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Seaweed reproductive biology: environmental and genetic controls

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Abstract: Knowledge of life cycle progression and reproduction of seaweeds transcends pure academic interest. Successful and sustainable seaweed exploitation and domestication will indeed require excellent control of the factors controlling growth and reproduction. The relative dominance of the ploidy-phases and their respective morphologies, however, display tremendous diversity. Consequently, the ecological and endogenous factors controlling life cycles are likely to be equally varied. A vast number of research papers addressing theoretical, ecological and physiological aspects of reproduction have been published over the years. Here, we review the current knowledge on reproductive strategies, trade-offs of reproductive effort in natural populations, and the environmental and endogenous factors controlling reproduction. Given that the majority of ecophysiological studies predate the "-omics" era, we examine the extent to which this knowledge of reproduction has been, or can be, applied to further our knowledge of life cycle control in seaweeds.

Keywords: endogenous control; environmental factors; fertilization; life cycle; seaweed reproduction.

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Introduction

Seaweeds are increasingly viewed as an important alternative source of food, feed, fuel and livelihood for humans. Global seaweed aquaculture has expanded at a rate of 8% per year in the past decade (FAO 2016). The combination of human population growth, stagnation in the world's fisheries as a result of depleting fish stocks, and the high environmental impact of certain types of aquaculture, such as intensive fish farming, are viewed as important incentives driving seaweed aquaculture. Expansion and a better integration of seaweed in marine aquaculture are regarded as pivotal for aquaculture to meet the growing global food demand (Duarte et al. 2009, Mazarrasa et al. 2014). Innovation in seaweed aquaculture and the rate at which new species become domesticated is, however, highly dependent on scientific effort (Mazarrasa et al. 2013). An excellent knowledge of the ecological and molecular factors controlling growth and reproduction of seaweeds is viewed as one of the fundamental aspects herein. The complex life cycles of algae, which often involve free-living diploid and haploid life stages, make understanding and controlling life cycles particularly challenging.

The relative dominance of the ploidy-phases and their respective morphology display tremendous diversity in seaweeds (Bell 1994, 1997). Consequently, the evolutionary and ecological aspects of this variation have been given considerable attention (Valero et al. 1992, Richerd et al. 1993, Mable and Otto 1998, Hughes and Otto 1999, Thornber 2006). Algal life cycles differ in the relative timing of syngamy and meiosis, and the degree of mitotic activity in the haploid and diploid phases (Coelho et al. 2007, Cock et al. 2014, Figure 1). In diploid life cycles, gametes are the only haploid cells, fusing immediately to form a new diploid cell, followed by a series of mitotic divisions before undergoing meiosis again. Conversely, in haploid life cycles, meiosis directly follows syngamy and the zygote is the only diploid cell in the life cycle. Mitotic divisions in both the haploid and diploid phases characterize haploid-diploid life cycles. Adding to the

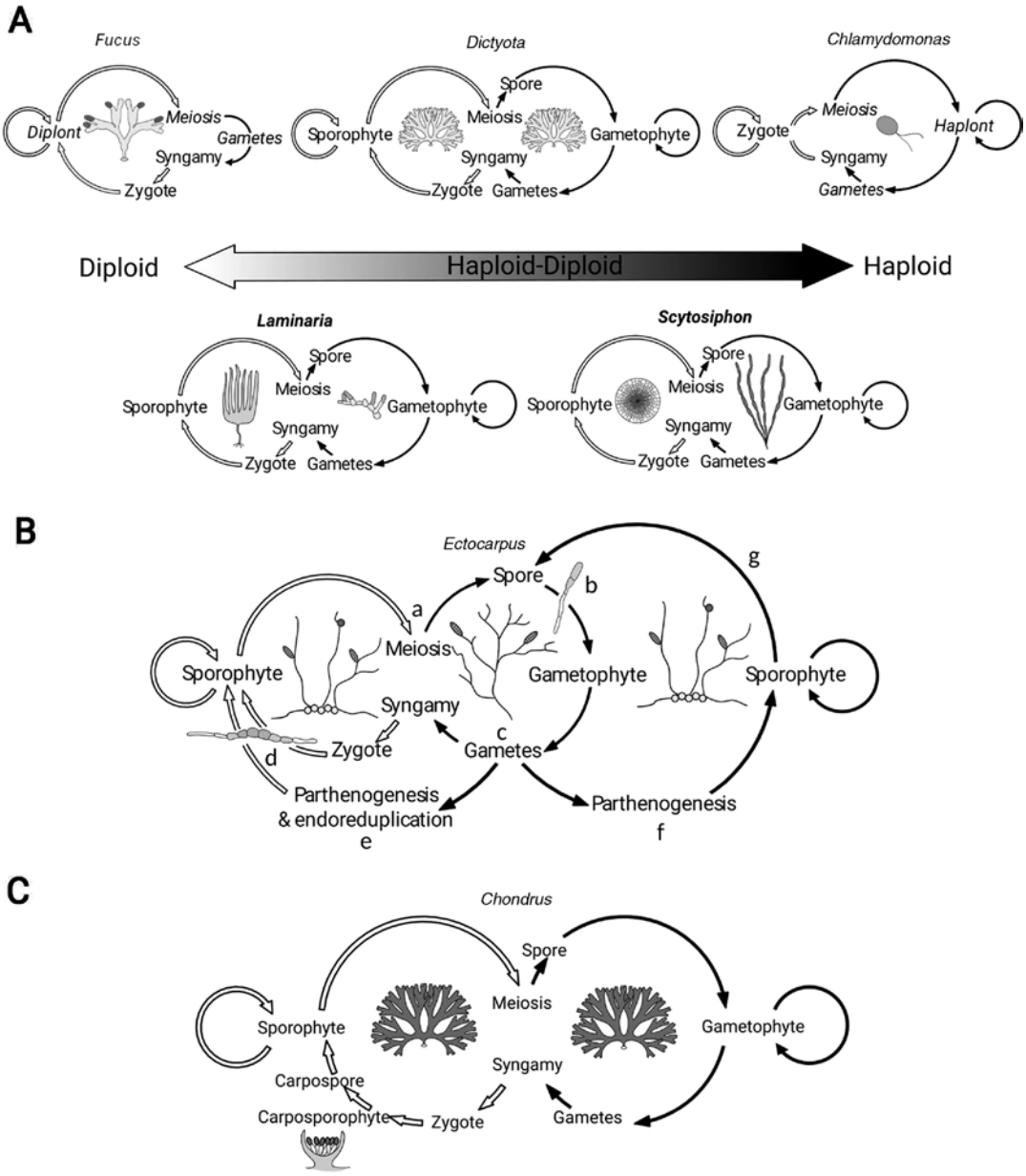

Figure 1: Schematic representation of algal life cycles.
Diploid and haploid stages are marked by white and black arrows, respectively. (A) Brown algal life cycle. Fucales are characterized by a diplontic life cycle. Meiosis in the reproductive tissue is immediately followed by gametogenesis and syngamy producing a diploid zygote. Most algae such as *Dictyota, Scytosiphon* and *Laminaria* exhibit a diplohaplontic life cycle where a haploid gametophyte alternates with a diploid sporophyte. Here following meiosis the resulting spore develops into a multicellular organism. Both haploid and diploid phases may be of identical morphology (isomorphic) (*Dictyota*), or the two phases may develop differently (heteromorphic) with either the gametophyte (*Laminaria*) or the sporophyte (*Scytosiphon*) being microscopic. Many unicellular algae (*Chlamydomonas*) are characterized by a haplontic life cycle where the formation of a zygote is immediately followed by a meiotic division. (B) Simplified diplohaplontic life cycle of *Ectocarpus siliculosus*. Meiosis (a) takes place in the sporophyte (diploid) to produce haploid spores. First cell division in germinating spores is asymmetric (b) and they grow into multicellular gametophytes. Gametophytes produce morphologically identical but physiologically differentiated male and female gametes (c), which fuse to form a zygote. After a symmetrical first cell division (d) the zygote grows into a diploid sporophyte. Alternatively, gametes that do not meet a partner of the opposite sex grow into diploid parthenosporophytes by means of parthenogenesis combined with endoreduplication (e) or into a haploid parthenosporophyte (f). The latter produces meiospores via a non-reductive apomeiotic event (g). (C) Life cycle of the red alga *Chondrus* showing three distinct stages: the gametophyte, the sporophyte and the carposporophyte, which develops parasitically on the gametophyte after fertilization. Loops connecting a generation with itself denote asexual reproduction mediated by vegetative reproduction (e.g. fragmentation, propagule formation) (*Fucus*, *Dictyota*), the formation of asexual spores (mitospores) (*Dictyota, Ectocarpus, Laminaria*), mitosis (*Chlamydomonas*) or parthenogenetic development of unfertilized (female) gametes (*Scytosiphon, Laminaria, Ectocarpus*). Figure adapted from Bogaert et al. (2013).

complexity, these two phases may be morphologically indistinguishable (isomorphic) or highly dissimilar (heteromorphic). Furthermore, in many species both haploid and diploid life cycle phases may replicate directly asexually, either through some form of vegetative fragmentation, asexual spores or parthenogenetic development of unfertilized gametes (Wynne and Loiseaux 1976, Clayton 1982, Santelices 1990). Besides having a free-living haploid and diploid phase, most red algae have an additional "third generation", the carposporophyte, which develops from the fertilized egg cell and depends for its nutrition on the female gametophyte. The carposporophyte releases diploid spores, carpospores, which grow into diploid tetrasporophytes (West and Hommersand 1981). Regardless of this large variation in life cycles, the core processes of life cycles, meiosis and syngamy, are conserved among virtually all eukaryotes (Cavalier-Smith 2002), leading to questions about the levels at which the ecological and molecular processes controlling these processes and their relative timing are conserved.

An alternation of haploid and diploid life stages mediated by meiosis and syngamy evolved at the base of the eukaryotic tree of life (Cavalier-Smith 2002, Speijer et al. 2015). A number of non-mutually exclusive theories, e.g. recombination, nutrition and repair theories have been put forward to explain why a sexual life cycle originally evolved. We refer to several excellent reviews for an in-depth discussion on the origin and maintenance of sexual reproduction (e.g. Maynard-Smith 1978, Bernstein et al. 1981, Michod 1993, Barton and Charlesworth 1998, Cavalier-Smith 2002). In the context of this review, the empirical observation that starvation is known to induce sexual reproduction in many protists is important. According to Cavalier-Smith (2002) the doubling of cell volume, which results from the syngamy of two individuals or gametes, would have significantly increased survival of the organism during periods of food or nutrient shortage, while smaller, haploid cells resulting from meiosis are advantageous under replete resource conditions. This trade-off between reproduction and growth, either in the number of individuals at the population level for unicellular organisms or thallus size for multicellular ones, forms the basis of theories of resource allocation which provide a framework for linking physiological performance and life cycle evolution (Reznick 1985, Jösson and Tuomi 1994, Obeso 2002). Therefore, the degree to which environmental conditions that trigger reproduction are conserved is also relevant from an evolutionary perspective.

The fundamental importance of life cycles and reproduction for an understanding of the biology of algae has spawned a whole series of reviews over the years focussing on ecological, evolutionary, physiological or molecular aspects (Table 1). This review does not intend to re-review the entire body of research. Rather, we provide a brief overview of the current knowledge, and examine the extent to which our ecological and physiological understanding of the factors triggering life cycle transitions in seaweeds has been embraced by present day "-omics" driven research. The review limits itself to the induction of fertility, either as meiosis or gamete formation. It does not cover processes such the release of gametes, pheromone signalling or fertilization. The focus is on seaweeds but, when appropriate, we draw on the extensive knowledge of a few well-studied microscopic algae (e.g. *Chlamydomonas*) for comparative purposes.

Resource allocation – balancing growth, reproduction, and survival

Evidence for trade-offs between reproduction, growth and mortality

An organism's life history is the result of combined trade-offs among different fitness components like survival, growth, and reproduction. As such, sexual reproduction imposes a demographic cost on the organism and, thus, the energy invested in reproduction is expected to affect growth and survival (Williams 1966a,b). De Wreede and Klinger (1988) reasoned that, if reproduction comes at a cost, organisms are likely to (i) have a certain size before becoming reproductive; (ii) reduce growth at the onset of reproduction; (iii) die after releasing reproductive structures or propagules; (iv) produce less reproductive spores or gametes in years with proficient growth or display reduced survival in the following year; (v) display an inverse correlation between the number of spores or gametes produced and their survival. Reviewing the evidence of resource allocation in seaweeds, De Wreede and Klinger (1988) suggested there was no apparent trade-off between growth and reproduction, and neither were there clear indications that the same resources could limit both seaweed growth and reproduction. The authors, however, stressed a general lack of data and rigorous experiments, which could demonstrate reproductive costs in algae. Since the review of De Wreede and Klinger (1988), evidence for trade-offs between reproduction and growth and or mortality has been gradually mounting.

Table 1: A chronological overview of review papers focusing on algal life cycles, fertility, and gamete release.

Author(s)	Focus of the review
Coleman (1962)	Genetic and environmental control of sexuality, cell fusion and chemotaxis of unicellular algae
Ettl et al. (1967)	An encyclopedic treatise of algal reproduction, vegetative reproduction, parthenogenesis and apogamy
Knaggs (1969)	Life histories of red algae
Dring (1970)	Photoperiodic effects on algal development and reproduction, with special emphasis on fertility in *Pyropia tenera*
Dring (1974)	Environmental control of fertility and release of spores and gametes, endogenous rhythms of fertility, chemotaxis and gamete fusion
Dixon and Richardson (1970)	Growth and reproduction of red algae as a function of photoperiodism
Wynne and Loiseaux (1976)	Life history variation in brown algae
Searles (1980)	The evolutionary advantage of a triphasic life cycle characteristic for many red algae
Lüning (1980a)	Environmental control of algal life cycles
Lüning (1981)	Effect of photoperiod on reproduction in algae
West and Hommersand (1981)	Life histories of red algae
Pedersen (1981)	Life histories of brown algae
Tanner (1981)	Life histories of green algae
Clayton (1982)	Variation in life history characteristics of Ectocarpales and their evolutionary significance
Dring (1984)	Photoperiodism, effects of daylength on development and life cycle control in algae
Hoffmann (1987)	An ecologically inspired review focusing on seasonal variation in fertility, endogenous and environmental factors controlling fertility and release of gametes and spores, dispersal of propagules
Dring (1988)	Photoperiodic responses of algae and photoreceptors involved in these responses
De Wreede and Klinger (1988)	Reproductive strategies and resource allocation, ontogenetic patterns of fertility, sporophyte/gametophyte and sex ratios, parthenogenesis
Breeman (1988)	Although strictly speaking a review of algal biogeography, the link between reproduction/growth and temperature is central in determining algal ranges
Clayton (1988)	Evolution and life histories of brown algae
Maggs (1988)	Intraspecific life history variation in red algae
Lüning and tom Dieck (1989)	Environmental control of fertility and growth in seaweeds, with a focus on large perennial species
Lüning (1990)	An influential textbook covering many aspects of seaweed biology, ecology, ecophysiology and biogeography, including life cycle control
Santelices (1990)	A monumental review discussing life cycles, sexual and asexual reproduction, resource allocation, sporophyte/gametophyte ratios, seasonality and ontogenetic patterns, release of gametes and spores, dispersal vectors and settlement and recruitment of propagules
Brawley and Johnson (1992)	Effect of environmental factors on gametogenesis, gamete release, fertilization (pheromones), monoecious reproduction and selfing, polyspermy blocks, parthenogenesis and ecology of the young zygote in unstable environments
Valero et al. (1992)	Diversity and theoretical considerations of the evolution and stability of life cycles
Klinger (1993)	Persistence of biphasic life cycles in algae
Bell (1997)	Evolution of brown algal life cycles
Mable and Otto (1998)	Diversity and theoretical considerations of the evolution and stability of life cycles
Brawley et al. (1999)	Gamete release and fertilization success in fucoid algae
Santelices (2002)	Fertilization in natural environments with an emphasis on gamete release and polyspermy blocking mechanisms
Coleman and Pröschold (2005)	Sexual reproduction in culture of unicellular algae
Thornber (2006)	Ecological and evolutionary aspects of isomorphic biphasic life cycles
Pearson and Serrão (2006)	Gamete release and fertilization success of fucoids
Coelho et al. (2007)	Diversity of life cycles with an emphasis on the molecular mechanisms governing life cycle transitions in plant model organisms and a discussion of how these can lead to a better understanding of algal life cycles
Bartsch et al. (2008)	A comprehensive review of the kelp *Laminaria* (sensu lato), including factors controlling fertility, spore release and chemotaxis
Luthringer et al. (2014)	Ecological implications and molecular basis of sexual dimorphism in seaweeds
Cock et al. (2014)	Diversity and regulation of brown algal life cycles

Age and size

The cost of reproduction and the dependence of reproductive structure on vegetative tissue for resources is often translated into a correlation of fecundity with age or size of the organisms (De Wreede and Klinger 1988, Guillemin et al. 2014). Several authors noted threshold sizes, i.e. minimal sizes below which individuals do not become fertile (Mathieson and Guo 1992, Zou et al. 2006). The age at which the seaweed first becomes reproductive varies widely among species. Available data have been summarized by De Wreede and Klinger (1988). For example, *Colpomenia peregrina* becomes reproductive after 2 days, while *Carpophyllum angustifolium* becomes reproductive only after 3 years. Among fucoids, several species of *Fucus* produce gametes after 2 years (Mathieson et al. 1976, Niemeck and Mathieson 1976) while *Ascophyllum nodosum* requires 4–5 years (Sideman and Mathieson 1983). Among kelps with heteromorphic life histories, microscopic gametophytes become fertile in a few days while macroscopic sporophytes require months to be reproductive (Bartsch et al. 2008). Even among relatively closely related species, reproduction can be age-specific or age-independent. Hence, a common pattern is difficult to ascertain. Studies carried out using *Sargassum polyceratium* demonstrated that resource availability plays a critical role in reproductive effort and size thresholds for reproduction. Individuals growing in deeper water with lower available resource levels (less light and water displacement) have been shown to have lower reproductive efforts and shorter reproductive seasons, as well as a smaller minimal size for reproduction (De Ruyter van Steveninck and Breeman 1987, Engelen et al. 2005).

Growth

Ang (1992) reported that fertile thalli of *Fucus distichus* manifested zero or negative growth, but no difference was found in longevity and mortality. Åberg (1996) demonstrated differences in the annual reproductive effort of *Ascophyllum nodosum* between small and large individuals, which were interpreted as a reproductive trade-off by arguing that small individuals are better off investing in growth, which offers them a better chance of survival, while larger individuals can afford to invest in reproduction. By removing either vegetative stems or reproductive structures in *Sargassum thunbergii*, Chu et al. (2011) demonstrated a trade-off between vegetative growth and reproduction. This study confirmed older observations by McCourt (1985) and Gillespie and Critchley (2001) of an inverse correlation between vegetative growth and reproductive effort among different *Sargassum* species in the Gulf of California and South Africa, respectively. Focusing on the commercial red alga *Gracilaria chilensis*, Guillemin et al. (2014) provided strong evidence for reproduction-associated costs. The photosynthetic performance and growth of vegetative thalli of male and female gametophytes, and of tetrasporophytes were significantly higher compared to the reproductive thalli of the corresponding stages of the life cycle. The authors hypothesized that nearby vegetative tissue or previously accumulated photosynthetic products are required to support the development of reproductive structures.

Mortality

Seaweeds display widely diverging life history strategies ranging from short-lived ephemeral species to extremely long-lived species, such as *Ascophyllum nodosum* (Åberg 1992a,b) or certain red algae (crustose red algae: Paine et al. 1979; *Cryptonemia*: Scott et al. 1982; coralline algae: Frantz et al. 2005) and green algae (e.g. *Halimeda*, Hillis-Colinvaux 1980). Likewise, reproduction strategies vary from semelparity (single reproductive event) to iteroparity (multiple reproductive events). The former is obviously more common in short-lived annual species which tend to grow to a certain size, reproduce and die. Semelparity as the putative ancestral mode of reproduction would be in line with starvation and repair theories whereby zygotes offer a better chance for surviving favorable ecological conditions, but not all semelparous species are short-lived. Tropical siphonous seaweeds (e.g. *Caulerpa*, *Halimeda*) are semelparous, yet many are apparently long-lived (Hillis-Colinvaux 1980, Clifton and Clifton 1999). Likewise, iteroparous species may also become fertile from an early age or size onward (e.g. *Sargassum polyceratium*, De Ruyter van Steveninck and Breeman 1987). This diverse array of life history strategies among seaweeds makes them attractive but largely unexplored models to assess evolutionary processes and trade-offs related to reproduction.

Demographic models

Reproduction-associated costs are also indicated by more indirect relationships, such as temporal patterns of growth and reproduction, and "reproductive effort" (i.e. the proportion of the total energy budget of an organism that is devoted to reproductive processes; Bell 1980, Santelices

1990). These characteristics should be interpreted in relation to a more general perspective of algal life-histories, which takes into account growth, longevity, and mortality. As the cost of reproduction can be expressed in these three processes, all have to be assessed together. Demographic studies are, however, quite rare in phycology and this is especially true for studies that combine models analysing trade-offs and their effects on population fitness. Demographic matrix models have been constructed for various fucoids (*Ascophyllum*: Åberg 1992a,b, 1996, Araújo et al. 2015; *Fucus*: Ang and DeWreede 1993, Araújo et al. 2014; *Sargassum*: Ang 1987, Engelen et al. 2005, Engelen and Santos 2009) and a few red seaweeds (*Gelidium*: Santos 1993, Vieira and Santos 2010; *Iridaea*: Ang et al. 1990, *Gracilaria*: Engel et al. 2001). For the long-lived fucoid, *Ascophyllum nodosum*, fitness is more sensitive to variation in survival than to variation in growth and fecundity (Åberg 1992a,b). For this reason, the reproductive effort of this species is restricted to a level that does not undermine future survival of thalli, and the costs would be expected to be expressed in reduced fecundity in the future. Small individuals investing in growth rather than reproduction have a higher survival because the cost of reproduction is high, whereas large individuals can allocate 70% of their net growth to reproduction without affecting their survival (Åberg 1996). Nevertheless, reproduction needs to be sufficient to guarantee persistence after disturbance events, such as ice scouring at high latitudes and storms and hurricanes at medium and low latitudes (Åberg 1992a, Engelen et al. 2005). More opportunistic fucoids like the invasive *Sargassum muticum*, which displays a very large reproductive allocation, seem to rely on the same strategy, irrespective of the state of invasion (Engelen and Santos 2009). Also, the red seaweed *Gracilaria gracilis* was characterized by high survival and low recruitment rates, consistent with an estimated longevity of 42 years (Engel et al. 2001). In contrast, short-lived ephemeral species are predicted to have a very high reproductive effort and associated costs as they do not have to balance costs with future vital rates. To our knowledge, no such species has been studied using demographic matrix models.

Costs required for reproduction and persistence are temporally and spatially variable, for example, along the distributional range of a species. Araújo et al. (2015) showed that *A. nodosum* individuals in populations close to their southern limit in northern Portugal allocate more resources to reproduction (despite their smaller size, Araújo et al. 2014), whereas more investment went into defence in more centrally located populations. It is uncertain whether there is a genetic basis for these differences in strategy as edge populations in *A. nodosum*, like other fucoids, are generally (strongly) genetically differentiated from central populations (Olsen et al. 2010). A systems biology approach in which hypotheses generated from demographic models are tested experimentally and subsequently adapted according to the new insights obtained, would be a preferred approach for the future in which "-omics" approaches can provide detailed insights into the mechanisms behind trade-offs.

A need for experimental evidence and demographic models

It should be pointed out that all studies addressing trade-offs between reproduction and other life history traits in seaweeds are based on correlation studies using naturally occurring variation or experimentally modified populations, in which neither the environment nor some life history trait was manipulated. In unmanipulated natural populations, the costs of reproduction can be difficult to detect, leading to the inaccurate conclusion that there are no associated costs when inter-individual variation in resource availability is large in relation to the variation in proportions allocated to reproduction (van Noordwijk and de Jong 1986). Correlative approaches are not without criticism, because inverse correlations observed between life-history traits may not be causal, but dependent, in opposite ways, on environmental conditions (Obeso 2002, Knops et al. 2007). Reznick (1985) would dismiss correlative as well as experimental evidence entirely, and emphasizes that indications of trade-offs should be tested by genetic correlation studies using quantitative genetic experiments under standardized conditions or selection experiments (Reznick 1985, Stearns 1989). In terrestrial plant studies aimed at understanding adaptive differentiation and life-history evolution, reproduction costs are typically determined by experimentally reducing fruit set (von Euler et al. 2012) or increasing reproduction through hand-pollination (Sletvold and Ågren 2015). Reproductive costs should preferably be changed by non-invasive manipulations. To the best of our knowledge, such experiments have not been conducted in any algal systems.

A molecular perspective on fertility

Genetic control

Sexual reproduction encompasses the fusion of two haploid gametes of opposite sex to form a diploid zygote,

followed by meiosis to restore the haploid state, either directly following syngamy or after development of the diploid life stage through mitotic divisions. From a molecular perspective, the factors involved in gamete formation, fusion and meiosis remain unknown for the vast majority of algal groups. Most of our knowledge is based on extensive genetic studies involving the green algal model organism *Chlamydomonas* (Goodenough et al. 2007, Lopez et al. 2015). In the following section we draw on the knowledge of *Chlamydomonas* to investigate the extent to which the molecular mechanisms involved in life cycle transitions are conserved among algae in general (Figure 2).

The genes involved in meiosis appear to be remarkably conserved across algal lineages and, by extension, across the eukaryotic tree of life (Supplemental Table S1). The presence of core meiotic genes (e.g. *SPO11, HOP1, HOP2, MND1*, etc.) is considered evidence for sexual reproduction (Schurko and Logsdon 2008). Also, in certain algae where sexual reproduction is very rarely observed (Trebouxiophyceae: Blanc et al. 2010, Fučíková et al. 2015), or has not yet been observed (*Ostreococcus*: Derelle et al. 2006; *Micromonas*: Worden et al. 2009), homologues of these core meiotic genes are present (Grimsley et al. 2010).

Gametogenesis has been thoroughly characterized in *Chlamydomonas*. Following nitrogen depletion, cells acclimate by upregulation of an N-starvation program, as well as starting the gamete program (Abe et al. 2004, 2005). The genes involved in gametogenesis, however, appear to be little conserved. For example, *FUS1*, initially characterized as a sex-specific gene located in the mt+ locus and essential for pre-fusion attachment between the plus and minus gametes (Ferris et al. 1996), is not found in other organisms, not even in the relatively closely related genera *Gonium* and *Volvox* (Ferris et al. 2010). Similarly, *MID* (the sex determination gene in *Chlamydomonas*; Lin and Goodenough 2007), *SAG1* and *SAD1* (encoding the plus and minus agglutinin, respectively), are not found outside of the Chlamydomonadales (Goodenough et al. 2007).

The seemingly non-conserved nature of genes involved in gametogenesis could result from rapid molecular evolution, and a consequent lack of sequence similarity of genes involved in sexual reproduction (Swanson and Vacquier 2002, Swanson et al. 2011), rendering

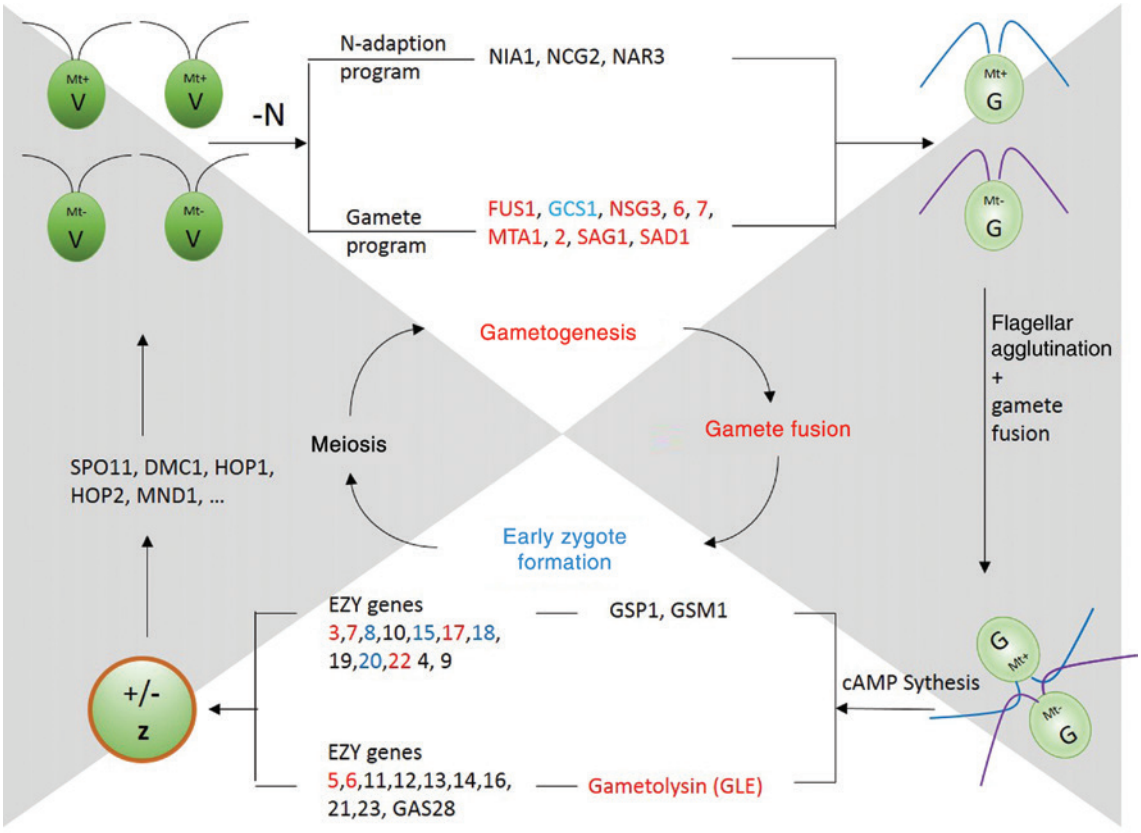

Figure 2: Synthetic overview of gamete formation, fusion and meiosis in *Chlamydomonas* with indications of the genes involved and their conservation in other algae (black, highly conserved; blue, somewhat conserved; red, not conserved).

BLAST-searches less effective. Interestingly, a generative cell specific 1 gene (*GCS1*), orthologous to *HAP2*, which was initially demonstrated to mediate membrane fusion of male and female gametes during fertilization in land plants (Mori et al. 2006) and later identified as an ancestral gamete, fusogen, due to its high conservation among distantly related eukaryotes (Liu et al. 2008, Wong and Johnson 2010, Speijer et al. 2015), seems to be highly conserved among species of Chlorophyta.

Following the attachment of opposite-type gametes in *Chlamydomonas*, release of lytic enzymes results in the rapid disassembly of the gamete cell wall (Matsuda et al. 1985). The newly formed zygote triggers the synthesis of a new zygote extracellular matrix (ECM). Among the studied genes involved in ECM formation (Rodriguez et al. 1999, Kubo et al. 2008), *EZY* (early zygote expressed) 12, 13 and 23 are highly conserved among all algae, while others (*EZY*5, 6, 11, 14 and *GAS28*) are not. The fusion of opposite mating type gametes initiates the diploid phase of the *Chlamydomonas* life cycle. Regarding the genetic mechanism underlying the full program of zygote development, *GSP1* originating from plus gametes and *GSM1* originating from minus gametes both contribute to zygote development, including the resorption of flagella, fusion of nuclei and chloroplasts, destruction of minus gamete G- chloroplast DNA, and secretion of a resistant cell wall (Wilson et al. 1999, Goodenough et al. 2007). Earlier studies showed that the ectopic expression of *GSP1* in minus gametes or of *GSM1* in plus gametes can switch the zygotic differentiation programme on, and the resulting zygotes could undergo a normal meiosis (Zhao et al. 2001, Lee et al. 2008). Further research has uncovered the functional homology between *GSP*1/*GSM*1 and KNOX/BELL, which regulate stem-cell specification in land plants (Lee et al. 2008). Both genes are conserved among algae, although they appear to be lost in some lineages (Trebouxiophyceae, *Gonium*, *Chondrus and Saccharina*, see Supplemental Table S1). The heterodimerization of *GSP1* and *GSM1* activates the zygote development program.

Compared to the detailed knowledge of *Chlamydomonas*, the genetics underlying life cycle control in multicellular algae is in its infancy. Knowledge of life cycle progression at the molecular level is accumulating rapidly for *Ectocarpus*, a brown algal model species with a haploid-diploid life cycle with subtle but distinct morphological differentiation between the sporophyte and gametophyte phases (Figure 1B). The complex life cycle of *Ectocarpus* has shown that life cycle transitions are controlled by genetic mechanisms instead of ploidy level, and can show a large degree of developmental plasticity (Müller 1967, Bothwell et al. 2010). However the identity of the molecular players is only just being revealed thanks to the combination of a whole genome sequence for *Ectocarpus* and life cycle mutants (Cock et al. 2010, 2014). Results have been published on two mutants, *immediate upright* (*imm*) and *ouroboros* (*oro*). The *imm* mutant exhibits partial conversion of the sporophyte generation into a gametophyte during early development, and the *oro* mutant generates a homeotic conversion of the sporophyte generation into a fully functional gametophyte (Peters et al. 2008, Coelho et al. 2011, Macaisne et al. 2017). Ongoing studies focus on detecting the genes underlying the *imm* and *oro* mutants, which would allow comparison of the diploid program with other model systems. Next to these studies, Lipinska et al. (2013, 2016) have characterized the transcriptome of male and female gametes and identified genes which may play a role in gamete recognition.

In multicellular red algae with complex triphasic life cycles, a number of recent studies have sought to determine the molecular machinery and genes controlling reproductive processes (García-Jiménez and Robaina 2015). Whole genome data of the economically important species *Pyropia yezoensis* (Nakamura et al. 2013) and *Chondrus crispus* (Collén et al. 2013) have provided a first glimpse into the gene repertoire involved in reproduction. Additional insights have been provided by transcriptomic analyses in a number of species, including *Pyropia* (Uji et al. 2013) and *Gracilariopsis* (Kamiya et al. 2011), which have identified sets of genes upregulated in different phases of the life cycle. In *Gracilaria*, *Hydropuntia* and *Grateloupia*, research has focused on the ornithine decarboxylase *GiODC* gene, which regulates carpospore maturation and liberation (Guzmán-Urióstegui et al. 2002, 2012, Sacramento et al. 2004b, García-Jiménez et al. 2009, reviewed in García-Jiménez and Robaina 2015). Variation in the expression of *GiODC* was observed during cystocarp development with levels reduced in fertile tissue (García-Jiménez et al. 2009). Ornithine decarboxylase has been characterized in several other algae (including *Chlamydomonas*, Theiss et al. 2002) where it is involved in cell growth and cell division.

Endogenous signaling

For morphologically complex seaweed species, e.g. Laminariales, sporogenesis occurs in different parts of the thallus (Leal et al. 2014). For some genera in the family Alariaceae, sporogenesis occurs on the surface of specialized laminae, called sporophylls, located at the base of the vegetative frond, while the nonsporophyllous genus

Pleurophycus produces sporogenic tissue on the blade and midrib. All members of the family Costariaceae, and most genera of Laminariaceae and Lessoniaceae, with a few exceptions, also form sori on their blades. The exceptions are the sporophyllous genera *Macrocystis* (Laminariaceae), and *Egregia* and *Eisenia* (Lessoniaceae), which have basal sporophylls where sporogenesis occurs (Leal et al. 2014). Distinctively, *Aureophycus aleuticus* forms sori on its semidiscoidal holdfast (Kawai et al. 2013). The above examples show apparent species-specific localization of reproduction. However, the typical reproduction area can also be altered experimentally or can be non-specific in some species. For example, *Alaria nana* was observed to produce sori on the vegetative blade after sporophylls were experimentally removed (Pfister 1991). However, natural populations of two other sporophyllous species, *Undaria pinnatifida* and *Alaria crassifolia*, were observed to produce sori on their blades and midrib (Sanbonsuga and Hasegawa 1967, Stuart et al. 1999, Kumura et al. 2006). In *Macrocystis*, apart from the sporophylls, different vegetative blades, such as frond initials, surface-canopy blades and apical scimitars, have been reported to bear sori and the spores produced are viable (Leal et al. 2014). Recently, sorus formation in the holdfast haptera of *Ecklonia radicosa* has been described (Akita et al. 2016), suggesting that sporogenesis in the holdfast is not distinctively unique to the "primitive" kelp *Aureophycus aleuticus*. In this regard, endogenous mechanisms are most likely involved in the location (i.e. different thallus parts) and timing of reproduction.

Findings on tissue-specific sporogenesis echo early results with *Laminaria digitata* by Buchholz and Lüning (1999) and Lüning et al. (2000). Excised portions from the vegetative blade above the meristematic zone produced sori when cultivated under 8–16 h of light per day and at temperatures between 6°C and 12°C, but not on blade discs cut from the meristem or in intact sporophytes cultivated under the same conditions. Subsequent studies have shown similar results in other *Laminaria* species (Nimura et al. 2002, Skriptsova and Titlyanov 2003). Such different responses between excised blades and intact sporophytes exposed to the same conditions strongly suggest that sporogenesis is not uniquely controlled by the environment. Furthermore, sporogenesis in *Saccharina latissima* was observed not only in isolated blade fragments but also in whole sporophytes with transverse cuts above the meristematic region (Pang and Lüning 2004). These results suggest the production of a putative sporulation inhibitor in the meristematic region of kelps (Lüning et al. 2000, Pang and Lüning 2004). The short day is thought to be the primary signal to reduce meristematic activity at the base of the blade and may also decrease the production of sporulation inhibitors down to a critical concentration allowing sorus formation in the distal blade portions. In the field, the observed sorus formation in Laminariales during low or no growth in autumn and early winter, points to a combined endogenously and environmentally controlled reduction in growth and putative sporulation inhibitors.

The exact nature of the regulating factors is still uncertain. Lüning et al. (2000) suggested that the inhibitor may not be a chemical substance after all, but signals (e.g. electrical currents) transmitted from cell to cell. In addition, whether the phytohormones of land plants are shared with algae is controversial, especially given the distinct evolutionary relationship. Many of the signaling pathway components are not present in basal early-diverging lineages of the Streptophyta and/or other algal lineages (De Smet et al. 2010, Lu and Xu 2015; Mori et al. 2017) making it less likely that a phytohormone function could have been inherited from a common unicellular ancestor. Nonetheless, evidence for phytohormone function in unicellular algae is beginning to accumulate, such as the role of abscisic acid and auxins in regulation of growth in unicellular green algae and diatoms (Kobayashi et al. 1997, Yoshida et al. 2004, Park et al. 2013, Lu et al. 2014, Amin et al. 2015). This is consistent with the hypothesis that hormones such as auxin might have served initially as growth-regulating hormones or pheromones in unicellular ancestors predating the advent of multicellularity (Cooke et al. 2002, Bogaert et al. 2013). While it is well established that algae (from cyanobacteria to brown algae) contain land plant phytohormones (reviewed in Tarakhovskaya et al. 2007, Stirk and Van Staden 2014, Lu and Xu 2015), compounds such as auxins may be breakdown products or intermediates from tryptophan metabolism and have been detected also in unikonts (Bertilsson and Palmér 1972).

The best explored putative phytohormones in brown algae are auxins, which exert a growth-promoting function in land plants, but most research has concentrated on the effects of indole-3-acetic (IAA) on growth and cell polarity, rather than its influence on fertility (Basu et al. 2002, Lin and Stekoll 2007, Le Bail et al. 2010). Auxin was shown to promote growth and inhibit sporogenesis when applied exogenously to *Saccharina japonica*, and the auxin oxidase activity in sporophyllous tissue was shown to be dramatically increased (Kai et al. 2006). Abscisic acid, in contrast, has been shown to promote sporogenesis in *S. japonica* (Nimura and Mizuta 2002). Among the red algae, two different phytohormones have emerged with a fertility-regulating role. Ethylene has been reported to induce tetrasporogenesis in *Pterocladiella capillacea*

(García-Jiménez and Robaina 2012). The maturation, liberation, and growth of carpospores in *Grateloupia imbricata* and *Hydropuntia cornea* (Guzmán-Urióstegui et al. 2002, 2012, Sacramento et al. 2004a, 2007), on the other hand, have been shown to be stimulated by polyamines.

The effects of phytohormones on algae should be considered also in a holobiont context (i.e. the algae including the interacting microorganisms) rather than focusing on the alga itself as reported for interactions with fungi (Fries 1988) and bacteria (Fries 1977) in fucoids. Recently, it was shown that IAA, synthesized by a *Sulfitobacter* species using tryptophan produced by the diatom *Pseudonitzschia multiseries*, promotes the growth of the latter (Amin et al. 2015). Growth-stimulating phytohormone-like substances such as thallusin and other compounds still to be identified have been also isolated from *Monostroma* and *Ulva* (Matsuo et al. 2005, Wichard et al. 2015). Similarly, the brown alga *Ectocarpus* was shown to interact with an alphaproteobacterium that harbors several proteins thought to be involved in the synthesis of algal hormones such as auxins and cytokinins (Dittami et al. 2014). Interactions have also been observed in land plants where pathogenic or symbiotic bacteria can influence the growth of a plant by manipulating its auxin homeostasis (Lambrecht et al. 2000, Frugier et al. 2008, Ludwig-Müller 2015). Therefore it is not certain if phytohormones are synthesized by algae themselves and metabolic auxotrophy may have evolved as a result of mutualism with microorganisms due to the aquatic environment (Kazamia et al. 2016, Mori et al. 2017).

In green algae, new compounds regulating fertility that are different from land plant phytohormones are emerging. In *Ulva*, the presence of sporulation inhibitors (SI) to maintain the vegetative state of the thallus has been described (Stratmann et al. 1996, Wichard and Oertel 2010). The release of these substances initiates the formation of either sporangia or gametangia. The first sporulation inhibitor (SI-1) has a high molecular mass that completely suppresses gametogenesis at concentrations lower than 10^{-14} M. SI-1 is excreted into the cell wall and leaks into the medium. The concentration declines continuously with age, subsequently making the frond reproductive (Nilsen and Nordby 1975, Stratmann et al. 1996). The second sporulation inhibitor, called SI-2, is a non-proteinaceous, low-molecular weight compound. SI-2 is excreted into the space between the two cell layers. Gametogenesis or sporogenesis can be induced by cutting the thallus into fragments and subsequent washing as observed in different *Ulva* species, since this is thought to result in the removal of both sporulation inhibitors (Stratmann et al. 1996, Wichard and Oertel 2010, Vesty et al. 2015). The SI-2–type sporulation inhibitor forms a gradient from the base to the top of the thallus, resulting in higher percentages of gamete formation and discharge from the apical regions (Wichard and Oertel 2010).

Environmental control of fertility

General patterns

Reproductive phenology is observed to vary with environment (Figure 3). Several seaweed species follow patterns that are related to latitude or climatic region, i.e. year-round fertility in tropical regions, bi-annual reproduction events peaking in spring and autumn in warm temperate regions, and reproduction restricted to summer to early autumn in cold temperate and polar regions (reviewed by Hoffmann 1987). However, there are also exceptions, such as seasonal fertility in the tropics being related to periods of lower water temperature (De Wreede 1976, Hoyle 1978, Engelen et al. 2005) and the late autumn/winter onset of sporogenesis in Arctic endemic *Laminaria solidungula* related to high ambient nutrient concentrations (Roleda 2016).

Experimental studies and field observations suggest that light, temperature or their combination often induce fertility in seaweeds (see Dring 1974, 1984, 1988, Lüning 1980a, 1981, Lüning and tom Dieck 1989). A series of papers, predominantly addressing fertility in red and brown algae under laboratory conditions (Supplemental Table S2) highlighted the importance of photoperiod (daylength) and temperature as the most important environmental factors controlling reproduction in most seaweeds. Lüning and tom Dieck (1989) discerned different types of response to synchronization of seasonal development of reproductive structures depending on whether environmental factors trigger reproduction directly (type 1) or whether the environment controls a circadian clock which then regulates reproduction (type 2). In a last type, for which there is currently no proof in seaweeds (type 3), the organism possesses a circannual clock which makes it more independent of environmental [or climatic?] factors directly influencing reproduction. The distinction between these types depends on the contrast between "ultimate factors", which control the onset of reproduction directly, and "proximate factors" which control a circadian clock. Temperature, irradiance and nutrients are considered "ultimate factors" controlling type 1 reproduction, which is expected to prevail in short-lived species. Type 2 reproduction is controlled largely by photoperiod. Given the distinction between "ultimate" and "proximate" factors,

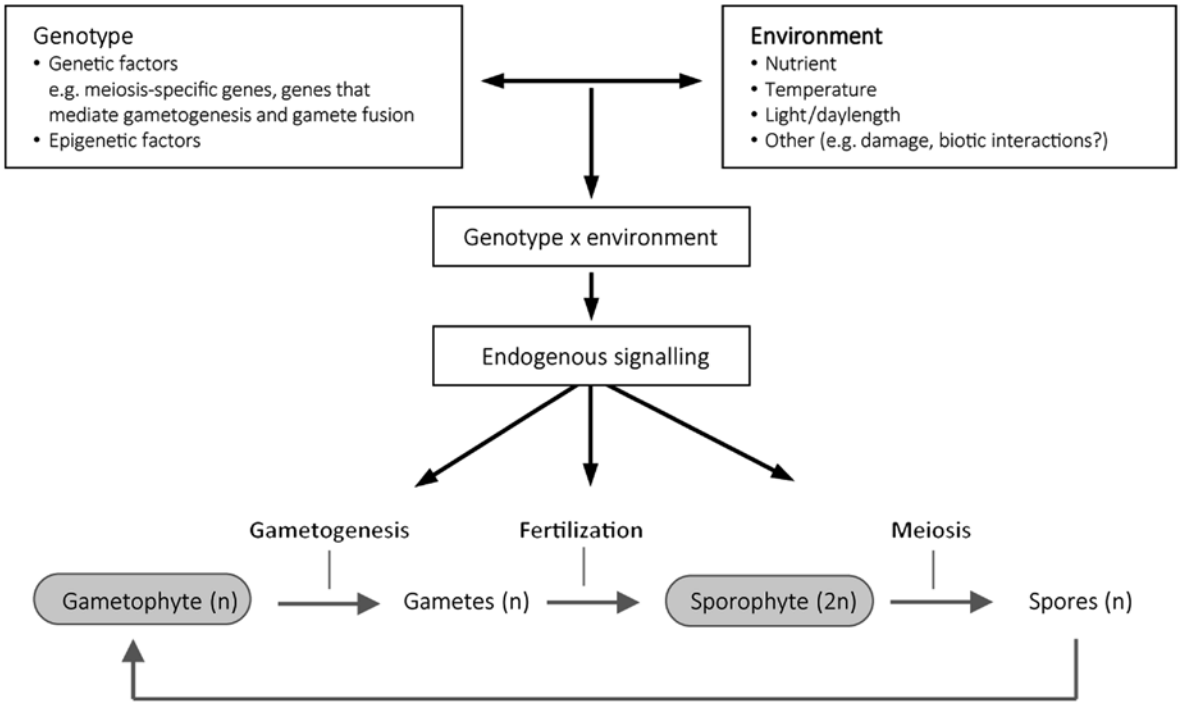

Figure 3: Life cycle control as a function of genotype and environmental factors.

it is important to discern genuine from non-genuine photoperiodic effects (Dring 1984, 1988). The list of studies in Supplemental Table S2 could best be interpreted in this framework. In order to classify an effect of daylength as a genuine photoperiodic effect, and not as a response to the total irradiance or any other parameter autocorrelated with daylength, daylength must control development or reproduction. Observations indicating that the dose rather than the timing of light may affect reproduction or growth would exclude these as genuine photoperiodic responses (Dring 1984). This is likely the case for several experimental studies that point to threshold irradiance values below which seaweeds do not become reproductive (see Dring 1970, *Callithamnion byssoides*: Kapraun 1978; *Desmarestia aculeata*: Chapman and Burrows 1970). Such results have been tentatively interpreted as an effect of increased photosynthesis, leading to higher food reserves, on reproductive effort (Dring 1974). Recently it was demonstrated that bacteria associated with *Arabidopsis* can determine the timing of flowering (Panke-Buisse et al. 2015), which opens the question of the extent to which algal-associated microbiomes are involved in reproduction and its timing.

Nutrients

Nutrients would qualify as "ultimate factors" triggering fertility. In freshwater green algae, the induction of fertility by nitrogen limitation has been studied extensively (e.g. *Chlamydomonas, Oedogonium, Scenedesmus*; see Coleman and Pröschold 2005). For seaweeds, evidence for a relationship between nutrients and fertility is rather limited. Critical levels of internal nitrogen and phosphorus are required to transform vegetative blades to sporangial sori in kelp species (Mizuta et al. 1999, Nimura et al. 2002, Kumura et al. 2006). In *Dictyota dichotoma*, nutrient limitation has been shown to have a positive effect on sporogenesis (Bogaert et al. 2016), reflecting the antagonism between growth and reproduction which is expected to be more pronounced in short-lived species. Similar results were presented for *Dictyota kunthii* by Hoffmann and Malbrán (1989). In a series of experiments with various temperatures, irradiances and photoperiods, a clear inverse correlation between growth and sporogenesis was most pronounced at 20°C. However, a gradual decrease in photoperiod resulted in an abrupt change in fertility, and consecutive interruptions of long 16-h dark periods over a 3 week period resulted in a cumulative decrease of the tetrasporangia (Hoffmann 1988). These observations would point to a genuine photoperiodic effect. Also nutrient concentrations have been shown to interact with photoperiodic effects in other seaweeds (*Rhodochorton purpureum*: Knaggs 1967, Dring and West 1983; *Bonnemaisonia hamifera*: Lüning 1980b; *Asparagopsis armata*: Oza 1977, Lüning 1981). Despite experimental evidence in several species, no physiological explanation is available

for the interaction effects between nutrient availability and photoperiod. Furthermore, the influence of nutrients vs. photoperiod on fertility complicates the classification of reproductive control into clear-cut primary (type 1) and proximate (type 2) factors controlling fertility (Lüning and tom Dieck 1989).

Light quality and identity of photoreceptors

Photoperiodic as well as non-photoperiodic responses have often been shown to be wavelength specific in algae. Especially the effects of blue and red/far-red light on fertility have been investigated extensively (reviewed by Dring 1984, 1988). Best studied in this respect is the effect of gametogenesis and egg release in various kelp species (Lüning and Dring 1972, 1975, Lüning 1980b). Blue irradiation increases the percentage of fertile gametophytes (Lüning and Dring 1972), but red light has an inhibitory effect which is most prominent at 15°C. However, at lower temperatures, some gametophytes become fertile in red light. Sporogenesis seems also to be influenced by light quality. In *Saccharina japonica* blue light promoted sporogenesis while red light inhibited sporangium formation (Mizuta et al. 2007). Bogaert et al. (2016) demonstrated that red light increased sporogenesis in *Dictyota*. Also the process of gamete release has been shown to be wavelength-specific. Blue light has been shown to induce gamete release in both *Fucus* and *Dictyota* (Kumke 1973, Pearson et al. 2004), but gamete release was inhibited by blue light in *Laminaria* (Lüning 1981) and *Ulva* (Wichard and Oertel 2010).

Despite these clear indications that light quality specifically induces or inhibits reproduction and growth, the quest for the underlying photoreceptors and signalling pathways has proved a hard nut to crack (Hegemann 2008). Phytochrome seems to be present only in streptophyte algae, some early diverging prasinophytes and stramenopiles, but not in red algae (Falciatore and Bowler 2005, Duanmu et al. 2014). Nevertheless, algae contain a rich set of photoreceptors (Hegemann 2008). Instead of phytochrome, stramenopiles possess their own blue light photoreceptor, aureochrome (Takahashi et al. 2007). The transcriptome of *Saccharina japonica* sporophytes under blue light was characterized by Deng et al. (2012), while differential gene expression under blue and red light was studied by Wang et al. (2013). The results indicated that the number of differentially expressed genes was significantly higher under red light conditions compared to blue light. However, the aureochrome and cryptochrome photoreceptor genes showed no significant differential expression among the different light qualities. These results are promising but also indicate that our understanding of the molecular mechanism of non-photosynthetic light perception and its control on a circadian clock is still limited, especially in comparison with *Chlamydomonas* (see Mittag et al. 2005).

Ecotypic variation

Given the importance for seaweeds to sense their environment, either through photoperiod or temperature, one should realize that these characteristics change across latitudinal gradients. So far, relatively little attention has been paid to measuring and understanding ecotypic latitudinal variation among strains. Most studies addressing intraspecific variation have concentrated on the effects of temperature regimes on growth and survival, and their biogeographic implications (e.g. Breeman 1988, Breeman and Pakker 1994, Molenaar and Breeman 1994, Molenaar et al. 1996, Breeman et al. 2002). Variation in the critical daylength for the short-day response of sporogenesis has been demonstrated for *Rhodochorton purpureum* (Dring and West 1983) and *Scytosiphon* (Lüning 1980a). However, the growing demand for seaweed in mariculture increases the need to better understand the degree of adaptation among latitudinal ecotypes and the limits of acclimation. So far studies are limited. For example, Lindstrom (2008) addressed ecotypic differentiation in the sporogenesis of *Porphyra*, and ecophysiological differentiation between Arctic and temperate populations of *Saccharina latissima* was studied by Olischläger et al. (2014) in a global change context. Efforts to combine quantitative genetics and breeding with genomic information in commercial seaweeds are leading to the identification of quantitative trait loci (e.g. Liu et al. 2010, 2011) and have the potential to combine traditional ecophysiological studies with "-omics" approaches.

Conclusion and perspectives

The diversity of life cycles in seaweeds is reflected in the wide variation of processes that control life cycle progression. A huge amount of research, mainly in the second half of the 20th century, has uncovered the critical roles of temperature, photoperiod, irradiance and, in some cases, nutrients as factors controlling reproduction in many species. There was a bias toward brown and red algae, with fewer studies addressing fertility in

green seaweeds. This ecological and ecophysiological information forms an excellent basis for future studies that address reproduction and life cycle progression at a molecular level. The growing demand for seaweed resources, either as feed, food or biomass, creates a need for sustainable seaweed exploitation. This societal demand presents a direct incentive to alleviate a number of major bottlenecks which currently impede mariculture practices (Charrier et al. 2017). An excellent knowledge of seaweed life cycles, including better control of the different developmental stages, which allows handling of seaweed in an aquaculture setting, is imperative. In contrast with the large number of ecophysiological studies to date, our knowledge of the underlying molecular basis of cell growth, development and reproduction falls short. For example, despite clear indications that photoperiod plays an important role in controlling reproduction, circadian clock genes have hardly been characterized from seaweeds, which is in contrast to the extensive knowledge on clocks in some unicellular algae (e.g. *Chlamydomonas*, *Ostreoccocus*: see Mittag et al. 2005, Corellou et al. 2009). In flowering plants, circadian clock genes control flower development, among other processes. Most genes have been characterized from genetic screening for mutants with altered flowering timing, or with defects in the circadian expression of reporter genes (Corellou et al. 2009). A similar approach, applied to seaweeds and drawing on the extensive existing ecophysiological data, has the potential to significantly increase our knowledge of seaweed reproduction. At present, considerable progress is being made by establishing a number of model organisms for which whole genome data are already available or are in the process of being generated, including *Ectocarpus* (Cock et al. 2010), *Pyropia* (Nakamura et al. 2013), *Chondrus* (Collén et al. 2013), *Saccharina* (Ye et al. 2015) and *Ulva* (see Wichard et al. 2015). These genomic resources, in combination with genetic maps and the possibility of creating developmental mutants for forward genetics (e.g. *Ectocarpus*, Fjeld and Borresen 1975, Cock et al. 2014) and a growing array of transformation protocols for reverse and forward genetics (reviewed in Mikami 2013, and recently, Oertel et al. 2015, Suzuki et al. 2016), should enable us to bring algal reproductive biology into the "-omics" age.

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