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Implications of clonal and chimeric-type thallus organization on seaweed farming and harvesting *

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Abstract

Clonal seaweeds are capable of regrowing from thallus fragments, while unitary seaweeds lack this capacity. This capability determines significant differences in the farming and harvesting models to be applied to the two types of algae. Farming of non-clonal species in general, requires more steps and a greater diversity of technologies than clonal seaweeds. In addition, clonal seaweeds may exhibit intra-clonal variation, considered here as an additional source of variation from those known for unitary seaweeds (e.g. intra-individual and inter-population variation). Intra-clonal variation may modify the efficiency and predictability of strain selection practices based purely on intra-individual and inter-population variation. Coalescence and formation of chimeric thalli occurs in many species of economic red algae. Coalescence affects recruitment success, survival and growth rates in many of these taxa. It is concluded that the farming and harvesting models derived from unitary organisms have to be modified when applied to seaweeds with clonal or chimeric-type thallus organization.

Introduction

According to their morphological differentiation and propagation capacity, seaweeds can be considered unitary, clonal or chimeric organisms (Santelices, 1999a). Unitary individuals exhibit morphological and physiological differentiation along the thallus and propagation is by zygotes or specialized cells (spores). Branches, branchlets or thallus fragments of these species normally do not function, survive or replicate the parental plant on their own (e.g. *Colpomenia, Durvillaea, Laminaria*).

Clones are organisms able to grow and propagate by self replication of genetically identical units (Harper, 1985; Jackson et al., 1985) as many seaweeds do (e.g. *Ectocarpus, Caulerpa, Gelidium, Pterocladia;* Santelices, 1992; Scrosati, 1998; Santos, 1994, 1995, 1998). The branches (ramets) can function and survive on their own if separated from one another by natural processes or by injury.

Studies considering seaweeds as clonal organisms started to appear over 15 years ago (Cousens & Hutchings, 1983) but progress has been slow and restricted in scope. A cluster of studies (Santelices, 1992; Santelices & Varela, 1993; Santelices et al., 1995; Meneses & Santelices, 1999; Meneses et al., 1999; Santelices, 2001) have explored intraclonal variation and its importance on strain selection practices. A second group of studies (Creed et al., 1998; Scrosati & DeWreede, 1997; Scrosati 1998; Santos, 1998) have concentrated on the population structure and dynamics of these clonal species, while a third approach (Collado-Vides, 1997) explored the ecological and evolutionary consequences related to modular construction in seaweeds. The overall conclusion emer-

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ging from these studies is that classical demographic and selection models based on unitary organisms should be revised when applied to clonal seaweeds.

Chimeric-type seaweeds originate by coalescence of genetically different plants and so far the process is known for red seaweeds only (e.g. *Gracilaria, Mazzaella, Chondrus, Sarcothalia*). When neighboring conspecific seaweed germlings grow close enough to one another, contacting cells from their sporelings establish secondary pit connections between adjacent cells and a common external cell wall is formed around the contacting discs. Many of the original germlings, however, maintain their independence regarding the capacity of producing upright axes within the coalesced mass. Thus, after the fusion process between compatible partners has occurred, no evidence can be seen with the naked eye or at the light microscopic level that the new thallus is, in fact, the product of two or more different spores and that the ‘individual’ is in reality a genetically polymorphic, chimeric organism (Santelices et al., 1996).

The capacity of some red algal sporelings to growth together to form a completely coalesced mass has been known for almost 70 years (Rosenvinge, 1931). However, only recently (Muñoz & Santelices, 1994; Santelices et al., 1996, 1999) has coalescence been examined experimentally. Results indicate coalescence is a widespread process, documented in members of roughly half the orders presently distinguished in the Florideophycidae (Rhodophyta). It involves not only morphological responses, but also ecological and probably physiological responses that should be considered when farming and managing red seaweeds.

Among the red algae, clonality and coalescence are not mutually exclusive conditions. For example, clonal growth is exhibited by coalescing (e.g. *Gracilaria, Mazzaella, Sarcothalia, Chondrus*) and non-coalescing (e.g. *Gelidium, Pterocladia, Ceramium*) species (Santelices et al., 1999). On the other hand, unitary organization aparently includes only non-coalescing species (e.g. *Porphyra*).

Since population and community concepts derived from unitary organisms do not necessarily apply to seaweeds with clonal or chimeric-type thallus organization (Santelices, 1999a), particular consideration should be given to these last two types and to their traits when applying demographic, natural selection or community models to them. In commercial crops, the kind of seaweed organization (unitary, clonal or chimeric) should determine very different approaches to farming (Santelices, 1999b) and harvesting. This study reviews such differences.

Clonality, coalescence and farming

Clonality and farming

Clonal versus non-clonal (unitary) organization imply that radically different farming methods must be used (Santelices, 1999b). Clonal seaweeds can be propagated directly through regrowth of thallus fragments. Therefore, the corresponding farming technique only requires the provision of the best possible growing condition for the clonal fragments to carry on growing. The fragments need to have a minimum size to successfully compete in the adult environment, and in time they will regenerate the adult form.

Fragments from unitary (non-clonal) seaweeds generally cannot survive and grow, and their propagation and farming has to be started from spores. In the case of anatomically complex seaweeds, their ontogenetic development may go through various morphologies. In seaweeds, different morphologies often require different environmental conditions. Therefore, each stage may require different facilities to be successfully farmed. This may lead to multi-step farming practices depending on the diversity of ontogenetic forms involved (Santelices, 1999b). In addition to the use of farming technology appropriate for the growth of the commercial stage, specialized nursery facilities may be required for sporelings and microscopic stages and another set of methods and a third set of facilities may be needed for growing the juvenile stages. In general, farming non-clonal species requires more steps than farming clonal species.

Clonality and strain selection

Once farming has been established for a given species, generally selection of a superior strain is the next step for improving the performance of cultivated seaweed crops. However, this process also seems to be affected by the kind of seaweed to be farmed.

Inter-individual and inter-population variation are the most important sources of genetic variation found in unitary organisms and genetic improvement and breeding of new strains has been successful in some commercial crops of these types of seaweeds, such as *Laminaria* (Wu & Lin, 1987) and *Porphyra* (Miura, 1975, 1976; Shin & Miura, 1990). Clonal seaweeds, on the other hand, may exhibit an additional source of variation, known as intraclonal variation, which may significantly modify the pattern of inter-genet or inter-population variation, reducing or increasing the efficiency and predictability of the strain selection practices.

Intra-clonal variation is any significant phenotypic difference exhibited by ramets derived from a single genet (Figure 1). It is a frequently observed process among clonal invertebrates, land plants and seaweeds (Buss, 1985; Harper, 1985; Santelices & Varela, 1993; Santelices et al., 1995) that can be produced by a) differences in the microenvironment surrounding each ramet; b) highly localized physiological or developmental difference among genetically similar ramets; c) pathogen infections in a given ramet, or d) genetic changes differentially affecting one or a few ramets. Sporeling coalescence has been added recently as an additional factor (Santelices et al., 1996) that seems to apply exclusively to seaweeds.

Intra-clonal variants is exhibited by replicated stages occurring in the life history of a given seaweed (e.g. among mitotically replicated ramets; among mitotically replicated carpospores of some red algae). Pigment and morphological variants are the most visible and, therefore, the most frequently described type of variants (for review, see Santelices, 2001) but physiological variants also occur. In fact, recent results gathered on *Gracilaria chilensis* suggest intra-clonal variation should be a rather common response in wild and cultivated seaweed populations due to frequent microenvironmental differences, high frequency of localized pathogen infections, or high frequency of genetic changes, as detected by DNA-fragment polymorphism. In *G. chilensis,* such changes are coupled to growth (Meneses et al., 1999; Meneses & Santelices, 1999) probably due to somatic recombinations and other kinds of DNA turn over that seem to be always occurring in various magnitudes during branch production.

Although over 30 studies have reported strain selection in a diversity of clonal seaweeds (see Santelices 1992 for review), with the exception of those in *G. chilensis,* none has explored the nature, frequency and consequences of intra-clonal variation on strain selection. Intra-clonal variation could either increase or decrease the magnitude of improvement of a given character selected by traditional means. On the other hand, the frequency of intra-clonal change would determine the stability of the selected strain. Therefore, there is strong need to characterize this type of variation in clonal species and to understand the re-

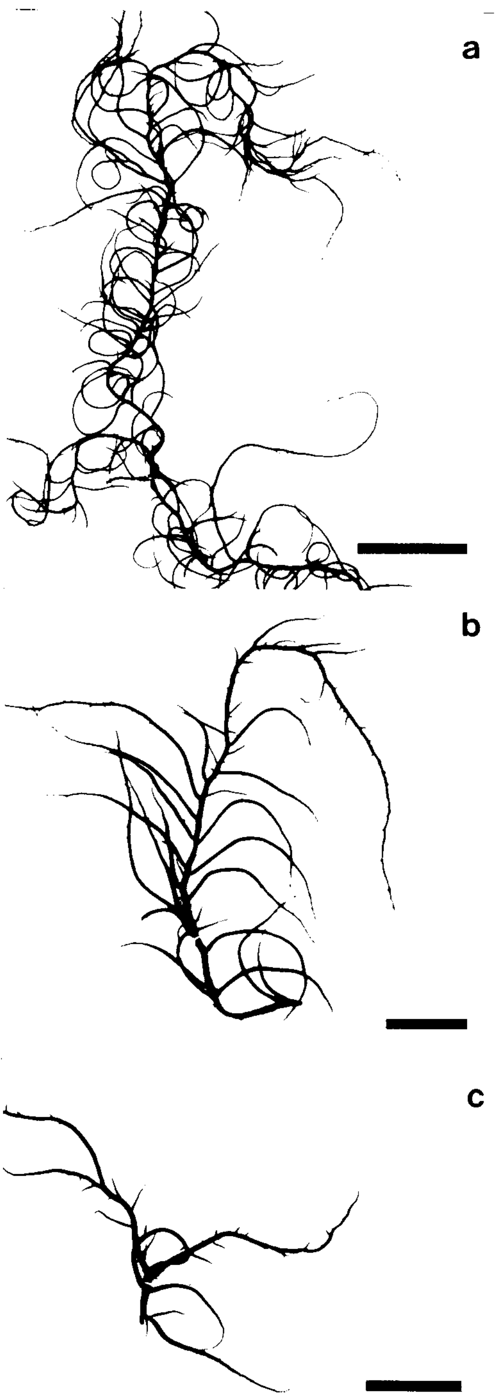

Figure 1. Example of clonal propagation and physiological intra-clonal variation in *Gracilaria chilensis.* All three clones (a, b, c) started from 1 cm-long branch tips excised from a single female thallus collected in Maullín, near Puerto Montt, in July 1999. The three clones were incubated for 120 days under similar laboratory conditions (45 μmol m^{-2} s^{-1}; 14 °C ± 1 °C; 12 h of daily light; SWM-3 culture medium exchanged every 6 days). Bar length is 5 cm in a and 2 cm in b and c.

lationships between this and the two classical sources of variability, in order to achieve genetic improvement in clonal seaweeds.

Coalescence and farming

Recent studies suggest that coalescing seaweeds exhibit a number of specific ecological responses that may be interpreted as adaptive traits because they increase survival, growth and reproductive potential of the coalesced individual (Santelices et al., 1999). Many of these responses should be considered when attempting to farm coalescing species. Thus, while germination success in non-coalescing species is inversely related to spore density, such an effect is not exhibited by the spores of coalescing species. Furthermore, survivorship of unisporic recruits of coalescing species in laboratory experiments have proved to be less successful than that of their multisporic counterparts (Santelices et al., 1999). In the field, multicellular recruits of coalescing taxa are likely to have a greater resistance to grazers, to mechanical dislodgment, and to overgrowth by juveniles of other competing species in comparison to unisporic and isolated recruits.

The importance of multisporic recruitment is also expressed during growth. For example, the total number of erect shoots differentiated by experimental individuals in laboratory cultures is a function of the initial number of spores (Figure 2; Santelices et al., 1996); unisporic sporelings had one or a few uprights while polysporic sporelings had many erect axes. In these experiments, erect axes in sporelings derived from one or a few spores generally were longer than those from multisporic germlings (Santelices et al., 1995, 1996, 1999). However, the sum of individual lengths of all erect axes and branchlets per sporeling increased with an increasing number of coalescing spores. Assuming that most of the photosynthetic tissues are concentrated in these axes and branches at this stage, coalescence of a large number of spores would generate a larger photosynthetic canopy than sporelings from a few or a single spore.

The above results strongly suggest that recruitment, survival and growth of coalescing species are greatly enhanced when the sporeling is multisporic. Nursery facilities used to incubate juvenile stages of coalescing species should consider the need to reduce interspore dispersal, facilitating multispore germination given the dependence of the above responses on initial number of spores. For example, this could be achieved, by increasing seeding densities or reducing the height of the water column between the seeding reproductive structure and the substratum to be inoculated.

Comparative studies with coalescing and non-coalescing Rhodophyta are in their infancy and results so far indicate the above responses are not equally significant in all coalescing species (Santelices et al., 1999). Future research is likely to further explore the interspecific differences in the above responses and identify the species that require multispore germlings for successful farming.

Clonality, coalescence and harvesting

Clonality and harvesting

In their summary review on the ecological effects of seaweed harvesting, Foster & Barilotti (1990) distinguished four types of harvest. One (Type IV) referred to the removal of beach cast plants, a situation that is outside the scope of this review. The characteristics of the other three types of harvest are summarized in Table 1. It is interesting to note that one of the main difference between Type I and the other two types of harvesting is the capacity for regrowth from basal attachment structures. That capacity is generally shown by clonal species and is generally absent from non-clonal species. It is true that some non-clonal species may regrow from basal structures following the first harvest (e.g. *Porphyra*, Schield & Nelson, 1990), but such regrowth is generally restricted to one or two additional months within a growing season only. This contrasts very strongly with the regeneration capacity of clonal species (e.g. *Gelidium, Pterocladia, Mazzaella, Gigartina*) often exhibiting post-harvest regrowth year after year. Thus, and similar to what happens with farming, clonal versus non-clonal organization determines important differences in the type of harvest to be done and on the ecological effects expected from such processes.

In order to define the best harvesting strategy from a given seaweed crop, authors have used one of two kinds of models, production models and structured population models. Production models simulate the dynamics of the total density or biomass of the population (e.g. Silverthorne, 1977; Seip 1980) while structured population models (Ang & DeWreede, 1993; Santos, 1993; Duarte & Ferreira, 1977; Santos & Nyman, 1998) simulate some demographically important

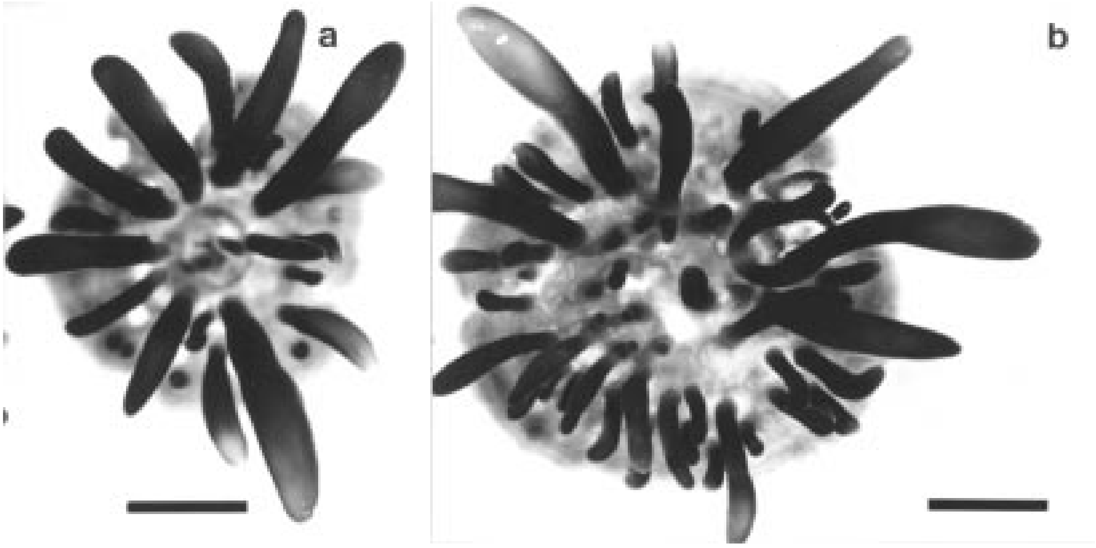

Figure 2. Example of the effects of coalescence on growth. Young thalli of *Mazzaella laminarioides* have been grown for 220 days under similar laboratory conditions (see Figure 1). The thallus on the left grew from a single spore; the one on the right grew from three coalescing spores. Bar = 2 mm.

Table 1. Types of seaweed harvesting, considering the portion of plant removed, the capacity of regrowth and the sources of repopulation (modified from Foster & Barilotti, 1990)

	Type I (Entire plant removed) e.g. *Porphyra*, *Laminaria*	Type II (Vegetative and reproductive structures removed) e.g. *Chondrus*, *Mazzaella*	Type III (Vegetative canopies removed) e.g. *Macrocystis*
Repopulation by	– immigrating spores – juveniles remaining in harvested area	– spores – juveniles remaining in the harvested area	– spores. – juveniles remaining in the harvested area
Regrowth	– none	– from basal attachment structures	– from harvested plants

vital rates (fecundity, survival, growth) according to population categories distinguished on the basis of age, size or developmental stages of the individuals in the population. In both kinds of models, however, there is a need to calculate demographic parameters in order to simulate the potential for population growth. However, population studies of seaweeds have only recently begun to appear (see Santos, 1998 for a review) and much of the theory has been adapted from models developed for terrestrial plant assuming that seaweeds have the same traits as land plants. Nevertheless, as Collado-Vides (1997) and Santos (1998) have remarked, application of demographic models to clonal seaweeds implies measuring characters and functions that are quite different from those measured in unitary seaweeds and focuss on ecological responses that up to now have been understood only as applied to unitary organisms. Analysis of the most important differences (Table 2) suggest that demographic studies with clonal seaweeds should consider ramets as equivalent to the individual of non-clonal seaweeds. Each ramet can be recognized as having characteristic time of birth and death, discrete lengths of life, and a characteristic mode of recruitment (Santos, 1998). In order to characterize any given function for a specific genet, the respective value of such a function for each

Table 2. A comparison of relevant demographic parameters and of birth and death determinants among unitary (non-clonal) and clonal seaweeds

	Unitary Seaweeds	Clonal Seaweeds
Demographic parameter		
– Population structure	Number and size of genets	Number and size of genets and ramets
– Longevity of the individual	Longevity of genet	Function of the number and longevity of ramets
– Fertility		
• Age 1^{st} reproduction	Size of genet	Size of ramet
• Reproductive effort	Size and area of genet	Integration of size and area of ramets
• Growth rate	Growth rate of genet	Average growth rate of ramets
Birth rate	Function of number of recruits	Function of number of recruits and number of active meristems
Death rate	– Herbivory on genets. May kill the individual – Competition may affect recruitment and growth	– Herbivory on ramets. May reduce number of ramets – Competition is more complex

and the total number of ramets needs to be taken into account.

Similar differences are found when the determinants of birth and death rate of clonal and non-clonal seaweeds are compared. As shown in Table 2, birth rate in non-clonal seaweeds is a function of the number of recruits reaching a given area. In clonal seaweeds, this is a function, not only of the number of recruits, but also of the number of active meristems generating new ramets.

Death rates in both types of organisms can be significantly influenced, among other factors, by herbivory and competitive exclusion. While herbivory on unitary seaweeds may kill or significantly affect survivorship of the individual, herbivory on clonal seaweeds principally affects the ramets. Intense grazing may effectively affect a large number of genets but generally it does not decimate all ramets within a genet. In fact, clonal organization had been interpreted (Harper, 1985) as a type of body construction that increases the probabilities of escape from moderate grazing on the population of genets.

Studies on competitive interactions among seaweeds or between seaweeds and other intertidal or subtidal space users (for reviews, see Lubchenco, 1990 and Paine, 1990) have documented negative effects on growth and reproduction. However, their experimental designs used in these studies do not allow differentiation of responses between clonal and non-clonal seaweeds. On theoretical grounds, competitive interactions involving clonal seaweeds are likely to be more complex than those documented for unitary organisms (Collado-Vides, 1997). Depending on the size of the clonal seaweed, ramets of a given genet may be simultaneously experiencing competitive interactions with other ramets of the same genet, ramets of different conspecific genets, ramets of allospecific genets and even invertebrates. Detailed experimental studies with seaweeds addressing this type of complex situation and its potential outcome cannot be predicted because most of the theoretical work on competition is based on interacting effects of unitary organisms.

Coalescence and harvesting

Since experimental studies on coalescence are only just starting, we lack information on the implications of this process on demographic and harvesting studies in seaweeds. However, Santos (1998) and Scrosati (1998) have recognized that coalescence could be a complicating factor because this process may lead to what appears to be a clump of modules of the genet when, in fact, they have originated from different zygotes. Under those circumstances genets are difficult to identify and population dynamics and structure has to be based on ramets.

Conclusions

Even though quantitative studies are only just starting, results gathered so far suggest thallus organization is a basic condition that should be taken into account when attempting to farm or to harvest seaweeds. Regeneration capacity, growth and production rates, sensitivity to mortality factors and competitive abilities are different in unitary, clonal and coalescing thalli. Therefore, different conditions seem to be required in order to optimize all these functions in these three major types of seaweeds.

Results also suggest that a number of demographic concepts, as well as population and community concepts, should be modified for their application to non-unitary seaweeds, and that many and more critical studies are required before we can formulate and compare more detailed predictions on the ecology and production patterns of these three kinds of seaweeds.

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