



A comparison of ecological responses among aclonal (unitary), clonal and coalescing macroalgae

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Abstract

Based on growth patterns, regeneration capabilities and genetic make up, benthic macroalgae include three groups of species. Similar to land plants, they include clonal and aclonal species, and, similar to colonial aquatic animals, seaweeds also include coalescing species, that have the capacity to fuse forming composite (chimeric) entities. Since the awareness of the differences between these three kinds of seaweeds is rather recent, most ecological studies have not discriminated among them. However, ecological models based on one kind of seaweeds will not necessarily apply to all kinds of seaweeds. This study reviews ecological responses of algae at the individual and community levels, and describes similarities and differences among both the three algal groups and with parallel groups in land plants and chimeric marine animals. The ecological responses reviewed are plant sizes and shapes; patterns of resource acquisition; algal life phases, reproduction and dispersal; genetic variability, intraspecific and interspecific competition and herbivory. Analysis of these responses supports the idea in distinguishing among the above three algal group, reveals the need for numerous additional ecological studies and advices on incorporating concepts from the biology of chimeric aquatic animals and from clonal theory of land plants into the study of benthic macroalgae.

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1. Introduction

Based on the ways how land plants add to their canopies above and below ground, since the mid-1970s, land plant ecologists have formally distinguished aclonal (also named unitary) from clonal plants (Harper, 1977, 1985; Harper and White, 1974). Aclonal plants

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form leaves and roots that are connected to the original axis, emphasizing growth in the vertical direction. In contrast, clonal plants emphasize lateral growth, forming potentially independent branches and root contacts. While aclonal plants concentrate their resources for growing taller and penetrating deeper into the substratum, clonal plants spread over the surface of the soil, with a propensity to occupy multiple microsites (Sachs and Novoplansky, 1997).

Theoretical and experimental studies developed over the last 30 years (see Jackson et al., 1985; van Groenendael and de Kroon, 1990; de Kroon and van Groenendael, 1997, for reviews) suggest significant differences among clonal and aclonal plants with respect to morphological construction, life history traits, demographic parameters, type and outcome of competitive interactions, dispersal syndromes and genetic variability.

On the other hand, and for well over a century, marine zoologists have distinguished between unitary and colonial animals (Giard, 1872; Brancroft, 1903). Colonial animals may have the capacity to fuse, forming composite entities. By now, fusions are known to occur (Buss, 1982, 1987; Grosberg, 1988; Hughes, 1989; Sommerfeld and Bishop, 1999) in all groups of modular animals including sponges, hydroids, corals, bryozoans and ascidia. Fused colonial animals exhibit significant differences with unitary organisms in their morphological construction, genetic make up, recruitment and growth patterns, competitive capacity to gain space and gamete exchange.

The marine benthic algae seemingly include three of the four kinds of organisms distinguished above. Similar to land plants, they exhibit clonal and aclonal species and similar to colonial invertebrates, seaweeds also include coalescing species, organisms that have the capacity to fuse forming composite (chimeric) entities.

Although, 20 years ago, Cousens and Hutchings (1983) used the terms genets and ramets while studying the density–weight relationships of some brown algae, it was only 12 years ago that Santelices (1992a,b) described the clonal characteristic of macroalgae and called for the need to incorporate concepts from theory of clonal organisms into the biological knowledge of the seaweeds. Progress thereafter has been slow and restricted in scope, with efforts concentrating in morphological plasticity, population structure, demography and intraclonal variation (see Santelices, 2001; Collado-Vides, 2002a for reviews).

On the other hand, the capacity of some algae to coalesce is known since the pioneer work by Rosenvinge (1931). Although the process was repeatedly described and illustrated in the past (see Santelices et al., 1999 for a review), only in the last 20 years (Maggs and Cheney, 1990; Muñoz and Santelices, 1994; Santelices et al., 1996, 1999, 2003a,b, in press) has coalescence been examined from the perspective of experimental ecology. Results suggest that this type of seaweed also differs from aclonal and clonal species in its morphological construction, genetic make up, recruitment and growth patterns.

Since the awareness of the differences between aclonal, clonal and coalescing seaweeds is rather recent, most ecological studies have not discriminated among them. Assuming that most seaweeds are unitary organisms, results gathered with one kind have been extrapolated to all kinds of benthic macroalgae. However, population and community models based on aclonal (unitary) seaweeds will not necessarily apply to clonal or coalescing macroalgae. Therefore, there is a need to review key aspects of the comparative

ecology of these organisms in order to evaluate if the similarities and differences described among asexual and clonal species of land plants and among unitary and chimeric colonial invertebrates have equivalent representation in the seaweeds. The first part of this study reviews ecological responses at the individual level, including plant sizes and shapes, patterns of resource acquisition, algal life history phases, reproduction and dispersal and genetic variability. The second part of the review focuses on some community responses, including intraspecific and interspecific competition and herbivory. Implications of the differences in growth style for seaweed farming and harvesting and on the demographic parameters often used to outline harvesting models have been revised somewhere else (Santelices, 2001).

This study does not intend to be an exhaustive review of each of the various topics included herein but to provide an overview of the need to reevaluate several key ecological concepts in light of the differences in growth patterns found among the algae. Topics and references in this review have been restricted to those where there is relevant information suggesting differential responses among the three types of seaweeds distinguished above. Many relevant areas lack enough information for a critical evaluation and therefore could not be incorporated into this study. Thus, the generalizations that emerge should in many cases be considered workable hypothesis rather than firmly established conclusions.

2. Ecological responses at the individual level

2.1. Definitions

Land plants grow by reiterating units of several different types, the two most common being shoot units and root units. In the case of seaweeds, the units are erect shoots and attachment structures (rhizoids, holdfast, basal crusts and others). Asexual seaweeds are defined as those species or free living life-history phases displaying predominantly vertical growth (Fig. 1), sometimes exhibiting morphological and physiological differentiation along the thallus and with their branches and branchlets distributed in such a way along the vertical axis that they may induce auto-shading over the lower parts of the erect axis (Alpert and Steufer, 1997; Collado-Vides, 1997; Santelices, 2001). Branches, branchlets or thallus fragments of these species or phases normally lack the capacity to function, survive or replicate the parental plant on their own if separated from it by natural means. The propagation of this type of seaweed normally is through haploid or diploid unicells.

In clonal plants, a higher order of modularity exists, as they grow by reiterating sets of shoot and attachment units, called ramets (Fig. 2). These ramets are vegetatively produced and they function and survive on their own if separated from the parent plant by natural processes or by injury. The vegetative units are termed ramets while the entire plant is termed genet (Harper and White, 1974). Genets develop from haploid or diploid unicells (Scrosati, 2001) and can propagate, in addition to unicells, by vegetative fragments (clonal fragmentation, Eriksson and Jerling, 1990), which are genetically identical to the parent plant. Among the algae, re-attachment to the substratum after clonal fragmentation with development of new individuals has been observed in species of the genera *Acanthophora*,

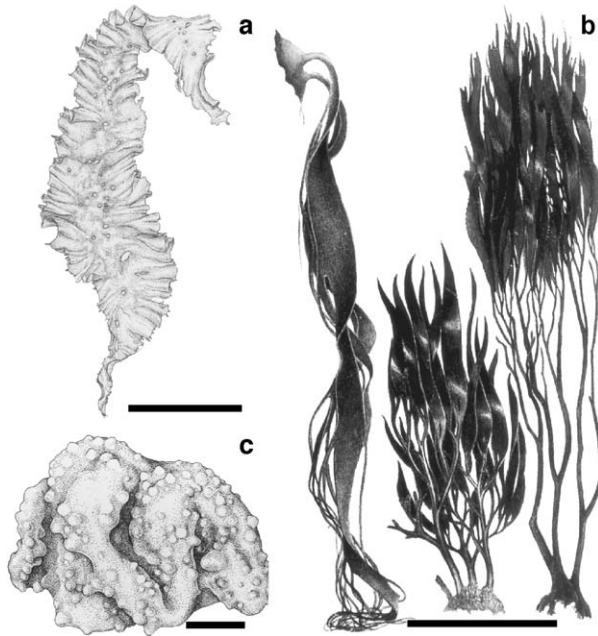


Fig. 1. Macroalgal species or life history phases representative of the aclonal (unitary) growth group: (a) *Ulva taeniata*, scale: 10 cm; (b) *D. antarctica* (left), *L. nigrescens* (center) and *L. trabeculata* (right), scale: 5.0 cm; (c) *Colpomenia trabeculata*, scale: 1 cm.

Caulerpa, *Gelidium* and *Halimeda* (Walters and Smith, 1994; Seoane-Camba, 1989; Meinesz et al., 1995; Collado-Vides, 2002a).

Coalescing seaweeds (Fig. 3) originate by the fusion of genetically different plants following the establishment of physical contact and growing together of two or more spores, groups of spore derivatives, sporelings or crustose basal portions of grown thallus in such a way that the resulting genetically heterogeneous individual responds as a discrete entity and some of the original cell lines no longer retain their morphological or anatomical individuality (Santelices et al., 1999, 2003a,b). Coalescing spores, sporelings or crusts may establish cellular connections among neighboring, genetically different cells.

Clonal and aclonal-type seaweeds seemingly are represented in the three main macroalgal divisions (Figs. 1 and 2). Typical examples of aclonal seaweeds are some green and red frondose forms such as *Ulva*, *Enteromorpha* and the frondose stage of *Porphyra*. The aclonal group also includes some brown algae such as fucoids (*Fucus*, *Selvetia*), the sporophytic (diploid) phase of kelps (*Laminaria*, *Hedophyllum*, *Lessonia*), the bull kelp (*Durvillaea*) and the sporophytic phase of several Scytosiphonales (*Endarachne*, *Petalonia*, *Scytosiphon*).

Clonal growth also is well represented within the three main macroalgal divisions (Fig. 2). Among the Chlorophyte, this growth pattern is especially well illustrated by species in genera such as *Caulerpa*, *Halimeda*, *Penicillus*, *Rhizoclonium*, *Rama* and *Cladophoropsis* (Fig. 2). Among the Phaeophyta, several genera in the ectocarpoids (*Ectocarpus*, *Hincksia*,

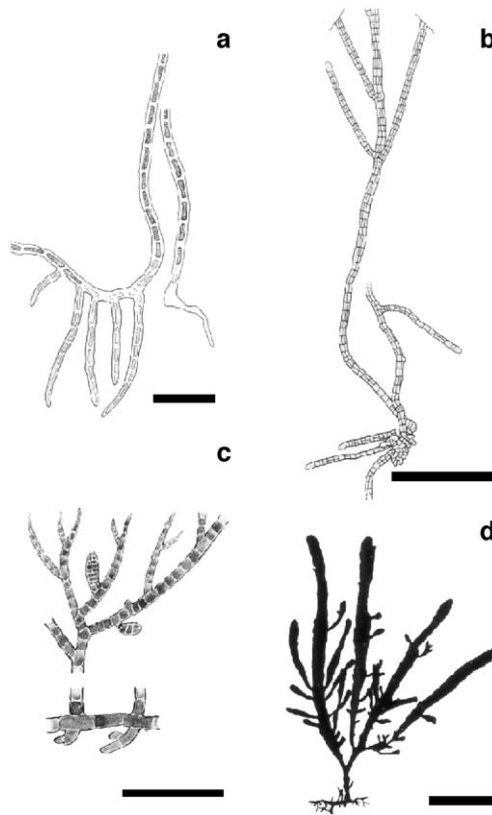


Fig. 2. Macroalgal species representative of the clonal growth group: (a) *Rama novae-zelandiae*, scale: 500 μm ; (b) *Sphacelaria furcigera*, scale: 500 μm ; (c) *Hincksia granulosa*, scale: 100 μm ; (d) *Gelidium chilense*, scale: 1 cm.

Spongonema), the Sphacelariales (*Sphacelaria*) and the alternate phase of Scytosiphonales and Laminariales are representative of clonal seaweeds. In the red algae (Rhodophyta), clonal growth is especially well represented among members of the Orders Batrachospermales, Gelidiales, Bonnemaisoniales and Ceramiales.

Coalescence has so far only been documented for red algae, including species from roughly half of the orders in the Subdivision Florideophycidae (Fig. 3; Santelices et al., 1999). However, the literature contains suggestions (Maggs and Cheney, 1990) that a similar process could also be occurring in some green algae (e.g. *Codium*).

As in land plants (Sachs and Novoplansky, 1997), in the seaweeds, there are probably numerous species with intermediate growth styles between clonal and aclonal growth. Even though in these cases a clear-cut separation may be difficult or even impossible, the different growth patterns among various species are very evident and the separation seems a valid and promising conceptual tool.

Clonality and coalescence are not mutually exclusive conditions (Santelices, 2001), which had led some authors (Scrosati, 2001; Collado-Vides, 2002a) to include

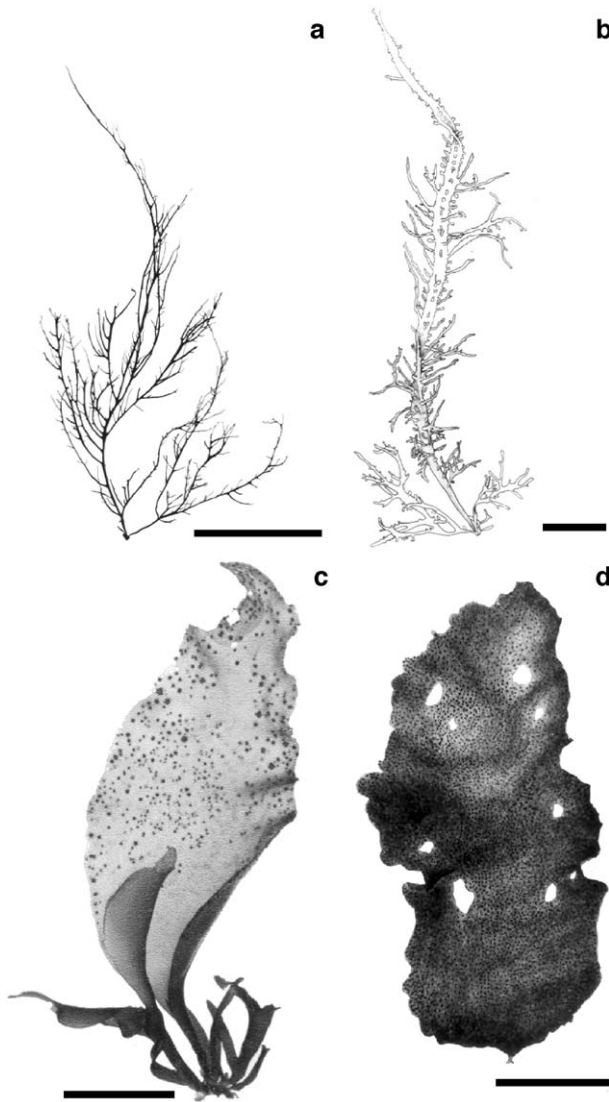


Fig. 3. Macroalgal species representative of the coalescing growth group: (a) *Gracilaria chilensis*, scale: 5 cm; (b) *Chondracanthus chamissoi*, scale 1 cm; (c) *Mazzaella laminarioides*, scale: 3 cm; (d) *Sarcothalia crispata*, scale: 3 cm.

coalescing seaweeds among clonal forms. However, there are several reasons to maintain them separated. First of all, coalescence is a unique growth style among the seaweeds with many genetic implications (see Section 2.5). In addition, there are many clonal species that lack the capacity to coalesce (e.g. *Gelidium*, *Bostrychia*, *Hincksia*). Although some coalescing species have the capacity to develop new individuals after the re-attachment of clonal fragments (e.g. *Gracilaria*, Santelices et al., 1984; *Corallina*, Littler and Kauker,

1984; *Chondrocanthus*, Bulboa and Machiavello, 2001), not all species of coalescing seaweeds have that capacity. It is true that the basal, often crustose, attaching portions of the plant in species of genera such as *Mazzaella*, *Sarcothalia* or *Gigartina* is able to regrow the crust or regenerate new erect shoots after fragmentation of the parent plant, provided that the base remains attached to the substratum. However, the frond fragments generally lack the capacity to regenerate under natural conditions.

2.2. Size and shape

Given the diversity of forms occurring within each seaweed group, it is difficult to outline exclusive patterns of size and shapes associated with asexual, clonal and coalescing-types of growth. In fact, Collado-Vides (2002a) has described and illustrated a diversity of forms and morphological architectures representing clonal growth. However, a few basic differences in size and shape seem to exist, at least among the most typical representatives of each major group (Fig. 1). The typical representative of an asexual seaweed has a main axis attached to the substratum at a single point. If devoid of branches, the axis may be elongated, cylindrical, flattened or globose, with apical or subapical growth of the meristems. If branched, primary branches are produced by the same axis that attaches the plant to the substratum. Branch and branchlet distribution is often related to light capture optimization. Size and thallus structure are variable, but some asexual forms are among the species with larger sizes in the seaweeds (e.g. kelps and bull-kelps).

A typical clonal seaweeds (Fig. 2) is a short, branched plant, attached to the substratum at several points by a creeping, prostrate axis with stoloniferous rhizoids. Erect axes originate from the creeping axis, often at points opposing the attachment structures. Erect axes may either be single or completely covered with branches and branchlets. Under some environmental conditions, these erect axes may become repent, develop additional attachment structures, thereby adopting the morphology of a creeping axis. If the continuity of the creeping axis is interrupted by biotic or abiotic factors (e.g. grazing, bleaching), the separated parts of the plant may continue to grow as independent entities. Similarly, if a fragmented ramet is allowed to re-attach (e.g. in low water movement areas), it will often have the capacity to continue growing, therefore regenerating the parent plant. A diversity of thin-filamentous (e.g. Ectocarpoids, Santelices, 1992a,b; *Brostrychia*, Collado-Vides, 1997), corticated-filamentous (*Gelidium*, *Pterocladia*, Santos, 1993), coenocytic (e.g. *Penicillus*, *Udotea*, Friedmann and Roth, 1977), green calcareous articulated (*Halimeda*, Collado-Vides, 2002a) and larger, corticated brown algae (e.g. *Ascophyllum nodosum*, Lazo and Chapman, 1998) all exhibit the capacity of clonal growth.

A typical member of the coalescing-type of growth (Fig. 3) is an algae attached to the substratum by a crustose holdfast, with one to many cylindrical (e.g. *Gracilaria*, Santelices et al., 1996) or flattened (e.g. *Mazzaella*, Santelices et al., 1999) erect axes arising from the basal crust. In plants with many erect axes, there is a tendency for the larger and thicker axis to be located to the center of the holdfast. Often, the size difference between these central axes and other axes generates significant size inequalities among the fronds (Martinez and Santelices, 1992). In some species (e.g. *Sarcothalia crispata*, Santelices et al., 1999), the centrally located fronds may be the only ones to develop to a large size (10–

20 cm long) and produce reproductive structures. At the mature stage, other blades may appear as dwarf projections of the holdfast.

So far, coalescence has been observed among spores or sporelings of corticated, cylindrical forms such as *Gracilaria* (Maggs and Cheney, 1990; Muñoz and Santelices, 1994), *Gymnogongrus* (DeCew and West, 1981) or *Ahnfeltiopsis* (Maggs et al., 1992); some frondose and blade-like forms, such as *Grateloupia* (Villalard-Bohnsack and Harlin, 1997), *Chondracanthus* (Guiry, 1984) and *Schizymenia* (DeCew et al., 1992) and some articulated (e.g. *Corallina*, Jones and Morjani, 1973) and non-articulated (*Hydrolithon*, Penrose, 1992) calcareous algae. All these can be considered coalescing species. Some green, non-calcareous crusts such as *Codium* might also belong in this group (Maggs and Cheney, 1990), but there is no evidence of fusion between different crusts in that genus yet.

Land plant ecologists (Lovett-Doust, 1981) have distinguished two morphological extremes in the clonal morphology, the “guerilla” and the “phalanx” growth styles. The stoloniferous habit of the first type has distant, loosely connected, spreading stolons, rhizomes or internodes. These are species with the capacity to explore and colonize open areas with few neighbors. The “phalanx”-type growth, by contrast, consists of tightly packed stands of thalli, able to resist the invasion of other clonal seaweeds and with capacity to exploit resources in a given site. This form is more frequent in densely populated areas.

The only application of the concepts of “guerilla” and “phalanx” type growth types to seaweed communities seems to be the work by McDermid (1988, 1990). Working with turfey seaweed communities on an intertidal reef in Hawaii, she found that a number of species (e.g. *Gelidiella acerosa*, *Laurencia brachioclados*) displayed the typical “guerilla” type of growth, while others (e.g. *Laurencia dotyi*, *L. crustiformans*) had a “phalanx” growth pattern. In these communities, morphology and growth patterns were found (McDermid, 1988) to be one of the most important factors influencing competitive ability of the species and the outcome of competitive interactions among them.

2.3. Resource acquisition

Extensive studies in land plants (see reviews by de Kroon and van Groenendael, 1990; Hutchings and Mogie, 1990; Marshall and Price, 1997; Oborny and Cain, 1997) have recognized spatial spread, resource-acquisition (foraging) and physiological integration as parts of a common strategy among clonal species. These studies recognize that the resources needed for growth are unevenly distributed in space and time in all natural habitats. Since clonal plants have the potential to alter their growth and are able to spread laterally, they have increased chances to exploiting favorable and avoiding unfavorable parts of their habitats. Thus, ramets placed at sites with greatest resource abundance specialize in enhanced acquisition of such resources while physiological integration between ramets redistributes the resources internally from sites of acquisition to clone parts located where the resources are scarce. This adaptation seems to be particularly effective in heterogeneous environments with significant differences in resource availability among microsites.

Equivalent ideas have only exceptionally been explored in the seaweeds because light and nutrients are thought to be very homogeneously distributed within the marine

environment at the scale pertinent to seaweed environment. In addition, all the seaweed surfaces are assumed to be involved in photosynthesis and nutrient uptake. The only exception so far seems to be the suggestion by Collado-Vides and Robledo (1999) that foraging for resources might be occurring in *Caulerpa cupressoides*. Most species of *Caulerpa* have a compact growth form in high light-high nutrient environments and a sparse growth form in low light-low nutrient environment. *C. cupressoides* may modify its morphology, which was interpreted as an adaptation to different growing conditions. A more sparsely branched, loose lying growth form in low nutrient conditions would allow the extension of new branches to more distant microsites, thereby increasing the probability of finding and exploiting microhabitats with locally higher nutrient concentrations (Collado-Vides, 2002b). However, experimental studies on nutrient loads, physiological integration and translocation in these seaweeds in these habitats are missing.

It is generally assumed (Lobban and Harrison, 1994) that long-distance translocation in seaweeds is relatively unimportant because, and in contrary to land plants, the distances between the alga surfaces absorbing light, CO₂ and nutrients are relatively minor. However, translocation can also serve to redistribute photo-assimilates from non-growing, strongly photosynthetic areas to rapidly growing regions, following a source-to-sink pattern of translocation. Translocation of photo-assimilates has been detected in aclonal (Lobban, 1978a,b,c; Buggeln, 1983) and coalescing (Gonen et al., 1996) seaweeds while nitrogen translocations occur in *Caulerpa*, a clonal macroalgae (Williams, 1984).

The scarce data available suggest that translocation may be playing different functions in the different types of seaweeds. In the case of aclonal macroalgae, the sinks include, in addition to intercalary meristems and young blades (Lobban, 1978b,c), the haptera and basal portions of plant. Due to the vertical growth of this type of seaweed, haptera and basal portions of these plants suffer autoshading and require photoassimilates to maintain the plant in position (North, 1971). In the case of coalescing seaweeds, differential translocation of the photosynthates toward the inner (central) parts of sporelings are thought (Maggs and Cheney, 1990; Santelices et al., 1999) to be partially responsible of the higher growth exhibited by the centrally located blades and the size inequalities often found in this type of seaweed. The stoloniferous, creeping axes of clonal seaweeds may colonize dark areas (e.g. crevices, underneath other algae), and perhaps translocation is helping these plant parts to survive and expand under suboptimal light conditions.

The supposed homogeneity of the marine environment with respect to nutrient supply for seaweeds is an additional point to be considered. It is becoming increasingly clear that many species, especially from sheltered reefs and sand flats, are able to absorb organic matter either dissolved in the water or accumulated as particles and sediments in microsites or over the seaweed surface (Williams, 1984; Larned and Stimson, 1996; Schaffelke and Klumpp, 1998; Schaffelke, 1999). Thus, the environment around the seaweed may be very heterogeneous, with patchy distributions of nutrients and significant differences between microsites. Environmental measurements and experimental data are needed to evaluate if there is any convergence in the seaweed strategies used in these habitats to forage for resources and those used by clonal land plants in heterogeneous environments.

2.4. Algal life phases, reproduction and dispersal

Algae exhibit a diversity of life histories. Some may involve development of only one multicellular, generally diploid phase, while others may exhibit an alternation of generations between haploid and diploid phases. In the latter, the alternating generations may have similar (isomorphic) or dissimilar (heteromorphic) morphologies.

Since alternation of generations is understood to be an adaptation to optimize the use of niches differing in some degree with respect to certain environmental characteristics (Keddy, 1989), some relationship may be expected between life history phases and growth patterns. Examination of a few cases suggests (Table 1) some interesting relationships. All growth styles can be found among the different life history phases that occur in seaweeds. However, there are differences in their relative abundances. Species with monophasic (diploid) life histories tend to have a clonal growth; however, they are less represented among the clonal species and notoriously scarcer among the coalescing seaweeds. In fact, the genus *Codium* is included with doubts in Table 1 because coalescence is suspected but not yet demonstrated in that genus.

Species with isomorphic alternation of generations exhibit representatives of the three growth styles, a situation clearly different from the species with heteromorphic life histories (Table 1). The macroscopic phases of heteromorphic species tend to be a clonal or coalescing, with infrequent representation of clonal forms. By contrast, the alternate, often microscopic phase of these species frequently has filamentous or crustose morphologies. These filaments often exhibit clonal growth, while the crusts may have propagation by fragmentation.

The absence of quantitative data on the abundance of species with the various growth patterns, the lack of information on the ecological responses of the microscopic alternate phases and the need to study coalescence among green and brown seaweeds do not allow a critical evaluation of the soundness of the above patterns at this time. However, it is tempting to conclude that the use of different environments by the alternating phases of heteromorphic species not only implies different morphologies but also different growth styles. On the other hand, the abundance of a clonal form among large-sized monophasic

Table 1
Macroscopic phase of several species characteristics of the different growth styles, (Life history type)

Growth style	Monophasic	Biphasic		
		Isomorphic	Heteromorphic	
			Macroscopic phase	Alternate phase
Aclonal	<i>Fucus</i> , <i>Durvillaea</i> , <i>Silvetia</i>	<i>Ulva</i> , <i>Enteromorpha</i>	<i>Laminaria</i> , <i>Porphyra</i> , <i>Scytosiphon</i>	Clonal (filaments or crusts)
Clonal	<i>Caulerpa</i>	<i>Gelidium</i> , <i>Ectocarpus</i>	<i>Ascophyllum</i>	Clonal
Coalescing	<i>Codium</i> ?	<i>Corallina</i> , <i>Mazzaella</i>	<i>Gymnogongrus</i> , <i>Ahnfeltiopsis</i>	Coalescing

(diploid) species and among equally large-sized diploid phases of heteromorphic species suggest that aclonal growth might be more appropriate than clonal or coalescing growth patterns for reaching large sizes in these diploid species and phases. The horizontal spread of clonal seaweeds in a highly variable environment such as the intertidal and shallow subtidal habitats, and the possibilities of propagation through fragmentations appear to ensure survival, growth and propagation but not the acquisition of large sizes. In turn, the scarcity of coalescing species among monophasic species may be related to the significant genetic disturbance that coalescence may incur to species without alternation of generations.

Various aspects of reproduction, dispersal and recruitment of seaweeds have been extensively reviewed in the last 15 years (e.g. Santelices, 1990a, 2002; Norton, 1992; Clayton, 1992; Brawley and Johnson, 1992; Amsler et al., 1992; Vadas et al., 1992), but the patterns and processes discussed have not distinguished between aclonal, clonal and coalescing seaweeds. In recent studies, however, the use of molecular techniques has allowed more accurate measurements, at least of dispersal distances in aclonal and clonal seaweeds. Working with the aclonal, macroscopic phase of *Postelsia palmaeformis* in California, Coyer et al. (1997) found that greatest dispersal occurred over distances of 1.5 m while the dispersal distances recorded for the clonal *Cladophoropsis membranacea* by van der Strate et al. (2002) frequently were 60 cm or less.

Seemingly, no one has measured with similar techniques the dispersal distances of coalescing seaweeds. Studying paternity relationships in *Gracilaria*, Engel et al. (1999) found that 80% of the matting pairs occurred within 85 cm of distance, but spore dispersal might follow a slightly different pattern than gamete dispersal. Recruitment studies done with several coalescing species suggest that (Santelices et al., 1999, 2003b) survival of early developmental stages is a function of aggregated recruitment, which, in turn, relates to spore density and distance from the spore source. Thus, dispersal in this type of seaweed is also expected to be short and probably shorter than in the other two types of seaweeds. Additional studies are needed to evaluate if there is a decreasing gradient of dispersal distance from aclonal to clonal and coalescing seaweeds.

In the seaweeds, there are numerous cases of long-distance dispersal (see examples in Santelices, 1990a; Norton, 1992). In the case of *C. membranacea*, van der Strate et al. (2002) found identical haplotypes at short (20 m) and long (5–10 km) distances. The short-distance dispersal could be explained by spore or gamete dispersal. The long-distance dispersal was more difficult to explain because long-distance gamete dispersal seems unlikely. The authors (van der Strate et al., 2002) suggested that plant fragments could be playing a key role in this process, by drifting away and releasing spores from parent plants.

Spore dispersal by plant fragments has been suggested in the past for aclonal (*P. palmaeformis*, Dayton, 1973; Paine, 1988) and clonal species (*Gelidium sesquipedale*, Seoane-Camba, 1966, 1969). However, there seem to be some more important differences between the two above seaweeds in relation to this process. While in *Postelsia* either fertile blades or the whole fertile plants are dislodged by water movement, in the case of *Gelidium*, only plant fragments are removed late in the fertile season. The percent age of detached fragments of *Gelidium* that are fertile is higher than those values found in the plant parts of the population that remain attached. Seoane-Camba (1969) suggested this to

be a natural spore dispersal method to ensure seeding other areas after seeding the areas around the parent plants.

The above two examples of long-distance dispersal with clonal seaweeds (*Cladophoropsis* and *Gelidium*) are particularly interesting because they suggest that fragmentation might be of some frequency among these types of seaweeds. In land plants, clonal fragments are able to reattach, enhancing asexual propagation, dispersal and invasion of new areas (Eriksson, 1997). In the seaweeds, by contrast, clonal fragments are unlikely to reattach except under calm water conditions. However, they may release sexual or asexual spores, thereby enhancing propagation, dispersal and establishment in new areas.

2.5. Genetic variation and compatibility systems

It is becoming increasingly clear that a great diversity of land plants, invertebrates and seaweeds violate Weismann's (1904) concept of genetic homogeneity of the individual (see reviews in Buss, 1982; Gill et al., 1994; Fageström et al., 1998; Santelices, 1999; Poore and Fagerström, 2000; Hughes, 2002). Among these organisms, two main forms of genetic heterogeneity are recognized. Mosaicism, generally thought to result from intrinsic genetic changes, and chimerism, resulting from grafting, fusion or coalescence among genetically different entities. Formally, a chimera is defined as any organism with two or more cell lines that are derived from different zygotes (Pineda-Krch and Lehtila, in press).

In a mosaic individual, the genetic heterogeneity may originate from somatic mutations, mitotic recombinations, mitotic gene conversions, genome duplications, changes in ploidy levels and transfer of nuclei between vegetative cells (see Santelices, 1999; Poore and Fagerström, 2000 for reviews). In organisms with rigid cell walls, such as land plants or seaweeds, the proliferation of the mutant cells may be localized. Thus, cell-lineage competition, as expected in organisms with mobile cells (e.g. invertebrates), does not occur among land plants nor seaweeds (Buss, 1987; Hughes, 2002). However, the genetic exchange may be inherited by subsequent generations if such exchange occurred in undifferentiated tissue with the capacity for further cell division (meristematic cells) or if it occurred in cells that later produce sexual or asexual propagules (Santelices and Varela, 1993; Poore and Fagerström, 2000, 2001).

Relatively few studies seem to have addressed the problem of genetic mosaicism in asexual seaweeds. In general, it is assumed that the longevity of asexual plants is limited by the accumulation of dead materials, metabolic errors or the physiological problems associated with large size. From that perspective, somatic mutations and other types of genetic exchanges may induce unrepairable metabolic errors and development instability in these organisms (Silander, 1985; Pineda-Krch and Lehtila, in press). However, no studies on the subject in seaweeds were found for this review.

Clonal seaweed exhibit mosaicism and this source of genetic variation seems to play an important function in these species. Since clonal propagation is asexual, without meiosis and fusion of gametes, it is often expected that clonal growth will lead to genetically uniform ramets. However, in both land and marine plants, authors (e.g. McLellan et al., 1997; van der Strate et al., 2002) have remarked on the high levels of genetic variation found in populations of clonal plants. Often this variation is comparable to populations of sexually reproducing organisms. Seemingly, this variability is achieved by intracolonial

variation derived from the genetic exchanges mentioned above (Poore and Fagerström, 2000). Thus, intraclonal genetic changes may constitute a powerful means to generate variation within a population, especially so in thalli that do not become sexually reproductive nor undergo meiosis or sexual recombination.

Coalescing seaweeds also may suffer mosaicism (Santelices and Varela, 1993). In *Gracilaria chilensis*, there are rapid within-individual genetic changes associated to growth (Meneses et al., 1999) or to changes in culture conditions (Meneses and Santelices, 1999). These changes may generate morphological intraclonal variation (Santelices and Varela, 1993) that in this particular species may be expressed in the branching patterns. Intraclonal variation, followed by fragmentation and re-attachment, may increase intra-population variation (Fig. 4). If the variants re-attach in habitats with different selection pressure than that of the original population, and, if the variation is heritable, there is a possibility of genetic differentiation among the two clonal populations (Silander, 1985; de Kroon and van Groenendael, 1990). As Poore and Fagerström (2000) have indicated, the few studies so far designed to detect this kind of variation (Santelices and Gonzalez, 2003; Santelices et al., 1995) indicate that in seaweeds there is the potential for selection upon this variation. In the case of invertebrates (aphids, Hughes, 2002), rapid population growth and amictic inheritance, when combined with strong selection pressure, has led to rapid intraclonal evolution. In the case of seaweeds, the above possibility is highest when the genetic exchanges occur in the free-living haploid state of the life cycle.

Interindividual fusion, coalescence or grafting occurs among the roots of some land plants, several kinds of fungi, modular colonial animals and some groups of red algae, resulting in chimeric organisms (Buss, 1987; Hughes, 1989; Sommerfeld and Bishop,

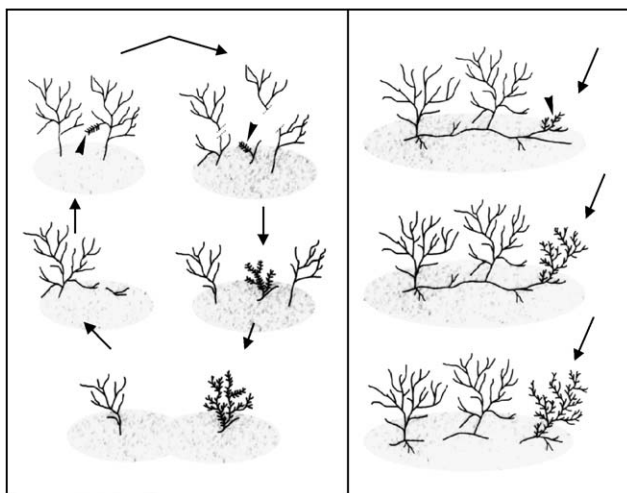


Fig. 4. Intraclonal variation becoming interpopulation variation in natural populations of macroalgae living on soft bottom (e.g. *Gracilaria*, left side diagram) or on rocky bottom (e.g. *Gelidium*, right side diagram). Intraclonal genetic changes may affect external morphology. The new variant (arrow head) may become separated from the parent plant due to fragmentation, grazing or any other natural process. Establishment and proliferation of the new variant as an independent plant would increase the total population variation in that habitat.

1999; Santelices et al., 1999). In fact, this process characterizes coalescing seaweeds. Fusion or coalescence leads to immediate size increase in the fused or coalesced organism. In turn, larger sizes may result in lower mortality due to predation or abiotic extremes and enhance competitive performance for space. In the seaweeds, larger sizes also implies a larger photosynthetically active canopy and higher productivity. Due to unequal growth and concentration of energy into a few, larger axes within the coalesced clumps, the onset of the first reproduction is earlier and the total reproductive output may be larger in coalescing than in non-coalescing individuals (Santelices et al., 1996, 1999, 2003a,b). In addition, the coalesced clumps have greater genetic variation (Fig. 5), which is expected to confer wider ranges of physiological plasticity.

As Hughes (2002) has noticed, among modular animals, the incidence and dynamics of chimera formation may depend on the risk of cell-lineage competition and parasitism. Because animals have mobile cells, one type of cell may replace the other type of cell after fusion (Buss, 1987). The less genetically related the two interacting individuals, the stronger cell-lineage competition and the associated fitness reduction will be. This would explain the evolution of allorecognition systems among chimeric animals. These systems govern whether somatic tissue contacts between individuals would lead to compatible fusion or to histoincompatible reactions, including rejection and non-fusion (Buss, 1987, 1990; Grosberg, 1988; Hidaka et al., 1997; Hart and Grosberg, 1999; Hughes, 2002).

In the case of land plants and seaweeds, the immobility imposed by the rigid cell walls would prevent any new lineage from becoming systemic (Buss, 1987; Hughes, 2002). Therefore, it is expected that land and marine plants would lack any allorecognition system

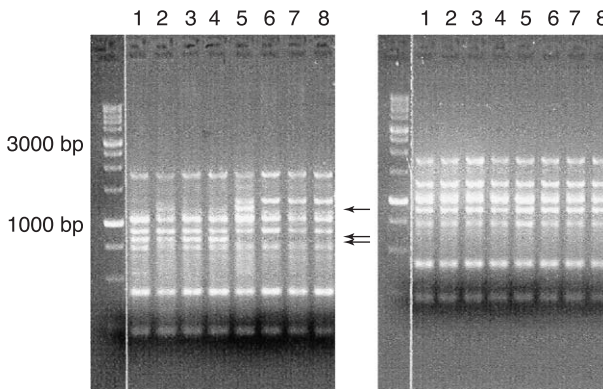


Fig. 5. Chimerisms in clumps of *M. laminarioides* from Maitencillo, Chile. The identity of erect blades taken at regular intervals across a holdfast of *M. laminarioides* was established using PCR-RAPD analysis. Each of the eight gels on the left correspond to individual erect blades from a field coalesced clump (plant no. 125; Santelices et al., 2003a,b). The eight gels on the right correspond to erect blades from a non-coalescing clump (plant no. 144; Santelices et al., 2003a). All blades were sterile gametophytes (resorcinol test), part of fertile cystocarpic clumps. The primer used was X-12 (5' -TCGCCAGCCA-3' ; see Faugeron et al., 2001 for methods). Based on the presence/absence of bands at 800 (double arrow) and 1200 bp (arrow), three haplotypes are distinguished among the blades on the left side group: haplotype 1 (gels no. 1–4) with the band at 800 bp; haplotype 2 (gel no. 5) with band at 1200 bp; and haplotype 3 (gels no. 6–8) with absence of both bands. Banding patterns in the eight gels from the non-coalesced clump are homogeneous, revealing only one haplotype.

that could control fusion or coalescence. Recent testing of this hypothesis with several species of coalescing red algae (Santelices et al., 2003a,b) indeed suggested that coalescence is a less sensitive process to genetic recognition than the colonial fusion described for animals and fungi or than the cell fusion processes described for red algae. Coalescence does not occur between different species, but it may occur between different phases of a similar species and among conspecifics of similar or different ages (Santelices et al., in press). In this seaweed, the most likely mechanism restricting successful coalescence to unispecific partners only seems to be the interspecific differences in growth rates, since a thick interphase with necrotic tissues is found in the contacting border between two interspecific partners. Differences in growth rates could result in the tissue of one partner compressing and eventually crushing the tissue of the other partner.

Even though there is no evidence for the existence of allorecognition systems preventing coalescence in seaweeds, some of the experimental results so far gathered (Santelices et al., 1996, 2003b) suggest interindividual incompatibility among coalescing cells during the differentiation process. Coalescing seaweeds such as *G. chilensis* or *Mazzaella laminarioides* differentiate erect axes from a basal crust. Germlings of both species differentiate comparatively less erect axes when the crust is formed by carpospores from different cystocarps (spores derived from different zygotes) than when formed by spores from the same cystocarp. The lower number of erect axes in the above experiments may indicate a proportionately larger number of initial spores or spore derivatives, unable to develop erect shoots by incompatibility between cells derived from different cystocarps. Additional experimental studies are needed to evaluate this possibility.

3. Ecological responses at the population and community levels

3.1. Intraspecific competition, crowding and the self-thinning law

Until recently, the general view on intraspecific competitive interactions among seaweeds was that traditionally held for any biological population. Under conditions of limiting resources, individuals of the same species will compete among themselves, especially when growing at high densities and the negative effects of this interaction could be measured in different stages of population development. Thus, negative effects on germination and growth could be found among crowded populations growing under constant laboratory conditions (see Santelices, 1990a for review). Newly recruited field populations would exhibit density reductions as the size of the individuals in the population increases (Black, 1974; Schiel and Choat, 1980; Chapman and Goudey, 1983; Santelices and Ojeda, 1984a). The effects of adult algal canopies on juvenile recruitment would generally be negative (e.g. Rosenthal et al., 1974; Santelices and Ojeda, 1984b, Kennelly, 1987a,b) due to irradiance reductions or by the sweeping action of the fronds on the juveniles. Among mature, well-established, monospecific stands of seaweeds, the negative relationship between density and mean weight (or, more properly, between density and stand biomass, Weller, 1987; Scrosati, 1996; Flores-Moya et al., 1996, 1997) would be an expression of intraspecific competitive interactions. In this last case, a negative linear relationship is expected between the logarithmic dimension of both

measurements, with a -1.5 slope and a maximum intercept of 4.3. The relation has been referred to as the $-3/2$ power law or the “self-thinning” law.

Laboratory and field results gathered with clonal and coalescing seaweeds over the last 10 years, however, are changing several of the above views. The crowding effect shown by germinating and growing sporelings does not occur with coalescing seaweeds. Under laboratory conditions, the number of germinating spores of coalescing species is a linear function of initial spore density (Fig. 6), while in clonal species (and probably in aclonal species) it is an optimality function, with maximum germination at intermediate spore densities (Santelices et al., 1999). Crowded cultures of aclonal or clonal species often exhibit high recruit mortality (Fig. 7).

Coalescing species also exhibit exceptional responses in relation to the fate of young sporelings overgrown by larger conspecifics. Traditionally, it has been assumed that overgrown young thalli would be killed by the overgrowing thallus, either due to tissue compression or due to drastic light or nutrient reductions. However, microscopic observations on laboratory cultured sporelings, as well as observations on field recruited spores and juveniles, indicate (Santelices et al., in press) that the young sporelings of coalescing species may be incorporated within the tissue of the larger, overgrowing germling or they may coalesce side-by-side with it, depending on precontact sporeling size

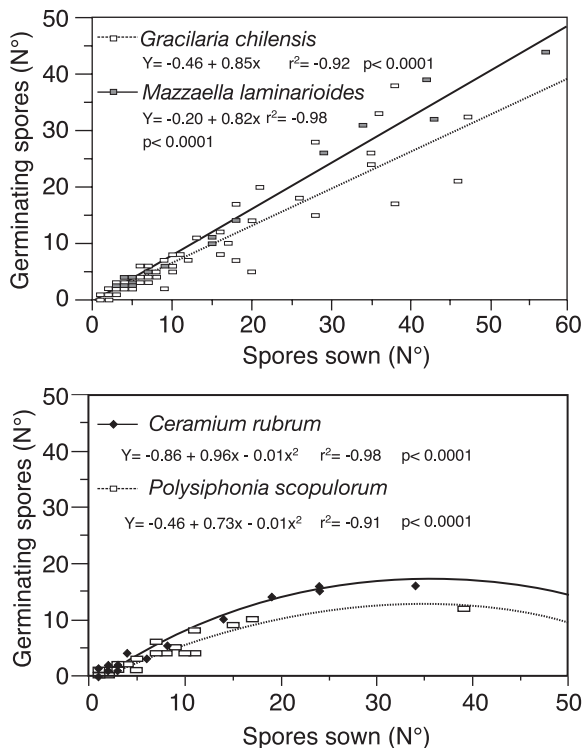


Fig. 6. Spore germination as a function of initial spore number among coalescing (upper figure) and clonal (lower figure) seaweeds (modified after Santelices et al., 1999).

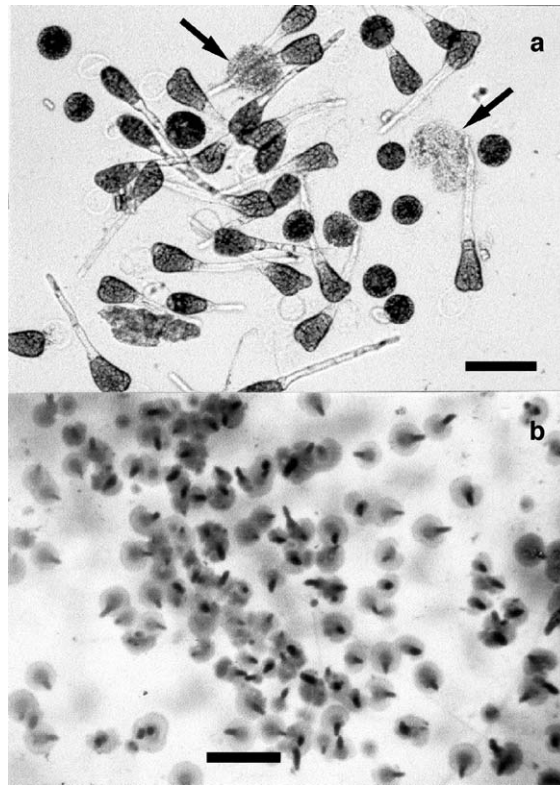


Fig. 7. Crowding effects on germination and early growth of a clonal species (*Gelidium lingulatum*, (a)) and a coalescing species (*Gracilaria chilensis*, (b)). Note the lack of germination (rounded spores without germination tube) and the dead spores (arrows) in *G. lingulatum*. In the case of *G. chilensis*, most sporelings have developed a basal crust and differentiated erect axes and many are coalescing. Scale is 60 μm in the upper figure and 200 μm in the lower figure.

(Fig. 8). Thus, young sporelings of coalescing species do not necessarily die when overgrown by their older, conspecific partners. Field-exposed plates suggest that these processes are common during natural recruitment and that many basal holdfasts of coalescing seaweeds are genetic chimeras due to the incorporation of small germlings into the larger, basal crust of field established clumps (Santelices et al., 2003a, in press).

The shading or the sweeping effects of adult canopies over conspecific recruits is a well-known process, but most of the cases in the literature refer to large-sized aclonal species or phases. In this algal type, shading effects are expected as a consequence of its growth along the vertical axis (e.g. *Macrocystis*, Rosenthal et al., 1974; Pearse and Hines, 1979; Dayton et al., 1984; Reed and Foster, 1984, Santelices and Ojeda, 1984a,b; *Egregia*, Black, 1974; *Durvillaea*, Hay and South, 1979; Santelices et al., 1980; *Laminaria*, Velimirov and Griffiths, 1979; *Ecklonia*, Kirkman, 1981; Kennelly, 1987a,b; *Lessonia*, Santelices and Ojeda, 1984c). This same effect, however, has been shown less often among coalescing or clonal seaweeds. In fact, recruitment of new plantlets in some

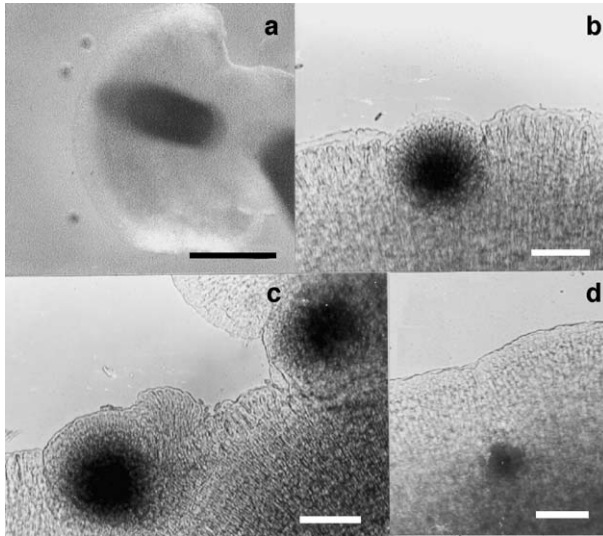


Fig. 8. Overgrowing of spores and germlings by an older and larger sporeling in a coalescing seaweed (*M. laminarioides*). (a) Indicates the position of spores experimentally placed around a laboratory grown, 3-month-old conspecific sporeling; scale: 0.5 mm. (b) Illustrates the younger germling being partially covered by the growing border of the larger sporeling; scale: 60 μm . (c) Shows two younger germlings being incorporated into the basal crust of the larger germling; scale: 60 μm . (d) Younger sporeling incorporated inside the basal crust of the larger sporeling; scale: 100 μm .

coalescing species (e.g. *M. laminarioides*) may be most effective underneath a canopy either of parent plants or of *Enteromorpha* or *Ulva*. Seemingly, the adult blades reduce desiccation of the *Mazzaella* recruits (Santelices and Norambuena, 1987).

The relationship between biomass and density also has been re-evaluated in recent years and results suggest the relationship is variable according to seaweed type. A negative correlation between biomass and density has been found among large kelps (e.g. *Macrocystis*, Reed and Foster, 1984; *Phyllariopsis*, Flores-Moya et al., 1996, 1997). These results are consistent with the assumption (de Kroon and Kalliola, 1995; Petersen and Jones, 1997) that the large size of these aclonal forms may predispose them to self-thinning.

Measurement of self-thinning in clonal seaweeds has yielded mixed results. Lack of self-thinning has been reported for *G. sesquipedale* (Santos, 1995) and *Ascophyllum nodosum* (Lazo and Chapman, 1998) while positive results were found for dense stands of *Asparagopsis armata* (Flores-Moya et al., 1996, 1997). In this last species, however, self-thinning takes place at densities above 2000 shoots m^{-2} , densities that could change seasonally or spatially. Among clonal land plants, self-thinning also seems to be a variable character. It is generally thought (Petersen and Jones, 1997) not to occur among clonal species with ramet densities below levels at which inter-ramet interference occurs. Thus, self-thinning is related to the great sizes of some clonal species and the consequent probabilities for greater intraclone size inequalities and shading. Perhaps, a similar pattern is occurring among the clonal seaweeds.

The few measurements of self-thinning done with coalescing seaweeds (*M. laminarioides*, Martinez and Santelices, 1992 and *Mazzaella cornucopiae*, Scrosati and De Wreede, 1997) indicate that the fronds of these species do not undergo self-thinning, even at the highest observed densities. A potential explanation is emerging from field and laboratory studies on coalescence (Santelices et al., 2003a). In the field, intraspecific encounters of coalescing seaweeds in species such as *Nothogenia fastigiata* or *M. laminarioides* were frequent, reaching up to 45% of the clumps within a growing season. After coalescence, the merging borders of the interacting clumps became the new center of the coalesced clump. Prior to coalescence, the erect fronds at the merging borders were typically short and dwarf. After coalescence, these same fronds developed longer and thicker erect axes, which eventually became the largest fronds in the clumps. Thus, although there is a re-arrangement of frond sizes within the coalesced clumps, it is not accompanied by frond losses. On the other hand, the number of erect axes arising from a juvenile crust is a function of the number of coalescing spores forming the crust (Santelices et al., 1999) and eventually of the number of crusts coalescing together. Thus, among coalescing seaweeds, the dynamics of the biomass–density relationship and the factors determining the results of this relationship appear to be completely different to those affecting density and biomass in clonal and aclonal seaweeds. In field populations of coalescing species, coalescence seems to replace intraspecific competition between conspecific partners (Santelices et al., 2003a).

The adaptive value of crowding has been further investigated by Scrosati (2000) studying the stand biomass and ramet density of a clonal (*Pterocladia capillacea*) and a coalescing (*M. cornucopiae*) seaweed species. He found that frond densities of both species were similar to the highest values reported for terrestrial plants, while stand biomass was higher than the average values expected from the terrestrial interspecific biomass–density relationship. Ramets of both species were found to be less slender than land herbs and to pack more biomass per unit of volume occupied than herbs. Scrosati (2000) suggested that crowding in the habitats where these species occur would help to reduce desiccation of ramets and to protect the understory from high irradiance during low tide (Hay, 1981). Crowding also probably reduces the rate at which temperature increases within the seaweed patches during the warmer season, and larger and more crowded seaweed patches would also survive strong water movement better than small or loosely packed patches. Although crowding could also result in mutual frond shedding, Scrosati (2000) suggested that this could be counter-balanced by periodic exposure of the shorter, overshadowed ramets to sunflecks aided by water movement. In addition, translocation and physiological integration may allow for the survival and growth of the overshadowed ramets. Therefore, predictions on the biomass–density relationships in the algae should consider the type of algal growth and the type of habitat where the population occurs.

3.2. Interspecific competition

Middle intertidal to shallow subtidal rocky bottom communities in temperate latitudes and low intertidal to shallow subtidal reefs in tropical latitudes are often characterized as habitats with intense inter- and intraspecific competition among sessile plants and animals (see Menge and Branch, 2001, Witman and Dayton, 2001 for recent reviews). Since space

may be limiting in these habitats and seaweed growth and production may surpass grazer control, seaweeds are among the organisms that traditionally have been regarded as important competitors (e.g. Dayton, 1975, Lubchenco, 1978, 1980; Lubchenco and Menge, 1978; Sousa, 1979; Santelices et al., 1980, 1981, 1990b; Foster, 1982, 1990; Underwood and Jernakoff, 1981; Kastendiek, 1982; Jernakoff, 1983, 1985; Johnson and Mann, 1986; Carpenter, 1990; Maggs and Cheney, 1990; Reed, 1990; Steneck et al., 1991; McCook and Chapman, 1993; McCook et al., 2001; Keats et al., 1997; Tanner, 1995; Hixon and Brostoff, 1996; Miller and Hay, 1996; Worm and Chapman, 1996, Creed et al., 1998; Figueiredo et al., 2000; Jompa and McCook, 2002a,b). Kelps, fucoids, calcareous and non-calcareous crusts, and some foliose red algae are among the taxa most frequently described as successful competitors in these intertidal and subtidal environments.

The possibility of experimentally demonstrating competition together with the interest in establishing its role as a factor causing and maintaining ecological patterns have stimulated the study of this interaction. Additionally, in intertidal and shallow subtidal communities, the existence of resources in shorter supply than those required by the diversity of species using them (e.g. two-dimensional space) and the often high intensity and permanence of the interactions among species in these communities (Underwood, 2000) have all contributed to the popularity of competition studies in these systems. However, competitive interactions are complex processes and some basic understanding of a few parameters are needed in order to set up an adequate experimental design (Underwood, 1986, 1992). These include, among others, understanding the scale of the process, some idea of the mechanism involved, proper identification of the competing partners, the expected outcome of the interaction and some approximation to the rate of renewal of the resource.

Comparative competition studies done with land plants suggest (Herben and Hara, 1997; Collado-Vides, 1997) differences in the expected outcomes of the interactions between asexual and clonal species, which also seems to apply to seaweeds. Interspecific competition among asexual plants is hierarchical and the outcome of the interaction is often of the type dominance/exclusion. In the case of clonal plants, with their horizontally extended thalli simultaneously exploiting many microsites, reversals in the direction of competition and competitive networks are frequent. In fact, several studies (reviewed in Herben and Hara, 1997) have shown long term coexistence of species-rich clonal plant communities. Architectural species constrains, intransitive competition and fine scale disturbances are the most relevant factors allowing coexistence of these species.

Similar comparisons in the seaweeds are lacking. However, some of the results so far gathered tend to support the above distinction especially when studying competitive interactions among species with similar growth styles. Thus, competitive interactions among asexual phases or species generally result in competitive displacement and exclusion. This is the cases, among others, with *Hedophyllum sessile* and *Lessoniopsis littoralis* (Dayton, 1975), *Lessonia nigrescens* and *Durvillaea antarctica* (Santelices et al., 1980), *Fucus evanescens*, *F. spiralis* and *F. vesiculosus* (Chapman, 1990, 1995; Chapman and Johnson, 1990), *Macrocystis pyrifera* and *Pterygophora californica* (Reed, 1990; Reed et al., 1991). The outcome of the interaction, in favor of one species or the other, may be mediated by grazing, abiotic extremes or both factors. However, the end result in all these cases seems to be the exclusion of one species or phase by the other.

Competitive interactions among clonal seaweeds have not yet been experimentally tested. However, there are field observations and measurements suggesting a similarity with the patterns observed in clonal land plants. In her study on the spatial and temporal relationships among benthic algal species in a subtropical intertidal habitat in Hawaii, McDermid (1988) found a competitive network that included 10–12 clonal species (Fig. 9). During the study period, some species such as *Hypnea chordacea*, *Laurencia majuscula* and *L. yamadana* consistently won space from other species. However, there were several examples of reversal. In addition, the network included several cases of symmetrical competition between species with neither species dominating, and intransitive interactions in which lower-ranking species outcompeted superior species (Fig. 9). In this system, some seasonal climatic changes did not result in discernible alterations in the mosaic spatial pattern of abundance of these seaweeds. Therefore, McDermid (1988) concluded that the coexistence of these many species was preserved by low-level abiotic disturbances and a balance of variable abilities of the algae to colonize, compete and persist.

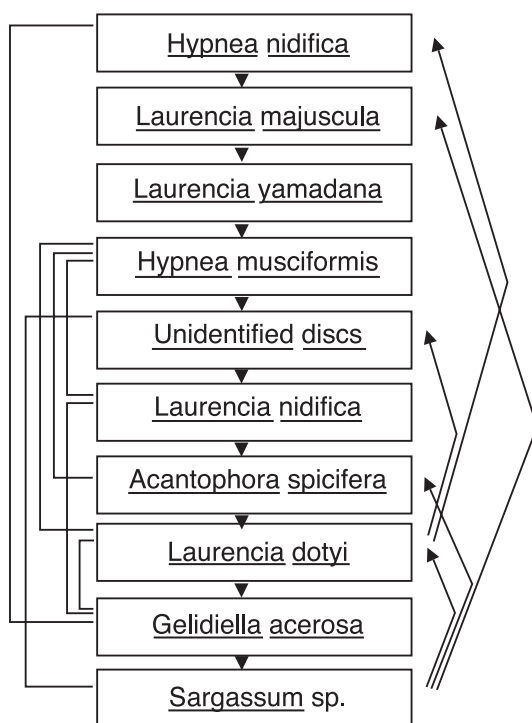


Fig. 9. Competitive network described for a subtropical turf seaweed community on an intertidal reef in Hawaii. Arrow heads indicate the dominance hierarchy and lateral arrows the competitive reversals observed. Cases of symmetrical competition are indicated by the solid lines on the left side of the species names. All taxa in the network identified to species have clonal growth. Reproduced after McDermid (1988) with permission from the author.

Although in temperate latitudes the competitive networks are likely to involve less species, coexistence might also occur. Working with *Gelidium lingulatum* and *G. chilense* (as *G. filicinum*), Montalva and Santelices (1981) found the two species overlapped along much of their vertical extent. There were seasonal changes in standing stocks of both species and these were negatively related among them. However, both species coexisted at the same tidal elevation, without exclusion.

Competitive networks with intransitive interactions and reversals also seem to characterize competition among coalescing species. Working with two species of *Pseudolithophyllum*, one species of *Lithothamnion*, another of *Lithophyllum* and the crustose base of *Bosiella*, Paine (1984) found that reversals in the direction of competition via overgrowth were common. Such reversals added uncertainty to the system, contributing to the potential coexistence of species by retarding the rate of competitive exclusion. In this case, coexistence was attributed (Paine, 1984) to the different species responses to grazing and biologically mediated disturbance. Some species could grow fast but were very sensitive to grazing. Others, with thicker, more grazing resistant crusts, had slower growth rates. More recently, Santelices et al. (2003b) have drawn attention to the need to evaluate the importance of crust thickness, growth rate and ways in which the crusts use the substratum in order to explain the outcome of competitive interactions during early growth between the coalescing *M. laminarioides*, *Nothogenia chilensis* and *S. crispata*. Differential use of the substratum may delay interspecific exclusion.

Competition may also occur among species with different growth styles (aclonal, clonal, coalescing), with a variety of outcomes that together illustrate the three general types of competition recognized in marine systems (Underwood, 2000). Low stature clonal species seem to be particularly effective in pre-emptive competition. In this type of interaction, the use of the space by these clones may prevent recruitment of other species that settle from the water column. This is the case with understory vegetation that prevent the recruitment of canopy forming species and, in general, is the case with clonal and ephemeral species that prevent the recruitment of other, often larger-sized, seaweeds (Lubchenco and Menge, 1978; Lubchenco, 1980, 1982, 1983; Underwood and Jernakoff, 1981; Sousa et al., 1981; Ojeda and Santelices, 1984; Hawkins and Hartnoll, 1983; Cubit, 1984; Dayton et al., 1984; Chapman, 1995; Kim, 1997). Although the clonal turf may prevent settlement or recruitment of many kinds of algae and even invertebrates, the group most frequently affected by pre-emptive competition seems to be the aclonal species, because they propagate exclusively by sexual or asexual spores.

Calcareous and non-calcareous coalescing crusts may also prevent settlement of propagules of other algal species. Allelopathic effects have not always been evaluated in this type of interaction and therefore cannot be ruled out (Worm and Chapman, 1996). However, most of the evidence suggests epidermis surface “sloughing” off may play a significant role in this process. Epidermis surface sloughing off has been reported for both calcareous and non calcareous crusts (Sieburth and Tootle, 1981; Johnson and Mann, 1986).

After recruitment and while growing, large-sized, aclonal species and phases are often involved in interference competition. The expansion of their attachment structures during growth gives them the capacity to overshadow, compress and eventually kill all other types of seaweeds (Kain, 1969; North, 1971; Dayton, 1975; Dayton et al., 1992; Santelices and Ojeda, 1984b; Stachowicz and Hay, 1999; Witman and Dayton, 2001). As indicated

earlier, the competitive outcomes of contests including large-sized aclonal species and phases are often of the suppression-exclusion type.

Among seaweeds, exploitative competition seems to have been infrequently studied and the few experiments done under laboratory conditions (Russell and Fielding, 1974; Enright, 1979). The limited number of studies on exploitative competition performed to date with macroalgae are insufficient to permit analysis regarding potential differences among aclonal, clonal and coalescing-type seaweeds with respect to their exploitation capacities of different resources.

3.3. Seaweed herbivory

Herbivory is one of the dominant factors affecting the distribution and abundance of seaweeds in marine systems (Hay, 1997). To persist in these systems, seaweeds must escape, tolerate or deter herbivores (Hay and Fenical, 1988; Duffy and Hay, 2001). Thus, escape mechanisms (in space, time or size) depend on morphology and size but also on algal life history, productivity and tolerance to abiotic extremes (Lubchenco and Gaines, 1981). Algal tolerance to herbivory depends (Carpenter, 1986; Lewis, 1986) on the capacity of ungrazed algal parts to regenerate grazed parts and on the possibilities that algal spores or vegetative portions will be able to withstand gut passage, a characteristic that has been related to life history strategies (Santelices and Ugarte, 1987; Buschmann and Santelices, 1987). Deterrence of herbivores depends on the presence and abundance of chemical deterrents in the algal thallus, morphological defenses, mechanical and structural components, food quality and phenotypic plasticity (Padilla, 1985; Hay and Fenical, 1988; Padilla and Allen, 2000; Duffy and Hay, 2001).

Since none of the above functions depends only on algal growth style, no obvious relationship is expected between growth pattern and herbivory. In fact, the complexities found in all the above responses conferring protection to seaweeds from herbivory have advised abandoning previous models (e.g. Littler and Littler, 1980; Steneck and Watling, 1982; Steneck and Dethier, 1994) describing general relations between algal morphology and herbivory. In addition, predictions of herbivory based on a single factor (e.g. morphology, growth style) are difficult to evaluate because morphological patterns can be confounded with other defensive mechanisms (e.g. chemical defenses) that may also correlate with morphology. Duffy and Hay (2001) have drawn attention to the case of coralline algae. The low palatability of these species was generally attributed to calcification (Lubchenco and Gaines, 1981). However, later research (Hay, 1984; Paul and Hay, 1986; Hay et al., 1994) found many calcified tropical seaweeds also produced chemical defenses. Thus, the low palatability of calcified species could be due to calcification, chemical deterrents or both.

The lack of correlation between growth styles and protective mechanisms from herbivory (escapes, tolerance and deterrents) are further substantiated by the simultaneous representation of all types of protective mechanisms among seaweeds with different growth styles (Table 2). In fact, some seaweeds might exhibit more than one protective mechanism, that may function either additively or synergistically to reduce susceptibility to consumers (Hay et al., 1994; Meyer and Paul, 1995; Duffy and Hay, 2001). The only

Table 2

Protective mechanisms against grazing in macroalgal species with different growth patterns

Growth style	Escape			Tolerance		Defenses	
	Time	Space	Size	Regrowth	Spore survival	Morphology	Chemical
Aclonal	<i>Petalonia</i>	<i>Ulva</i>	<i>Durvillaea</i>	?	<i>Ulva, Porphyra</i>	<i>Lessonia</i>	<i>Fucus</i>
Clonal	<i>Rhizoclonium</i>	<i>Bostrychia</i>	<i>Sargassum</i>	<i>Rhizoclonium</i>	<i>Cladophora, Gelidium</i>	<i>Halimeda</i>	<i>Caulerpa</i>
Coalescing	<i>Gigartina</i>	Upper intertidal <i>Ahnfeltia</i>	<i>Gigartina skottsbergii</i>	<i>Gracilaria Porolithon</i>	<i>Mazzaella</i>	Calcareous crusts	<i>Plocamium</i>

exception to this pattern (Table 2) is the absence of aclonal species from those able to tolerate herbivory through regrowth.

4. Conclusions

The combination of biological characteristics and ecological responses discussed above support the idea of distinguishing three macroalgal groups, aclonal (unitary), clonal and coalescing species, based on their growth styles, their regeneration and fusion capabilities and the resulting genetic make-up. In some of the above characteristics and responses, these algal groups reproduce patterns that parallel the distinctions of clonal from aclonal land plants (e.g. morphology, self-thinning responses) and colonial from unitary animals (e.g. genetic variation, adaptive value of coalescence). However, the seaweeds also exhibit their own characteristics (e.g. translocation, alternation of generations) probably related to their own history as a group.

Assigning individual algal taxa to aclonal, clonal or coalescing groups may be a difficult task due to several factors. First of all, there is a lack of knowledge on growth patterns, life history processes and ecological response of many seaweeds in the field. Sometimes key ecological processes (e.g. clonal growth, translocation) have been demonstrated in one or just a few species in a major taxonomic group and it may not always be accurate to expand those findings to all members of such taxonomic groups, especially when these are morphologically and physiologically variable. Other times, processes that now appear relevant (e.g. coalescence) have not previously been studied in different groups or their experimental analysis has been too recent to include enough representative species of different phylogenetic groups. Second, some of the group separations are not mutually exclusive. For example, some coalescing seaweeds may also respond as clonal species due to their regeneration capabilities. Finally, there is a need to quantify the frequency and to test the generality of key events related to the nature of some of the algal groups here distinguished. One such case is coalescence. Under laboratory conditions, coalescence has been observed in over three dozen species, yet under field conditions it has been only quantified in one species (Santelices et al., 2003a, 2004). At present, we know nothing with respect to the frequency coalescence occurs during the life time of the individuals in a given population, nor if it is an obligatory process in any seaweed species.

Difficulties encountered in assigning a given species to one group or other, however, should not result in to ignoring the existence of these groups. Future research with additional species would help to better define the above algal groups, to validate the differential responses outlined above, and also it may contribute to uncovering additional groups with yet unknown growth styles among the seaweeds.

Algal grouping based on growth styles, regenerating capabilities and genetic make up should not be confused with the form-function hypothesis (Littler and Littler, 1980), which also attempted to predict ecological responses in various algal groups based on external morphology. As Collado-Vides (2002a) explained, the clonal growth style in the algae may be exhibited by a diversity of species with different morphologies, including coenocytic (e.g. *Caulerpa*), filamentous (e.g. *Hincksia*), thin corticated (e.g. *Gelidium*), thick corticated (e.g. *Ascophyllum*) and articulated calcareous (e.g. *Halimeda*) species. Although morphologically less diverse, the aclonal group also comprises a variety of morphological constructions, including thin, membranous forms (e.g. *Ulva*, *Enteromorpha*), kelp-like, forms (e.g. *Durvillaea*, *Lessonia*), tubular and globose forms (e.g. *Adenocystis*, *Colpomenia*) and fucoids (e.g. *Fucus*, *Pelvetia*). Even though the group of coalescing species appears morphologically more homogeneous than the other two groups, it still includes calcareous crustose (e.g. *Mesophyllum*), calcareous articulated (e.g. *Corallina*), thin corticated (e.g. *Gracilaria*) and frondose (e.g. *Sarcothalia*) species, and perhaps, coenocytic forms (e.g. *Codium*).

The diversity of forms included in each group involves major conceptual differences with the form-function hypothesis (Padilla and Allen, 2000). In the present proposal, arrangement is based on a specific function (growth style, including re-growth and fusion capacities) and species are allocated to groups based on that criterion and independent of morphology. In contrast, the form-function hypothesis assigns species to groups solely based on their external form and the functions are inferred. Authors (Littler and Littler, 1980; Steneck and Watling, 1982; Steneck and Dethier, 1994), assumed that all functions, including primary productivity, growth rates, competitive ability, resistance to herbivores, resistance to physical disturbance and tolerance to physiological stress, were correlated with each other and similarly correlated with morphology. Later studies have experimentally shown these supposed correlations do not hold true (see Padilla and Allen, 2000 for review).

Future studies testing growth patterns and ecological responses among seaweeds should be aware of the problems associated to phylogenetic relatedness. Closely related species are expected to have more similar features and growth styles, than more distantly related species (de Kroon and van Groenendael, 1990; Padilla and Allen, 2000). This lack of independence due to a shared phylogenetic or evolutionary history means that testing correlations between growth styles and other specific responses should only include distantly related taxa or take evolutionary relatedness into account statistically (Felsenstein, 1985). Perhaps, the greater homogeneity of forms and ecological responses presently observed among coalescing species may be influenced by this factor.

While reviewing modes of fertilization, reproduction, dispersal and recruitment in the seaweeds, Santelices (1990a, 2002) found the macroalgae may combine their own processes and responses typical of seaweeds with patterns and responses analogues to those of land plants and marine invertebrates. For example, this is the case of external

fertilization. In many brown and green algae, the process is similar to that of broadcasting invertebrates, whereas fertilization in red algae is internal and much closer to the brooding process, a pattern also found in terrestrial (e.g. wind-pollinated) plants (Santelices, 2002). Grouping macroalgae by growth styles, as proposed here, reproduces the above situation in the sense of including patterns known for land plants (clonal, aclonal growth) with others known for aquatic animals (interindividual fusion and chimerism). The parallel with land plants is perhaps related to phylogenetic relationships (Karol et al., 2001), which not only involves cellular and subcellular components, but also some general patterns of body organization and growth. The similarity with growth responses of aquatic invertebrates, on the other hand, may be interpreted as a case of ecological convergence, determined by the co-occurrence of aquatic invertebrates and seaweeds in the same environment. Therefore, it seems that in order to understand ecological patterns and processes in the seaweeds, there is a need to understand not only their own responses but also those related to their history and to the type of habitat they occupy. Future research would probably indicate how much of the present theory on clonal organisms and relevant ideas on chimeric colonial animals could be applied to the seaweeds. Today, both theoretical bodies are useful reference frameworks to advance the unstudied biological aspects of the macroalgae and to search for transphyletic ecological patterns associated to different growth styles.

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