



Priming of Marine Macrophytes for Enhanced Restoration Success and Food Security in Future Oceans

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Marine macrophytes, including seagrasses and macroalgae, form the basis of diverse and productive coastal ecosystems that deliver important ecosystem services. Moreover, western countries increasingly recognize macroalgae, traditionally cultivated in Asia, as targets for a new bio-economy that can be both economically profitable and environmentally sustainable. However, seagrass meadows and macroalgal forests are threatened by a variety of anthropogenic stressors. Most notably, rising temperatures and marine heatwaves are already devastating these ecosystems around the globe, and are likely to compromise profitability and production security of macroalgal farming in the near future. Recent studies show that seagrass and macroalgae can become less susceptible to heat events once they have been primed with heat stress. Priming is a common technique in crop agriculture in which plants acquire a stress memory that enhances performance under a second stress exposure. Molecular mechanisms underlying thermal priming are likely to include epigenetic mechanisms that switch state and permanently trigger stress-preventive genes after the first stress exposure. Priming may have considerable potential for both ecosystem restoration and macroalgae farming to immediately improve performance and stress resistance and, thus, to enhance restoration success and production security under environmental challenges. However, priming methodology cannot be simply transferred from terrestrial crops to marine macrophytes. We present first insights into the formation of stress memories in both seagrasses and macroalgae, and research gaps that need to be filled before priming can be established as new bio-engineering technique in these ecologically and economically important marine primary producers.

Keywords: DNA methylation, plasticity, stress memory, bio-engineering, seagrass, macroalgae farming, kelp restoration, heat hardening

INTRODUCTION

Marine macrophytes, including seagrasses and macroalgae, form the foundational basis of some of the most productive and diverse coastal marine ecosystems on the planet (Larkum et al., 2006; Costanza et al., 2014; Klinger, 2015; Teagle et al., 2017) that provide ecosystem services worth US\$ 28.9 ha⁻¹ year⁻¹ (Costanza et al., 2014). Moreover, macroalgae, traditionally cultivated in Asia (Chopin, 2017; Hu et al., 2021) at an annual value of US\$ 13.3 billion (FAO, 2020), are increasingly recognized in Europe and America as a target for a new, highly profitable, and environmentally sustainable bioeconomy (Skjermo et al., 2014; Stévant et al., 2017; Grebe et al., 2019; Araújo et al., 2021).

Marine macrophytes are increasingly threatened by a variety of anthropogenic stressors, including coastal development, invasive species, agricultural run-offs, dredging, aquaculture, and rising sea levels (Orth et al., 2006; Krumhansl et al., 2016; Chefaoui et al., 2018; Filbee-Dexter and Wernberg, 2018). Nearly one-third of global seagrass areas have disappeared over the last 100 years (Waycott et al., 2009) and 60% of macroalgal forests have been in decline over the past 2–5 decades (Wernberg et al., 2019).

Above all, temperature is the most important range-limiting factor for marine macrophytes (Jueterbock et al., 2013; Repolho et al., 2017; Assis et al., 2018; Duarte et al., 2018; Martínez et al., 2018). Rising ocean temperatures, interfering with reproduction, development, and growth (Breeman, 1990; Short and Neckles, 1999), are fundamentally altering genetic diversity and adaptability (Coleman et al., 2020; Gurgel et al., 2020), and devastating macroalgal forests and seagrass meadows around the globe (Arias-Ortiz et al., 2018; Filbee-Dexter et al., 2020; Smale, 2020). In response, large-scale restoration efforts aim to avert severe ecological and economic consequences (Eger et al., 2020; Fredriksen et al., 2020; Layton et al., 2020; Tan et al., 2020; Vergés et al., 2020). Modeling studies, based on projected carbon emission scenarios, predict that poleward range shifts will intensify (Jueterbock et al., 2013; Valle et al., 2014; Assis et al., 2016, 2017; Chefaoui et al., 2018; Wilson and Lotze, 2019). Even if rising sea temperatures remain below lethal limits, they reduce macroalgal growth and performance (Nepper-Davidsen et al., 2019; Hereward et al., 2020; Smale et al., 2020), increase disease outbreaks and biofouling (Harley et al., 2012; Nepper-Davidsen et al., 2019; Qiu et al., 2019; Smale et al., 2020), and radically alter ecological interactions that determine persistence (Provost et al., 2017; Vergés et al., 2019)—thus compromising future sustainability of natural habitats, and production security of associated industries.

PRIMING POTENTIAL IN MARINE MACROPHYTES

Priming, a Common Technique for Crop Enhancement

In agriculture, priming (**Box 1**) is a commonly employed technique to enhance crop resistance to environmental

challenges, including pathogen infections, hot, cold, dry, or saline conditions (Ibrahim, 2016; Pawar and Laware, 2018; Wojtyla et al., 2020); in some cases even across generations (transgenerational priming, **Box 1**) (Herman and Sultan, 2011; Lämke and Bäurle, 2017; Benson et al., 2020). For example, reproductive output of F3 *Arabidopsis* progeny increased five-fold under heat stress (30°C) if the F0 and F1 generations had previously experienced the same stress (Whittle et al., 2009). Seed priming also synchronizes germination and improves vigor, leading to improved crop establishment and yield (Pawar and Laware, 2018). Priming is now considered a promising strategy for crop production in response to future climate (Wang et al., 2017; Mercé et al., 2020), and may have large potential to alleviate negative climate change impacts on marine macrophytes as well as to enhance yield in macroalgal production.

Mechanisms Underlying Priming

Priming relies on the formation of a molecular stress memory (**Box 1**), a process that can include epigenetic mechanisms such as microRNAs (miRNAs), histone modifications, and DNA methylation (Iwasaki and Paszkowski, 2014; Balmer et al., 2015; Crisp et al., 2016; Hilker et al., 2016; Wojtyla et al., 2016; Gallusci et al., 2017; Lämke and Bäurle, 2017; Bäurle, 2018; **Figure 2**). Epigenetic mechanisms do not alter the DNA sequence but have the potential to change gene expression (Bossdorf et al., 2008). Stress memory based on non-coding RNA and histone modifications generally lasts no longer than several hours or days (Mathieu et al., 2007; Cedar and Bergman, 2009; Lämke and Bäurle, 2017; Kumar, 2018), with some exceptions (Huang et al., 2013; Bilichak et al., 2015; Morgado et al., 2017). In contrast, DNA methylation is more stable, and can even be heritable across generations (Boyko et al., 2010; Ou et al., 2012; Verhoeven and van Gurp, 2012; Bilichak and Kovalchuk, 2016; González et al., 2017). For example, mediation of transgenerational priming via inherited DNA methylation has been demonstrated in the plant *Polygonum persicaria*, in which demethylation of offspring with zebularine removed the adaptive effect of parental drought exposure in the form of longer root systems and greater biomass (Herman and Sultan, 2016).

Indications of Priming in Macrophytes

Recent studies show that seagrass can become less susceptible to heat events if it has been primed to stressful temperatures (**Figure 1**). For example, primed individuals (6 days at 29°C,

BOX 1 | Glossary of priming-related terms.

Priming—A plant's ability to acquire a stress memory, enhancing its performance when exposed to a second stress by allowing it to respond faster, stronger, or in response to a lower threshold compared to a naive plant (**Figure 1A**). Priming is often used synonymously with hardening, conditioning, or acclimation.

Stress memory—A stress-induced alteration in epigenetic state that may last under mitotic cell divisions and results in priming.

Transgenerational priming—Stability of a stress memory under meiotic cell divisions across at least one generation that benefits the progeny of primed parental plants.

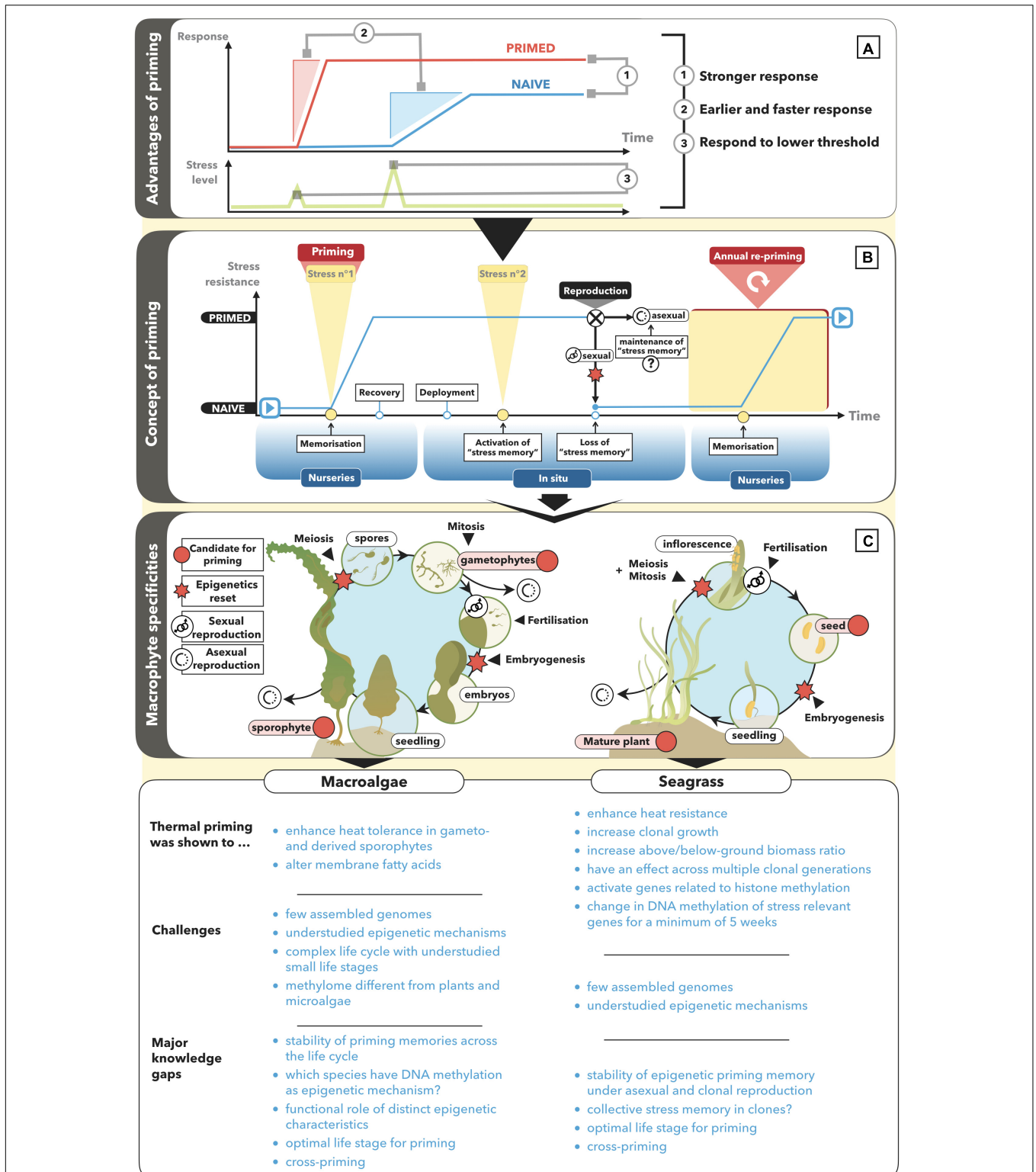


FIGURE 1 | Concept of priming and potential for its application in macroalgae and seagrass. **(A)** A primed organism responds faster, earlier, stronger or to a lower threshold of a stressful triggering stimulus as compared with a naïve organism. **(B)** A naïve organism is primed by building up a memory of a certain stress stimulus. The stress memory is more likely to be heritable across asexually produced generations than across sexually produced generations because of epigenetic reprogramming under gametogenesis (meiosis) and embryogenesis. **(C)** At which stage priming is best applied depends on the stability/transfer of a priming memory across the life cycle stages of kelp and seagrass. The state of the art, challenges and knowledge gaps to establish priming as a novel bio-engineering technique in marine macrophytes are listed for macroalgae and seagrass, respectively.

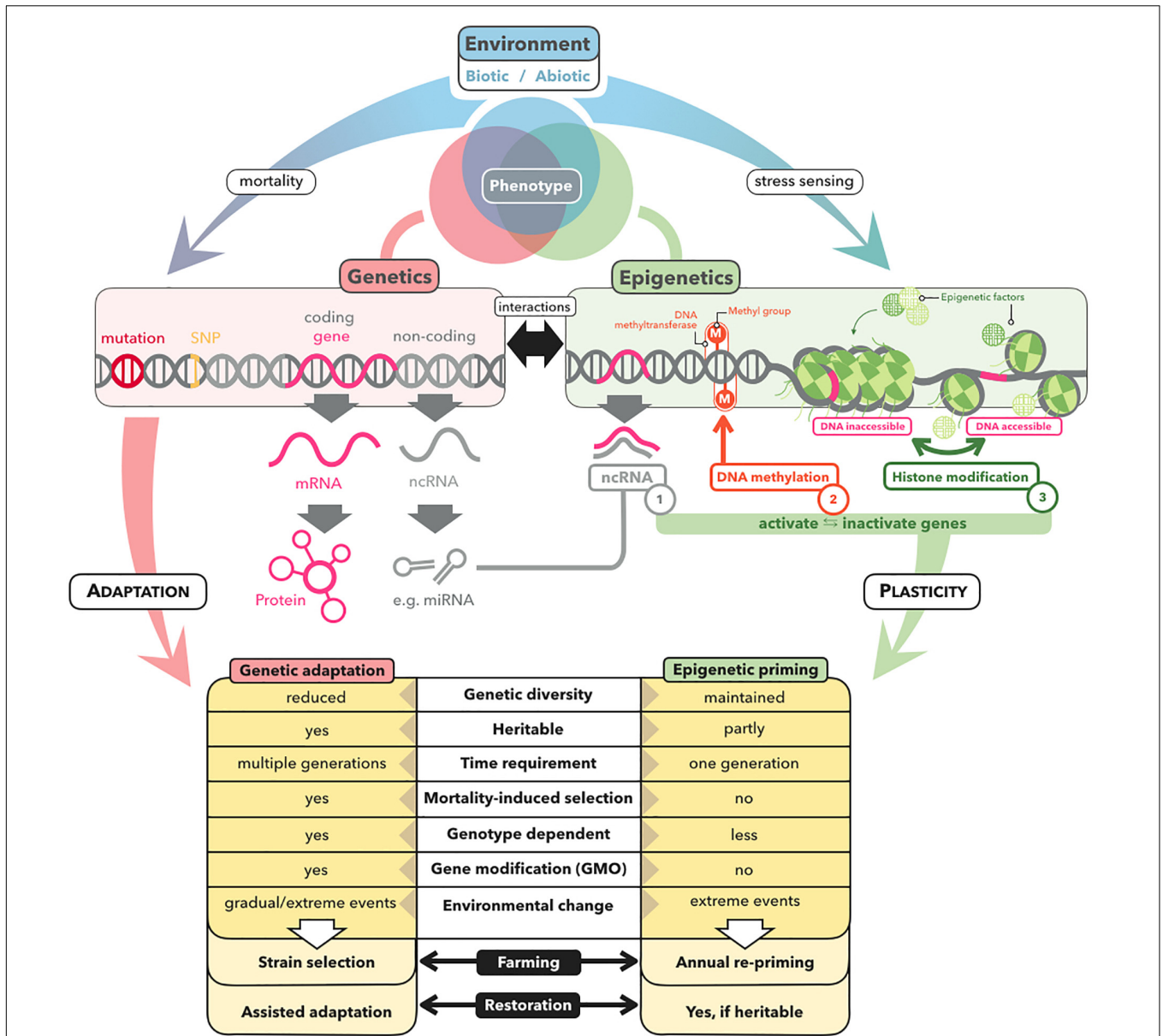


FIGURE 2 | Genetic versus epigenetic mechanisms underlying stress adaptation and their relevance for restoration and farming of marine macrophytes. Environmental stress can alter the phenotype of marine macrophytes by positive selection of pre-adapted genotypes or of new beneficial mutations, resulting in genetic adaptation of the population within several generations. In contrast, epigenetic mechanisms, comprising ncRNAs, DNA methylation, and histone modifications, contribute to phenotypic plasticity by altering the expression patterns of genes within a single generation. The key characteristics with respect to the application potential of genetic and epigenetic mechanisms for farming and restoration of marine macrophytes, are listed at the bottom.

4°C above natural conditions) of the seagrass species *Zostera muelleri* and *Posidonia australis* showed significantly enhanced photosynthetic capacity, leaf growth, and chlorophyll *a* content after exposure to heat stress (32°C for 9 days) compared with naïve plants (Nguyen et al., 2020). Moreover, previous exposure of *Zostera marina* to simulated warming (15°C for 45 days, 2°C above control temperature) resulted in an increase in clonal shoot production and shoot length, as well as a decrease in leaf growth rates and in the ratio of below to above ground biomass (DuBois et al., 2020). Vegetatively grown shoots of

primed parental plants could maintain biomass production under a second warming event (ca. 16°C for 40 days) but not shoots of naïve parental plants. The changes, which lasted for several years across multiple clonal generations after the stress was removed, would likely be adaptive in a warmer environment by reducing the respiratory burden of non-photosynthetic tissues. As discussed in Nguyen et al. (2020), heat priming may explain why the Mediterranean seagrass *Posidonia oceanica* did not suffer high mortality rates after intense and long-lasting heat-waves in 2012, 2015, and 2017 (Darmaraki et al., 2019),

in contrast to an extensive die-off after the 2006 heatwave (Marbà and Duarte, 2010).

Evidence that epigenetic modifications contribute to form a thermal stress memory in seagrass is suggested by significant stress-induced regulation of methylation-related genes, in particular histone methyltransferases (Nguyen et al., 2020), and a change in DNA-methylation patterns that lasted for at least 5 weeks following exposure to heat stress (Jueterbock et al., 2020). A 5-week heat-stress memory is potentially long enough to heat-harden the same generation of previously exposed shoots. This methylation memory involved CG hyper-methylation and, thus, potentially constitutive upregulation (Zhang et al., 2006; Yang et al., 2014; Dubin et al., 2015; Niederhuth and Schmitz, 2017) of genes involved in the breakdown of heat-denatured proteins (Feder and Hofmann, 2002); which would be expected to provide a faster or stronger protective response upon exposure to a second heat stress.

In furoid macroalgae, priming was shown to enhance resistance to dry and cold conditions (Schonbeck and Norton, 1979; Collén and Davison, 2001). Moreover, in the kelp *Laminaria digitata*, gametophyte exposure to low temperatures (5°C versus 15°C) significantly enhanced growth of the derived sporophytes under benign conditions (5 and 15°C) (Liesner et al., 2020). A small number of studies suggest that macroalgal performance under heat stress may be bio-engineered by thermal priming (Figure 1). First, priming the gametophyte generation of the kelp *Alaria esculenta* for 3 days at 22°C (compared with 12°C) enhanced their survival under increased temperatures, and the growth of the derived sporophyte generation (Quigley et al., 2018). Second, cultivation of *Saccharina japonica* gametophytes at 22–24°C increased the heat-tolerance of the derived sporophytes by 2°C (Wu and Pang, 1998) in Bricknell et al. (2021). Third, in the furoid brown alga *Fucus vesiculosus*, storage of parental tissue at a higher temperature (14°C versus 4°C), or acclimation of embryos to 29°C significantly increased their survival by 30–50% under 33°C (Li and Brawley, 2004). Fourth, individuals of the red alga *Bangia fuscopurpurea* primed for 3 days at 28°C could survive 1 week at 32°C significantly better than naïve individuals (Kishimoto et al., 2019). The priming stress caused an increase in the saturation level of membrane fatty acids, suggesting that altered membrane fluidity is part of the species' heat stress memory. However, this memory lasted for only 5 days after the primed individuals were returned to benign conditions (15°C).

DISCUSSION – PROSPECTS AND CHALLENGES OF PRIMING IN MARINE MACROPHYTES

Distinguishing Priming From Selection

Just as thermal stress in natural settings can cause mortality and selection (Coleman and Wernberg, 2020; Coleman et al., 2020; Gurgel et al., 2020), priming induced mortality could inadvertently result in selection of pre-adapted genotypes—which may explain the observed transfer of positive effects from the

primed gametophyte to the derived sporophyte generation of kelp (Quigley et al., 2018; Liesner et al., 2020). In order not to falsely ascribe improved stress tolerance to the formation of a molecular stress memory, it is critical to distinguish between priming and selection. This could be achieved through establishing correlations between positive priming effects and priming-induced epigenetic shifts that are independent from priming-induced genetic shifts by using partial mantel tests and multivariate redundancy analysis (Foust et al., 2016; Gugger et al., 2016; Herrera et al., 2016; Oksanen et al., 2016; Jueterbock et al., 2020). Moreover, tests for outlier loci that have become dominant allelic variants under positive selection (Narum and Hess, 2011; Günther and Coop, 2013; Ahrens et al., 2018) should be carried out in order to prove that positive priming effects cannot be explained by the survival of adapted genotypes.

Specificities of the Brown Algal Methylome

While the presence of cytosine methylation has been reported for green algae, red algae, dinoflagellates, and diatoms (Maumus et al., 2011; Tirichine and Bowler, 2011; Veluchamy et al., 2013; Bräutigam and Cronk, 2018; Lee J. M. et al., 2018), it is still not clear which brown algae share a lack of DNA methylation with the filamentous brown alga *Ectocarpus* sp. (Cock et al., 2010), in which epigenetic variation may be instead mediated at the chromatin level by histone modifications (Bourdareau et al., 2020) or via stress responsive miRNAs (Cock et al., 2017). Recently, DNA methylation was detected in the kelp *S. japonica* (Fan et al., 2019). The kelp methylome has been shown to change between life-cycle stages, to correlate with gene expression, and to differ from that of plants and microalgae. For example, methylation occurs predominately in CHH sequence contexts, which transfer methylation less reliably across mitotic cell divisions than CG sites (Law and Jacobsen, 2010). Moreover, DNA methylation appears to rely on a DNA methyltransferase (DNMT2) that is of low efficiency compared with other DNMTs, belonging to a class that mainly catalyzes tRNA methylation in plants and animals (Fan et al., 2019). How these specificities affect the functional role of the kelp methylome with respect to molecular stress memory remains unexplored.

Integrative Analyses

Parallel recording of epigenetic and transcriptomic priming responses can allow the identification of priming-induced epialleles that correlate with gene expression patterns and therefore potentially explain enhanced stress resistance (e.g., heat shock proteins). For example, that heat-induced methylation changes could be involved in stress acclimation of the red alga *Pyropia haitanensis*, was suggested by their correlation with the expression of stress-responsive genes (Yu et al., 2018). Penalized regression methods present promising integrative multi-locus models to test for statistical relationships between different “omics” data sets as they can overcome the challenge of having a small number of individuals (n) relative to the number of parameters (p) (Pineda et al., 2015; Lien et al., 2018; Zhong et al., 2019). Causal effects of DNA methylation on improved

phenotypes may be possible to model with structural equation modeling (SEM), an established multivariate method that is relatively new to the field of molecular biology (Igolkina and Samsonova, 2018; Fatima et al., 2020). To demonstrate a causative relationship between priming memories and adaptive phenotypic changes requires experimental removal of DNA methylation, e.g., using Zebularine or 5-Azacytidine (Griffin et al., 2016), or targeted modifications of epigenetic marks, e.g., using the CRISPR-Cas system (Xu et al., 2016).

Inferences about the functional effect of molecular priming memories rely on the availability of annotated genomes, which are still scarce for marine macrophytes. Genomes have been published for six brown macroalgae: *Ectocarpus* sp. (Cock et al., 2010), *S. japonica* (Ye et al., 2015), *Undaria pinnatifida* (Shan et al., 2020), *Cladosiphon okamuranus* (Nishitsuji et al., 2016), *Nemacystus decipiens* (Nishitsuji et al., 2019), and *Sargassum fusiforme* (Wang et al., 2020). Published seagrass genomes include *Z. marina* (Olsen et al., 2016), *Z. muelleri* (Lee et al., 2016), and *Halophila ovalis* (Lee H. et al., 2018). Thus, the assembly and annotation of genomes, particularly of species of high ecological or commercial relevance, is a key priority in priming-related research.

Stability and Transfer of the Priming Memory

Multi-generational stability of the priming memory (transgenerational priming) is more important for the application of priming in restoration than in cultivation. Macroalgal cultivation naturally allows for annual re-priming during the few weeks the macroalgae are cultivated under controlled laboratory conditions. For example, for kelps, priming could be annually applied to either the haploid gametophyte cultures or to the young diploid sporophytes before being deployed at sea until harvest. While priming of the gametophytes would require the least resources (i.e., space and water), it is not clear to what extent epigenetic reprogramming during fertilization would affect transmission of a priming memory to the sporophyte generation. To characterize the transfer of priming memories via small life-cycle stages such as meiospores, gametes, and zygotes may become possible with new single-cell 'omics technologies (Wang and Bodovitz, 2010; Zhu et al., 2020) that allow to sequence at DNA quantities which are too low for more traditional high-throughput sequencing technologies.

For restoration of kelp forests and macroalgae beds, thermal priming could be applied to the newly developed restoration tool "Green gravel," where macroalgae are seeded on rocks and reared in the laboratory until reaching a size of 2–3 cm (Fredriksen et al., 2020). Specifically, priming could be used to enhance initial survival of gametophytes and juvenile sporophytes to the generally harsher conditions in degraded areas where an adult canopy is lacking. However, if not transferred across generations, any positive priming effect will last, at most, until the primed individuals have died, and will not provide long-term protection against recurrent stress. Some macroalgae grow vegetatively (e.g., *Ecklonia brevipes*; Coleman and Wernberg, 2018), allowing to compare the longevity of priming effects under

different modes of reproduction in macroalgae being applied in a restoration context.

In seagrass meadows, priming memories are likely to be more stable across vegetatively/mitotically grown generations than across sexually produced generations because epigenetic marks are often reset during meiosis and embryogenesis (Figure 1C; Hirsch et al., 2012; Douhovnikoff and Dodd, 2014; Dodd and Douhovnikoff, 2016; González et al., 2017). While direct tests for predicted sexual-aseexual differences in the transgenerational stability of epigenetic marks are virtually lacking (Verhoeven and Preite, 2014), a unique system to test these differences is provided by the dramatic range in clonal diversity and life history strategies of seagrasses, ranging from predominantly vegetative to predominantly sexual reproduction (Kilminster et al., 2015).

Clonal seagrass meadows further provide a unique potential to study whether communication of epigenetic information across physically connected shoots allows the acquisition of a collective stress memory to prepare interconnected ramets for a range of future environmental challenges (Latzel et al., 2016). The transport of epigenetic information from somatic tissue to the germline via miRNAs (small ncRNAs that can cross cell barriers) has been demonstrated in humans and the nematode *Caenorhabditis elegans* (Creemers et al., 2012; Devanapally et al., 2015; Sharma, 2015; Szyf, 2015). Whether such communication may extend across interconnected ramets of the same clone has never been tested.

Prospects to Explore Priming as Biotechnological Tool in Marine Macrophytes

Priming has a large potential to enhance restoration success of macroalgal forests and seagrass meadows, and to ensure production security of macroalgal biomass under environmental challenges. Because primed organisms are not considered genetically modified, they can be grown in countries where GMO restrictions apply. Moreover, priming would likely be a less controversial and more socially acceptable way to boost resilience in macrophytes relative to the proposed gene editing approaches (Coleman and Goold, 2019). However, priming cannot be simply transferred from terrestrial plants to marine macrophytes. In particular, brown and red macroalgae are distantly related to terrestrial plants, and kelps have complex heteromorphic life cycles with free-living gametophyte generations. Thus, in order to identify whether priming can be established as a novel bio-engineering technique for marine macrophytes, we need ambitious fundamental research that uses complex experimental setups combined with multivariate analyses that can integrate multiple high-throughput sequencing datasets to test at which intensity, duration, and life-cycle stage priming has a positive and long-term effect without inducing selection or high mortality. For priming to be of commercial value to the macroalgae farming industry, we must further assess whether the cost factor added to the cultivation process pays off by enhancing yield even in years where the macroalgae are not exposed to stress or by providing cross-protection to other relevant stressors (Hilker et al., 2016). Despite these knowledge gaps, priming should be explored as

a tool to boost resilience of both seagrass and macroalgae to secure their ecological and economic values in future oceans.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

AJ wrote the first draft of the manuscript. AM created the figures. JC, MC, TW, LS, RR, JZ, and Z-MH contributed to the article by commenting and re-writing sections, and approved the submitted version. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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