



The evolution of the life cycle of brown seaweeds

GRAHAM BELL

Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3S 1B1

Received 27 September 1995, accepted for publication 9 February 1996

The brown seaweeds (Phaeophyta) are well-suited for testing theories of the evolution of the sexual alternation of haploid and diploid generations because of the great diversity of life cycles within the phylum. Three theories are investigated in this paper. (1) Diploid growth evolves because it has the effect of complementing deleterious recessive mutations. This is rejected because (a) ancestral haplonty is not a parsimonious inference from current phylogenies; (b) the exaggeration of diploid growth does not evolve in a comb-like fashion; (c) forms with predominantly haploid growth have evolved from smaller isomorphic ancestors; and (d) there is no correlation between haploid growth and monoecy. (2) Diploid growth evolves when gamete dimorphism leads to intense sexual selection, favouring the production of genetically diverse gametes through meiosis. This is rejected because there is no correlation between the dominance of the diploid generation and the degree of gamete dimorphism. It is possible to show that gamete dimorphism itself has evolved in the Phaeophyta through the increase in size of the macrogamete in forms that have evolved larger sporophytes. (3) Microthalli become specialized as gametophytes because fusion is promoted by releasing gametes into the boundary layer; macrothalli become specialized as sporophytes because dispersal is promoted by releasing zoospores into the water column. This is consistent with the sexual and reproductive biology of Phaeophyta. The classic sexual cycle can then be interpreted as evolving from an asexual alternation of microthallus and macrothallus, governed largely by environmental factors, through selection for the appropriate association of ploidy with vegetative size. The exceptions to this general rule are forms in which gametes are released from macrothalli, where a different suite of sexual characters has evolved.

©1997 The Linnean Society of London

ADDITIONAL KEY WORDS: — haploidy – diploidy – sex – alternation of generations – Phaeophyta – gamete dimorphism – mutation – sexual selection – fertilization – dispersal.

CONTENTS

Introduction	22
The complementation of deleterious recessive mutations	24
The antagonism of natural and sexual selection	27
The evolution of gamete dimorphism in Phaeophyta	28
Gamete dimorphism and the balance of haploid and diploid growth	28
The biology of spores and gametes	30
Simple direct cycles	32
Direct cycles with differentiation	33
Complex reproductive cycles	33
Complex sexual cycles	35
Forms with gamete-releasing macrothalli	36

Acknowledgments	36
References	36

INTRODUCTION

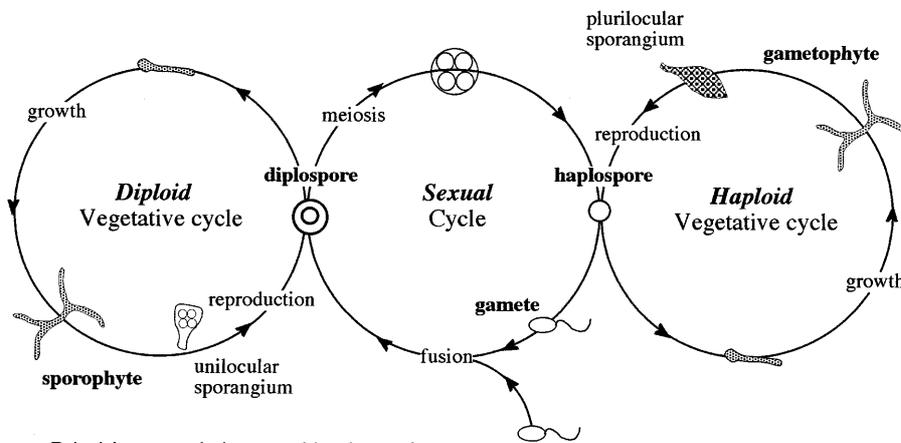
The balance of haploid and diploid growth is one of the main features of the life cycle of multicellular eukaryotes. In some cases (such as mosses) the familiar macroscopic body is haploid, and diploid structures are relatively small and insignificant, whereas in others (such as ferns) the large conspicuous plant is diploid, and the haploid phase is greatly reduced. In extreme cases, there is no diploid growth at all, because gamete fusion is followed immediately by meiosis (as in charophytes), or no haploid growth at all, because the products of meiosis are gametes (as in animals). These patterns have been known for many years, but despite a recent stirring of interest among theoreticians (for example, the symposium volume edited by Kirkpatrick, 1994) have not yet been satisfactorily explained.

The brown seaweeds, phylum Phaeophyta, represent one of the four or five major clades in which large multicellular forms have evolved independently. Compared with animals, fungi, rhodophytes and the chlorophyte-plant lineages their construction is rather simple, but they nevertheless exhibit a vast range of sizes, from minute prostrate filaments, crusts and tufts to the massive thalli of the rockweeds and kelps. Moreover, almost the whole range of life cycles is represented, including forms in which the haploid individual is the larger, forms in which haploid and diploid individuals are of similar size, whether small or large, and forms in which the diploid individual is the larger, up to an extreme at which haploid growth is almost entirely suppressed. This diversity of life cycles, in a well-defined and rather uniform phylum with a restricted ecological distribution along the narrow rim of the oceans, offers an excellent context for developing and testing theories of haploid and diploid growth.

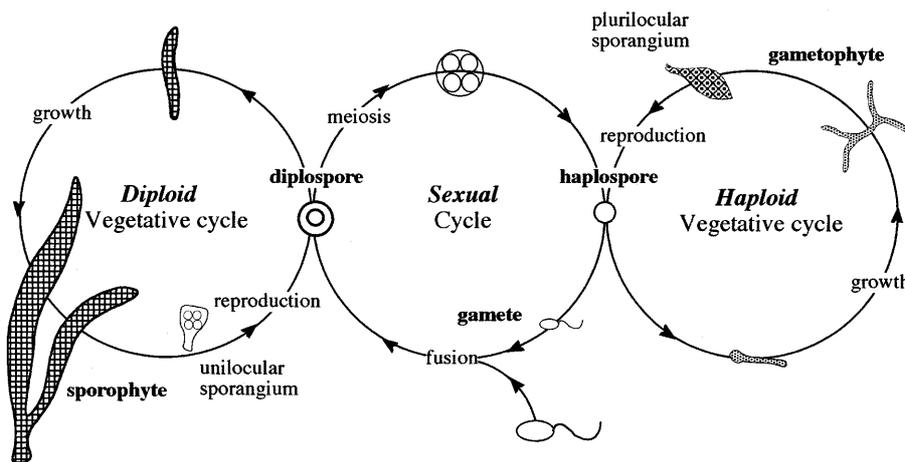
The phylogeny of the phylum as presently understood on the basis of DNA sequence information (Tan & Druehl, 1993) is shown in Figure 2, where it is used as the basis for analysing character evolution. Briefly, the Phaeophyta belongs to an early-diverging clade of eukaryotes that also includes chrysophytes, oomycetes and various amoebas. Its closest sister taxon appears to be the Xanthophyta, in which case primitive character states for the common ancestor of Xanthophyta and Phaeophyta include filamentous organization, branched or unbranched, with diffuse growth; motile spores; isogamety; and a dormant zygospore. Important shared primitive characters of Phaeophyta are thus trichothallic growth; physiological anisogamety; and a subitaneous zygote, the dormant or resistant phase being a filament. The phylum comprises two major clades, which I shall call for the purposes of this article Clade I and Clade II. Clade I includes Ectocarpales, Scytosiphonales, Chordariales and Dictyosiphonales; these are mostly small filamentous or pseudoparenchymatous forms. Clade II includes Ralfsiales, Syringodermatales, Sphacelariales, Fucales, Dictyotales and Laminariales; though some forms are small and simple, this clade includes all the 'seaweeds' with massive thalli. Unfortunately, the phylogeny of Phaeophyta is too poorly understood for stringent comparative tests to be applied, and I shall often use simple species comparisons, interpreted in the light of the little phylogenetic information available.

The classical interpretation of the life cycle of Phaeophyta (Fig. 1) is the alternation of a diploid sporophyte with a haploid gametophyte. The sporophyte bears

unilocular sporangia which are the site of meiosis and normally bear four spores. The meiospores germinate into gametophytes bearing plurilocular sporangia whose contents differentiate as gametes. There is a tendency for diploid growth to become exaggerated in larger and more highly-derived forms, in a manner akin to land plants. Thus, there is a progressive increase in size, accompanied by an increasing disparity between haploid and diploid individuals, from isomorphic filamentous forms in Ectocarpales, through the much larger isomorphic Dictyotales, leading to the massive sporophytes and minute gametophytes of Laminariales, and ultimately to the condition in Fucales, where a two-celled gametophyte is sessile on the sporophyte, and the only free-living haploid stage is a gamete. I shall argue below



Primitive state is isomorphic alternation of filamentous individuals with isogametic sexuality



Advanced state is heteromorphic alternation of gametophytic microthallus with sporophytic macrothallus; anisogametic or oogametic sexuality

Figure 1. The classical interpretation of the sexual life cycle in Phaeophyta. This way of representing the life cycle, as a series of linked cycles, was introduced by Bell (1994).

that this simple picture is inadequate to represent or understand the evolution of life cycles in the phylum.

THE COMPLEMENTATION OF DELETERIOUS RECESSIVE MUTATIONS

The most widely-accepted theory of diploid growth in multicellular organisms is that it causes a transient reduction in mutational load. If a lineage in an outcrossed haploid population expresses prolonged diploid growth, novel deleterious mutations will be complemented by wild-type alleles, and subsequent recessive mutations will be unexpressed and therefore neutral. This provides an immediate advantage for the lineage, and the genes responsible will increase in frequency (Muller, 1932; Kondrashov & Crow, 1991; Perrot, Richerd & Valero, 1991; Otto, 1994). This process is essentially irreversible, because in a diploid population the number of loci bearing recessive mutations will increase through time, so that any reversion to haploid growth would entail an immediate loss of fitness.

It should be noted that this theory will apply to loci that are expressed only in the diploid, or sporophytic, stage. Its application to forms with free-living gametophytes is uncertain, because the overlap between gene expression in sporophyte and gametophyte is unknown; in flowering plants a large fraction of the genome is expressed in both sporophyte and gametophyte (see Mulcahy & Mulcahy, 1975).

The corollary that the evolution of diploidy is irreversible leads to the prediction of a comb-like pattern of character evolution, the more highly-derived forms having successively more exaggerated degrees of diploid growth, with no reversions to increased haploid growth. The phylogeny used here shows no unequivocal example of a reversion; the phylum is as yet too sparsely sampled to assign ancestral states with confidence. In one sense, however, it is more parsimonious to regard diploid growth as the ancestral state. In order for haplonty to be ancestral, it is necessary to assume that three lineages were haplontic: the ancestor of the entire clade, the ancestor of the in-group (Phaeophyta) and the ancestor of Clade II (Fig. 2A). Diploid growth then arose independently on four occasions, in Chordariales-Dictyosiphonales in Clade I, and in Syringodermatales, Fucales and Laminariales in Clade II. In order for diplonty to be ancestral, it is necessary to assume only that either of two lineages were diplontic: either the ancestor of the entire clade, or the ancestor of the Phaeophyta (Fig. 2B). Diploid growth was then repressed (and haploid growth exaggerated) on one occasion, in the ancestor of the Ectocarpales-Scytosiphonales of Clade I. This inference is unexpected, but not entirely unreasonable; the sister taxon of the Xanthophyta-Phaeophyta in the phylogeny used here is the Bacillariophyta (diatoms), which are diplontic. A more extensive phylogeny is needed to resolve this issue.

Nor does the phylogeny clearly support a comb-like evolution of diploidy. Even if it were granted that haplonty is the ancestral state, on the four occasions where a more or less marked exaggeration of diploid growth has evolved, the sister-groups seem to be more or less isomorphic. In particular, the diplontic life cycle of Fucales did not evolve from the exaggerated diploid growth of Laminariales, which retain a free-living gametophyte; instead, Laminariales branch early in the clade, and the sister-group of Fucales is the isomorphic Dictyotales. (This latter inference from the molecular data is in conflict with morphologically based interpretations, and continues to be controversial.) Highly reduced gametophytes have also evolved in

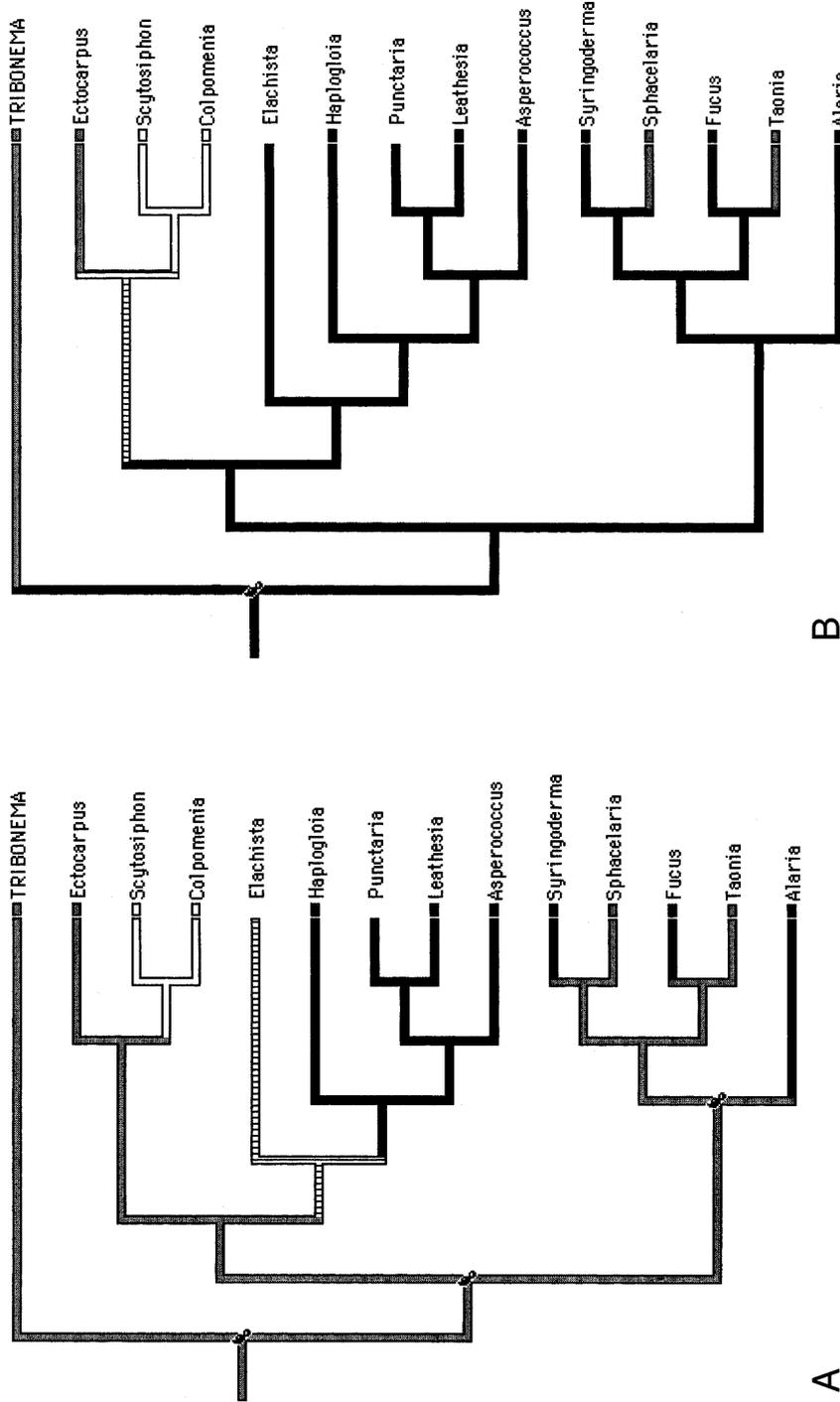


Figure 2. The evolution of the life cycle in Phaeophyta, using the rRNA phylogeny given by Tan & Druehl (1993). Key: open, haploid individuals larger; stipple, isomorphic; solid, diploid individuals larger; barred, uncertain (Elachista is asexual). In order to interpret character evolution unambiguously, it is necessary to designate certain nodes arbitrarily as representing ancestors with predominantly haploid or diploid growth. A. For haploid growth to be ancestral, it is necessary to designate three nodes (indicated by paintbrushes) as haploid. B. For diploid growth to be ancestral, it is necessary to designate only one node as diploid. These figures were drawn in MacClade (Maddison & Maddison 1992).

Syringoderma, and in one species are sessile on the sporophyte (Henry, 1984); here, a case for the sequential evolution of diploidy might be made, but there are no intermediate forms with freeliving gametophytes of moderate size.

It is a peculiarity of this theory that it can explain the exaggeration of diploid but not of haploid growth. It seems incompetent to explain the life cycle of Scytosiphonales, where the conspicuous tabular thalli are haploid gametophytes, and the diploid generation is a prostrate filament (for references to culture studies, see

TABLE 1. A brief digest of sexual life cycles in Phaeophyta.

This table covers only sexual forms with freeliving gametophytes, for which recent unialgal culture studies of the entire life cycle are available. The general state of Dictyotales (where I can find no such studies) is the only exception. The characters abstracted are as follows. Mac: Form of macrothallus. Fil: unaggregated filaments. PP: aggregated filaments, pseudoparenchymatous thallus. Par: parenchymatous thallus. Alt: Alternation of generations. H: haploid individual larger than diploid. I: isomorphic. D: diploid individual larger. HSp: Haploid sporophytes observed in culture. Scored yes or no. Gen: Gender (of gametophytes). D: dioecious M: monoecious. SC: Self-compatibility. C: self-compatible, clonal fusion observed. I: self-incompatible. Note: all dioecious forms are scored as self-incompatible. GD: Gametodimorphism. I: isogametic. A: anisogametic. O: morphologically oogametic

Order	Genus	Mac	Alt	HSp	Gen	SC	GD	Authority
Ectocarpales	<i>Ectocarpus</i>	Fil	I	yes	D	I	I	Muller, 1972, 1977
Chordariales	<i>Chordaria</i>	PP	D	no	M	C	I	Peters, 1992a
	<i>Myriogloia</i>	PP	D	yes	D	I	I	Peters, 1992b
	<i>Sphaerotrichia</i>	PP	D	yes	D	I	I	Peters <i>et al.</i> , 1987
	<i>Stilophora</i>	PP	D	yes	D	I	I	Novaczek, Bird & McLachlan 1986a Peters & Muller, 1986b
Scytosiphonales	<i>Colpomenia</i>	PP	H	yes	D	I	A	Clayton, 1979
	<i>Scytosiphon</i>	PP	H	yes	D	I	A	Clayton, 1980
Dictyosiphonales	<i>Adenocystis</i>	PP	D	yes	D	I	I	Muller, 1984
	<i>Dictyosiphon</i>	PP	D	yes	D	I	I	Peters, 1992c
	<i>Hummia</i>	PP	D	no	D	I	A	Fiore, 1977
	<i>Myriotrichia</i>	PP	D	yes	D	I	I	Peters, 1988
	<i>Scytothamnus</i>	PP	D	yes	D	I	I	Clayton, 1986
Desmarestiales	<i>Phaeurus</i>	PP	D	yes	D	I	O	Clayton & Wiencke, 1990
	<i>Himantothallus</i>	PP	D	no	D	I	O	Wiencke & Clayton, 1990
	<i>Desmarestia</i>	PP	D	yes	D	I	O	Anderson, 1982
	<i>Desmarestia</i>	PP	D	yes	M	C	O	Ramirez <i>et al.</i> , 1986
Sporochneales	<i>Carpomitra</i>	PP	D	?	M	?	O	Motomura, Kawaguchi & Sakai, 1985
	<i>Perithalia</i>	PP	D	yes	D	I	O	Muller, Clayton & Germann, 1985
Sphacelariales	<i>Sphacelaria</i>	Par	I	yes	D	I	A	Hoek & Flinterman, 1968
Syringodermatales	<i>Syringoderma</i>	Par	D	yes	D	I	I	Henry & Muller, 1983
Dictyotales	<i>Dictyota</i>	Par	I	?no	D	I	O	[generally]
Laminariales	<i>Alaria</i>	Par	D	yes	D	I	O	Blinn & Markham, 1969
	<i>Chorda</i>	Par	D	yes	M	C	O	Maier, 1984
	<i>Chorda</i>	Par	D	yes	D	I	O	Novaczek <i>et al.</i> , 1986b
	<i>Phyllariopsis</i>	Par	D	no	D	I	O	Henry, 1987
	<i>Pseudochorda</i>	Par	D	no	M	?	O	Kawai & Kurogi, 1985
	<i>Saccorhiza</i>	Par	D	yes	M	?	O	Henry, 1986
	<i>Saccorhiza</i>	Par	D	no	D	I	O	Norton, 1972

Table 1). These shared a common ancestor with Ectocarpales, which are typically filamentous and isomorphic.

The most vulnerable prediction of the theory is suggested by recent work by Otto & Marks (unpublished; cited and epitomized in Otto, 1994). Briefly, complementation will be less effective in inbred organisms, where partners are likely to bear mutations identical by descent. The exaggeration of diploid growth will therefore occur only, or at least will be more pronounced, in outbred species. There are no direct estimates of inbreeding in Phaeophyta. However, gametophytes may be dioecious or monoecious; and monoecious gametophytes seem to be self-compatible in most cases where observations of gamete fusion are available (Peters, 1992a, in *Chordaria*; Ramirez, Muller and Peters, 1986, in *Desmarestia*; Maier, 1984, in *Chorda*; Hardy & Moss, 1978, in *Halidrys*). Indeed, I am not aware of any monoecious types that have been demonstrated to be self-incompatible. It seems a fair test of the mutation-complementation hypothesis to propose that haploid growth, or isomorphism, will be associated with monoecious gametophytes, and diploid growth with dioecious gametophytes. This is not the case. Gametophytes are generally dioecious, regardless of vegetative form. Thus, there is an excess of dioecious species in relatively small and simple forms such as Chordariales and Dictyosiphonales, as well as in large and complex macroalgae such as Dictyotales and Laminariales. Monoecious forms are scattered throughout the phylum, for example in *Chordaria* (Chordariales), *Carpomitra* (Sporochnales), and *Chorda* (Laminariales). Forms with largely haploid growth (Scytosiphonales), haploid and diploid growth (Dictyotales) and largely diploid growth (other orders) are all typically dioecious. Moreover, in several cases monoecy and dioecy are found in the same genus, with no substantial variation in life cycle: for example *Desmarestia* (Anderson, 1982; Ramirez *et al.*, 1986), *Chorda* (Maier, 1984; Novaczek, Bird & McLachlan, 1986b) and *Saccorhiza* (Norton, 1972; Henry, 1986). The only generalization that one might advance is that in many cases morphological monoecy seems to be accompanied, not by the exaggeration of diploid growth, but by the loss of sexual ability altogether: for example *Arthrocladia* in Desmarestiales (Müller & Meel, 1982) and generally in Tilopteridales (e.g. Kuhlenskamp & Müller, 1985).

In short, the lack of evidence for a sequential accumulation of diploid growth, the evolution of forms with predominantly haploid growth from isomorphic ancestors, and the lack of any correlation between diploid growth and dioecy, offer no support for the mutation-complementation hypothesis.

THE ANTAGONISM OF NATURAL AND SEXUAL SELECTION

I have advanced an alternative theory of the life cycle (Bell, 1982). Briefly, a major difference between life cycles in which growth is largely restricted to haploid or to diploid individuals is the genetic diversity of gametes produced by an individual. A haploid individual produces genetically uniform gametes by mitosis; in a diplontic life cycle, gametes are the immediate products of meiosis in a diploid individual, and are thus genetically diverse. If there is intense sexual selection, so that only a small fraction of exceptionally well-endowed gametes are likely to succeed in fusing, individuals that produce a wide diversity of gametes will be favoured, and genes that establish a diplontic cycle will spread; conversely, where there is little sexual

selection, and the qualities that promote the success of gametes are nearly the same as those that promote the success of zoospores, a haplontic cycle in which gametes are equally component will be favoured. This argument can be expressed algebraically to obtain conditions for the spread of genes directing haplontic or diplontic development, in terms of the degree of antagonism between vegetative and sexual function (Bell, 1994).

We know very little about the operation of sexual selection in organisms such as Phaeophyta. However, sexual selection will be intense when one gamete gender is present in great excess, leading to the inference that diplonty should be favoured when male gametes are numerous and small, whereas female gametes are few and large. We are therefore led to predict that the relative extent of diploid growth should be correlated with the relative size of male and female gametes.

The evolution of gamete dimorphism on Phaeophyta

The size of gametes has two opposed effects on fitness: larger gametes may give rise to more successful zygotes, but fewer can be produced from a given mass of tissue. It can be shown that gamete dimorphism will tend to evolve if the survival or subsequent growth of zygotes increases disproportionately with their size (Parker, Baker & Smith, 1972; Charlesworth, 1976; Bell, 1976; this and other theories reviewed by Hoekstra, 1987).

Two types of relationship between the size of propagules and the size of multicellular individuals can be imagined. First, larger individuals might give rise to larger propagules; secondly, larger propagules might give rise to larger individuals. In Phaeophyta, the latter proposition is correct (Fig. 3). Larger zygotes are associated with larger sporophytes; larger meiospores are associated with larger gametophytes. Conversely, there is no correlation between the size of sporophytes and spores, or between gametophytes and zygotes or gametes. The main assumption of the hypothesis, that large propagules are necessary for the subsequent development of large individuals, is therefore quantitatively supported. The shape of the relationship between propagule size and individual size cannot be determined from the data.

The evolution of small, motile microgametes and large immotile macrogametes is conventionally supposed to involve the reduction in size of the male gamete, past the point where an unfused male gamete could support subsequent embryogenesis. This is not the case in Phaeophyta. Gamete copulation is very generally, perhaps universally, anisogametic; even in isogametic forms, the female gamete, initially motile, settles before fusing with a motile male gamete. Where male and female gametes differ not only in activity but also in size, male gametes are not consistently smaller than zoospores; instead it is the female gamete that increases in size (Fig. 4). The evolution of gamete dimorphism in Phaeophyta thus hinges on the specialization of female gametes, for larger size that yields a larger zygote that can develop into a larger sporophyte.

Gamete dimorphism and the balance of haploid and diploid growth

The predicted relationship between increased gamete dimorphism and the exaggeration of diploid growth is shown in the series from the nearly isomorphic and

isogametic Ectocarpales, through the isomorphic and moderately anisogametic Sphacelariales, and the heteromorphic and strongly anisogametic Desmarestiales, to the extremely anisogametic and heteromorphic Laminariales and Fucales (Fig. 5). However, there are two exceptions that preclude any general rule. Dictyotales are oogametic but have sporophytes and gametophytes of similar size and form. This might be interpreted as a lag between the initial evolution of gamete dimorphism and the subsequent evolution of diploid growth. (Tilopteridales are likewise oogametic and isomorphic, but largely or entirely asexual.) However, in Chordariales and Syringodermatales, diploid growth may be exaggerated even in isogametic taxa.

The hypothesis also makes the directional prediction that the evolution of gamete dimorphism should precede the evolution of exaggerated diploid growth. This is not supported by the phylogeny of the phylum. In the Chordariales-Dictyotales clade of Clade I, only the most highly-derived genus (*Asperococcus*) is anisogametic, the more basal genera (such as *Haplogloia*) being isogametic when they are sexual at all; and yet the entire clade shows a tendency towards large sporophytes. In Clade II, where

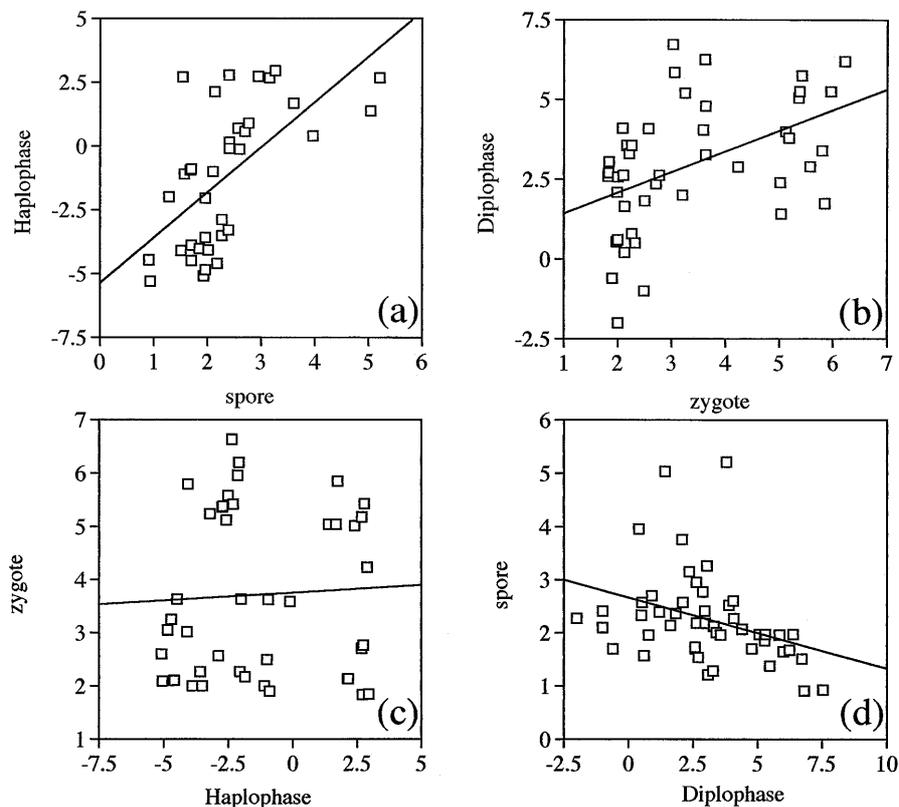


Figure 3. The relationship between propagule size and vegetative size. Plotted points are species. Data were drawn from a wide variety of sources, including those listed in Table 1. The size of vegetative individuals was estimated (no doubt with substantial error) from drawings and photographs, and are expressed in units of mm^3 . The size of propagules was estimated in the same way, or taken directly from measurements in the original papers, and expressed in units of μm^3 . Size is expressed as \log_{10} in both cases (a) Haplophase (y) on spore (x): $y = 1.782x - 5.352$, $r^2 = 0.38$, $P < 0.01$. (b) Diplophase (y) on zygote (x): $y = 0.648x + 0.781$, $r^2 = 0.22$, $P < 0.01$. (c) Zygote (y) on haplophase (x): $y = 0.029x + 3.754$, $r^2 = 0.003$, $P > 0.05$ (d) Spore (y) on diplophase (x): $y = -0.133x + 2.662$, $r^2 = 0.12$, $0.01 < P < 0.05$.

exaggerated diploid growth is common, the ancestral state of the gametes cannot be determined from the phylogenetic information currently available.

THE BIOLOGY OF SPORES AND GAMETES

An alternative interpretation of the life cycle in terms of natural and sexual selection hinges on the different properties of spores and gametes. These two classes of propagule serve, not merely different, but opposite ends. Spores are reproductive propagules that can germinate directly and develop into new individuals; they distribute the lineage into new sites, and are thus adapted for dispersal. Gametes are sexual propagules that are adapted for fusion. Dispersal implies a more or less wide separation; fusion implies close proximity. Moreover, the success of spores and gametes in achieving dispersal or fusion will depend not only, or even primarily, on

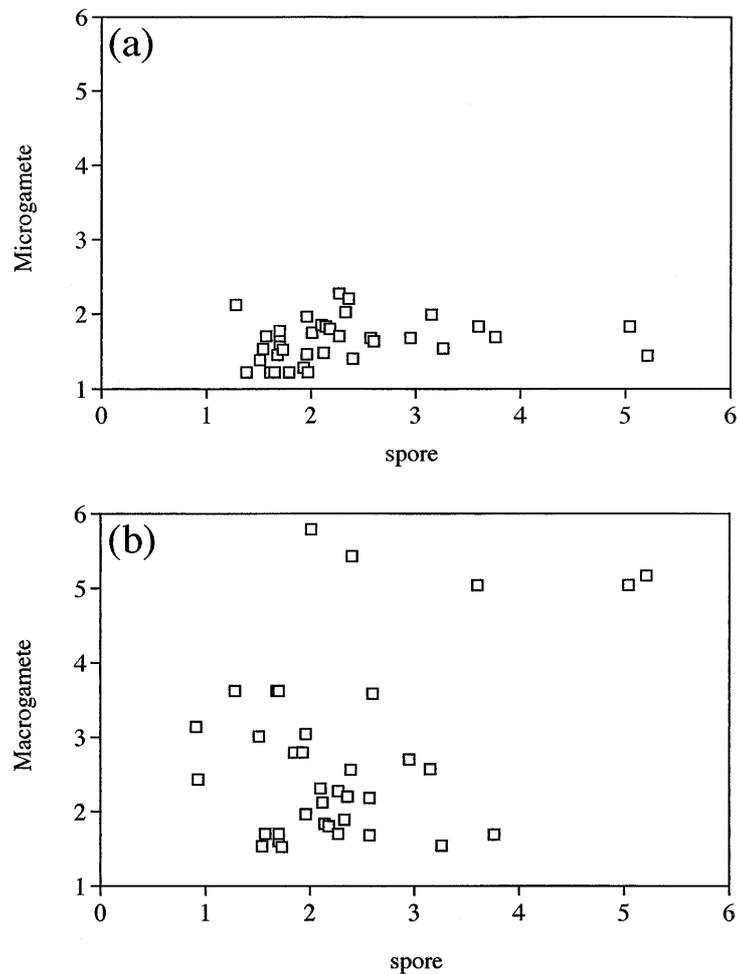


Figure 4. Gamete size in the context of spore size. Units are μm^3 . (a) Microgametes are uniformly comparable in size to small zoospores. (b) Macrogametes vary widely in size over the same range as spores.

their intrinsic properties, but also on the properties of the spore-releasing and gamete-releasing individuals. In heteromorphic life cycles, the microthallus is generally a creeping filament or disc closely appressed to the substrate, whereas the macrothallus is a large sac-like or blade-like thallus extending into the water column.

Thus, propagules released by the microthallus enter a viscous, low-velocity environment in or close to the boundary layer (see Amsler, Reed & Neushul, 1992). Self-propulsion by flagella will often be rapid relative to water flow, and chemical gradients can be maintained. These propagules are therefore appropriately specialized for fusion as gametes.

In contrast, propagules released by the macrothallus enter a more turbulent, high-velocity environment in which water flow is much faster than self-propulsion and where chemical gradients are difficult to maintain (see Norton, 1992). These propagules are appropriately specialized for dispersal as zoospores.

The microthallus is thus appropriately specialized as a gametophyte, and the macrothallus as a sporophyte. This interpretation is similar to that advanced long ago for land plants by Bower (1908; see Keddy, 1981). It is clearly consistent with the usual organization of the life cycle in sexual Phaeophyta. However, the most convincing evidence in favour of the theory is that on closer inspection the conventional interpretation of the life cycle is inadequate in one important respect. Careful culture studies reported during the last 15 years have shown that completely

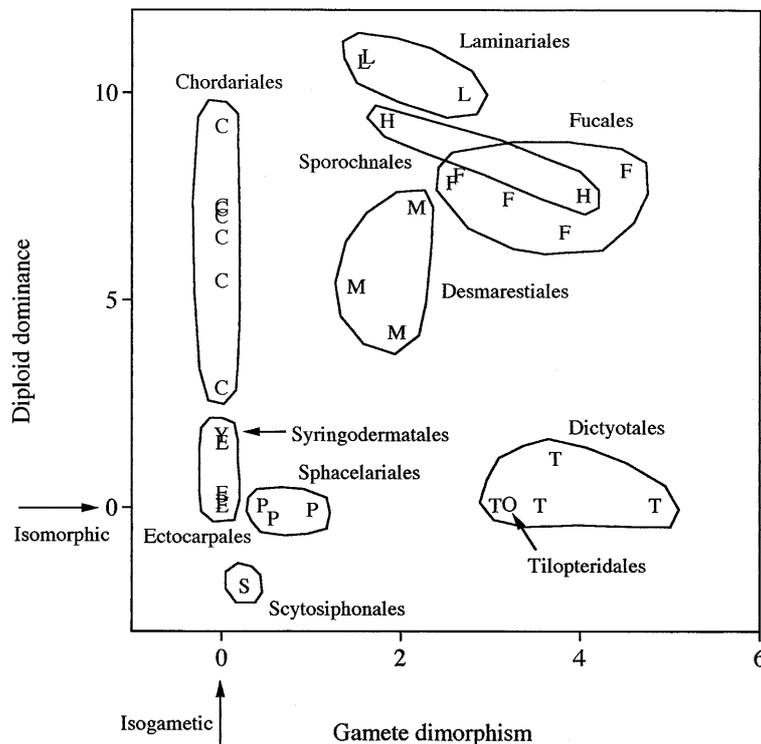


Figure 5. How the balance of haploid and diploid growth varies with the disparity in gamete size. Diploid dominance is expressed as log (diploid size/haploid size), and gamete dimorphism as log (macrogamete size/microgamete size).

asexual life cycles may display a heteromorphic alternation of microthallus and macrothallus.

Simple direct cycles

The xanthophyte outgroup taxon, *Tribonema*, is an unbranched filament. The primitive state of Phaeophyta seems to be a prostrate system of branched filaments, reproducing by motile spores (Fig 6A). The intercalation of sex into this cycle would lead merely to an isomorphic alternation of nearly indistinguishable filaments. In such cases, such as *Ectocarpus* (e.g. Müller, 1972), the diploid individual is often the more 'robust', with slightly thicker filaments, presumably because of the increase in cell size that is generally associated with increase in DNA content or ploidy.

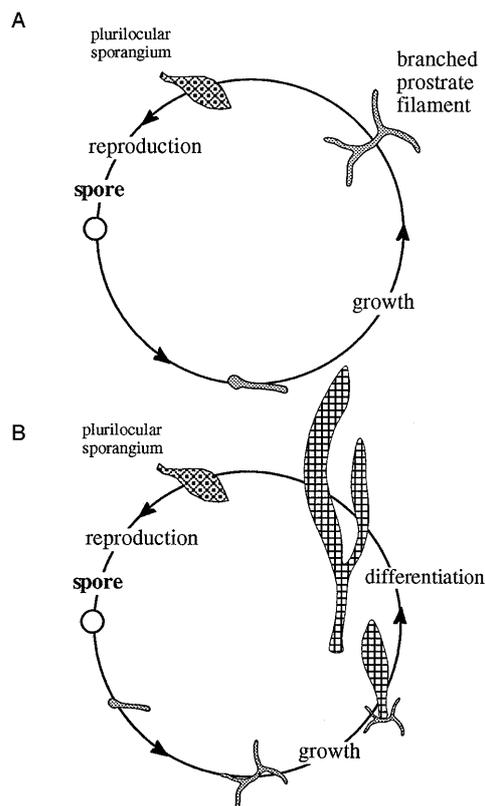


Figure 6. Sexual and asexual life cycles in Phaeophyta. The diagrams show all possible transitions between forms. Not all of them actually occur: for example, the sequence {unilocular sporangium (reproduction) diplospore (meiosis) haplospore gamete (fusion) diplospore} is unknown, and could certainly not be repeated indefinitely. A, simple direct cycle. B, direct cycle with differentiation. C (facing page), complex reproductive cycle. D (overleaf), complex sexual cycle, including both haploid and diploid microthallus and macrothallus.

Direct cycles with differentiation

Horizontal growth on a substrate is constrained by competition for space; the evolution of larger size then requires an erect system of filaments or sheets of tissue that extend into the water column. The organism then grows first as a prostrate filament, securing attachment and persistence, on which arises erect axes that permit extended growth through photosynthesis and absorption (Fig. 6B). The prostrate and erect systems of the mature individual thus divide physiological labour in a manner somewhat similar to the root and shoot of a land plant. Again, sex does not necessarily introduce any complications, because it will lead most straightforwardly to an isomorphic alternation of macrothalli, as in Sphacelariales and Dictyotales.

Complex reproductive cycles

Instead of an upright thallus developing from one of the cells constituting the prostrate system, it may instead develop from a propagule produced by the prostrate system. The result is a complex life cycle involving the alternation of a filamentous microthallus with a parenchymatous or pseudoparenchymatous macrothallus (Fig. 6C). There is no sexual process involved, but only two kinds of asexual spore: one produced by the microthallus and giving rise to the macrothallus, the other produced

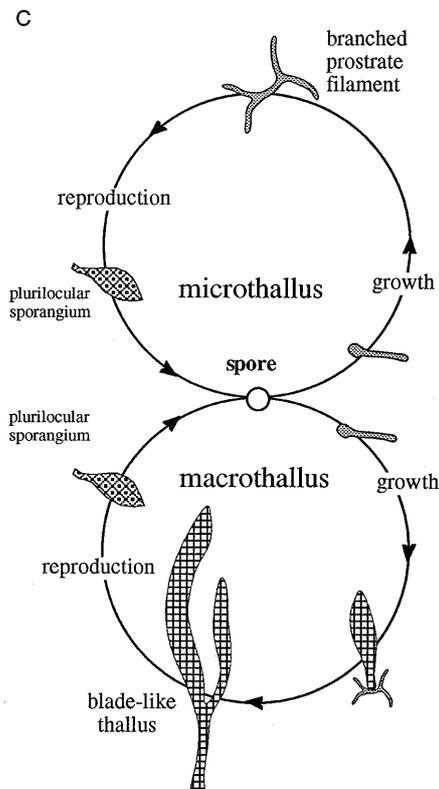


Figure 6C. See caption facing page.

by the macrothallus and returning the macrothallus. (This need not be an obligate alternation; the spore produced by either thallus may iterate the same phase for several generations.) This can be called a Steenstrup alternation, in that it resembles the life cycles of hydrozoans, salps and trematodes described by Steenstrup (1845), where there is a succession of morphological forms developing from propagules without any change in ploidy. I am not aware of any attempt to develop an evolutionary theory of Steenstrup alternation. It is conceivable that microthallus and macrothallus require different conditions for successful growth, and thus benefit from dispersal as an alternative to direct differentiation.

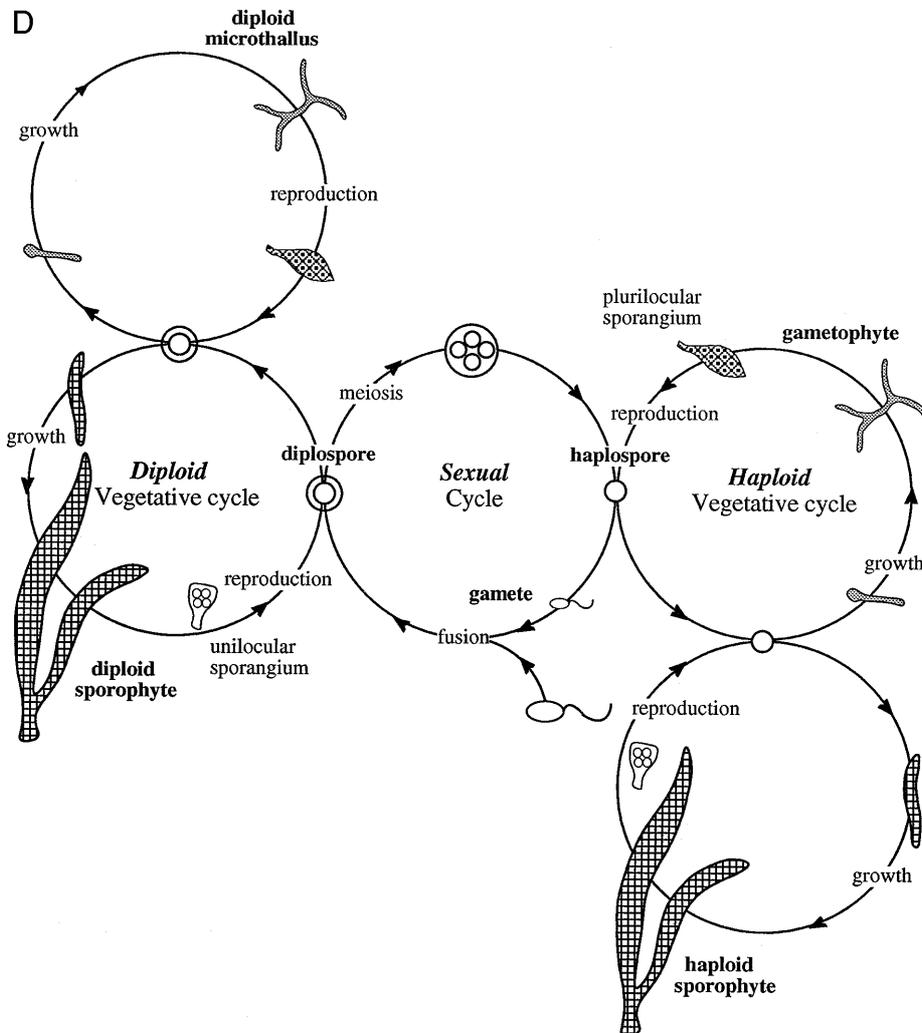


Figure 6D. See caption on p.32.

Complex sexual cycles

When sex occurs in life cycles of this sort, serious complications arise in the form of unfamiliar concepts that do not appear in the usual paradigm (Fig 6D).

The first is the haploid sporophyte. Haploid spores produced by the microthallus may germinate and develop into the macrothallus rather than fusing as gametes. Even if they are capable of acting as gametes, they may develop parthenogenetically if they fail to find fusion partners within a certain period of time. The concept of a haploid sporophyte may seem odd, but careful culture studies have shown that it is very widespread (see Table 1). Indeed, there are few careful culture studies involving the complete life cycle of a sexual species outside the Fucales-Dictyotales clade that has failed to uncover a haploid sporophyte.

The corresponding phenomenon is the diploid microthallus. The prostrate filament developing from the zygote may produce diploid propagules that develop into new microthalli or macrothalli. This filament, sometimes called a plethysmothallus, is morphologically similar to a gametophyte, although of course it cannot act as one. Life cycles involving a diploid microthallus as well as a morphologically similar haploid gametophyte have been reported from Chordariales (see Peters & Muller, 1986a) and Dictyosiphonales (see South, 1980).

The force of these examples, and especially the very widespread occurrence of the haploid sporophyte, is to demonstrate that the association of gametophyte and sporophyte with characteristic morphological states is not necessarily regulated by ploidy. It may instead be regulated either by environmental factors, such as temperature or daylength, or by developmental history. A spore may be switched into one developmental pathway or another according to whether conditions require a persistent stage or permit extended growth without reference to ploidy, even in sexual species.

The generalized life cycle of Phaeophyta thus involves both an asexual alternation of forms and a sexual alternation of ploidy. The association of ploidy with morphology arises when the haploid stage becomes specialized as a gametophyte (through a reduction in the frequency of the haploid sporophyte), whereas the diploid phase is specialized as a sporophyte (through the reduction of the diploid microthallus). Given the different characteristics of zoospores and gametes, it is easy to understand why this happens. There are two ways in which the sexual cycle might become heteromorphic.

The first possibility is that the haploid microthallus becomes specialized as a gametophyte, shedding motile chemotactic gametes into a low-velocity environment close to the substrate. The zygotes, which are dispersed only very locally, give rise to a diploid macrothallus specialized as a sporophyte, shedding motile or immotile spores into a high-velocity environment away from the substrate, so they will be more widely dispersed.

The alternative is that the diploid microthallus becomes specialized as a sporophyte, shedding haploid spores into a low-velocity environment which makes wide dispersal unlikely. These spores germinate into haploid macrothalli, producing gametes that are likely to be swept away by water currents, become widely dispersed, and never fuse.

Clearly, the first possibility is consistent with the basic biology of gametes and spores, whereas the second is not.

Forms with gamete-releasing macrothalli

The main objection to this thesis is the existence of groups that seem to contradict it, especially Scytosiphonales, Dictyotales and Fucales. From a cytological point of view, these taxa are strongly contrasted: Scytosiphonales have a heteromorphic cycle with haploid macrothalli, Dictyotales have an isomorphic cycle in which both phases are large individuals, and Fucales are diplontic or nearly so. However, from the point of view of gamete biology they are very similar: in all three cases, the somatic structure that releases gametes is a macrothallus that extends into the water column. The situation may be compared with that in land plants. The dependence of flagellated gametes on water explains why the gametophytes of plants such as ferns are small and subaerial: but the end-point of the reduction of the gametophyte in land plants is essentially the release of male gametes (strictly, of course, gametophytes) from large erect individuals. This is made possible by an adaptive syndrome that includes the retention of the female gametophyte on the sporophyte, elaborate methods for transporting and trapping the minute male gametophyte, and the release of male gametes within sporophytic tissue, which they penetrate by extension rather than by flagellar motion. The evolution of large gamete-releasing structures in Phaeophyta can be understood in analogous terms: the combination of low flow and chemotaxis is replaced in such cases by an alternative adaptive syndrome. Male gametes are released synchronously, through some environmental cue; thus, the release of gametes, but not spores, is triggered by the lunar cycle in *Dictyota*. The female gametophyte or gamete may be temporarily retained on the sporophyte; thus, in *Fucus*, Sargassaceae (Fucales) and Seirococcaceae (Fucales) the packets liberated from a conceptacle are embedded in mucus that sticks them to the outer surface of the conceptacle until they are fertilized — the mucus may also trap sperm — and drop off. These adaptations are accompanied by the breakdown of the previous adaptive syndrome, and in particular by the loss of pheromonal taxis by male gametes; instead, a pheromone secreted by the mature egg triggers the explosive release of sperm in Laminariales, Sporochnales and Desmarestiales. These phenomena have been reviewed by Brawley & Johnson (1992). The general pattern suggested here thus fails only in particular and predictable circumstances.

ACKNOWLEDGMENTS

This work was supported by a Research Grant from the Natural Sciences and Engineering Research Council of Canada.

REFERENCES

- Amsler CD, Reed DC, Neushul M. 1992.** The microclimate inhabited by algal propagules. *British Phycological Journal* **27**: 253–270.
- Anderson RJ. 1982.** The life history of *Desmarestia firma* (C. Ag.) Skottsb. (Phaeophyceae, Desmarestiales), *Phycologia* **21**: 316–322.
- Bell G. 1976.** The evolution of anisogamy. *Journal of Theoretical Biology* **73**: 247–270.
- Bell G. 1982.** *The Masterpiece of Nature*. London: Croom Helm; Berkeley: The University of California Press.
- Bell G. 1994.** The comparative biology of the alternation of generations. *Lectures on Mathematics in the Life Sciences* **25**: 1–26.

- Blinn DW, Markham JW. 1969.** Development of gametophytes of *Alaria marginata* P. & R. and *Hedophyllum sessile* (C. Ag.) Setch. in saline pond water from British Columbia. *Phycologia* **8**: 51–55.
- Bower FO. 1908.** *The Origin of a Land Flora*. London: Macmillan.
- Brawley SH, Johnson LE. 1992.** Gametogenesis, gametes and zygotes: an ecological perspective on sexual reproduction in the algae. *British Phycological Journal* **27**: 233–252.
- Charlesworth B. 1976.** The population genetics of anisogamy. *Journal of Theoretical Biology* **73**: 347–357.
- Clayton MN. 1979.** The life history and sexual reproduction of *Colpomenia peregrina* (Scytosiphonaceae, Phaeophyta) in Australia. *British Phycological Journal* **14**: 1–10.
- Clayton MN. 1980.** Sexual reproduction — a rare occurrence in the life history of the complanate form of *Scytosiphon* (Scytosiphonaceae, Phaeophyta) from southern Australia. *British Phycological Journal* **15**: 105–118.
- Clayton MN. 1986.** Culture studies on the life history of *Scytothamnus australis* and *Scytothamnus fasciculatus* (Phaeophyta) with electron microscope observations on sporogenesis and gametogenesis. *British Phycological Journal* **21**: 371–386.
- Clayton MN, Wiencke C. 1990.** The anatomy, life history and development of the Antarctic brown alga *Phaeurus antarcticus* (Desmarestiales, Phaeophyceae). *Phycologia* **29**: 303–315.
- Fiore J. 1977.** Life history and taxonomy of *Stictyosiphon subsimplex* Holden (Phaeophyta, Dictyosiphonales) and *Farlowia onusta* (Küsting) Kornmann in Kuckuck (Phaeophyta, Ectocarpales). *Phycologia* **16**: 301–311.
- Hardy FG, Moss BL. 1978.** The attachment of zygotes and germlings of *Halidrys siliquosa* (L.) Lyngb. (Phaeophyceae, Fucales). *Phycologia* **17**: 69–78.
- Henry EC. 1984.** Syringodermatales ord. nov. and *Syringoderma floridana* sp. nov. (Phaeophyceae). *Phycologia* **23**: 419–426.
- Henry EC. 1986.** Primitive reproduction characters and a photoperiodic response in *Saccorhiza dermatodea* (Laminariales, Phaeophyceae). *British Phycological Journal* **21**: 127–137.
- Henry EC. 1987.** The life history of *Phyllariopsis brevipes* (= *Phyllaria reniformis*) (Phyllariaceae, Laminariales, Phaeophyceae), a kelp with dioecious but sexually monomorphic gametophytes. *Phycologia* **26**: 17–22.
- Henry EC, Müller DG. 1983.** Studies on the life history of *Syringoderma phinneyi* sp. nov. (Phaeophyceae). *Phycologia* **22**: 387–393.
- van den Hoek C, Flinterman A. 1968.** The life history of *Sphacelaria furcigera* Kütz. (Phaeophyceae). *Blumea* **16**: 193–215.
- Hoekstra RF. 1987.** The evolution of sexes. In: Stearns SC, ed., *The Evolution of Sex and Its Consequences*. Basel: Birkhäuser Verlag, 59–91.
- Kawai H, Kurogi M. 1985.** On the life history of *Pseudochorda nagaii* (Pseudochordaceae fam. nov.) and its transfer from the Chordariales to the Laminariales (Phaeophyta). *Phycologia* **24**: 289–296.
- Keddy PA. 1981.** Why gametophytes and sporophytes are different: form and function in a terrestrial environment. *The American Naturalist* **118**: 452–454.
- Kirkpatrick M. (editor) 1994.** *The Evolution of Haploid-Diploid Life Cycles. Lectures on Mathematics in the Life Sciences volume 25*. Providence, Rhode Island, U.S.A.: American Mathematical Society.
- Kondrashov AS, Crow JF. 1991.** Haploidy or diploidy: which is better? *Nature* **351**: 314–315.
- Kuhlenkamp R, Müller DG. 1985.** Culture studies on the life history of *Haplospora globosa* and *Tilopteris mertensii* (Tilopteridales, Phaeophyceae). *British Phycological Journal* **20**: 301–312.
- Maddison WP, Maddison DR. 1992.** *MacClade: Analysis of Phylogeny and Character Evolution*. Version 3. Sunderland, Massachusetts: Sinauer.
- Maier I. 1984.** Culture studies of *Chorda tomentosa* (Phaeophyta, Laminariales) *British Phycological Journal* **19**: 95–106.
- Motomura T, Kawaguchi S, Sakai Y. 1985.** Life history and ultrastructure of *Carpomitra cabreræ* (Clemente) Kützting (Phaeophyta, Sporochneales). *Japanese Journal of Phycology* **33**: 21–31.
- Mulcahy DL, Mulcahy GB. 1975.** The influence of gametophytic competition on sporophytic quality. *Theoretical and Applied Genetics* **46**: 277–280.
- Müller DG. 1972.** Life cycle of the brown alga *Ectocarpus fasciculatus* var. *refractus* (Kütz.) Ardis. (Phaeophyta, Ectocarpales) in culture. *Phycologia* **11**: 11–13.
- Müller DG. 1977.** Sexual reproduction in British *Ectocarpus siliculosus* (Phaeophyta). *British Phycological Journal* **12**: 131–136.
- Müller DG. 1984.** Culture studies on the life history of *Adenocytis utricularis* (Phaeophyceae, Dictyosiphonales). *Phycologia* **23**: 87–94.
- Müller DG, Clayton MN, Germann I. 1985.** Sexual reproduction and life history of *Perithalia caudata* (Sporochneales, Phaeophyta). *Phycologia* **24**: 467–473.
- Müller DG, Meel H. 1982.** Culture studies on the life history of *Arthrocladia villosa* (Desmarestiales, Phaeophyceae). *British Phycological Journal* **17**: 419–425.
- Muller HJ. 1932.** Some genetic aspects of sex. *The American Naturalist* **66**: 118–138.
- Norton TA. 1972.** The development of *Saccorhiza dermatodea* (Phaeophyceae, Laminariales) in culture. *Phycologia* **11**: 81–86.
- Norton TA. 1992.** Dispersal by macroalgae. *British Phycological Journal* **27**: 293–301.
- Novaczek I, Bird CJ, MacLachlan JL. 1986a.** Culture and field study of *Stilophora rhizoides* (Phaeophyceae, Chordariales) from Nova Scotia, Canada. *British Phycological Journal* **21**: 407–416.

- Novaczek I, Bird CJ, McLachlan JL. 1986b.** The effect of temperature on development and reproduction in *Chorda filum* and *Chorda tomentosa* (Phaeophyta, Laminariales) from Nova Scotia. *Canadian Journal of Botany* **64**: 2414–2420.
- Otto SP. 1994.** The role of deleterious and beneficial mutations in the evolution of ploidy levels. *Lectures on Mathematics in the Life Sciences* **25**: 69–96.
- Parker GA, Baker RR, Smith VGF. 1972.** The origin and evolution of gamete dimorphism and the male-female phenomenon. *Journal of Theoretical Biology* **36**: 529–553.
- Perrot V, Richerd S, Valero M. 1991.** Transition from haploidy to diploidy. *Nature* **351**: 315–317.
- Peters AF. 1988.** Culture studies of a sexual life history in *Myriotrichia clavaeformis* (Phaeophyceae, Dictyosiphonales). *British Phycological Journal* **23**: 299–306.
- Peters AF. 1992a.** Culture studies on the life history of *Chordaria linearis* (Phaeophyceae) from Tierra del Fuego, South America. *Journal of Phycology* **28**: 678–683.
- Peters AF. 1992b.** Distinction of South American *Haplogloia andersonii* and *Chordaria linearis* (Phaeophyceae) based on differences in sexual reproduction, morphology, ecophysiology, and distribution. *Journal of Phycology* **28**: 684–693.
- Peters AF. 1992c.** Culture studies on the life history of *Dictyosiphon hirsutus* (Dictyosiphonales, Phaeophyceae) from South America. *British Phycological Journal* **27**: 177–183.
- Peters AF, Muller DG. 1986a.** Culture studies on the life history of *Myringloea chilensis* (Mont.) Llaña (Phaeophyceae, Chordariales). *Botanica Marina* **29**: 43–48.
- Peters AF, Muller DG. 1986.** Sexual reproduction of *Stilophora rhizoides* (Phaeophyceae, Chordariales) in culture. *British Phycological Journal* **21**: 417–423.
- Peters AF, Novaczek I, Muller DG, McLachlan J. 1987.** Culture studies on reproduction of *Sphaerotrichia divaricata* (Chordariales, Phaeophyceae). *Phycologia* **26**: 457–466.
- Ramirez ME, Müller DG, Peters AF. 1986.** Life history and taxonomy of two populations of ligulate *Desmarestia* (Phaeophyceae) from Chile. *Canadian Journal of Botany* **64**: 2948–2954.
- South GR. 1980.** Observations on the life histories of *Punctaria plantaginea* (Roth) Greville and *Punctaria orbiculata* Jao (Punctariaceae, Phaeophyta). *Phycologia* **19**: 266–272.
- Steenstrup JJ. 1845.** *On the Alternation of Generations: or, the Propagation and Development of Animals through Alternate Generations.* English translation by Busk G. London: The Ray Society.
- Tan IH, Druehl LD. 1993.** Phylogeny of the Northeast Pacific brown algal (Phaeophyceae) orders as inferred from 18S rRNA gene sequences. *Hydrobiologia* **260/261**: 699–704.
- Wiencke C, Clayton MN. 1990.** Sexual reproduction, life history and early development in culture of the Antarctic brown alga *Himantothallus grandifolius* (Desmarestiales, Phaeophyceae). *Phycologia* **29**: 9–18.