



Unravelling the secret life of MultiAnnual delayed gametophytes in the order of the *Laminariales*

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ABSTRACT

Research within the *Laminariales* in nature has predominantly focused on the sporophyte phase, often overlooking the other half of a bi-phasic life cycle; the gametophytes which can grow and propagate independently. This study examines the potential function that gametophytes might have within the *Laminariales*, focussing primarily on the understudied MultiAnnual Delayed (MAD) gametophyte, and comparing it with the typically researched newly formed single celled or delayed gametophyte. MAD gametophytes, characterized by extended vegetative growth before reproduction, display notable morphological and functional differences compared to their single-celled or younger multicellular counterparts. Key fundamental questions arise when discussing the evolutionary pressures that result in the formation of these older gametophytes. Why do MAD gametophytes actually exist? Why can MAD gametophytes seemingly live forever? Why do MAD gametophytes grow vegetatively and seemingly without limits? We posit an updated life cycle model for *Laminariales*, hypothesizing two phenotypically different gametophyte types, each with unique morphologies, functionalities, and reproductive behaviors. This life cycle model puts more focus on the understudied MAD gametophytes and their role in nature, thereby aiming to push for more research and thus comprehensive understanding of the in-culture selection pressures and *in vivo* life cycle dynamics that affect MAD gametophytes. An understanding that is pertinent since unravelling the secret life of MAD gametophytes is fundamental to the success of future kelp domestication and large scale rewilding efforts.

1. Introduction

The Laminariales, known for their haplo - diplontic life cycle, evolved to propagate independently in both their haploid as well as their diploid life phase (Bell, 1997). While much work has been done on understanding the life cycle of the *Laminariales* (Bartsch et al., 2008), and evolution of brown algae (Bringloe et al., 2020), fewer studies have examined the evolutionary significance and behaviour of the haploid gametophyte (Lüning and Tom Dieck, 1989; Bell, 1997; Carney and Edwards, 2006; Destombe and Oppliger, 2011). As of yet, no definitive answers have been articulated on why gametophytes have evolved to grow vegetatively (Hollenberg, 1939), why they can asexually multiply through fragmentation (Destombe and Oppliger, 2011), or why they have the ability to live vegetatively for prolonged periods of time (Shao-

Jun and Chao-Yuan, 1996, Carney, 2011, Zhang et al., 2019). Relatively little research has been conducted involving the gametophyte phase compared to the sporophyte phase. Much more is understood about the macroscopic sporophyte phase, resulting in a better understanding of their nutrient uptake mechanics (Lubsch and Timmermans, 2019), morphology (Zhu et al., 2021), their fertility cycle (Bartsch et al., 2008) and subsequent sporulation (Nagasato et al., 2020), their growth dynamics (Wheeler and Druehl, 1986), population dynamics (Bell, 1997), fouling (Matsson et al., 2019; Visch et al., 2020), and subsequent mortality (Sogn Andersen et al., 2011). There is a long and rich history of gametophytes being researched in a similar way under invitro conditions (Harries, 1932; Lüning and Dring, 1972; Motomura and Sakai, 1984; Dieck, 1993; Choi et al., 2005; Martins et al., 2017; Veenhof et al., 2022a). However in contrast, little is known of these traits in

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gametophytes within their natural setting. This stark dichotomy in our limited understanding of the microscopic gametophyte phase compared to the macroscopic sporophyte phase makes it difficult to hypothesize how the *Laminariales* behave/survive on large spatial and temporal scales, why they evolved the way they did, let alone hypothesize how external pressures like climate change will impact their survivability.

The challenge of directly observing sessile gametophytes of *Laminariales* in their natural habitats has significantly limited our understanding of their behaviour (Carney and Edwards, 2006) and have not been fully assessed in aquatic ecosystems in the three decades since the work of Chapman (1987) and Hoffmann and Santelices (1991) as described in Schoenrock et al. (2021). Studies in the past were limited to *in situ* recruitment studies using out-planted zoospores (Deysler and Dean, 1986; Reed et al., 1991). However prior studies (Ladah et al., 1999; Robuchon et al., 2014) have provided indirect evidence of these gametophytes on natural substrates, asking for a deeper investigation into their *in vivo* abundance and behaviour. A notable *in vivo* blind spot is the gametophytes ability to propagate vegetatively, which might offer valuable insights into the evolution of their independent life cycle alongside the sporophyte phase. Current consensus suggests that gametophytes remain dormant under adverse environmental conditions with suboptimal nutrient conditions (e.g. low Fe concentrations; Motomura and Sakai, 1984), or suboptimal light conditions (e.g. low red light conditions; Sato et al., 2020). These suboptimal conditions delay sexual reproduction in favor of vegetative growth (Lüning, 1980; Ratcliff et al., 2017; Edwards, 2022). These delayed gametophytes can persist vegetatively for extended periods (Carney, 2011; Barrento et al., 2026), even decades (Murúa et al., 2021), forming into so called pompoms (Fig. 1), and becoming MultiAnnual Delayed (MAD) gametophytes (Liang et al., 2023). Furthermore, recent studies have begun to shed light on the dispersal mechanisms of delayed gametophytes, contributing to a more comprehensive understanding of their ecological roles within the *Laminariales* life cycle (Destombe and Oppliger, 2011; Veenhof et al., 2022a).

Sessile organisms, including gametophytes, typically disperse *via* abiotic (e.g. gravity, water currents) and biotic (e.g. animal interactions) means. Recent studies have highlighted the dual dispersal capabilities of sessile delayed gametophytes. Destombe and Oppliger (2011) showed that male gametophytes can disperse through fragmentation, leveraging water currents for abiotic distribution. Similarly, Veenhof et al. (2022b) found that delayed gametophytes can endure the digestive systems of micrograzers, indicating biotic dispersal pathways. This feat of seaweed dispersal through biotic means has been observed recently in other

seaweed species as well, such as *Gracilaria gracilis* whose spermatia were carried on the bodies of small isopods (Lavaut et al., 2022). The remarkable longevity of gametophytes in combination with the multiple ways of dispersal suggest that older delayed gametophytes play a much larger role in the life cycle and genetic progression of the *Laminariales* than just being the dormant or resting stage. Yet, gametophyte research in the last 50 years predominantly focused on newly formed single-celled or newly formed delayed gametophytes, overlooking the more complex behaviors that were observed in older MAD gametophytes (Ebbing et al., 2020; Murúa et al., 2021; Liang et al., 2023). At the same time, in recent years more focus is placed on MAD gametophytes for the goal of breeding, thermal priming, and genetic research (Liesner et al., 2022; Martins et al., 2019, 2020; Monteiro et al., 2019; Strasser et al., 2022; Silva et al., 2022; Gauci et al., 2022; Liboureau et al., 2024; Veenhof et al., 2024). Although these studies are critical in our understanding of how (a)biotic factors influence MAD gametophyte behaviour, none looked comparatively into age or the long term culture conditions as an important factor that could influence gametophyte behaviour as well. This highlights the need for a more focused investigation into how the intricate behaviors of MAD gametophytes could differ from that of newly formed gametophytes, and how age or the culture conditions of MAD gametophytes could be a crucial factor in the observed behaviour.

We propose a hypothetical novel way of looking at the lifecycle of the *Laminariales* (Fig. 3), positing the existence of two distinct age related gametophyte phases, each characterized by unique phenotypes that diverge in their developmental functions and behaviors. This hypothesis functions as a substantiated call to further research MAD gametophyte behaviour more in-depth. This starts with the acknowledgement of our limited understanding of this complex part of the *Laminariales* lifecycle, both within their natural environment as well under cultured conditions. We propose to use a conservative temporal age boundary of a year between these phenotypes, with MultiAnnual delayed (MAD) gametophytes representing gametophytes that have been vegetative for more than one year (Ebbing et al., 2021a; Liang et al., 2023). This conservative temporal boundary aims to reliably differentiate between the two distinct age related gametophyte phenotypes and hopes to promote the study of specific MAD gametophyte traits, to complement the more generally researched newly formed single celled and delayed gametophytes. These studies are presently needed to aid kelp aquaculture and rewilding efforts, since MAD gametophytes are increasingly becoming a cornerstone of novel cultivation methods (Goetze et al., 2020; Kerrison et al., 2020; Umanson et al., 2021). Our hypothesis also calls for in-depth

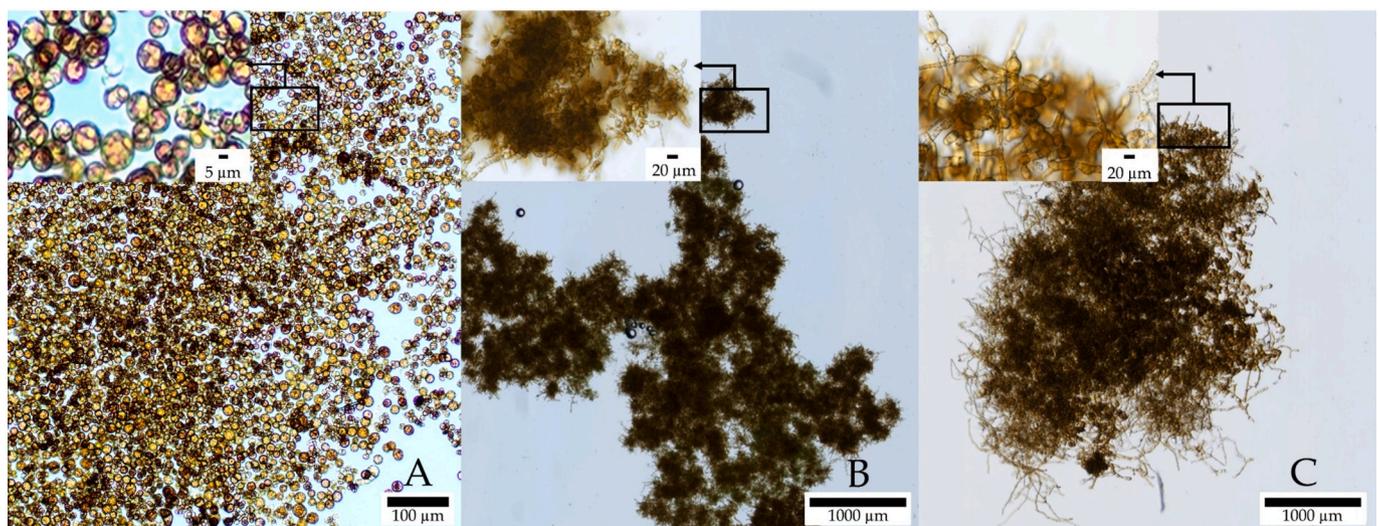


Fig. 1. ; three pictures that show the morphological differences between (A) single celled newly formed gametophytes, (B) Male- and (C) Female- MultiAnnual Delayed gametophytes (*Saccharina latissima*).

in vivo studies to explore the elusive secret life of MAD gametophytes in their natural settings. Here we substantiate how these two gametophyte phenotypes are morphologically, functionally, and behaviorally distinct, possible necessitating the representation as separate phases in an updated life cycle mode.

1.1. The fundamental rationale of differentiating between two gametophyte phenotypes in the order Laminariales

In order to make the case that an additional life phase is necessary to accurately represent the life cycle of the *Laminariales*, it is important to define what a life phase is in the first place. Different nomenclature have been used for the definition “life phase” in the past (e.g. life generation or life stage), making these definitions interchangeable and therefore slightly ambiguous (Willson, 1981; Ottaviano and Mulcahy, 1986; Coelho et al., 2007). Here we use the definition “life phase” as is described by Willson (1981), to refer both the alternating haploid – diploid components of the life cycle and subsequently to any intervening, asexually produced progenies. Wilson describes that while the point is made that the genetic identity of asexual parents and offspring cannot be assumed, this does not alter the general idea that asexually produced young are more similar than those produced sexually and that the clone is still the unit of selection. Based on Wilson’s definition of a life phase we hypothesize that newly formed gametophytes and the asexually propagating MultiAnnual Delayed (MAD) gametophytes could embody separate life phases, by showing the observed difference in morphology, developmental functionality, and reproductive behaviour. For our analysis we initially distinguish between single celled gametophytes and MAD gametophytes since they represent the two edges of the temporal range in the life of a gametophyte, with the delayed gametophyte embodying the transition period between the two life phases.

1.2. Morphology

The overall morphology is the most apparent phenotypical difference between newly formed gametophytes and the older MAD gametophyte life phase, with delayed or MAD gametophytes being multicellular in comparison to single celled newly formed gametophytes before initiating reproduction (Fig. 1). This transition from single celled and a delayed gametophyte is characterized by biomass augmentation through vegetative mitotic growth, forming undifferentiated, filamentous cells. These cells exhibit Hollenberg’s (1939) described tendency for developing separable branches, which either eventually self-fragment (Destombe and Oppliger, 2011) or cleave due to external factors (Zhang et al., 2019). The subsequent biomass accumulation, as the result of vegetative growth, becomes an important differentiating biotic factor in sexual reproduction. The influence of increasing biomass on the sexual reproduction is especially apparent in cultured conditions, since increases in culture density are invertedly correlated with decreasing reproductive success rates. This correlation is observed in both initial zoospore densities (Reed et al., 1991; Choi et al., 2005; Schwoerbel et al., 2022) as well as gametophyte densities (Carney and Edwards, 2010; Ebbing et al., 2021b). Density, as a biotic factor influencing reproduction, becomes a strong natural differentiator between newly formed gametophytes and the older MAD gametophytes. Whereas young gametophytes rarely will encounter high densities in the vastness of the ocean, this might be different with MAD gametophytes that vegetatively will grow into a high gametophyte density within their own micro-verse. The transformational point, from single-celled and newly formed gametophytes to multicellular gametophytes happens rather quickly, within a couple of weeks (Avila-Peltroche et al., 2022). However, it is far from clear whether behavioural changes, which are observed in MAD gametophytes (i.e. the (a)biotic factors needed to initiate sexual reproduction described in chapter 1.4), occur at the onset of becoming multicellular.

1.3. Developmental functionality

The developmental functionalities of a life phase in algae encompass various biological processes that enable these organisms to grow, reproduce, and adapt to their environment (Coelho et al., 2007). For example, eukaryotic sexual life cycles involve recurring life cycle transitions between diploid and haploid phases with meiosis facilitating the transition of the diploid to haploid phase (Willson, 1981). While this fundamental structure is shared across various life cycles in nature, differences can be observed in two key aspects: the relative duration of each phase (i.e. the amount of time spent in haploid versus diploid state) and the extent of mitotic activity in each phase, including the clonal multiplication of haploid and/or diploid cells (Mable and Otto, 1998; Coelho et al., 2007). It is this observed phase duration and mitotic activity that is a major divider between the functionality of either newly formed or MAD gametophytes, with the behavioural dependence on the sporophyte’s seasonality as key differentiator.

Life cycle transitions are often timed seasonally due to a combination of environmental, biological, and evolutionary reasons, with the goal to increase the chances of successful reproduction and subsequent survival of the offspring (Lüning and Tom Dieck, 1989). The proposed difference in functionality between newly formed- and MAD gametophytes lies in their dependence from the sporophyte for their reproductive strategy. In other words, we hypothesize that the seasonal timing for the initiation of gametophyte sexual reproduction, the reproductive synchronization between gametophytes, and thus of a new generation of sporophytes, is either oriented autonomously or dependently from their parental sporophytes.

Sporophytes use circannual rhythms to time the formation of sorus tissue (Lüning and Tom Dieck, 1989; Mizuta et al., 1998; Bartsch et al., 2008), time their zoospore release (Nagasato et al., 2020), and therefore time when newly formed gametophytes initiate sexual reproduction or decide to delay reproduction. These seasonally changing factors exert selective pressures, with reproduction starting when the primary environmental factors are deemed favourable. This is described by Lüning and Tom Dieck, 1989 as a Type-1 seasonal synchronization of the development of an organism. The longer newly formed gametophytes delay their reproduction, the more autonomous the gametophyte needs to become in order to correctly synchronize their reproduction to seasonal changes, and by doing so optimize their chances of successful syngamy with surrounding gametophytes. This is described by Lüning and Tom Dieck, 1989 as a Type-2 reproductive synchronization, and needs more reliable and predictive environmental cues for successful reproduction. These more reliable cues are called proximate factors and are used by organisms that have attained higher levels of autonomy from their immediate environmental conditions (Dring, 1988; Breeman, 1988). The autonomy necessary for MAD gametophytes to correctly synchronize and time their reproduction, with the surrounding MAD gametophytes and fertile sporophytes, is what functionally differentiates them from the more sporophyte dependent reproductive timing of newly formed gametophytes. Functionally speaking, MAD gametophytes are “autonomously propagating gametophytes”, while newly formed gametophytes are “sporophyte dependent propagating gametophytes”. However, actually assessing when these gametophytes functionally transition between the two developmental stages is not yet clear, bringing us to the reason why we propose to use a conservative one-year boundary with MAD gametophytes.

One unexplored question is whether gametophytes immediately operate autonomously at the onset of multicellular development, or whether it is dependent of their age—be it a week, a month, or even six months. Another unexplored question is whether gametophytes possess, in what Lüning and Tom Dieck, 1989 describe as, a Type-3 reproductive synchronization. In their work, they explore how gametophytes reproductive timing can be influenced by an internal biological clock, a phenomenon they termed ‘Type-3 reproductive synchronization.’ This suggests that gametophytes may delay reproduction to temporally

synchronize with upcoming seasonality. We use this timeframe of a year to account for the possibility of this internal timing mechanism operating over a longer vegetative phase. This internal zeitgeber keeps the procreating gametophytes dependent of the zoospore release timing of their parental sporophyte. The older the gametophyte becomes the more necessary it becomes to reliably know whether the observed reproductive behaviour is triggered by a zeitgeber or not. This zeitgeber is subsequently the underlying reason why we make this clear distinction between delayed gametophytes and MAD gametophytes. By remaining vegetative for at least one year they transgress all seasons and therefore any potential type 1 or type 3 synchronized sexual reproduction. MAD gametophytes have remained vegetative for more than a year, not showing any indications of an internally active zeitgeber that triggered a predetermined reproductive event. This is why MAD gametophytes can be considered to be autonomously “type-2” synchronizing organisms with a much higher degree of confidence (Fig. 2). Subsequently, this conservative temporal distinction makes MAD gametophytes a much more reliable model organism to research compared to regular delayed gametophytes. Future research, particularly temporal gene expression studies, should aim to pinpoint this functional transition, or the presence of a zeitgeber, more precisely. For now, a conservative approach is needed and recommended in distinguishing newly formed and delayed gametophyte behaviour from that of MAD gametophytes.

1.4. Reproductive behaviour

Careful observations have been made suggesting that delayed gametophytes, and in particular MAD gametophytes, initiate reproduction under different environments than their newly formed gametophyte counterparts. To our knowledge, the first observations of changing reproductive behaviors in delayed gametophytes were described by Carney and Edwards (2010) and Carney (2011), who observed that delayed gametophytes had much faster recruitment (i.e. sporophyte production) than newly formed gametophytes (4-fold reduction in time). Their explanation for this difference in reproductive speed was accounted by the fact that delayed gametophytes may utilize a nutrient-poor delay period to build up their lipid reserves in order to promote more rapid sporophyte production once conditions improve. To our

knowledge only one publication comparatively examined changing reproductive behaviour between MAD gametophytes and newly formed gametophytes (Murúa et al., 2021). They observed that the reproductive success of their MAD gametophytes (20 years old) and newly formed gametophytes had different light intensity optimums. In this case newly formed *Macrocystis pyrifera* gametophytes reached their optimal reproductive success at much higher light intensities than their MAD gametophyte counterparts. The starkest difference was found in a *M. pyrifera integrifolia* subvariety, where newly formed gametophytes had their highest reproductive success at a light intensity of 120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, while their MAD gametophytes reached optimal reproductive success between 50 and 70 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Subsequently, comparing several full factorial experiments, *S. latissima* MAD gametophytes some careful early signs were observed they become increasingly selective to temperature before initiating sexual reproduction. *S. latissima* MAD gametophytes had a narrow range of 1.4 °C in which their optimal reproductive success was achieved (Ebbing et al., 2021a). Compare this to the much broader optimal reproductive ranges observed in newly formed *S. latissima* gametophytes with 10 °C (Lüning, 1980) or 7 °C (Lee and Brinkhuis, 1988) respectively. The apparent increased environmental or abiotic selectivity of MAD *S. latissima* gametophytes results in a more narrow optimal reproductive success range than newly formed gametophytes which is described more in detail schematically in Fig. S1. Interestingly, when we look at the selectivity of newly formed compared to MAD gametophytes of other *Laminariales* species, we continue to observe these broad bands of optimal reproductive success as a recurring phenomenon. Broad optimal temperature gradients were observed in *Laminaria ochroleuca* (+/- 6 °C; Izquierdo et al., 2002), *Laminaria digitata* (+/- 10 °C; Martins et al., 2017), and *Undaria pinnatifida* (> 5 °C; Morita et al., 2003).

Despite the limited number of physiological, ecological, genetic, and behavioural studies of MAD gametophytes, there are other indications of increased selective responses of MAD gametophytes to their direct environment. For example, MAD gametophytes need relatively specific initial male/female gametophyte sex ratios and biomass densities before initiating sexual reproduction (Ebbing et al., 2021a). There is an apparent species specific light intensity optimum in MAD gametophyte reproduction towards the *in vivo* conditions where *Alaria esculenta* and

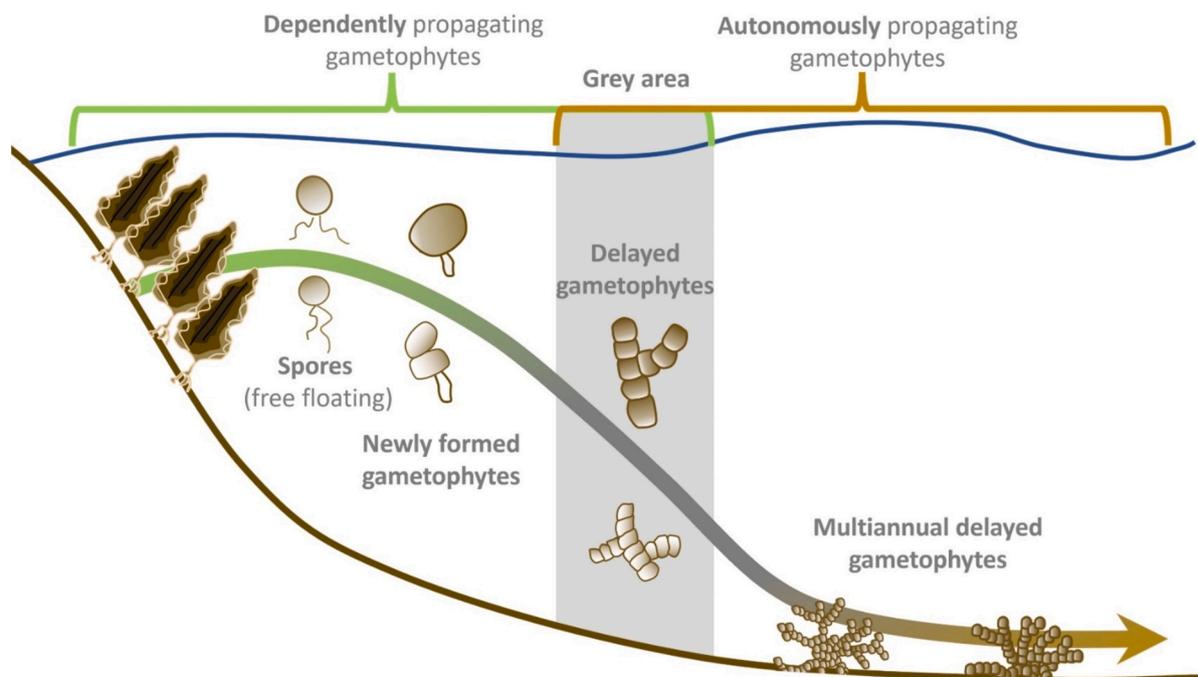


Fig. 2. ; visualization of the increasing autonomy of the MAD gametophyte through time.

Laminaria Digitata sporophytes thrive (Silva et al., 2022). MAD gametophytes use specific interactive light/temperature conditions to time their sexual reproduction, as proposed in the seasonal lag hypothesis (Ebbing et al., 2021a). Aging female gametophytes became less fertile through time in conditions normally considered favourable for newly formed gametophytes (Kinlan et al., 2003), an observation that could be explained by an increased selective response to their environment instead of infertility. If indeed the summation of these careful early observations of increased selectivity in MAD gametophytes persist in future studies, it would add to the validation that gametophyte behaviour indeed changes over time from a more generic type-1 reproductive synchronization towards a more autonomously controlled, selective, type 2 synchronization.

2. Discussion

Following the definition of a life phase described by Willson, 1981 referring to both the alternating haploid – diploid components of the life cycle and subsequently to any intervening, asexually produced progenies, it seems plausible that indeed there are two phenotypically different gametophyte phases within the life cycle of the order of *Laminariales*. Both single-celled newly formed gametophytes as well as the under-studied MultiAnnual Delayed (MAD) gametophytes might have fundamentally different functions in the *Laminariales* life cycle, and as such we hypothesize a novel way of looking at the lifecycle including two distinctive gametophyte phases (Fig. 3). The cumulative differences observed in morphology, their functional differences, and their reproductive behaviour all add to the necessity for more studies to better understand the role that MAD gametophytes have in the life cycle of the *Laminariales*.

The life cycle of the *Laminariales* is often described as being haplo-diplontic (Bartsch et al., 2008), with somatic growth in both the diplontic as well as the haplontic life phase (Mable and Otto, 1998). The fact that the *Laminariales* are able to close their life cycle through successful sexual reproduction between two single-celled newly formed

gametophytes makes their lifecycle actually, by definition, diplontic instead. The definition is based on the fact that in the diplontic life cycle version the somatic development is present only in the diploid phase, without any somatic growth in the haploid phase (Hughes and Otto, 1999; Coelho et al., 2007). It makes the life cycle of the *Laminariales* diplontic, as well as haplo-diplontic. There is even an added possible reproductive pathway possible between the two life cycle versions, where the diplontic lifecycle version and the haplo-diplontic lifecycle version can reproduce sexually with each other. The possibility of having an interconnected haplo-diplontic as well as a diplontic life cycle also allows for the possibility that the two life cycle versions exhibit different reproductive strategies that influence the reproductive behaviour of the gametophytes (MacArthur and Wilson, 1963; Pianka, 1970). We hypothesize that there is a behavioural divergence developing between strong r-selected reproductive strategies in newly formed gametophytes towards increasingly more K-selected reproductive strategies in MAD gametophytes. The r-strategists produce many offspring, thrive in unstable or unpredictable environments with the focus on quick reproduction. All the while K-strategists produce fewer offspring and devote less energy in reproduction than in vegetative growth, they do well in more stable environments with limited resources, and focus on long-term survival (MacArthur and Wilson, 1963; Santelices, 1990). In land plants it has been suggested that ecological succession involves a shift from r- to K-selection with increasing age or maturity of the community (Odum, 1969; Wilbur et al., 1974; Newell and Tramer, 1978). This might also apply in the oceans in case for the autonomously operating MAD gametophytes, resulting in the inter-operability between the two reproductive strategies of the diplontic and haplo-diplontic life cycles, potentially even in combination with parthenogenic sporophyte formation (Doust and Doust, 1988).

We are aware that a lot of research is still needed to further validate this hypothetical lifecycle model that includes MAD gametophytes. Validating this hypothesis needs more quantifiable data on the reproductive behaviour of MAD gametophytes than is readily available in published literature as of yet. The differences between newly formed

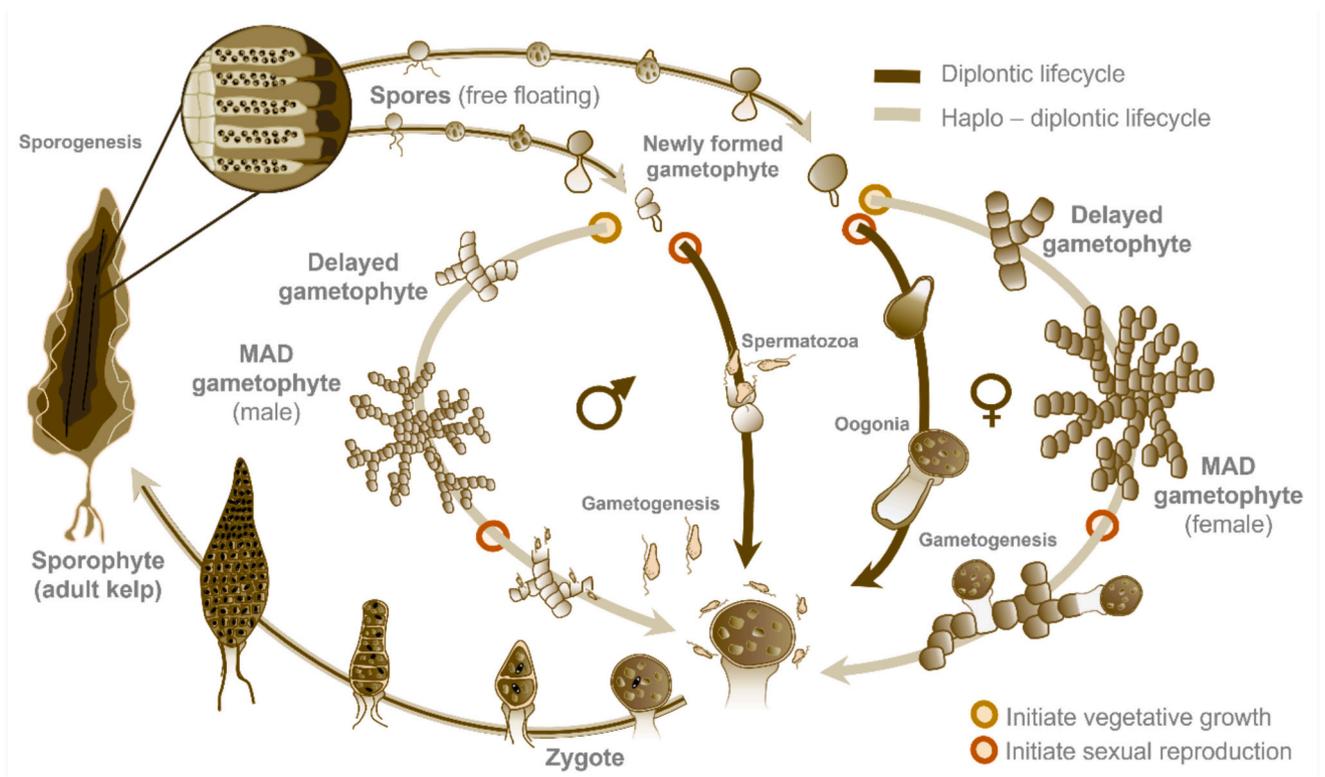


Fig. 3. ; Adapted life cycle of the *Laminariales* that includes the added life phase of MultiAnnual Delayed (MAD) gametophytes.

single celled, newly formed delayed, and MAD gametophytes should be clearly observable by their reproductive behavioural differences but, as of yet, different scenarios are still possible. For example, in the case we find long term stable behavioural changes at the onset of multicellularity the need for using the term “MAD” gametophytes becomes obsolete, since the term “delayed” will cover the entire behavioural spectrum. Moreover, not only is the body of MAD gametophyte research still limited, the findings that are available for younger gametophyte cultures are also too divergent to clearly discern recurring behavioural patterns. The variability in the utilized light intensity and light quality (Fig. 4), temperature (Fig. S2) and light period (Fig. S3) in scientific experiments is high, making a comparative analysis challenging. We observed this high variability in both vegetative growth conditions as well as in the conditions for the induction of sexual reproduction. This high variability was observed intraspecifically as well as interspecifically between the species *S. latissima*, *S. japonica*, *U. pinnatifida*, and *M. pyrifera*. This high interexperimental variation of the abiotic factors that were used all imply for the need for experimental standardization and the possibility of additional understudied (a)biotic factors that influence the reproduction of gametophytes like biomass density, genetic diversity, microbiome interactions, and in the case of MAD gametophytes, the age of a culture.

Apart from age being a possible important biotic factor influencing the behaviour of MAD gametophytes there is also the very real possibility that in-culture selection between MAD gametophytes in long term cultured conditions could have strong behavioural effects (Dieck, 1993; Ebbing et al., 2021a). Lakeman et al., 2009 describes the phenomenon of in-culture selection within micro-algae cultures, summarizing several different ways of artificial pressures changing *in vitro* populations through time. They delved deep into processes like genetic drift, inbreeding, selection, and how these different forces can influence a culture over prolonged periods of time. The vegetative growth of delayed gametophytes and in particular MAD gametophytes is a key driver for in-culture selection (Ebbing et al., 2021a). One scientific route to try and minimize the effects of long term in-culture selection is by utilizing the remarkable capabilities of gametophytes to survive in absolute darkness for up to 18 months (Dieck, 1993), since minimizing the vegetative growth of gametophytes also minimizes the effects that in-culture selection might have. Regardless of vegetative growth, recent

studies showed that thermal stress in cultured conditions could induce photoinhibition and influence reproduction (Strasser et al., 2022; Liboureau et al., 2023). Overall, considering the fact that decades worth of cultured conditions could influence MAD gametophytes reproductive behaviour (Murúa et al., 2021), makes it even more apparent that focus is needed on *in vivo* MAD gametophytes observations, allowing for the possibilities to distinguish nature from nurture in the future.

The fact that we need to make a clear distinction between gametophyte types is apparent, since perpetually maintained MAD gametophytes are the gene banks and germplasm collections upon which kelp domestication depends for a developing kelp aquaculture industry (Goecke et al., 2020; Wade et al., 2020). It has become increasingly apparent that MAD gametophytes are an essential part in large-scale seaweed cultivation, rewilding efforts, and environmental protection (Barrento et al., 2026; Visch et al., 2019; Kerrison et al., 2020; Umanzor et al., 2020). The way they can be cultured and stored, gametophytes may hold the key to designing and implementing proactive management and conservation strategies to secure the future of kelp forests (Veenhof et al., 2022b), and rediscover the ancient regenerative impact they had on biodiversity (Johnston, 2022). However, much is unknown, except our understanding that MAD gametophytes indeed behave uniquely and deserve to be researched as such. If MAD gametophytes would be observed in nature it would change the way we look at *Laminariales*. Or as Edwards (2000) so eloquently described it for *Desmarestia* sp. gametophytes; “they would be regarded as alternate life-history stages that simply maintain populations under a different set of environmental conditions than the macroscopic sporophytes do, rather than as “dormant” or “resting” stages. Or in other words, the gametophyte stage and in particular the much older MAD gametophyte stage might have a much more profound role and impact on how the *Laminariales* behave, adapt, and ultimately evolved the way they did.

CRediT authorship contribution statement

Alexander Ebbing: Writing – original draft, Visualization, Validation, Resources, Investigation, Formal analysis, Data curation, Conceptualization. **Scott Lindell:** Supervision. **Harald Holm:** Visualization, Investigation. **Yoichi Sato:** Supervision. **Klaas Timmermans:** Writing – review & editing, Supervision, Funding acquisition.

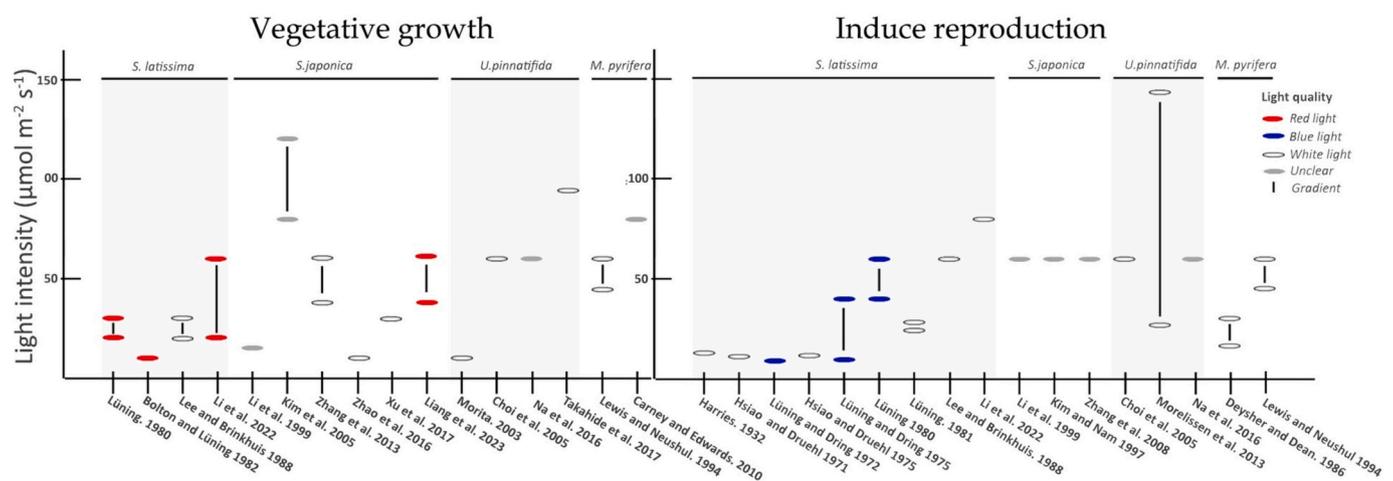


Fig. 4. ; A literature study on the variability in light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and light quality (Legend) that was used to keep cultures vegetative or induce reproduction of newly formed and newly formed delayed gametophyte cultures within the order of the *Laminariales*. The research papers on the x-axis cover several species including *Saccharina latissima*, *Saccharina Japonica*, *Undaria pinnatifida*, and *Macrocyctis pyrifera*. Light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is described on the y-axis while the colour of the datapoint is giving insight in the light quality that was used (Legend). When a line between the two datapoints is included it was a study that used a gradient in light intensity. The goal of this overview is to show the variability in light intensity and light quality that was used between studies over time, within the order of *Laminariales*. The research papers described on the x-axis are not hyperlinked, but can nonetheless be found in the reference list below. (Bolton and Lüning, 1982; Hsiao and Druehl, 1971; Huang et al., 2022; Kim et al., 2005; Kim and Nam, 1997; Lewis and Neushul, 1994; Li et al., 1999, 2022; Morelissen et al., 2013; Na et al., 2016; Takahide et al., 2017; Zhang et al., 2008, 2013; Zhao et al., 2016).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2025.152081>.

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