

Intraclonal Variation in Macroalgae: Causes and Evolutionary Consequences

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Recent studies documenting the presence of intraclonal variation in macroalgae indicate that there is considerable potential for selection in algae at levels other than among genets. As in other modular organisms, genetic changes that occur in algal somatic tissues may contribute to variation among sexual or asexual progeny. Several unusual aspects of algal reproduction and genetics increase the likelihood of intraclonal variation in contrast to the more familiar organisms that have strongly influenced much evolutionary theory. Somatic mutation, mitotic recombination, ploidy changes and rapid changes in genotype have all been documented in clonal lineages of macroalgae. The rarity of sexual processes in many algal populations suggests that this intraclonal genetic variation may contribute substantially to levels of genetic variation. Mechanisms that buffer the effects of somatic mutation in higher plants (e.g. stochastic meristems, diploidy) are often absent in algae, and thus intraclonal genetic variation has a high probability of being inherited and expressed in the phenotype of algal offspring. The presence of intraclonal variation, and some additional unusual aspects of algal biology, affect our concepts of the individual in biology.

Keywords: Modular organisms, mosaicism, individuality, somatic mutation, complex life histories

1. Introduction

It has long been known that modular organisms do not conform to August Weismann's doctrine of the separation of the germ line and the soma (Buss, 1983). As a consequence of the late development of the germ line, genetic variation within an individual resulting from changes during somatic development may contribute to variation among sexually derived progeny. It may also result in genetic variation among offspring that are produced asexually. If this variation is heritable and results in differential reproduction and survival, natural selection can occur among these mitotically derived entities in a way analogous to that of Darwinian selection among individuals produced sexually (Jerling, 1985). There is a growing body of theoretical (Judson and Normark, 1996; Fagerström et al., 1998) and empirical (e.g. Sunnucks et al., 1998; Sanders, 1999) work to suggest that asexual lineages are not evolutionary dead ends. These findings may be reconciled with

traditional evolutionary theory if we accept that natural selection may occur among different types of individuals, not just those that result from a zygote, and at different levels of biological organisation (i.e. between cells, between ramets, between genets, Tuomi and Vuorisalo, 1989).

While it is well established that modular organisms may consist of mosaics of cells with different genotypes (Gill et al., 1995), the evolutionary consequences of intraclonal genetic variation remain largely untested and have been considered for only a few groups of multicellular organisms (predominantly long-lived higher plants, Whitham and Slobodchickoff, 1981, and parthenogenetic arthropods, e.g. Sunnucks et al., 1998). Organisms that lack a predetermined germ line, however, are widely distributed across life on Earth and in fact occur in a majority of phyla (Buss, 1983). In this review, we aim to broaden the scope of research into intraclonal variation by considering the potential for adaptive evolution in the absence of sexual processes among several large groups that have received little attention in this regard – the multicellular algae (divisions Phaeophyta, Chlorophyta and Rhodophyta). We propose that there are many aspects of algal genetics

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and reproduction that increase the likelihood of selection within a clonal lineage relative to that within more familiar study organisms. Like other modular organisms, algae do not sequester cells for the production of reproductive propagules, and consequently, any genetic change that occurs during somatic development may be inherited by subsequent generations. Specifically, we discuss the production of intraclonal genetic variation, its distribution and inheritance, and the potential for selection upon that variation. We further discuss how this variation, and some additional unusual aspects of algal biology, affect our concepts of the individual.

2. Algal life histories

Algae have some of the most complex and variable life histories of any known organisms. Many aspects of their reproduction and genetics are unusual when compared to the organisms that have been the focus of most evolutionary biology. The potential thus exists for evolution in algae to proceed in ways not predicted by traditional evolutionary theory. Sexual reproduction in algae, as in all organisms with sexual life histories, involves an alternation between haploid and diploid phases (Fig. 1). Unlike higher plants and most animals, however, most algal life histories involve extensive multicellular development of the haploid phase (Klinger, 1993). Algal life histories may be broadly classified as monophasic, with multicellular development of only one phase (Fig. 1A), biphasic, with development of both haploid and diploid phases (Fig. 1B), and triphasic, a condition found only in the red algae with an additional diploid phase (Fig. 1C) (see reviews in Hawkes, 1990; Santelices, 1990; Murray and Dixon, 1992). Monophasic life histories may involve multicellular development of only the diploid phase (Fig. 1A, e.g. the brown alga *Sargassum*), or the haploid phase (e.g. the green alga *Spirogyra*). Among biphasic and triphasic algal life histories, there is great variation in the duration, morphology, and relative abundance of haploid and diploid phases (Santelices, 1990). The two phases may be isomorphic, with both phases morphologically similar (Fig. 1B, e.g. the brown alga *Dictyota*), or heteromorphic, with morphological and ecological differences between the two phases (e.g. the giant kelp *Macrocystis pyrifera*

with a 60 m diploid phase and a microscopic haploid phase).

Adding to the complexity of the sexual cycles, asexual reproduction of one or both of the free-living phases is common in most groups of macroalgae. This may involve both vegetative propagation (e.g. spreading stolons or rhizoids, fragmentation, specialised branches) and the production of a wide variety of unicellular propagules (e.g. mitotic or apomeiotically derived spores, parthenogenetic gametes) (Hawkes, 1990; Santelices, 1990; Murray and Dixon, 1992). There is great variation in the relative amount of sexual and asexual reproduction among taxa and many species show considerable intraspecific variation in life history (Santelices, 1990). Reproductive anomalies, such as the production a haploid phase epiphytic on the diploid phase, the production of gametangia and sporangia on the same individual ("mixed phase" reproduction), or male reproductive structures on female individuals, are regular occurrences in many algal groups (Maggs, 1988; Destombe et al., 1989). As a consequence of algal life history variation, many types of replicating entities exist – derived from uni- or multicellular precursors, and mitotic or meiotic processes (Fig. 1).

3. Production of genetic variation within a mitotic cell lineage

While clonal reproduction generally produces identical copies of the unit being replicated, there are several means by which genetic variation may arise in a mitotic cell lineage. In addition to classical mutations occurring during DNA replication, variation may result from intragenomic recombination, mobile genetic elements, gene duplication, and ploidy changes (Buss, 1985). The evolutionary importance of this variation relative to that produced by sexual processes is dependent on both the rates at which this variation is produced, and clone longevity (i.e. the number of mitotic cell divisions between meiotic events). Evidence from genetic studies suggests that several of these possible sources of intraclonal genetic variation are common among algae. This variation may be of considerable evolutionary importance if sexual reproduction is rare, as is the case for many algal taxa.

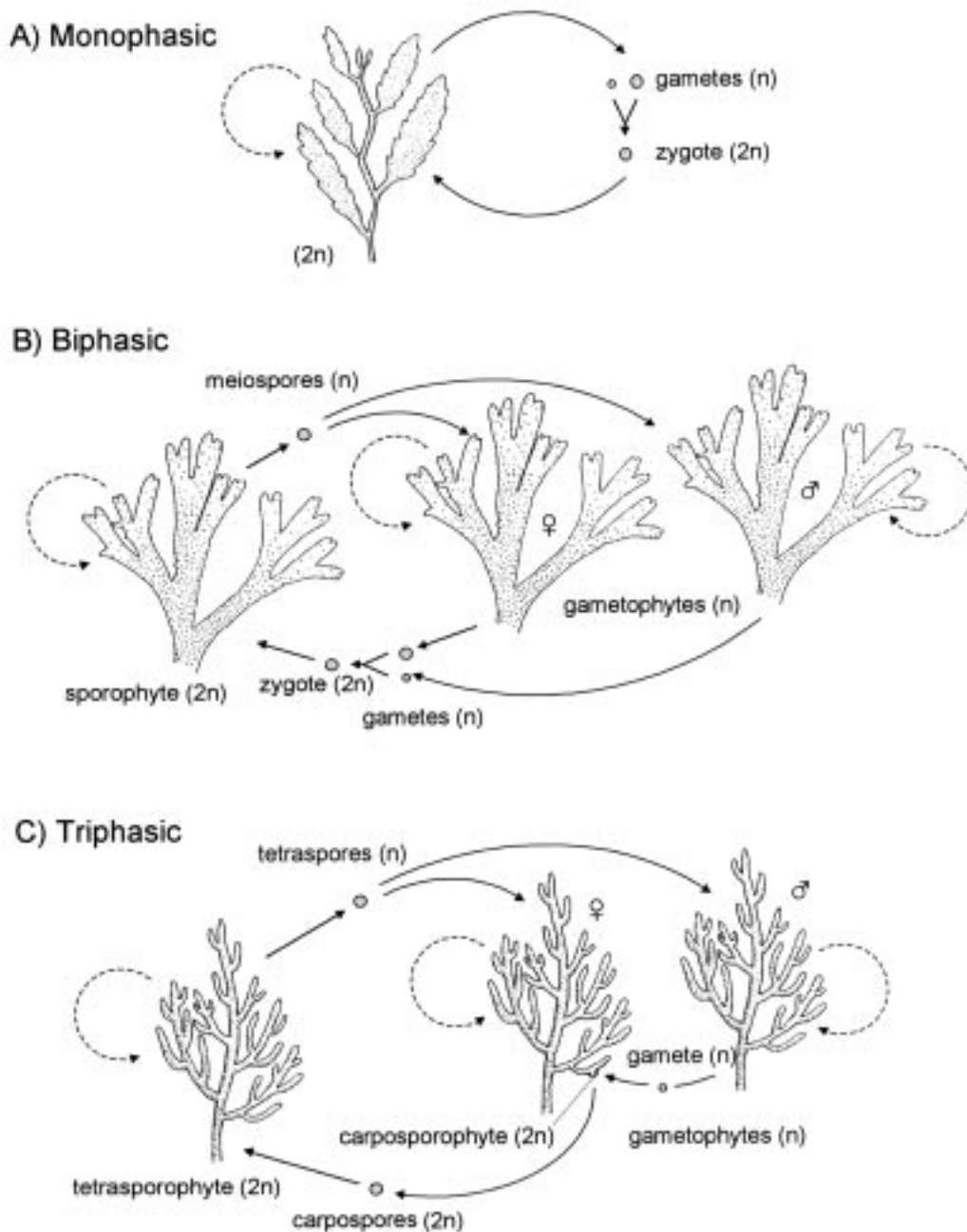


FIG. 1. Generalised algal life histories. A) Monophasic life histories involve multicellular development of only the diploid or the haploid phase. In life histories with a dominant haploid phase (not illustrated), the zygote is the only diploid cell and undergoes meiosis immediately. B) Biphasic life histories involve multicellular development of both haploid and diploid phases. The diploid sporophyte produces haploid spores via meiosis which develop into haploid gametophytes. The gametophyte produces gametes mitotically which fuse to form a diploid zygote and subsequently a mature sporophyte. C) Triphasic life histories, found only in the Rhodophyta, feature an additional diploid phase, the carposporophyte, which develops from the zygote and remains attached to the female gametophyte. The carposporophyte releases, via mitosis, diploid carpospores which develop into the diploid phase (the tetrasporophyte). In each life history (A–C), some or all of the phases may have capacity for clonal replication via dispersive propagules, vegetative propagation or fragmentation (dashed arrows).

3.1. Sources of intraclonal genetic variation

Algae have been shown to be a rich source of mutations (Russell, 1986) and many of the documented

mutations are the result of mutation during somatic growth, resulting in altered plant sectors (van der Meer, 1990). These mutations have been shown to affect a wide variety of phenotypes including mor-

phology, pigmentation, chemical composition and even the expression of sexual characters (e.g. in the red alga *Gracilaria tikvahiae*, where a heritable somatic mutation resulted in the development of a bisexual frond on a male plant, van der Meer et al., 1984). Somatic mutation rates are variable among taxa and strains, but may be high in some populations. Colour mutants are frequently found in field populations of the red alga *Chondrus crispus* and usually occur as plant sectors, indicating that somatic mutations are common in natural populations of that species (van der Meer, 1981a). In the green alga *Ulva mutabilis*, the frequency of mutations among individuals derived from asexual reproduction (parthenogenetic gametes or zoospores) is as high as 4% for one known laboratory strain (Fjeld and Løvlie, 1976).

Mitotic recombination has been shown to occur at high frequencies in *Gracilaria tikvahiae* (van der Meer and Todd, 1977; van der Meer, 1981b). Patches of recombinant tissue were identified as differently coloured spots on diploid tetrasporophytes known to be heterozygous for a recessive pigment mutation. These patches also differed from the surrounding tissue in producing both male and female gametangia (normally found in the haploid phase of this alga) as the recombination had resulted in tissue homozygous for the gene controlling sex determination. Such "mixed phase" reproduction has been reported for a wide variety of red algae (Maggs, 1988), although the degree to which somatic recombination is responsible for these observations remains untested. Mitotic recombination has been shown to occur at high frequencies for other species of *Gracilaria* (van der Meer, 1990) and has been suggested to contribute to differences in RAPD banding patterns between parents and their offspring in the red alga *Lophocladia trichocladus* (van Oppen et al., 1996).

While most of the genetically characterised mutants in algae are stable, a few have been shown to revert to wild type phenotypes. In three species of *Gracilaria*, unstable green mutations that frequently revert to wild type have been isolated, resulting in patches of wild type red tissue on otherwise green individuals (van der Meer and Zhang, 1988). These phenotypes and the results of crosses with wild type individuals suggest the involvement of mobile genetic elements. No direct evidence is available, how-

ever, and the potential importance of mobile genetic elements in producing genetic variation remains unknown for algae.

Polyploidy is common in many algal groups (Goff and Coleman, 1990) and rapid changes in ploidy levels (autodiploidization) are known to occur with individual development. This is especially prevalent within the green algal order Siphonocladales (Kapraun, 1993) – in *Valonia utricularis*, for example, haploid germlings may contain nuclei with DNA contents corresponding to the diploid phase after seven months of somatic development (Beutlich et al., 1990). Similarly, in some florideophyte red algae, sequential changes in ploidy levels of cells occur during development (Goff and Coleman, 1990). In a well-studied example, the apical meristem cells in species of *Polysiphonia* are highly polyploid with branch development involving regular reductions in the ploidy level of nuclei further from the apex. Ploidy levels of the apical cells also decline with age.

An unusual source of genetic variation among cells within a mitotic cell lineage, unique to red algae, is that of nuclear migration between vegetative cells. The most well-known example involves the transfer of nuclei between cells in *Polysiphonia* during the formation of secondary pit connections (Goff and Coleman, 1990). These connections form between adjacent cells that are not derived from a common cell division and result in the transfer of one or more nuclei from a donor to a recipient cell. Secondary pit connections are found in a wide variety of red algal taxa and may form between cells within the same clone or between genetically unrelated cells (Maggs and Cheney, 1990; Goff and Coleman, 1990). As a result of nuclear transfers, algal tissue may be a mosaic of cells with different numbers of nuclei, or may be heterokaryotic if transfers have occurred between unrelated cells.

If one or more of these sources of genetic variation are as widespread as the genetic studies suggest, clonal lineages of algae would not be expected to be genetically stable. Recent experimental studies with the red alga, *Gracilaria chilensis*, have indeed shown that clone genotypes change with time. Genetic changes within a clonal lineage, as detected by variation in RAPD markers, was recorded within only 30 days (Meneses and Santelices, 1999). Furthermore, this genetic variation increases with

growth, supporting the hypothesis that mitotic recombination (or other mechanisms associated with mitotic cell division) can result in significant levels of genetic variation among clonally produced offspring (Meneses et al., 1999).

3.2. *The frequency of sex*

The evolutionary importance of genetic variation produced in the absence of meiosis and recombination increases as the frequency of sexual reproduction decreases. A greater number of mitotic cell divisions between meiotic events is thought to lead to a greater frequency of mutations among gametes (Klekowski, 1988). Similarly, there should be greater variation between asexually produced progeny, and thus a greater potential for adaptive evolution in the absence of sex. While most algal individuals are short lived (certainly with respect to higher plants), there may be long intervals between sexual events due to the prevalence of asexual reproduction in many macroalgae.

In many taxa, asexual reproduction is the main source of new algal tissue and there are some taxa in which sexual reproduction has not yet been reported (Hawkes, 1990). A well-known example that emphasises the importance of asexual reproduction, is that of the invasive green alga *Codium fragile* ssp. *tomentosoides*. In the last 100 years, this alga has spread from the western Pacific to the eastern Pacific, New Zealand and both sides of the Atlantic reproducing exclusively by fragmentation and the production of parthenogenetic gametes (Trowbridge, 1996).

Algal populations often vary greatly in the relative frequency of sexual and asexual reproduction (Santelices, 1990). Species that reproduce sexually in some populations may reproduce exclusively by asexual means in other populations (Maggs, 1988). Unfortunately, there is little quantitative data on the relative frequency of sexual and asexual reproduction among algal populations (Klinger, 1993), and thus no direct estimates of clone ages. It is clear, however, that many taxa and populations exist in which sexual processes are rare. In these cases, intracolonial genetic variation may contribute substantially to the levels of genetic variation within algal populations.

4. **Distribution of genetic change within and among modules**

A cell in which a somatic mutation, or other form of genetic change, has occurred has three possible fates within an organism: extinction, fixation within a meristem or reproductive structure, or persistence within a chimeric organism (Fagerström et al., 1998). The first fate has no evolutionary significance, while the others may result in genetic change being distributed among future generations and thus being exposed to natural selection. Several aspects of the development of algal meristematic and reproductive tissues affect the probability that a mutant cell is a precursor of new growth, either as a meristem or as a reproductive propagule.

4.1. *Fate of genetic change within a module*

Mutant cells may only increase in frequency within a growing module if they occur in undifferentiated tissue with the capacity for further cellular division. This is obviously true for algae with diffuse growth, in which all cells are capable of mitotic divisions (e.g. various filamentous and sheet-like forms). The spread of mutant cell types in these algae is conceptually similar to that within a population of single celled organisms. In most algae, however, growth is localised in meristems. Several theoretical studies have investigated the probabilities of mutations being incorporated into meristems of different types and the ability of selection within an organism ("diplontic selection") to remove deleterious mutations or fix advantageous mutations (Klekowski, 1988; Otto and Orive, 1995; Pineda-Krch and Fagerström, 1999). These probabilities depend strongly on meristem type with chimeras less likely to persist in structured meristems, where an initial cell remains undifferentiated and is the source of all daughter cells, than in stochastic meristems, where initial cells are selected from a pool of available cells. Inheritance of genetic change is most likely in the most simple of the structured meristems, those with single apical cells, where a mutant cell genotype will be passed on to all subsequent tissue derived from that cell. Structured meristems are expected to preserve unfavourable mutations at a higher rate than stochastic meristems (Klekowski,

1984), but should also increase the rate of spread of a beneficial mutation.

Structured meristems occur in a large number of algal taxa and are often unicellular. Single apical meristem cells occur in many simple filamentous forms but also in more complex forms such as the brown algae in the orders Sphacelariales, Dictyotales and Syringodermatales (Clayton, 1990). Over 95% of all red algae have a filamentous construction with apical growth. The inheritance of mutations in algae with single-celled meristems should be similar to that within other groups with unicellular meristems (e.g. ferns, Klekowski, 1984). Unusual aspects of algal biology, however, may necessitate the development of theory particular to algae. Nuclear transfers between cells, for example, as seen in red algae, may result in cells losing their mutant genotype.

4.2. Inheritance of genetic change by new modules

Even if a mutant cell type becomes fixed within a given module, it may still be lost if that module does not reproduce, either through vegetative propagation, or by the production of sexual or asexual propagules. The level of developmental determinism seen in modular organisms strongly governs the probabilities that genetic changes within a clonal lineage will be inherited (Buss, 1983). Mutations are more likely to be passed on to a new module in organisms with low levels of developmental determinism (i.e. any tissue may become reproductive). In the most extreme example, that of unstructured development, the spread of mutant cell types within an organism is similar to that within bacterial populations (Otto and Orive, 1995).

Unstructured development of reproductive tissue is seen in many algal groups and in particular, the green algae, where there are no specialised reproductive structures (Phillips, 1990). In the abundant green algal genus, *Ulva*, for example, any part of the thallus may become reproductive with gametes or zoospores developing from transformed vegetative cells (Phillips, 1990). Other algal divisions do have specialised reproductive structures and as the number of parts that may become reproductive increases, the probability that genetic change is inherited increases, as does the potential contribution of intracolonial genetic variation to the variation among

propagules (sexual or asexual). In addition to the production of reproductive propagules, many algae have a high capacity for vegetative propagation with algal fragments often able to form new independent individuals. In these cases, as the production of sexual propagules in *Ulva*, all tissue has the capacity to create new modules.

Algal propagules are produced by mitotic or meiotic cell division, and may be unicellular or multicellular (Fig. 1, Santelices, 1990). While spores or gametes produced by mitotic cell divisions are all expected to carry a given mutation (barring reverse mutations), propagules produced by meiosis may not, depending on the genetic nature of the mutation and the pattern of segregation. The type of reproduction, sexual or asexual is thus expected to have a strong influence on the inheritance of somatic mutations. Multicellular propagules are expected to contain a greater mutational load than unicellular propagules due to the higher number of genomes capable of bearing mutations (Kondrashov, 1994; Otto and Orive, 1995). As with unicellular meristems, chimeric individuals will not persist when life histories repeatedly pass through a single-celled stage but may persist with continual asexual reproduction with multicellular propagules.

The way in which reproductive cells are sampled from the parent organism also affects the levels of genetic variation within an individual with multicellular propagules that are recently derived from a single cell expected to contain fewer mutations than those with more distantly related cells (Kondrashov, 1994). In many algae, new modules are formed with multicellular precursors, both by multicellular dispersive propagules and by fragmentation. Fragments with the capacity to regenerate may be viewed as propagules with an especially large number of relatively distantly related cells, and subsequently have a high probability that mutations are inherited by subsequent module generations. For multinucleate algae, reproductive cells with few nuclei could act in a similar way to unicellular propagules in reducing the likelihood of mutational inheritance (Kondrashov, 1994).

5. Selection within algal clones

Natural selection among cells or clonally reproduced entities may result in evolutionary change if

these entities display heritable variation that is correlated with phenotypic traits affecting their ability to replicate. Theoretical studies suggest that intra-organismal selection has the potential to increase the rate at which deleterious mutations are removed, and promote the spread of beneficial mutations (Otto and Hastings, 1988). The likelihood that genetic variation produced within a clone is expressed as phenotypic variation and is exposed to such selection is particularly high among macroalgae due to the prevalence of free-living haploid stages in the life cycles of many algae. Recent empirical studies document high levels of intracolonial variation in macroalgae and thus, considerable potential for selection to act at levels other than that among genets.

5.1. Ploidy levels in algae

Multicellular haploid phases are present in most algal life histories and are the only free living phase in present in some groups (see above, Fig. 1). While mutations in haploid organisms are less likely to occur than in diploid organisms, due to the reduced genome size, all mutations in coding DNA will be phenotypically expressed. As most mutations are recessive, diploidy thwarts selection within a clonal lineage (Klekowski, 1988). Sexual reproduction in biphasic and triphasic life histories (Fig. 1B, C) involves a change in ploidy levels between parents and offspring, while clonal reproduction produces offspring with the same ploidy levels. The relative amounts of sexual and asexual reproduction is thus expected to have a strong influence on the inheritance of a mutation within an algal population with these life histories. Model simulations of the spread of a beneficial allele in biphasic life histories confirm this expectation, with the greatest variation in time to fixation for life histories in which sex is relatively rare (Poore and Fagerström, in press).

There is great variation in the morphology, relative abundance and longevity of the haploid phase relative to the diploid phase among those algae with biphasic and triphasic life histories. In most taxa with morphologically similar phases, the diploid phase is more abundant than the haploid phase (De Wreede and Klinger, 1988). There are, however, some widespread and abundant taxa in which the reverse is true (e.g. the red algal order Gigartinales, Scrosati and De Wreede, 1999). As diploidy slows

the spread of beneficial mutations, this variation in the relative abundance of haploid and diploid phases is expected to strongly affect the rate at which a mutation spreads within an algal population (Poore and Fagerström, in press).

The effect of haploidy in exposing mutations to selection is modified in multinucleate cells. These are found in some red algae (Goff and Coleman, 1990) and in the coenocytic green algae which lack transverse cell walls (orders Caulerpales, Siphonocladales, and Cladophorales, Kapraun, 1993). Cells with many nuclei are expected to be buffered from mutations. The timing of DNA replication with respect to cell division is also important. Goff and Coleman (1990) reported that most red algae examined have nuclei in the G2 stage of mitotic cell division, and thus multiple copies of each gene are present.

5.2. Evidence for intracolonial phenotypic variation

Although few studies have been designed to detect intracolonial phenotypic variation in algae, it has been documented in both genetic and culture studies. The classical genetic studies working with phenotypic markers clearly demonstrate phenotypic variation within a clone (reviewed in van der Meer, 1990 and discussed above). Some of the documented mutations have large effects on algal phenotype and would be expected to result in strong selection, especially those that result in changes to reproductive traits (e.g. van der Meer and Todd, 1977).

Phenotypic variation within clones has also been demonstrated in continuously varying traits such as growth, survival and morphology in culture studies (Santelices et al., 1995). Santelices and Varela (1993) demonstrated significant variation in growth rates and branching patterns among ramets produced by two replication systems in the red alga *Gracilaria chilensis*. Variation was found both among vegetatively propagated ramets and among germlings reared from carpospores (see Fig 1C, derived mitotically from the same cystocarp). Also in *G. chilensis* (as *G. secundata*), Lignell and Pedersén (1989) obtained eight distinct and stable strains that differed in morphology and in agar composition from vegetative propagation of a single plant. The genetic basis of intracolonial variation is unknown in both studies, although Meneses and Santelices

(1999) have since provided evidence that clones of *G. chilensis* display rapid changes in genotype with time, as detected by variation in RAPD markers.

As with terrestrial plants (Gill et al., 1995), most evidence of intraclonal variation in algae derives from algae in culture rather than from natural populations and there is little data correlating genetic with phenotypic variation. The occurrence of significant intraclonal variation in the few studies designed to detect that variation, however, indicates that there is certainly potential for selection upon this variation, both in natural systems, and as a means for strain selection in algal aquaculture (Santelices et al., 1995).

6. Individuality in algae

Clonal reproduction, late development of the germ line, and the presence of genetic variation within clonal lineages, all challenge commonly held concepts of the individual in biology. Despite the notion of the individual being central to much ecological and evolutionary theory, there has been no consistent definition of an individual (Hull, 1980; Fagerström et al., 1998; Santelices, 1999). Individuals in algae are particularly difficult to define, both in practice and in theory, due to the problems inherent in all modular and clonal organisms (Buss, 1985), but also due to some additional unusual aspects of algal biology.

Fagerström et al. (1998) recognised that individuals have been traditionally defined by their ontogeny or by their genetic origin. In the ontogenetic definition, individuals are assumed to be those entities that are derived from a single cell. In the genet-centered definition, individuals are assumed to be those entities that derive from a zygote, the product of fertilisation of gametes formed by meiosis. Combining these definitions, they showed that organisms are distributed among three types of individuals; those derived from a unicellular precursor that was the product of meiosis, those derived from a unicellular precursor that was the product of mitosis, and those from multicellular precursors derived from mitotic cell division. Algae clearly include each of these three types of entities, commonly within the same species (Fig. 1).

Santelices (1999) recognised that individuals have been commonly characterised by genetic

uniqueness, genetic homogeneity, and autonomy and physiological unity. Again, macroalgae do not conform to any of these traditional concepts of the individual. As in all other clonal organisms, genetic uniqueness in algae is violated due to the prevalence of asexual reproduction. Genetic homogeneity may be violated in many algae due to the presence of intraclonal genetic variation (as outlined above), but also due to some unusual aspects of cell division. Genetic mosaics occur without mutation in some red algae simply due to the position of meiosis in the life history. In species of *Porphyra*, for example, meiosis occurs in the germinating spore rather than prior to spore release (Mitman and van der Meer, 1994). The resulting tissue thus contains cells of different genotypes, each resulting from the separate products of meiosis. The thallus may be divided in two longitudinally, with one half producing male reproductive structures and the other half female due to the segregation of the sex determining gene at meiosis. Similar mosaics occur in *Polysiphonia* with the cells of the base and apex being derived from different meiotic products. Four sectorised plants have been observed in species of *Gracilaria* resulting from the independent segregation of colour mutations and sex determining genes (van der Meer, 1977).

Autonomy and physiological unity is also a variable trait among macroalgae, with sporeling coalescence and cellular fusion being widely reported (Maggs and Cheney, 1990; Santelices et al., 1999). In culture conditions, cellular fusion between unrelated tissue may occur, and even between tissue of different sex (e.g. between male and female filaments in *Griffithsia tegis*, Goff and Coleman, 1990) or different life history phase (e.g. *Chondrus crispus*, González and Correa, 1996). The coalescence of germinating spores resulting in what appears, morphologically, to be a single individual has been reported from several red algal orders (Santelices et al., 1999). This mode of development is not restricted to culture studies, and is an ecologically important phenomenon in field populations of some red algal species. In *Sarcothalia crispata*, for example, 37% of recruits were formed from aggregations of more than one spore (Santelices et al., 1999).

The failure of traditional definitions of the individual for macroalgae further emphasises the notion that there are many types of individuals, with potentially different ecological and evolutionary proper-

ties (Fagerström et al., 1998; Santelices, 1999). The type of individuality displayed by a given organism should be viewed as a derived trait that requires evolutionary explanation (e.g. Michod, 1997), not a fixed trait assumed to be invariant for all organisms. Rather than seek a single definition of an individual, we should aim to explain the distribution of different types of individual among different taxa and environments.

7. Conclusions

The presence of genetic and phenotypic variation within algal clonal lineages indicates that there is considerable potential for selection to occur at levels not traditionally considered as evolutionarily important. As with similar findings for higher plants and clonal invertebrates, this strongly challenges the widespread notion that the only evolutionarily important selection processes are those among those individuals that arise from zygotes (i.e. genets). Consideration of other levels of selection seems particularly important for macroalgae due to the widespread occurrence of several mechanisms that result in genetic variation in the absence of meiosis and recombination, the rarity of sexual processes in many populations, and the widespread absence of the mechanisms assumed to buffer the effects of somatic mutations (diploidy, stochastic meristems).

Macroalgae offer an excellent opportunity to experimentally test the evolutionary consequences of intracolonial variation. Their fast growth, genetic plasticity, variety of clonally produced entities, and the speed with which intracolonial variation has arisen in experimental studies suggest that hypotheses regarding the importance of intracolonial variation may be more easily tested with macroalgae than with higher plants. Much of the relevant data are currently limited to the red alga *Gracilaria* and it is unknown to what degree such variation is evolutionarily important in a wide variety of algal taxa.

Intracolonial variation and the life history variation displayed by algae provide a wide variety of replicating entities among which selection may act. Evolutionary theory for algae, and other modular organisms, must consider this variation and the hierarchical nature of selection in modular organisms (Tuomi and Vuorisalo, 1989). Existing theoretical studies aimed at predicting how variation in patterns

of plant development affect the fate of somatic mutations (Klekowski, 1988; Pineda-Krch and Fagerström, 1999) have not considered complex life histories. One approach is to consider selection at the modular level, which allows for variation among modules as a result of intracolonial genetic variation, and offers the opportunity to contrast of a wide variety of life histories (Fagerström, 1992; Poore and Fagerström, in press). Models of selection at this level enable study of how life history variation in complex life histories – mixtures of meiotic, mitotic, sexual and asexual reproduction – affect evolutionary processes.

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