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Clonal architecture in marine macroalgae: ecological and evolutionary perspectives

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Abstract. The study of the ecological and evolutionary consequences of clonal growth in vascular plants has been widely addressed; however, marine macroalgae, which are interesting modular organisms that combine 'simple' morphologies and complex life cycles, have been almost ignored. This paper presents a review and analysis of the ecological and evolutionary consequences of clonality in marine macroalgae, including three main subjects: (1) modular construction; (2) life cycle and evolutionary perspectives, and (3) ecological perspectives of clonality in marine macroalgae. The main biological attributes of clonality are present in marine macroalgae such as high longevity of the genet by the continual renewal of modules, and variable morphological plasticity of ramets and modules in relation to environmental conditions. However, experimental work is still needed to solve questions such as the effect of crowding on survival rates and use of resources, as well as its effect on sexual or asexual patterns of reproduction. I expect that the study of the evolutionary consequences of the combined presence of alternation of generations and clonal growth in marine macroalgae will make important contributions to clonal plant theory.

Key words: Macroalgae, clonal, marine algae, algal architecture modules, rammets

Introduction

The architecture of any organism is the result of the developmental rules of growth that determine the form of the adult individual. In modular organisms, architecture refers to the construction of an individual based on the repetition of multi-cellular units or modules (metamers; Harper and Bell, 1979; Harper, 1981; Hardwick, 1986; Mackie, 1986; Williams, 1986). In architectural terms, the modular form is determined by 'rigid' (genetic) iterative rules (branching) and differential responses of the parts to localized environmental variation (morphological plasticity; Franco, 1986). In other words, growth is the result of the iteration of connected multi-cellular units (Waller and Steingraeber, 1985). These units are functional, semi-autonomous, ecologically interactive and reproductive (Toumi and Vuorisalo, 1989).

The fact that modular growth is the iteration of functional semi-autonomous units implies that the development of a genetic individual (defined as the program from zygote to zygote) is achieved by progressive, iterative growth (Harper, 1981, 1985). Plant development, in contrast to animal development, is a flexible, life-long process because plants have an open organization with no programmed events in early ontogeny such as cleavage and gastrulation (Niklas, 1994).

The ecological and evolutionary consequences of modular, clonal construction in plants have been widely analyzed in vascular plants (Schmid, 1990) and invertebrates (Jackson *et al.*, 1985). However, algae have usually been ignored in this context. At the same time ecological and evolutionary studies on marine macroalgae have rarely made an attempt to apply concepts and predictions developed for clonal plants. I will try and incorporate clonal plant theory as background for studying the ecology and evolution of marine macroalgae. Consequently, the goal of this paper is (a) to mention different forms of clonal growth in marine macro-algae, (stoloniferous, common holdfast, crusts), (b) to identify the basic units of construction (modules and ramets) of those forms, and (c) to analyze some likely ecological and evolutionary consequences of clonality in this group of organisms. For the purpose of this review, marine macroalgae will be defined as any kind of algae that are bigger than 1 cm in size and that belong to one of the three main algal divisions Chlorophyta (green algae), Rhodophyta (red algae) and Phaeophyta (brown algae).

The paper is organized into three main sections. First, I will give a brief description of different morphological types of clonal growth in marine macroalgae followed by a discussion of the units of construction in clonal macroalgae. The second topic focuses on aspects of the life cycle of marine macroalgae, thereby exploring possible evolutionary consequences of the alternation of generations and clonal growth. Finally, I will address some ecological consequences and perspectives of clonality in the context of longevity, and the relationship between the form and density in population studies of marine macroalgae.

Clonal growth in marine macroalgae

Clonal growth in algae is present within the three main algal divisions Chlorophyta (green algae), Rhodophyta (red algae) and Phaeophyta (brown algae). 'Heterotrichy' is a stoloniferous type of growth that manifests itself in a thallus (i.e. plant body) consisting of two distinct parts: a prostrate creeping system (stolon) usually exhibiting apical growth and giving rise to an erect system, which is usually branched (Fritsch, 1935; Fig. 1A). A frequent stoloni-

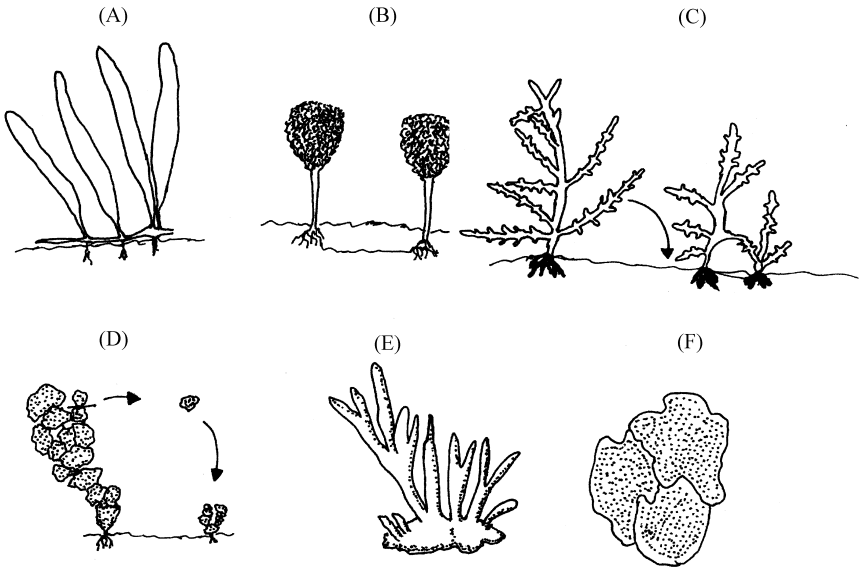

Figure 1. Different types of clonal growth present in marine macroalgae. (A) Stoloniferous growth of a coenocytic *Caulerpa*. (B) Buried stolon giving rise to two potential ramets in *Penicillus*. (C) Branching bending and re-attachment in *Laurencia*. (D) Fragmentation in *Halimeda*. (E) Fronds growing from a holdfast. (F) Crustouse growth.

ferous mode of growth occurs in filamentous brown algae of the order Ectocarpales. In the red algae this type of growth is found in species such as *Gelidium sesquipedale* (Santos, 1993), *Bostrychia radicans* (Collado-Vides *et al.*, 1997), and also in coenocytic (i.e. multinucleate single cell organisms) green algae such as in the genera *Caulerpa* (Jacobs, 1994; Meinesz *et al.*, 1995), *Penicillus*, and *Udotea* (Friedmann and Roth, 1977; Hoeck *et al.*, 1995).

Another type of clonal growth in macroalgae, the 'common holdfast growth', is achieved by the production of an initial, prostrate, basal system, from which one or more erect thalli may develop (Coomans and Hommesand, 1990; Fig. 1E). Examples include the red algae *Corallina officinalis* (Littler and Kauker, 1984) the green algae *Blidingia minima* (Garbary and Tam, 1989), the red algae *Mazzaella cornucopiae* (Scrosati and De Wreede, 1997, 1998), and the brown algae *Ascophyllum nodosum* (Lazo and Chapman, 1998).

Crusts are also a clonal mode of algal growth. They are characterized by apical activity at the margin of the plant body, resulting in a horizontal cover of the substrate without any erect axis (Fig. 1F). Common red crust include species of *Mesophyllum*, and some brown crusts belong to the genus *Ralfsia*. Crust are common in almost all marine substrates from temperate to tropical areas (Taylor, 1960; Steneck and Adey, 1976; Paine, 1984).

Clonal growth can also be realized by the bending of erect branches and by the re-attachment of the apical cell to the substrate, initiating the growth of a new thallus also. Asexual propagation can occur (Fig. 1C) by means of algal fragments that re-attach to the substrate (Fig. 1D).

Modules and ramets

As in vascular plants, the plant body or genetic individual (genet) of marine macroalgae is the result of the development of a single zygote into a sessile branched organism with an inherent hierarchical architecture that consists of a set of modules and/or ramets.

Modules

The module is defined as 'the multi-cellular unit of construction that is iterated in the process of growth' (Harper *et al.*, 1986). Some algal cells divide throughout their lifespan. They are permanently dividing like a multicellular meristem, thereby giving rise to branched organisms with different levels of organization. Patterns of thallus growth and the morphological complexity of marine macroalgae have been described in detail elsewhere (Fritsch, 1935). In this review I will focus on their modular construction.

Filamentous thalli are constructed by the iteration of a single cell. These algae can be simple or branched single cell series, and the module can be defined as result of the apical, basal or intercalary cell that is constantly dividing (Fig. 2A). The result of the division of the apical cell is either the elongation of the main axes of the filament or a new growing axes (a branch). Branches are the iterated units in the process of growth, then branches are the modules. Medullar organisms are tightly packed filaments where the medullar branch is the module. The module is the result of the apical, intercalary or basal cell that is constantly dividing (Fig. 2C). Parenchymatous organisms are the result of a change in the plane of division of the apical cell; as a consequence, they are medullar branched organisms (Fig. 2D), and each branch can be identified as a module.

Coenocytic organisms are multinucleate, single cells with different levels of morphological complexity ranging from simple filamentous forms, such as *Caulerpa* species, to highly organized forms as a result of the intermingling of filaments, like *Halimeda* and *Codium*. In these cases, the module as a multicellular unit is difficult to identify because no cell walls exist in the thallus. However, these algae also grow by iteration of similar units, such as erect fronds or branches rising from an stolon (Fig. 2B). As a result we have branched sessile organism without cell walls, where the module is any part of the single cell organism that can be identified as a branch.

All clonal macroalgae, including coenocytic thalli, are sessile, branched organisms with a hierarchical organization (presence of modules, ramets and

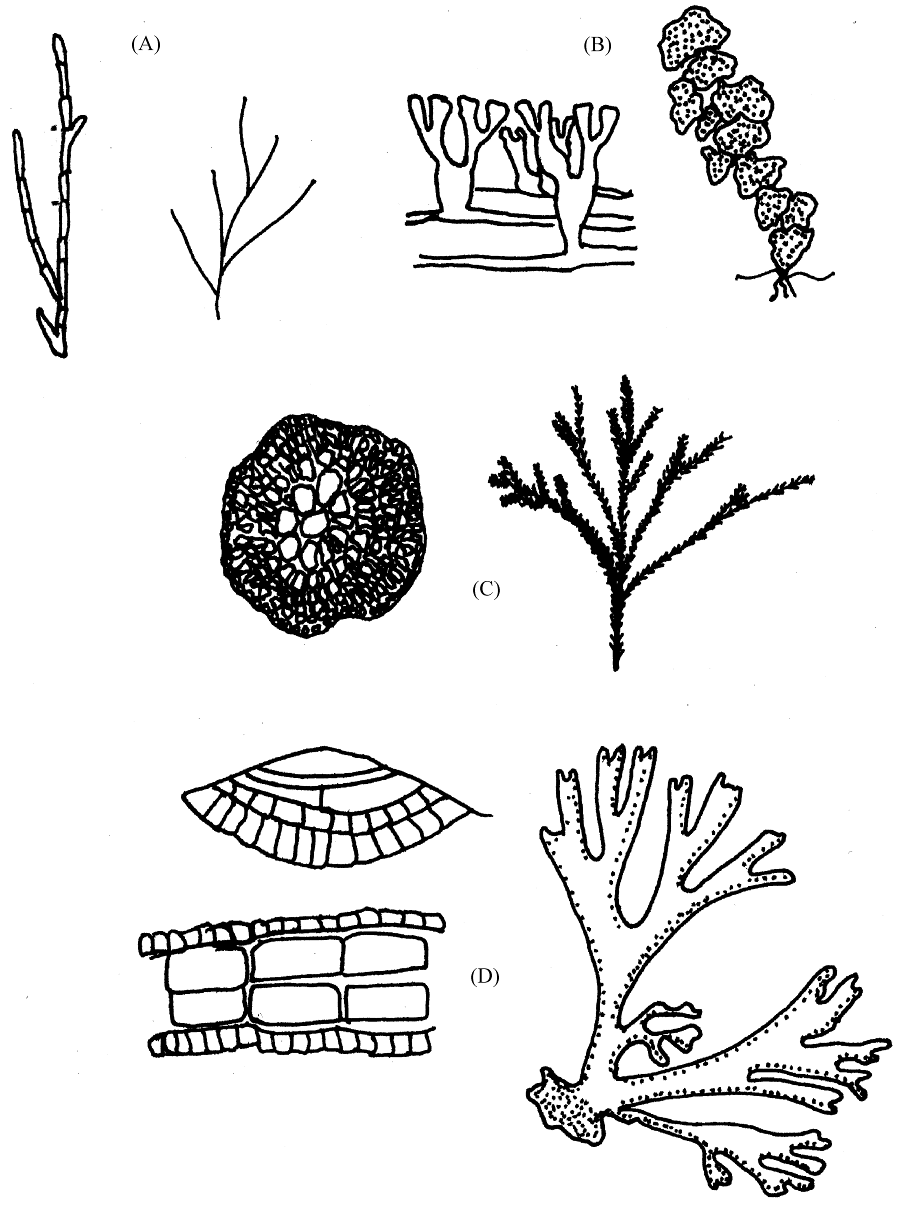

Figure 2. Different levels of organization in marine macroalgae. (A) Uniseriate branched filament. (B) Coenocytic organization. (C) Medullar or pseudo-parenchymatouse organization. (D) Parenchymatouse organization.

genets). The module is either a filament branch, a medullar (with a parenchyma or only packed filaments) branch, or a coenocytic branch.

Ramets

Ramets are potentially independent units and they are defined as the smallest physiologically integrated parts of a genet (Toumi and Vuorisalo, 1985). Some modular organisms have the ability to disintegrate and give rise to plant parts that behave as independent organisms. There is a continuum of organisms, ranging from those in which modules remain physically attached to forms where modules become physiologically and physically independent. A consequence of this architectural variation is that natural selection may act on different hierarchical levels of biological organization (i.e. cells, ramets and genets). Independent ramets act as ecological and functional individuals but they belong to the same genetic individual or genet (Eriksson and Jerling, 1990). Because algae lack organ differentiation, any module (branch) has the potential to became an independent individual, and became a ramet in functional terms. It is known that in marine macroalgae almost any segment of the branched thallus has the ability to produce a new individual. This is exemplified by the case of species where any branch can give rise to a new organism, such as many red algae (Santelices and Varela, 1993). Therefore, the definition of ramet should be any algal fragment with the ability to reattach to the substratum and develop as a new individual. Not all the branches will fragment from thalli; many of them will remain attached to the genet. No information exists on how long a ramet will remain attached. Studies that analyze the morphology and ecology of different groups of algae in relation with ramet biology are still needed.

Fragmentation: ramet examples

In marine marcroalgae, totally independent individuals (independent ramets) are produced by the process of fragmentation, which is very common in all algal divisions. Small pieces such as segments in the calcified, branched green algae *Halimeda* (Walters and Smith, 1994) and the red algae *Corallina* (Littler and Kauker, 1984) have the ability to reattach to the substrate and form a new individual which functions as an independent ecological unit. The same is true for broken branches in many fleshy red algae such as *Acantophora spicifera* and *Hypnea nidifica* (Mshigeni, 1978) or in the commercial production of *Gracilaria chilensis* (Meneses and Santelices, 1999) by fragmentation. The process of fragmentation is particularly important for the spread of the invasive coenocytic species *Caulerpa taxifolia* in the Mediterranean sea, as this is the only known way of dispersion in this species (Meinesz *et al*., 1995). Fragmentation followed by re-attachment can counteract the negative effects of damage (e.g. by herbivory) on algal populations, possibly leading to an increase in plant numbers after grazing in reef habitats (Walters and Smith, 1994). In seaweeds, fragmentation is a frequent mean of maintaining freefloating populations (Lobban and Harrison, 1997). In fact fragments are likely to grow and spread faster than spores or other types of microscopic propagules (Meneses and Santelices, 1999).

Coalescence of sporelings and fusion of individuals

A process that complicates the identification of ramets and genets in algae is the coalescence of sporelings and the fusion of individuals. Sporeling (first stages of spore growth) coalescence (the capacity of some red algae sporelings to grow together to form a completely merged, mass giving rise to genetically polymorphic thallus) has been described for some red benthic macroalgal species (Maggs and Cheney, 1990; Santelices *et al*., 1996, 1999). Fusion of crusts is also a process that combines genetically different individuals. Paine (1984) mentions the fusion of marine crusts in a common garden experiment. In both cases (coalescence and fusion) the genetic identity of erect branches is difficult (if not impossible) to assess. Coalescence and fusion may lead to the presence of more genets within one ramet.

Algal life cycles

Life cycles in algae are complex and variable. Sexual reproduction may involve only one multicellular phase, or an alternation between haploid and diploid phases with extensive multicellular development within both phases. In diploid individuals, known as diploid phase (2N phase individuals), meiosis occurs and produces meiospores . There spores give rise to individuals with half of the genetic content known as haploid or N phase individuals (Fig. 3). Some algal life cycles are characterized by the alternation of erect, branched thalli and horizontal crusts such as *Petalonia fascia*. Other species have life cycles with morphologically similar thalli in both phases, such as many *Polysiphonia* species.

Asexual reproduction can occur by parthenogenesis in the haploid phase (N), and by asexual production of spores in the diploid phase (2N) (Fig. 3). We cannot assume a genetic uniformity of all ramets produced during one life cycle. Therefore, haploid and diploid phases should be considered parts of different genets. It is noteworthy, however, that both haploid and diploid free living individuals have different interactions with the environment and different demographic patterns. De Wreede and Green (1990), for instance, have found evidence for differences in spatial distribution between gametophytes (haploid individuals) and sporophytes (diploid individuals) in the red algae *Iridaea cordata*. Dyck and De Wreede (1995) found that gametophytes and sporophytes of the red algae *Mazzaella splendens* have different temporal distribu-

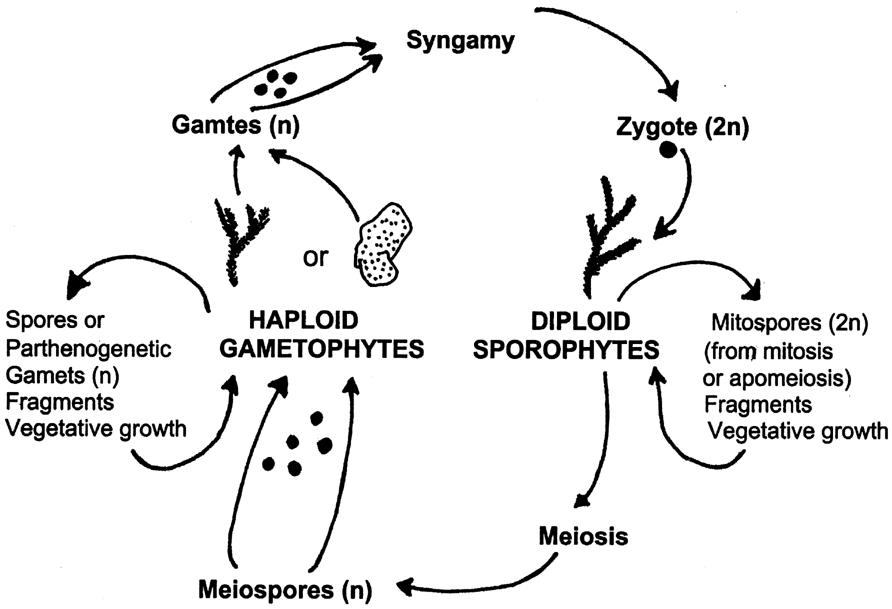

Figure 3. Schematic representation of an alternating phase life cycle in marine macroalgae.

tion. Differences in the demography and population dynamics of haploid and diploid phases deserve to be studied in more detail in order to evaluate possible changes in the genetic characteristics of each phase as is discussed in the following section.

Effects of the existence of alternation of generations on genetic diversity

In species with alternation of diploid and haploid generations, a balance of allele frequencies is achieved by sexual reproduction and hence, no genetic differentiation among the two phases should be expected (Coyer *et al.*, 1994). In the case of predominant asexual over sexual reproduction we can expect a reduction of gene flow between the two alternating phases (2N and N), resulting in genetic differentiation within population by genetic drift, as has been shown in the case of some species of *Gelidum* (Rhodophyta; Sosa *et al.*, 1998).

Intraclonal genetic variation can be the result of the occurrence of genetically different mitotic cell-lineages within an organism, known as genetic mosaics. Genetic mosaics are common and well documented in all major taxa (Gill *et al.*, 1995). This aspect has been studied in several algae (van der Meer and Todd, 1977; van der Meer, 1990) and is particularly well known for commercial algal strains as *Gracilaria chilensis* where genetic changes may occur with the initiation of branches in a new environment (Santelices and Varela, 1993;

Santelices *et al.*, 1995; Sosa *et al.*, 1998; Meneses *et al.*, 1999; Meneses and Santelices, 1999).

If the life cycle is dominated by one phase (diploid or haploid) with clonal growth, the appearance of new genotypes through sexual recruitment may become a very rare event. The presence of genetic variation in *C. taxifolia* provides an excellent example for this fact. *Caulerpa taxifolia* reproduces only by vegetative growth, and the invasive form from the Mediterranean is known to differ genetically from other individuals of the same taxon which can be found elsewhere in the world (Benzie *et al.*, 2000). The invasiveness of this particular strain is supposed to be the result of mutations that occurred during its aquarium culture, which made this particular strain resistant to lower temperatures (Meinesz *et al.*, 1995) and is inherited by vegetative reproduction leading to a genetic drift from the native strains.

If evolutionary change can occur without sexual reproduction, it is conceivable that genetically different individuals have originated from a succession of genetically different ramet generations without involving sexual reproduction (Fagerström *et al.*, 1998; Pineda-Krch and Fagerström, 1999), as in the case of *C. taxifolia*. In marine macroalgae, the production of mitotically derived and genetically different individuals can occur during different phases (diploid and haploid) of their life cycle, so we can expect that intraclonal variation will contribute substantially to levels of genetic variation of each phase and of the general population (Poore and Fagerström, 2000, 2001).

Ecological implications of clonality

Longevity

Dixon (1965) argued that the survival of the creeping thalli (stolon) is critical to the longevity of several marine algal species with prostrate as well as upright portions. He showed that the fleshy red algae *Pterocladia capillacea* survived in the field at least 36 years, by the survival of prostrate basal remnants from which new growth was resumed in the growing season. This biological attribute is particularly evident in crustose algae e.g., *Ralfsia expansa*, *Hildenbrandia rubra*, *H. occidentalis* (Kennish *et al.*, 1996) and *Petrocelis franciscana* (Sussman and De Wreede, 2001) Paine *et al.* (1979) concluded from an 88 month study on the red crust *Petrocelis middendorffii* that an average size crust of this species is probably between 25 and 87 years old.

Clonal growth affects algal longevity by continued production of modules, which balances the senescence of older parts of the plant, thereby avoiding senescence and death of the individual. This has been exemplified for *C. taxifolia* (Meinesz *et al.*, 1995), which follows a seasonal growth pattern with mortality of fronds in winter and recovery of the population in spring by new vegetative growth from the remaining stolon. This system is at least more than 18 years old, since the first colony was discovered in 1984. Persistence in periods of adverse environmental conditions by prostrate structures, as well as continued rejuvenation of the genet by the production of new ramets is a clonal attribute of plants that is clearly affecting the longevity of marine macroalgae. I expect that more detailed studies on the lifespan of clonal marine macroalgae may reveal surprising results. These organisms are commonly seen as short-lived species with a fast turn-over rate for individuals, but algal populations might in fact comprise very old individuals.

Form and density

The form, size and shape of clonal organisms is the result of the module production rate, and the spatial distribution of new modules (Harper and Bell, 1979). Two different approaches from the clonal plant literature, density effects and plasticity, will be used to analyze the form and shape of algae.

Crowding and self-thinning have been studied in several algal groups. Some studies have shown a negative correlation between growth and density (Reed and Foster, 1984). The distribution of lamina in vertical layers in tall brown algae (kelps) results in shade effects on smaller, younger algal lamina, whose growth may be limited by low light availability. In contrast, the relationship between growth and density have been reported to be positive by other authors in small red algae and brown intertidal species of algae (Schiel and Choat, 1980; Schiel, 1985; Martínez and Santelices, 1992; Lazo and Chapman, 1998). The reasons for the differences found in the above studies are due to both the particular environmental constraints and morphological attributes of the species. Marine clonal macroalgae survive high degrees of water movement and desiccation stress in the intertidal rocky shore by crowding (Santelices and Ojeda, 1984; Scrosati, 2000). In this particular environment, a high density has several advantages over low-density stands which affect survival in the intertidal zone. Crowding protects thalli from strong water movement, decreases desiccation by accumulating water and prevents photo-damage by auto-shading during low tide hours (Scrosati and De Wreede, 1997, 1998). Crowded populations are likely to have low sexual reproduction, a high self-fertilizing reproducing system, or massive spawning in the case of coenocytic algae in the Caribbean (Clifton and Clifton, 1999). Low-density populations will have a higher rates of sexual than asexual reproduction, a longer distance dispersal of zygotes (fertilized cell before germination) such as shown for several kelps (Santelices, 1990; Brawley and Johnson, 1992). Questions on the importance of crowding vs. low density growth as well as the ability to modify those growth patterns have yet to be determined.

Plasticity and foraging

Ecological consequences of phenotypic plasticity in clonal marine macroalgae have yet to be studied. It is well known that marine macroalgae show generally high levels of plasticity (Lobban and Harrison, 1997) but its analysis under the clonal plant perspective has been poorly addressed. To my knowledge only one study has focused on the spatial distribution of ramets. Collado-Vides *et al.* (1997) modeled the growth form and space utilization of *B. radicans* using L-Systems. They describe the growth of *B. radicans* as regular and compact, equivalent to the phalanx growth form in vascular plants (Lovett-Doust, 1981). This growth form allows for an intensive use of resources, creates a barrier to neighbors and increases interactions at the intraspecific level, as has been shown for *B. radicans* in mangrove habitats (King and Puttock, 1989). Ecological consequences of differences in the growth form (e.g. phalanx vs. guerilla) of marine macroalgae have to be addressed experimentally.

Foraging for resources has been suggested to occur in some clonal macroalgae such as *Caulerpa* in a tropical reef system (Collado-Vides and Robledo, 1999; Collado-Vides, 2002). In these studies species living in environments with high light availability and high water movement had a compact growth form, while species living in low light habitats with low water movement had a more sparse growth form. One of the studied species, *C. cupressoides*, was able to modify its morphology showing a compact pattern in high light, high water environments, and adopting a less compact growth in a low light, low water movement environment. This result suggests that not all species have the ability to modify their growth pattern. Species that do show architectural plasticity, however, are able to widen their spatial distribution by optimizing the relationship between their morphology and specific environmental characteristics. Experimental studies are needed to demonstrate that this behavior is adaptive (i.e. a search or avoidance syndrome) and not a constraint.

Conclusions

The marine macroalgae are an open world to discuss clonal plant theory in a system with complex life cycles and simple plastic morphologies.

The combination of clonal growth and complex life cycles can give new insights into evolutionary questions such as: How can asexual reproduction lead to a genetic differentiation between two phases of the same organisms? How long can an individual (haploid or diploid) live without any sexual reproduction? Which are the ecological consequences of having a single strain and a single phase for invasive species? Which is the relative importance of sex in creating genetic diversity compared with long term genetic drift of an asexual strain, and what are its consequences for evolution and speciation?

Several marine macroalgae species have been introduced and some of them have became invasive. Some clonal examples belong to the genus *Codium*, *Sragassum*, and recently *Caulerpa*. A high ability to invade space, fast colonization rates by fragmentation and vegetative growth, long distance dispersal by transportation of fragments, genetic differentiation of strains due to somatic mutations dispersed and replicated by vegetative growth are some of the traits that ensure the big success of these algae as invasive organisms (Meinesz *et al.*, 1995). All of those characteristics are attributes of clonal plants. Understanding algae as clonal organisms may help managers to make effective decisions when a new introduced species is in its initial stage of colonization.

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