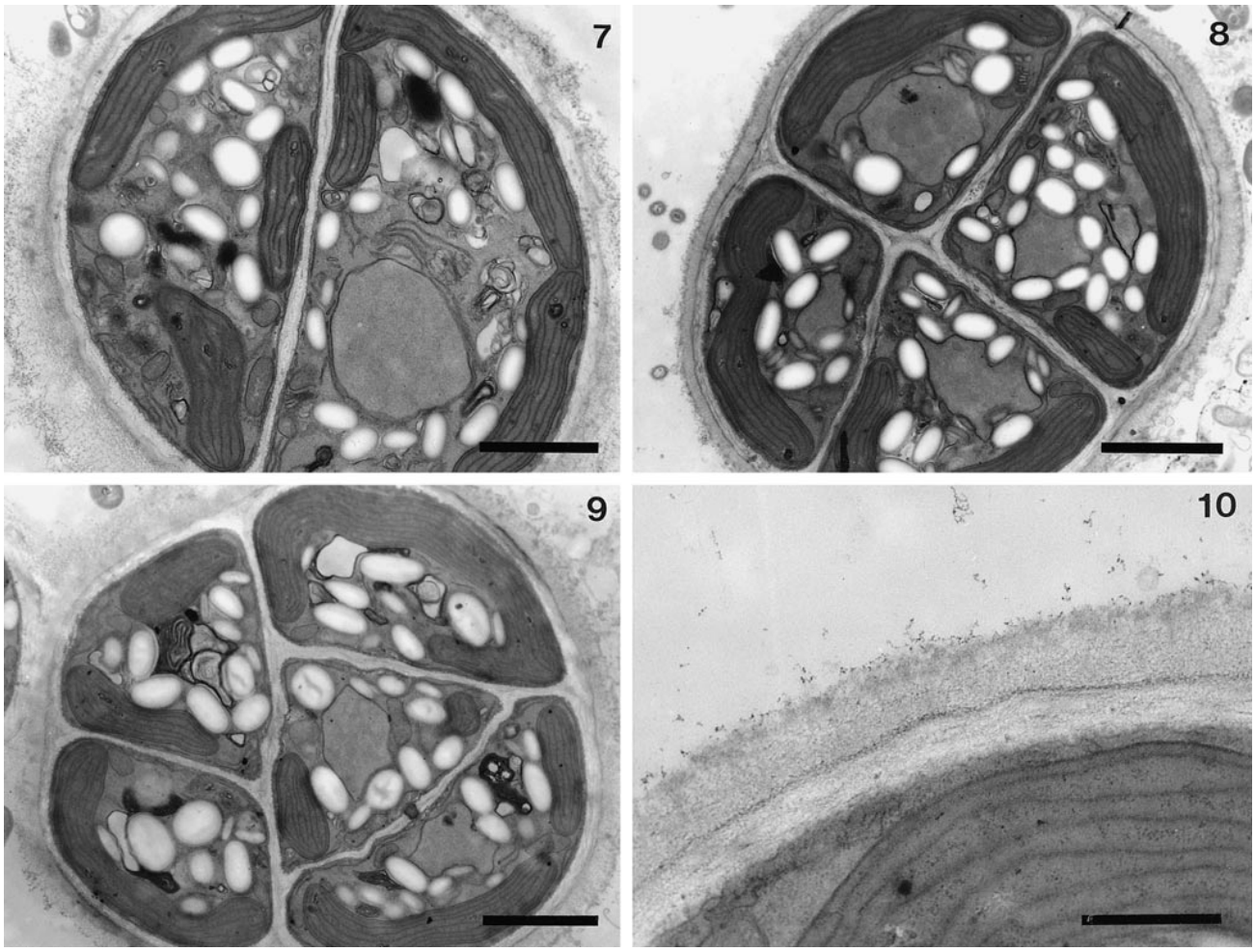
TABLE 3. Taxa in Rhodophyta that do not form crusts or coalesce.

Order	Genera and species	Germination	References
Acrochaetiales	*Acrochaetium asparagopsis*	*Nemalion*-type	5
	Acrochaetium bonnemaisoniae (as *Colaconema*)	*Nemalion*-type	1
	Acrochaetium chylocladiae	*Nemalion*-type	1
	Acrochaetium coespitosum	*Nemalion*-type	1
	Acrochaetium endophyticum	*Nemalion*-type	5
	Acrochaetium infestans	*Nemalion*-type	5
	Acrochaetium thuretii	*Nemalion*-type	1
	Rhododraparnaldia oregonica	*Nemalion*-type	30
Batrachospermales	*Batrachospermum breutelii*	Bipolar-type	31
	Batrachospermum carpocontortum	Bipolar-type	15
	Batrachospermum heterocoricum	*Nemalion*-type	25
Bonnemaisoniales	*Bonnemaisonia asparagoides*	*Naccaria*-type	1
	Bonnemaisonia geniculata	*Naccaria*-type	9
	Bonnemaisonia nootkana	*Naccaria*-type	3
	Naccaria wiggii	*Naccaria*-type	1, 35
Ceramiales	*Aglaothamnion herveyi*	Bipolar-type	29
	Aglaothamnion priceanum	Bipolar-type	26
	Anisoschizus propaguli	Bipolar-type	13
	Bostrychia bispora	Bipolar-type	28
	Callithamnion baileyi	Bipolar-type	11
	Caloglossa leprieurii	Bipolar-type	8
	Crouania pleonospora	Bipolar-type	10
	Deucalion levringii	Bipolar-type	13, 23
	Hypoglossum rhizophorum	Bipolar-type	17
	Janczewskia morimotoi	Bipolar-type	12
	Laurencia brachyclados	Bipolar-type	24
	Laurencia nipponica	Bipolar-type	32
	Mazoyerella arachnoidea	Bipolar-type	7
	Microcladia californica	Bipolar-type	19, 20
	Microcladia coulteri	Bipolar-type	19, 20
	Monosporus australis	Bipolar-type	13
	Pterothamnion plumula (as *Antithamnion*)	Bipolar-type	6
Gelidiales	*Acanthopeltis japonica*	*Gelidium*-type	2
	Gelidiella acerosa	*Gelidium*-type	2, 8
	Gelidium latifolium	*Gelidium*-type	2
	Gelidium maggsiae	*Gelidium*-type	33
	Gelidium pulchellum	*Gelidium*-type	2
	Gelidium pusillum	*Gelidium*-type	2
	Gelidium sp.	*Gelidium*-type	1, 6
	Pterocladiella melanoidea (as *Pterocladia*)	*Gelidium*-type	21
	Pterocladiella capillacea (as *Pterocladia pyramidale*)	*Gelidium*-type	2, 6
Gigartinales	*Dawsoniocolax bostrychiae*	Bipolar-type	18
	Hummbrella hydra	Bipolar-type	14
Nemaliales	*Gloiophloea scinaioides*	*Nemalion*-type	16
	Helminthocladia calvadosii (as *H. purpurea*)	*Nemalion*-type	1
	Helminthora divaricata	*Nemalion*-type	1
	Liagora californica	*Nemalion*-type	34
	Liagora harveyana	*Nemalion*-type	22
	Nemalion sp.	*Nemalion*-type	1, 4
	Scinaia furcellata	*Nemalion*-type	1
Rhodogorgonales	*Rhodogorgon ramosissima*	*Nemalion*-type	27

References: 1. Chemin 1937. 2. Boillot 1963. 3. Chihara 1965. 4. Dawson 1966. 5. White and Boney 1969. 6. Dixon 1973. 7. Gordon-Mills and Womersley 1974. 8. Bold and Wynne 1978. 9. Shevlin and Polanshek 1978. 10. Prince 1979. 11. Whittick and West 1979. 12. Nonomura and West 1981. 13. Huisman and Kraft 1982. 14. Hawkes 1983. 15. Sheath et al. 1986. 16. Huisman 1987. 17. Ballantine and Wynne 1988. 18. West and Calumpong 1988. 19. Gonzalez and Goff 1989a. 20. Gonzalez and Goff 1989b. 21. Fredriksen and Rueness 1990. 22. Guiry 1990a. 23. Guiry 1990b. 24. McDermid 1990. 25. Sheath and Cole 1990. 26. Maggs et al. 1991. 27. Ogden 1992. 28. West et al. 1992. 29. Aponte et al. 1994. 30. Sheath et al. 1994. 31. Sheath and Whittick 1995. 32. Masuda et al. 1997. 33. Rico and Guiry 1997. 34. Hall and Murray 1998. 35. Jones and Smith 1970.



FIGS. 1–6. Ultrastructure of carpospores of coalescing Rhodophyta from the moment of release up to 4 days in culture. C = chloroplast, M = mitochondria, N = nucleus, S = starch granules. Sp 1 = spore no. 1, Sp 2 = spore no. 2. Scale bars = 3 μm (Fig. 1), 1 μm (Figs. 2, 3), 500 nm (Figs. 4, 5), and 300 nm (Fig. 6). FIG. 1. Naked spore of *Chondrus canaliculatus* at the time of release. No extracellular wall material is observed at this stage. The central nucleus appears surrounded by numerous starch granules, and the lobes of the plastid appear scattered within the cytoplasm. FIG. 2. Naked spore of *Mazzaella laminarioides* at the time of release. Plasmalemma (arrow) is associated with mitochondria, endoplasmic reticulum (arrowheads), and electron-opaque vesicles heterogeneous in texture. FIG. 3. Naked spores of *Ahnfeltiopsis furcellatus* 24 h after release. Large accumulation of electron-opaque vesicles in close proximity with the plasmalemma. In most of these vesicles, the content seems condensed, leaving a pale halo around the material. FIG. 4. Spores of *Chondrus canaliculatus* 24 h after release. Release of electron-opaque substance (arrowheads), clearly connected with microtubular structures (arrows) located perpendicular to the cell surface. FIG. 5. Spore of *Ahnfeltiopsis durvillaei* 24 h after release. Vesicles containing electron-opaque material underneath the plasmalemma have disappeared, and very thin fibrils begin to accumulate immediately outside the plasmalemma (arrows). Granules of electron-dense substance remain on the cell surface (arrowhead). FIG. 6. Closely settled spores of *Chondrus canaliculatus*. Cell fusion 4 days after release. Arrow indicates fusion of the plasmalemma.



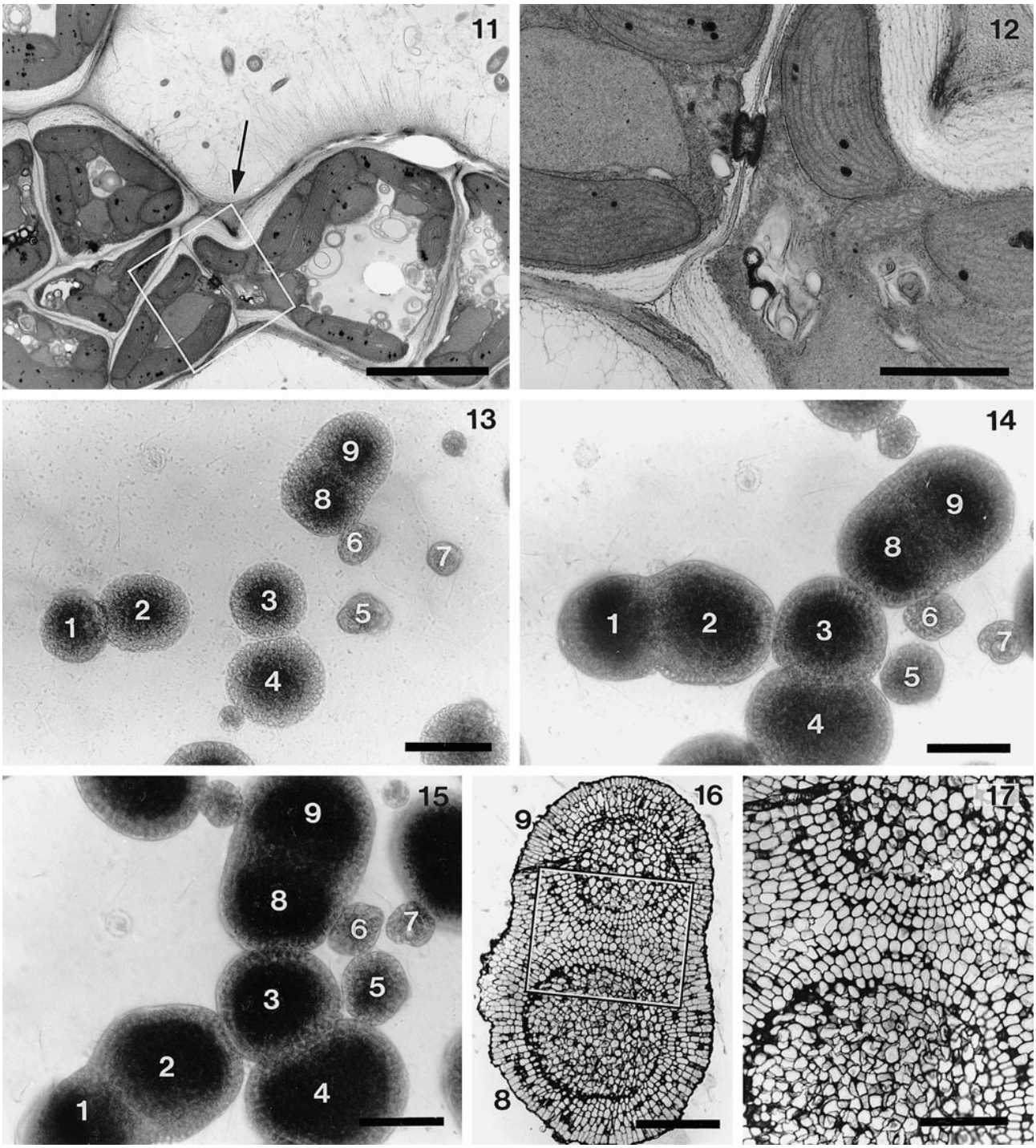
FIGS. 7–10. *Ahnfeltiopsis furcellatus*. Post-settlement development in laboratory culture. Scale bars = 3 μm (Figs. 7–9) and 500 μm (Fig. 10). FIG. 7. First mitosis in a 4-day-old sporeling. Immediate cell wall forms a pale septum dividing the two daughter cells and extends around the external face of each. This immediate cell wall is thin and surrounded by a thicker, fibrous external cell wall. Plastids have migrated toward the periphery and appear with clearly distinguishable thylakoids. Starch granules are less numerous, and the vacuole is still not apparent. FIGS. 8, 9. Second and third mitosis in a 4-day-old sporeling. Cell division is not accompanied by enlargement, and the resulting daughter cells are small. FIG. 10. Close-up of the two-layer outer cell wall of a 4-day-old sporeling. The fibrillar inner layer or immediate cell wall remains surrounded by a finely granular outer layer.

ling. The interface between the two layers was thin and condensed. The diameter of the two-celled embryo was similar to the diameter of the original spore.

Ultrastructure of individual cells within each sporeling exhibited only minor changes during the following divisions (Figs. 7–9). Starch grains tended to diminish, with the nucleus remaining at the center of the cell and the plastid adopting a parietal position just beneath the plasmalemma. The large number of small vesicles with fibrillar or compacted electron-opaque material, which were quite abundant in the spores after release, were no longer detected in cells of sporelings. Subsequent stages of embryonic development did not significantly modify the cell wall (Fig. 10). Thus, from very early in development, sporeling cells of the studied species appeared surrounded by a complex cell wall.

Two different patterns of early development were detected following the first mitosis. One was observed in *Mazzaella laminarioides* and *Sarcothalia crispata*. It consisted of more or less symmetric divisions that resulted in diskoid sporelings. The second pattern was observed in a few cases in *Ahnfeltiopsis durvillaei, A. furcellatus,* and *Chondrus canaliculatus*. It was characterized by asymmetric divisions that resulted in sporelings of various shapes. However, a typical diskoid crust developed afterward in these species.

The extent of coalescence at these early developmental stages varied from one species to another. In *Ahnfeltiopsis durvillaei,* complete coalescence, including the establishment of secondary pit plugs, was observed at day 4, when sporelings were less than 10 cells in size (Figs. 11, 12). In *Ahnfeltiopsis furcellatus,* coalescence was detected at sizes smaller than 10 cells but sporelings were older (day 13) than in *A. durvillaei*.



FIGS. 11–17. Coalescence after postsettlement. Scale bars = 4 μm (Fig. 11), 1 μm (Fig. 12), 100 μm (Figs. 13–16), and 50 μm (Fig. 17). FIG. 11. Coalescence between six-celled and two-celled sporelings of *Ahnfeltiopsis furcellatus*. Total fusion of the outer cell wall and a pit plug between contacting cells (insert below the arrow) is observed. FIG. 12. Close-up of the interface between the two coalescing sporelings of *A. furcellatus* showing the pit plug. FIGS. 13–15. Sequence of coalescence in *Sarcothalia crispata*. The same individuals (numbered 1–9) were recorded at 13 days (Fig. 13), 18 days (Fig. 14), and 20 days (Fig. 15). FIG. 16. Section parallel to the substratum through the product of coalescence of two initially separated sporelings after 30 days in culture. FIG. 17. Close-up of the insert in Figure 16 showing complete compatibility between the tissues of the two coalescing sporelings.

Coalescence in older (2–4-week) sporelings was observed in all the species included in this study. At this stage, sporelings were diskoid crusts and maintained a radial symmetry if no other embryo was nearby. Serial observations (Figs. 13–15) indicated that neighboring crusts completed fusion within 5 to 7 days after contact. Coalesced sporelings, 18 to 30 days old, looked like the number 8. They were formed by two groups of small cells surrounded by a common external tissue formed by larger and radially oriented cells (Fig. 16). A single outer cell wall encircled the 8-like sporelings. At this stage, no evidence indicating that tissues were of different embryological origin was observed. No evidence of scars or healing responses was detected at the light microscopic (Fig. 17) or ultrastructural levels.

Ecological Studies

Germination as a function of initial number of spores. The pattern of percentage germination as a function of initial number of spores differed among coalescing and noncoalescing species (Fig. 18). Percentage germination in the four coalescing species was a linear function of the initial spore density (Fig. 18A). Although significant differences were seen in the slope of the four species (ANCOVA, mean square = 208.39, $F = 32.95$, df = 3, $P < 0.0001$), which is determined by their respective average germination rates, the best fit for the response of these four species was a linear curve. In contrast, germination in the four noncoalescing species (Fig. 18B) reached a maximum and then gradually decreased as spore density increased. For these species, the best fitting was a quadratic polynomial curve, suggesting that maximum germination occurs at intermediate densities.

Aggregated versus solitary recruitment. Examination of sporelings on poxy–putty plates collected from the field (Fig. 19) indicated that recruits from coalescing species may originate either from solitary spores or from aggregations of up to 10 coalesced spores. The frequency of coalescing recruits varied among the species from 37% in *Sarcothalia crispata* to 18% in *Mazzaella laminarioides.* In contrast, sporelings from noncoalescing species always originated from solitary propagules; recruits were seen to grow so close to one another that their bases became entangled. However, the axes of individual uprights always originated from well-defined, noncoalescing holdfasts.

Aggregated versus solitary survival. In laboratory cultures, uni- and multisporic plantlets of coalescing species formed gradually expanding, irregularly circular disks. Conspecific sporelings with a high number of coalescing spores (Fig. 20) appeared to have better survivorship than plantlets arising from one or from a few spores. Such differences were minor (~5%) in *Mazzaella laminarioides,* intermediate (25%–40%) in *Gracilaria chilensis* and *Chondrus canaliculatus,* and high (>90%) in *Sarcothalia crispata.*

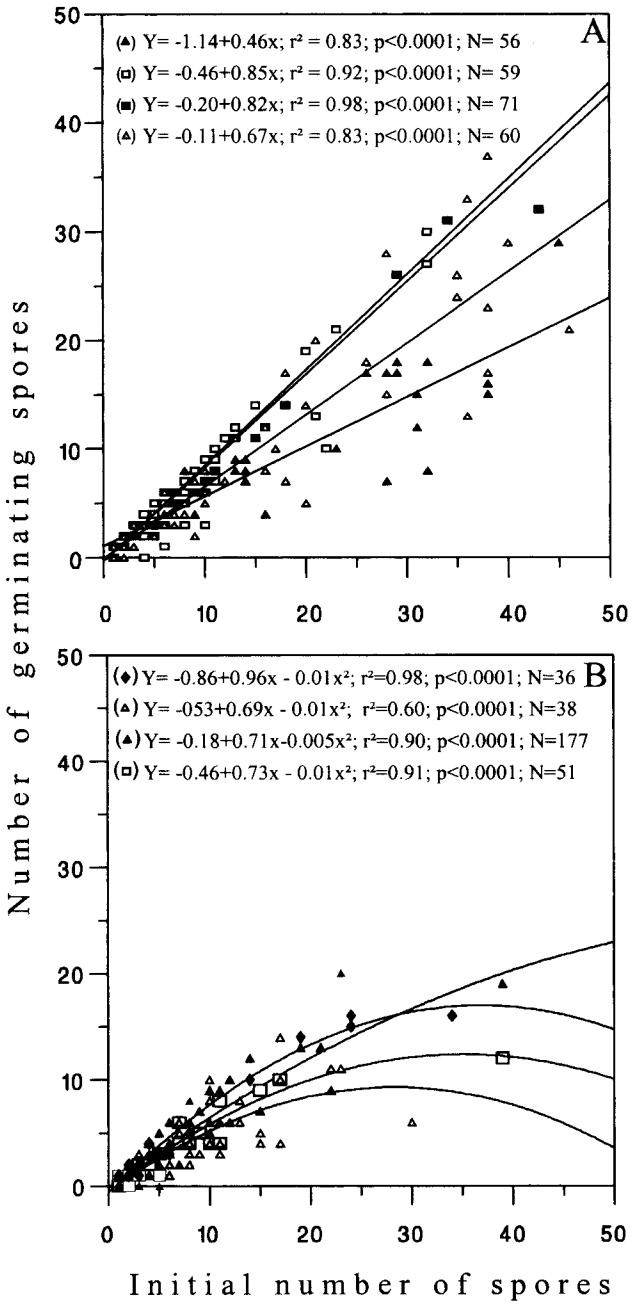


FIG. 18. Spore germination as a function of initial number of spores. A = coalescing species: (▲) *Chondrus canaliculatus,* (□) *Gracilaria chilensis,* (■) *Mazzaella laminarioides,* (△) *Sarcothalia crispata;* B = noncoalescing species: (♦) *Ceramium rubrum,* (▲) *Gelidium lingulatum,* (△) *Laurencia chilensis,* (□) *Polysiphonia scopulorum.*

In the previously described experiments, grouping of sporelings with approximately similar number of spores allowed us to obtain an average survival value but did not allow for replication values among sporeling groups. Thus, no statistical comparisons could be made among groups with a different initial number of spores. When survival of all four species was plotted as a function of the initial number of spores, the correlation (Fig. 20) indicated a statisti-

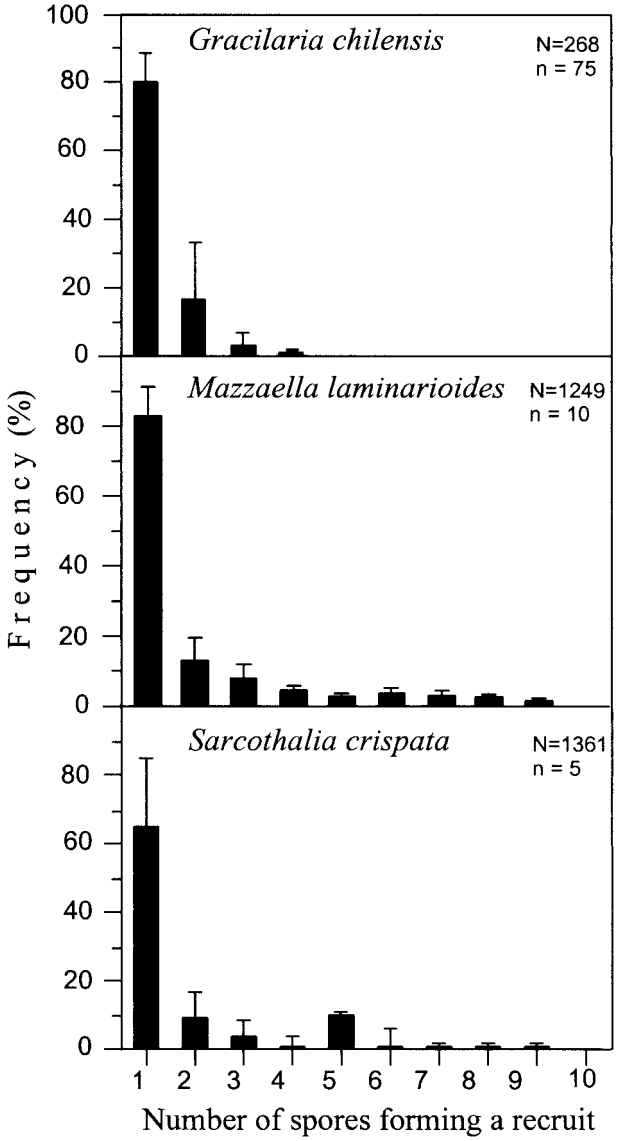


FIG. 19. Solitary and aggregated recruitment in coalescing species. n = number of poxy–putty plates; N = total number of recruits found in the plates; bars = SE.

cally significant trend of increased survival rates with increasing number of spores, up to a maximum number, where 100% survival is achieved. According to these experiments, all the sporelings formed by 12 or more spores did survive.

Comparisons of field survival on poxy plates (Fig. 21) showed that survival rates of aggregated recruits were significantly higher than from solitary recruits. Microscopic examination suggested that mechanical dislodgment by water movement, grazing, or overgrowth by faster-growing juveniles of opportunistic algae (*Enteromorpha, Ulva*) affected solitary recruits more frequently than coalescent ones. In addition, during field exposure, some solitary crusts eventually coalesced with neighboring crusts.

Growth as function of initial number of spores. In laboratory cultures, the time of appearance of erect axes in the four species studied ranged from the third to the seventh week of cultivation (Fig. 22). In *Mazzaella laminarioides* and *Gracilaria chilensis,* a tendency was observed in the plantlets that formed from two or more coalescing spores to differentiate uprights earlier in development. However, the regression value was statistically significant for *M. laminarioides* only. In *G. chilensis,* the probability value was slightly higher than 5%. This pattern was not shown by *Chondrus canaliculatus* or by *Sarcothalia crispata.* In the former species, a tendency was observed for plantlets from two or more spores to differentiate uprights later in development, whereas *S. crispata* differentiated erect axes at roughly similar times regardless of the number of spores giving rise to the plantlets.

The total number of erect axes produced by the coalescing mass was a logarithmic function of the initial number of spores (Fig. 23). The initial number of erect axes first increased with increasing number of spores, but with further spore increments it remained constant. This numerical relationship determined clear morphological differences among plantlets originating from different number of initial spores (Figs. 24–26). Thus, thalli originating from one or a few spores were elongated plants with a single or a few main axes bearing lateral branches. In contrast, individuals that grew from many coalescent spores appeared bushy, with many short, sparsely branched erect axes arising from a diskoid holdfast.

When the total length of all individual erect axes produced by a single plantlet was added and plotted as a function of the original number of spores (Fig. 27), plantlets of all four species exhibited a tendency to have a greater total length of erect axes with increasing spore numbers. In *Chondrus canaliculatus, Gracilaria chilensis,* and *Sarcothalia crispata,* differences in the sum of total length of erect axes between plantlets with the fewest and those with the greatest initial number of spores were statistically significant.

Spatial distribution of reproductive fronds. Data on frond height or stipe diameter distribution along the basal disk indicated in wild populations a significant increase in frond length or stipe diameter toward the center of the basal coalescing disks ($P < 0.001$ for all curve fitting and $P < 0.001$ for Jonckheere test in all species; Fig. 28). Thus, in all species studied (see also Fig. 26), the central blades were the longest. Among these taxa, *Sarcothalia crispata* exhibited the most pronounced size inequality. Each clump was formed by a central single, large (up to 25 cm long, 10 cm wide) blade surrounded by one to seven dwarf (1–2 cm long, 1–2 cm wide) blades. In contrast, *Gracilaria chilensis* exhibited the less pronounced size inequality, with the central axes slightly wider than the peripheral axes. In young laboratory cultures (Fig. 29), a similar growth

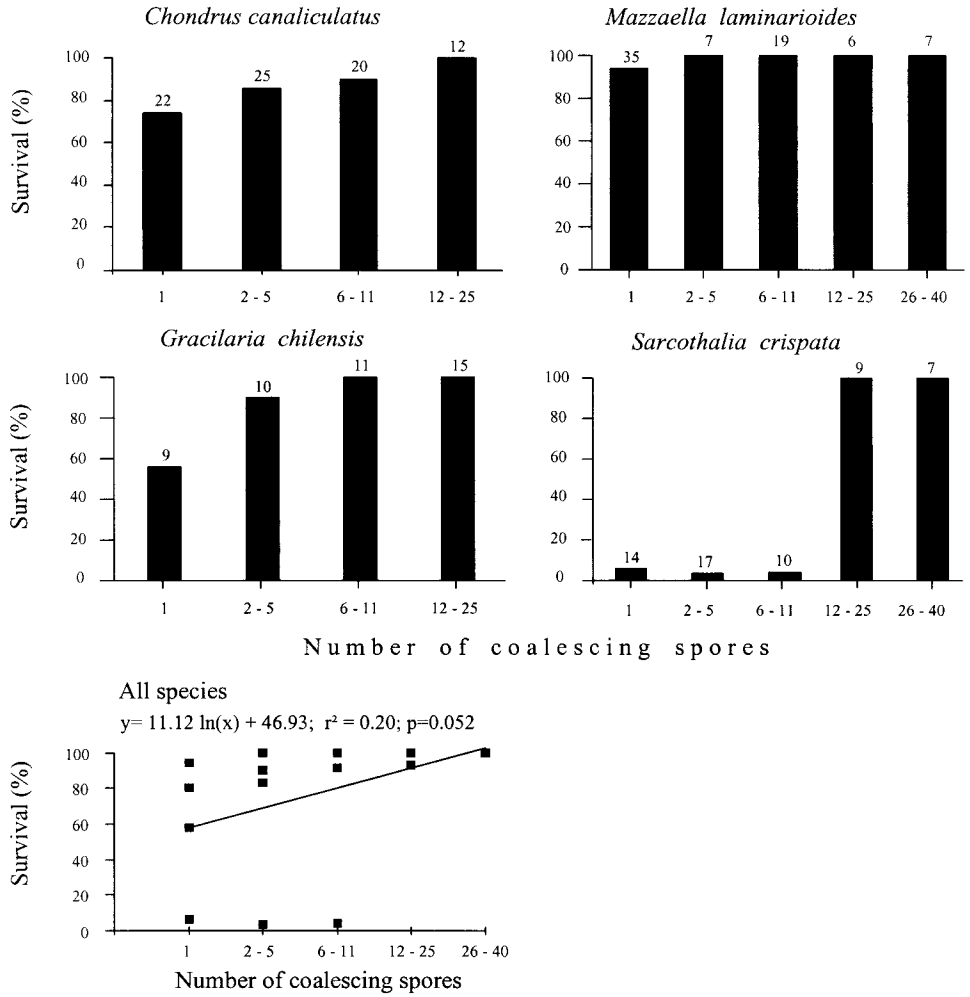


FIG. 20. Laboratory survival of sporelings as a function of the number of coalescing spores. The number at the top of each column indicates the number of replicates considered to calculate survival of each sporeling group. The regression value in the bottom figure (all species) includes results of the four coalescing species.

pattern was observed (see also Figs. 24, 25), with the longest erect axes toward the center of the clump.

Only the largest axes produced spores (either tetraspores or carpospores; Figs. 26, 28). In *Sarcothalia crispata,* this was restricted generally to the single large, central blade. In *Chondrus canaliculatus* and *Mazzaella laminarioides,* more than one reproductive blade per clump may exist, but generally the size of the reproductive blade was distinctively larger than the remaining sterile blades. In *Gracilaria chilensis,* although the reproductive axes were among those centrally located in the holdfast, they were not necessarily the largest in the clump.

DISCUSSION

The combination of results obtained in this study suggest that sporeling coalescence is a most important process, exhibiting three distinctive characteristics in the Rhodophyta. First, it is a widespread phenomenon, documented for members of roughly half the orders presently distinguished in the Florideophycidae. Second, it is a convergent response, as at light and ultrastructural levels the process is similar regardless of the phylogenetic affinities of the species concerned. Third, it is a complex process, as it involves not only morphological responses but also ecological and probably physiological responses that can be understood as adaptive traits associated with coalescence.

Generality of the response. The information gained through this taxonomic survey suggested that coalescence occurs mainly in species with diskoidal germination (*Dumontia*-type germination; Chemin 1937). Disks later expand into crusts, which in 83% of the cases studied exhibited coalescence.

The taxonomic affiliation of these species included seven historically related orders. They are found in the Rhodymeniales and the Palmariales, an order that was established (Guiry 1978) for species previously included in the Rhodymeniales. Coalescent species are also found in the Gigartinales and in four other orders recently derived from it, including Ahnfeltiales (Maggs and Pueschel 1989), Corallinales (Silva and Johansen 1986), Gracilariales (Fredericq and Hommersand 1989), and Halymeniales (Saunders and Kraft 1996).

The information gathered in the taxonomic survey documents the widespread occurrence of coa-

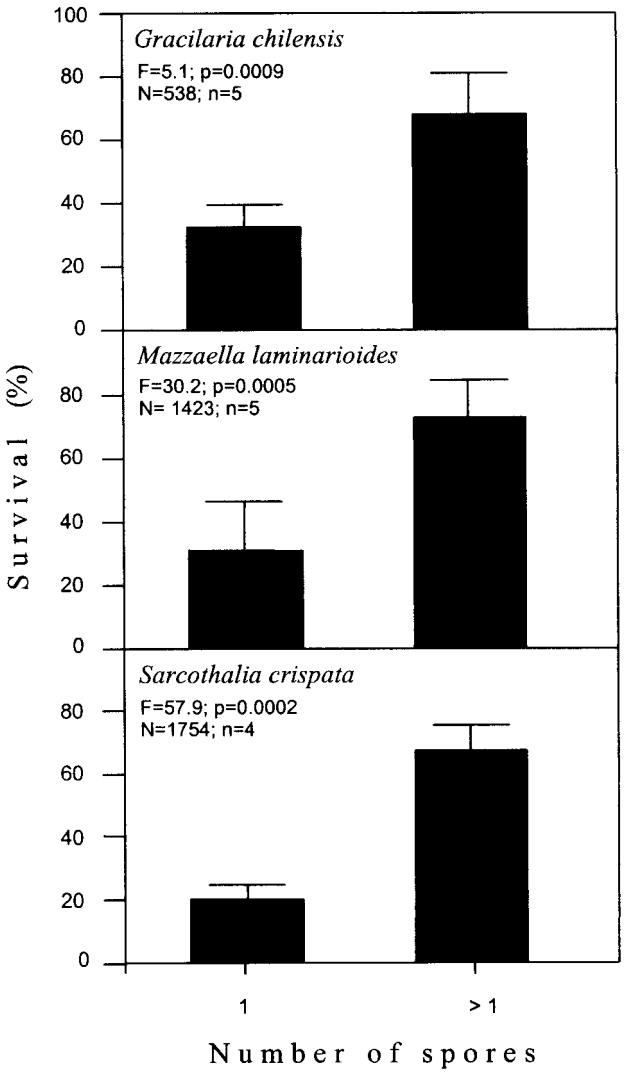


FIG. 21. Field survival of solitary and aggregated recruits of coalescing seaweeds on poxy–putty plates. Statistical values refer to *t*-test comparisons between treatments. n = number of replicate poxy–putty plates; N = total number of recruits considered; bars = SE.

lescence, and TEM studies show common patterns despite the diversity of species exhibiting it. In these species, the integration of two separate individuals into a single, morphological and functional unit can take place in two different ways. Recently released naked spores may fuse into a single cell. This was not frequent among the species studied, but it was clearly demonstrated in *Chondrus canaliculatus*. To our knowledge, this is the first report of naturally occurring cell fusions among red algal spores. Protoplast fusions of color mutants of *Porphyra* were induced under laboratory conditions (Saga et al. 1986, Fujita and Migita 1987), and fusions followed by exchange of nuclei are known to occur in host–parasite associations in red algae (Goff and Coleman 1984, Goff and Zuccarello 1994). In coalescing seaweeds, cell fusion may enhance variability by incorporating two genomes into a single cell.

More frequently, recently released spores may remain in contact, but each cell maintains its individuality and eventually develops a cell wall. Coalescence secondary to the formation of cell wall during germination may occur, with the establishment of cellular connections (secondary pit connections) between cells of different origins, similar to what has been described for *Gracilaria chilensis* (Santelices et al. 1996). The role of these connections remains to be determined.

Rapid secretion of a cell wall occurred immediately after spores settled. The first division is perpendicular to the substratum and is followed by other divisions, parallel and perpendicular to the substratum. At these or later stages, and provided that sporelings are spatially close, they fuse, leaving no evidence of scars or tissue incompatibility when observed at either light or ultrastructural levels. Furthermore, secondary pit plugs are established between some cells of coalescing germlings at the fusion zone. These results are in full agreement with those reported earlier for *Gracilaria chilensis* (Santelices et al. 1996), and they demonstrate that coalescence follows a similar pattern among several species within two red algal orders.

Species in almost half the orders in the Florideophycidae exhibit nondiskoidal germination. However, this group of species is developmentally heterogeneous and includes four types of germination in which the only common feature is the establishment of an apical-to-basal polarity either in the germinating spore or among the initials soon after germination. The best known of such examples, and the one that contrasts most sharply with diskoidal germination, is the *Ceramium* type of germination (Chemin 1937, Dixon 1973). In this type of germination, spores develop two opposite primordia, one originating a rhizoid and the other an apical cell from which the erect frond develops. In the *Nemalion* and the *Gelidium* types, germinating spores form a germ tube into which the cytoplasm passes. Subsequently, a transverse septum separates the empty cell wall of the original spore from the germ tube. In Acrochaetiales, Nemaliales, Batrachospermales, and Rhodogorgonales, the first cell formed during the development of the germ tube functions as an apical cell. In the Gelidiales, one end of the first cell forms a rhizoid, whereas the opposite end divides to form a mass of cells within which one or several apical cells eventually differentiate (Dixon 1973). Similarly, the *Naccaria* type of germination of the Bonnemaisoniales differentiates apical cells early in development by transverse divisions of the individual spores or of the spore derivatives.

Available information (for a review, see Waaland 1990) does not explain how polarity and cleavage planes of germinating carpospores are determined. A few experimental studies (Weber 1960, L'Hardy-

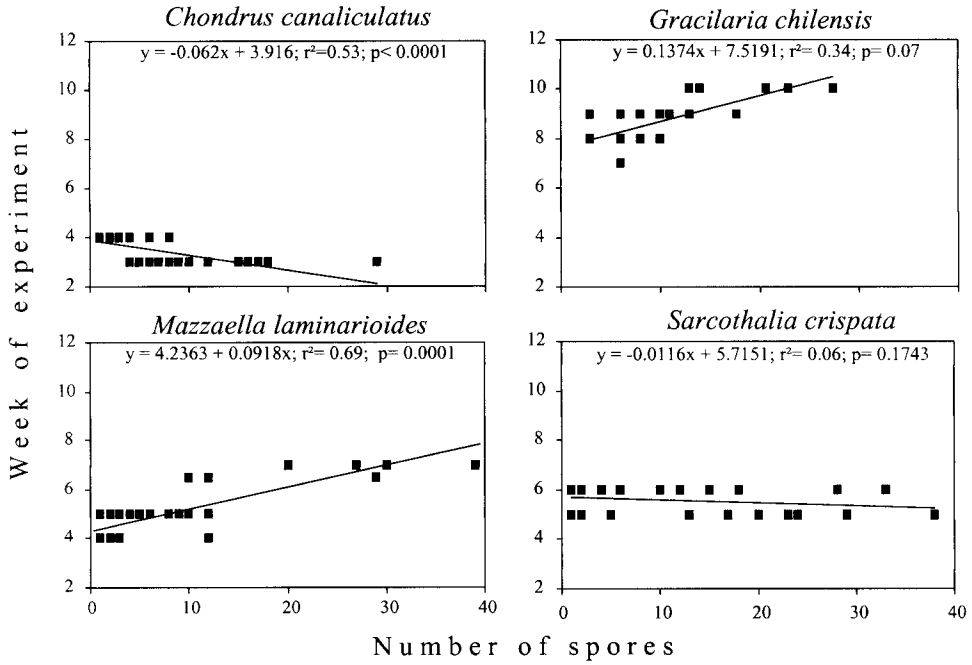


FIG. 22. Time of appearance of erect axes as a function of initial number of spores.

Halos 1971) have reported a lack of environmental effects on spore polarity of the Ceramiales, and the culture results included in Tables 2 and 3 additionally suggest that the type of germination within a group is a conserved trait that is unaffected by the culture condition used.

Comparative data from fucoid zygotes suggest that cell polarization and determination of cleavage planes is a complex process involving significant changes in cell symmetry and organization (e.g. Quatrano 1973, Brawley and Quatrano 1979, Kropf 1992, Stafford et al. 1992, Swope and Kropf 1993, Shaw and Quatrano 1996, Quatrano and Shaw 1997). Enzymatic removal of the cell wall prevents axis fixation (Kropf et al. 1988), and cell wall from different areas (thallus vs. rhizoid) of an embryo contains factors that can determine cell fate in apolar cells (Berger et al. 1994). Similar studies in red algae are needed to explain the different germination patterns and specifications of cell fate, which in turn determine the capabilities for early coalescence and for construction of chimeric thalli.

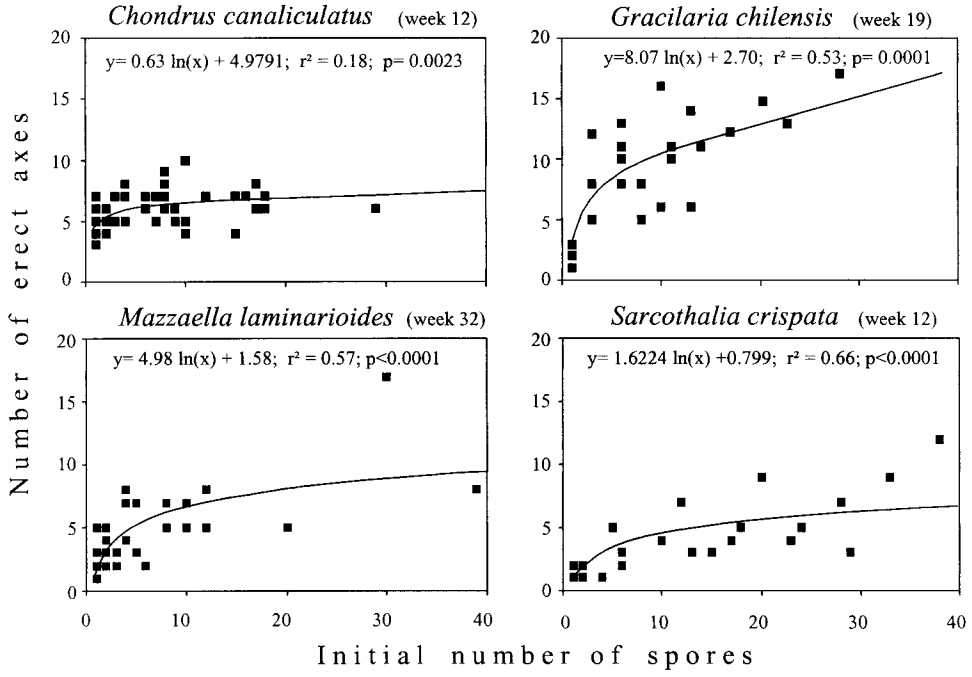
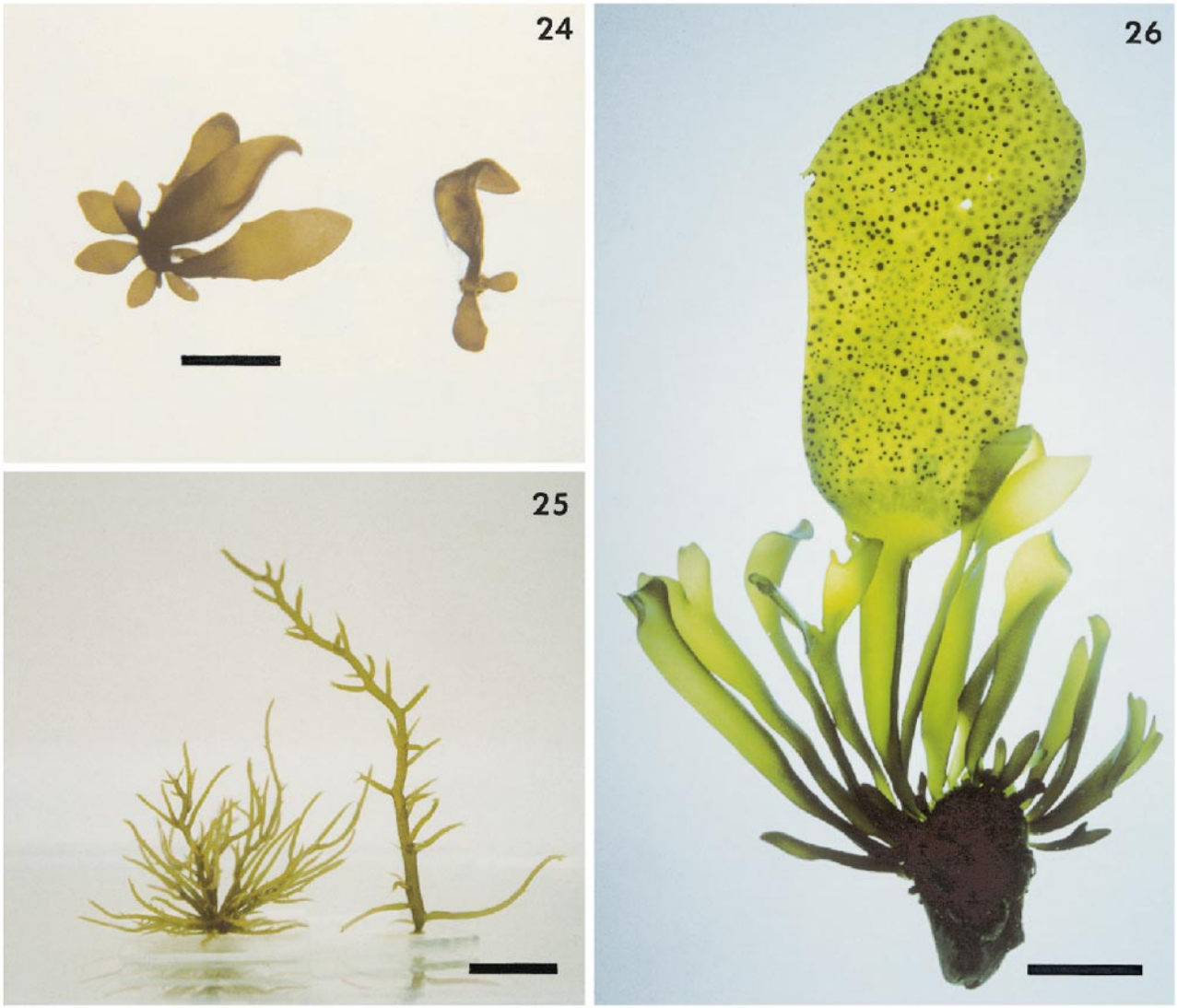


FIG. 23. Total number of erect axes as a function of initial number of spores.



FIGS. 24–26. Morphological variation and size inequalities in coalescing Rhodophyta. Scale bars = 2 cm (Figs. 24, 25) and 1 cm (Fig. 26). FIG. 24. Sixteen-week-old laboratory-grown plantlets of *Sarcothalia crispata*. The plantlet on the left grew from 11 coalescing spores, whereas the one on the right arose from two coalescing spores. Note size inequality, with the larger blades to the center of the clump. FIG. 25. Thirty-five-week-old laboratory-grown thalli of *Gracilaria chilensis*. The plantlet on the left grew from 14 coalescing spores, whereas the one on the right grew from one spore. Note size inequality in the bushy plant on the left, with the larger axis to the center of the clump. FIG. 26. Size inequality in field-collected specimen of *Mazzaella laminarioides*. All erect axes originate from a common disk settled on top of a black mussel. Note extensive cystocarp development only in the larger blade.

Adaptive traits. Coalescing seaweeds exhibit a number of specific ecological responses that can be interpreted as adaptive traits because they increase survival, growth and productivity, and reproductive potential of the coalesced individuals.

Contrary to what could be anticipated in other seaweeds (see Amsler et al. 1992, Vadas et al. 1992, Kendrick 1994), germination and early recruitment of coalescing taxa are characterized by positive rather than by negative interactions. In noncoalescing species, germination success is inversely related to spore density, an effect not exhibited by the spores of the coalescing species used in our studies. Furthermore, in the laboratory, survivorship of unisporic recruits was less successful than that of their multisporic counterparts. Because some mortality of individual spores occurs in all plantlets, regardless of the initial number of spores, chance mortality of one or two spores in one- or few-cell sporelings may result in the disappearance of the entire recruit. On the other hand, in the field, multicelled recruits are likely to have a greater resistance to grazers, to mechanical dislodgment, and to overgrowth by juveniles of other competing species in comparison to unisporic and isolated recruits, emphasizing the importance of positive interactions among individuals of coalescing species in the field. It should be remembered that in traditional ecological theory, which is heavily influenced by the study of unitary, noncoalescing organisms, positive interactions often

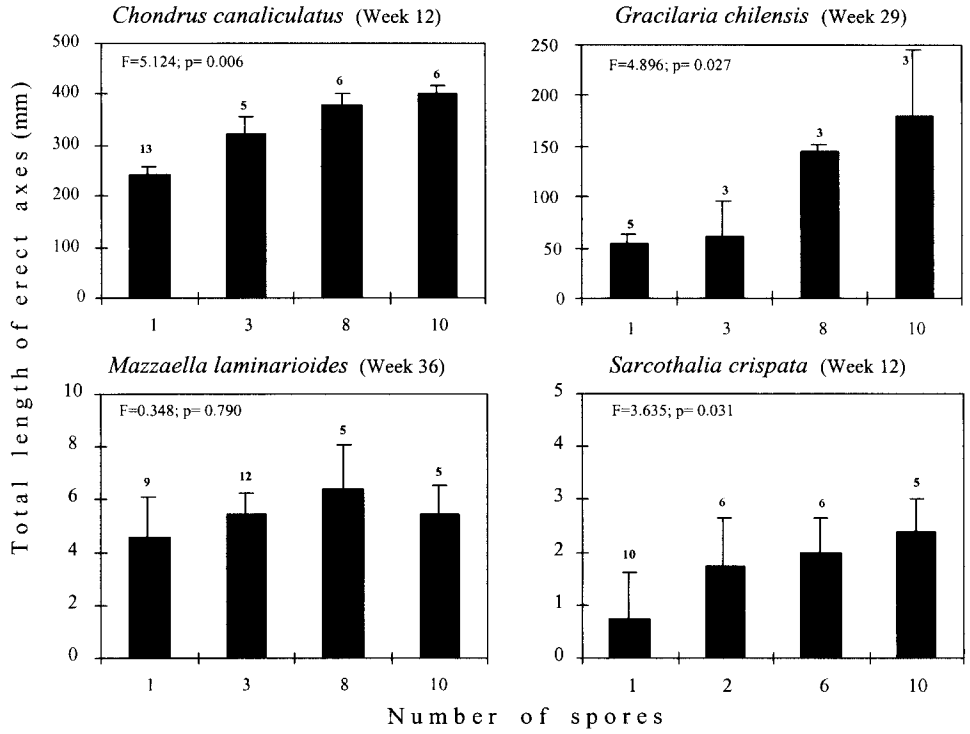


FIG. 27. Sum of total length of erect axes in four coalescing species as a function of initial number of spores in each sporeling. The numbers on top of the columns indicate the total number of replicates. Bars = SE; *F*- and *P*-values refer to *t*-test comparisons between treatments with the fewest and largest initial number of spores.

have been treated as exceptions in biological systems (see review in Santelices 1999). Further, in coalescent seaweeds, the importance and complexity of positive interactions probably have been underestimated.

Earlier studies (Jones 1956, Tveter and Mathieson 1976, Maggs and Cheney 1990) reported earlier initiation, faster growth, and a greater number of erect shoots in coalescent compared to noncoalescent sporelings. These three responses would confer important competitive advantages in nutrient uptake and light capture as well as the possibility of emerging earlier from under sandy or muddy bottoms. Previous studies with *Gracilaria chilensis* (Muñoz and Santelices 1994, Santelices et al. 1996) have documented that coalescing sporelings exhibit only one of these responses (increased number of erect shoots), suggesting that quantitative screening of other species was needed before generalizations could be made. Our study confirms these results, but these show interspecific variability. In *Mazzaella laminarioides* and *Gracilaria chilensis,* a tendency was observed in plantlets formed from a few coalesced spores to differentiate upright earlier than plantlets originated from many spores. In the other two species, such a difference was not detected.

In the species used in our study, the total number of erect shoots was a function of the initial spore number. This relation had been described already for *Gracilaria chilensis* (Santelices et al. 1996) and explained as a consequence of the growth pattern for coalescing spores. Polysporic plantlets in all four species are formed by grouped cell clusters, each with an initial spore and its derivatives that, with TEM, appear as discrete units surrounded by a common external cell wall. Cells in adjacent clusters may fuse, establishing secondary pit plugs, but within each cluster active cell division produces numerous derivatives of the initial spore. The capacity for growth as an independent unit, to form uprights eventually, seems retained by the spore derivatives in each cluster, and this would explain the numerical relationship found between the initial number of spores and the number of erect shoots.

Although erect axes in sporelings derived from one or a few spores are generally longer than those from multisporic germlings (Santelices et al. 1995), the sum of individual lengths of all erect axes and branchlets per plantlet, in any of the four species considered in this study, increased with an increasing number of coalescing spores. Assuming that at this stage most of the photosynthetic tissues are concentrated in these axes and branches, coalescence of a large number of spores generates a larger photosynthetic canopy than plantlets from a few spores or a single spore.

As growth continues, erect axes within a given plantlet gradually become heterogeneous in size, with a tendency for larger and thicker axes to be located at the center of the holdfast. Although size inequalities occur in both laboratory-grown and field-collected clumps of the four species studied, the magnitude of the response differs among species. *Gracilaria chilensis* and *Chondrus canaliculatus* exhibit size inequality only at some stages of the growth cycles, in young clumps in *G. chilensis* and in

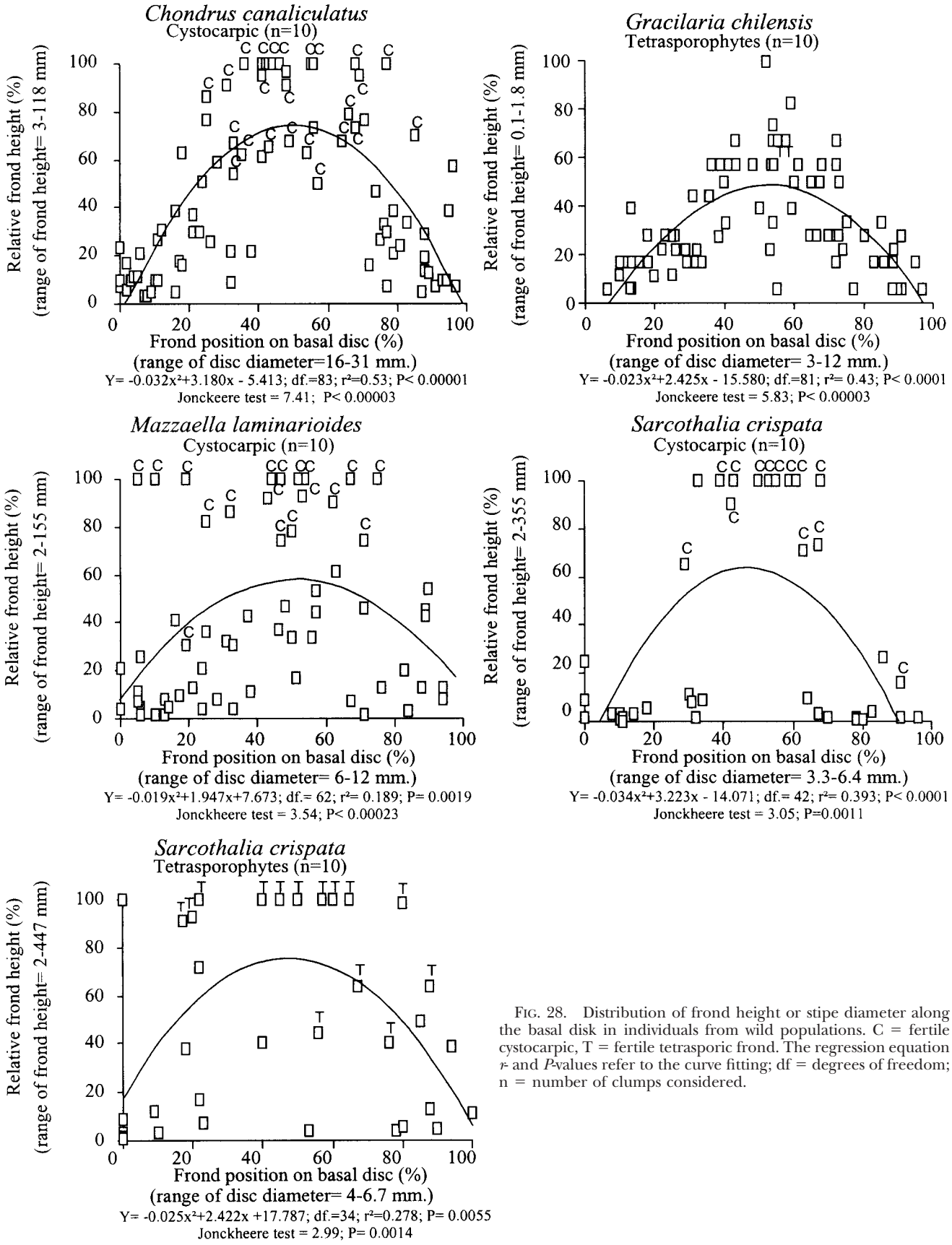


FIG. 28. Distribution of frond height or stipe diameter along the basal disk in individuals from wild populations. C = fertile cystocarpic, T = fertile tetrasporic frond. The regression equation *r*- and *P*-values refer to the curve fitting; df = degrees of freedom; n = number of clumps considered.

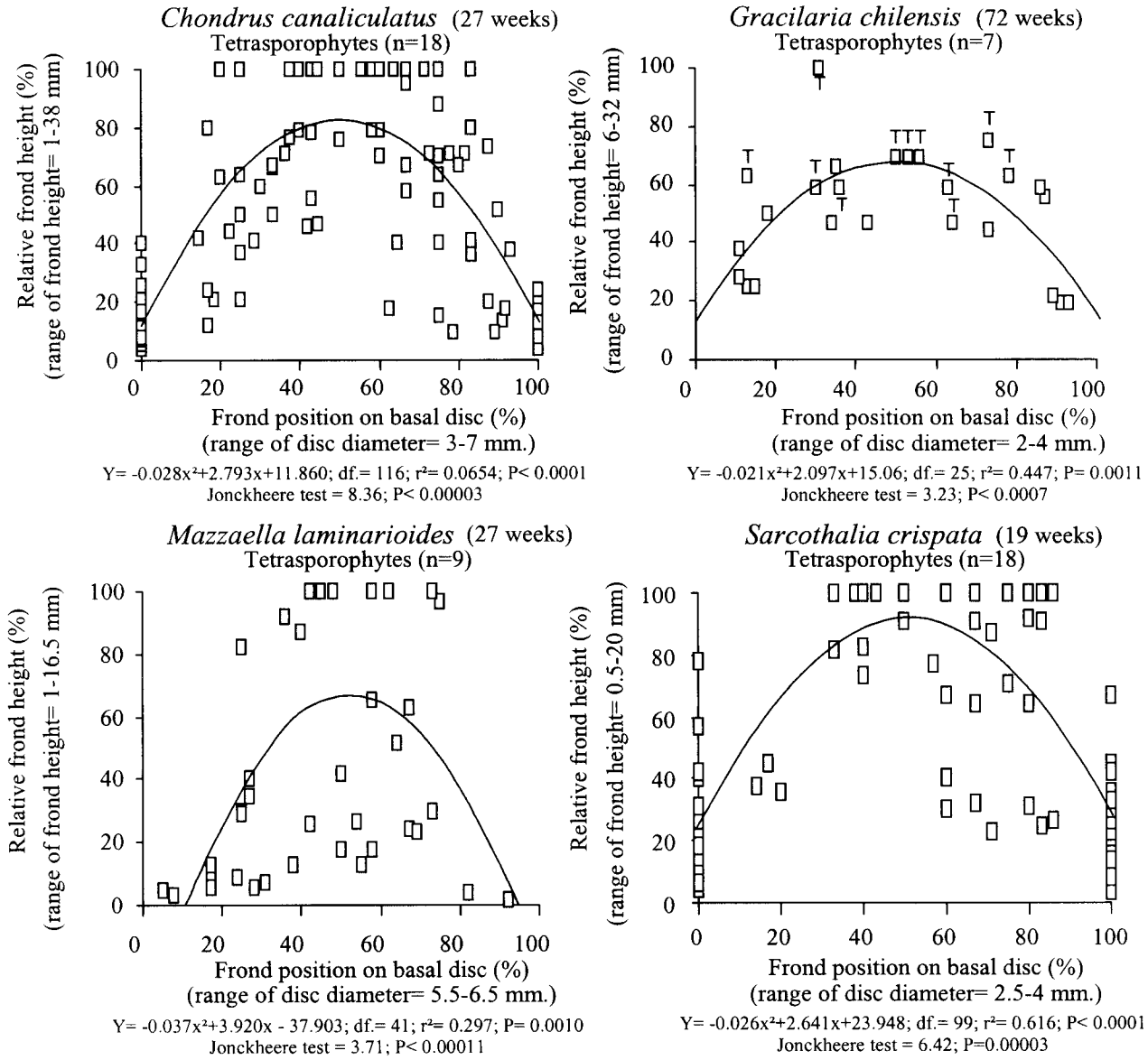


FIG. 29. Distribution of frond height or stipe diameter along the basal disk in laboratory-grown populations. T = fertile tetrasporic frond. The regression equation r- and P-values refer to the curve fitting; df = degrees of freedom; n = number of clumps considered.

mature clumps in *C. canaliculatus*. This pattern is disrupted by thallus fragmentation and branching in *G. chilensis,* and it is not found in young (<5 cm in height) clumps of *C. canaliculatus*. On the other hand, size inequalities are present throughout the life span of clumps of *Mazzaella laminarioides* and *Sarcothalia crispata*. In the latter species, normally one or two of the 6 to 10 blades forming a clump reach macroscopic dimensions (15–20 cm long, 7–10 cm wide); the other blades remain ≤1 to 2 cm long.

Morphological descriptions of species included in the seven red algal orders exhibiting coalescence (e.g. Abbott and Hollenberg 1976, Womersley 1994) suggest that size inequality is a common response among coalescing species with erect axes. However, data are still insufficient to conclude that this is a general pattern. Precise measurements of erect axes in taxa that seemingly lack this pattern (e.g. *Ahnfeltiopsis, Ahnfeltia,* and coralline algae) are still needed.

The factors producing size inequalities are unknown. Size differences between peripheral and central thalli in experimental clumps of *Gracilaria chilensis* were thought to be a protective response conferred by peripheral thalli against sediment deposition, grazing, or high nutrient concentrations (Santelices 1990a). However, the response also occurs in laboratory-grown clumps and in a variety of habitats. Maggs and Cheney (1990) suggested the existence of growth regulation within the sporeling mass and differential translocation of photosynthates toward the inner sporeling. Nutrient avail-

ability and other factors affecting algal productivity are likely to play a role also, as coalescing clumps of *Mazzaella laminarioides* in low-nutrient habitats are smaller than clumps in high-nutrient habitats and show almost no size inequalities (Martínez and Santelices 1992).

Formation of cystocarps and tetrasporangial sori in many red algal species imposes an energy cost to the fertile thalli (see reviews by DeWreede and Klinger 1988, Santelices 1990a). In the case of coalescing seaweeds, this probably explains why only the few larger fronds in each clump become reproductive. Coalescence, growth regulation, physiological integration, photosynthate translocation, and size inequality are all factors that allow accumulation of enough energy in a single or a few blades in a clump to produce reproductive cells. Noncoalescing plantlets of these species or plantlets derived from a few spores either do not become reproductive or take longer to reach maturity.

In summary, the specific ecological responses exhibited by coalescing seaweeds suggest adaptive traits that increase survival during germination and recruitment, increase production because of a larger photosynthetically active canopy during growth, and earlier or more abundant reproduction due to unequal growth and concentration of energy in a few larger blades within a clump. Together with the widespread occurrence of coalescence in the Florideophycidae and the similarity of the coalescence process among the various groups, these adaptive traits suggest that coalescence constitutes a unique growth style that is widespread among red algae and that divides the species now included in the Florideophycidae into two major groups of coalescing and noncoalescing species.

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