



Climate Change Impacts on Seagrass Meadows and Macroalgal Forests: An Integrative Perspective on Acclimation and Adaptation Potential

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Marine macrophytes are the foundation of algal forests and seagrass meadows—some of the most productive and diverse coastal marine ecosystems on the planet. These ecosystems provide nursery grounds and food for fish and invertebrates, coastline protection from erosion, carbon sequestration, and nutrient fixation. For marine macrophytes, temperature is generally the most important range limiting factor, and ocean warming is considered the most severe threat among global climate change factors. Ocean warming induced losses of dominant macrophytes along their equatorial range edges, as well as range extensions into polar regions, are predicted and already documented. While adaptive evolution based on genetic change is considered too slow to keep pace with the increasing rate of anthropogenic environmental changes, rapid adaptation may come about through a set of non-genetic mechanisms involving the functional composition of the associated microbiome, as well as epigenetic modification of the genome and its regulatory effect on gene expression and the activity of transposable elements. While research in terrestrial plants demonstrates that the integration of non-genetic mechanisms provide a more holistic picture of a species' evolutionary potential, research in marine systems is lagging behind. Here, we aim to review the potential of marine macrophytes to acclimatize and adapt to major climate change effects via intraspecific variation at the genetic, epigenetic, and microbiome levels. All three levels create phenotypic variation that may either enhance fitness within individuals (plasticity) or be subject to selection and ultimately, adaptation. We

review three of the most important phenotypic variations in a climate change context, including physiological variation, variation in propagation success, and in herbivore resistance. Integrating different levels of plasticity, and adaptability into ecological models will allow to obtain a more holistic understanding of trait variation and a realistic assessment of the future performance and distribution of marine macrophytes. Such multi-disciplinary approach that integrates various levels of intraspecific variation, and their effect on phenotypic and physiological variation, is of crucial importance for the effective management and conservation of seagrasses and macroalgae under climate change.

Keywords: seagrasses, kelp forests, physiology, epigenetics, microbiome, modeling, early life stages, global climate change

CLIMATE CHANGE IMPACT ON MARINE MACROPHYTES

Burning of fossil fuels since the eighteenth century Industrial Revolution increased the atmospheric CO₂ concentration from a pre-industrial level of 280 ppm to >400 ppm (reached in 2013), a level that has not been reached over the past few million years (Monastersky, 2013). Increasing levels of CO₂ enhance the greenhouse effect, trapping more solar radiation near the earth surface, which causes an increase in global temperatures (Keller, 2009). About 80% of the excessive heat is absorbed by the ocean. Consequently, average global ocean temperatures have increased by 0.9°C in the upper 700 m during the twentieth century (Domingues et al., 2008), and currently (2001–2005 average) rank among the highest levels recorded during the past 1.4 million years (Hansen et al., 2006). Concomitantly, ocean uptake of atmospheric CO₂ leads to ocean acidification (Doney et al., 2009). Further consequences of rising temperatures are ranging from changes in atmospheric and ocean circulation, over changes in season succession, as well as in storm and precipitation patterns, to drought periods and altered thermal environments (Reay et al., 2007; Poloczanska et al., 2013). A cascade of extreme thermal events became particularly evident in the last years, with severe increases in both frequency and intensity (Reay et al., 2007; Field et al., 2012), and affected phenological cycles in both adult forms and early-life stages of many marine organisms (Poloczanska et al., 2013). Summer warm extremes have increased by about 10% since the 1960's to 1970's in China and Europe (Yan et al., 2002; Klein Tank et al., 2003; Alexander et al., 2006) and the European heat waves in summer 2003 and 2010 (Beniston and Stephenson, 2004; Schär and Jendritzky, 2004; Barriopedro et al., 2011) caused major community shifts and local species extinctions (e.g., Garrabou et al., 2009; Sorte et al., 2010). Increasing ocean temperature and changing chemistry affects physiological performance, behavior, and population dynamics of all marine organisms, from primary producers to upper-trophic-levels, including fishes, seabirds, and marine mammals (Doney et al., 2012).

With the exception of hydrothermal vents in the deep sea, photosynthetic primary producers are at the base of all food webs. Here, we focus on macrophytes as key primary producers

in marine benthic habitats, commonly known as seagrasses (marine angiosperms) and brown macroalgae. Seagrasses are Archaeplastida, the primordial photosynthetic eukaryote group which includes also green and red algae. In contrast, brown macroalgae are Stramenopiles (SAR), a lineage that gained chloroplasts in some groups by secondary endosymbiosis from other eukaryotes. Brown macroalgae (hereafter referred to as macroalgae) include fucoids that grow mainly in the intertidal, and kelps, a term used to designate large subtidal brown algae, most with a heteromorphic life cycle in the orders Laminariales, Tilopteridales, and Desmarestiales. An exception is bull kelp that is classified as a fucoid. Taxonomic understanding of both groups remains incomplete and in need of further refinement (reviews Hartog and den Kuo, 2006; Bartsch et al., 2008; Bolton, 2010), despite recent advances (Lane et al., 2006; Aires et al., 2011; Coyer et al., 2013; Rothman et al., 2015, 2017; Jackson et al., 2017). The continued application of genome-wide markers and multigene phylogenies will likely reveal previously overlooked taxonomic and biogeographic lineages (e.g., Tellier et al., 2009, 2011).

Both seagrasses and brown macroalgae are not only key primary producers, but also foundation species that influence ecosystem structure and function by creating locally stable conditions and habitat for other species, while supporting some of the most productive and diverse coastal marine ecosystems on the planet (Costanza et al., 1997; Spalding et al., 2007; Chung et al., 2011; Smale et al., 2013; Thomson et al., 2015; Teagle et al., 2017). Marine macrophytes further provide ecosystem services, such as food for invertebrates and fish, a blue carbon sink, nutrient fixation, and protection of the coastline from erosion (Procaccini et al., 2007; Harley et al., 2012). While macroalgae predominate on rocky shores in temperate to polar regions (Steneck et al., 2002; Bolton, 2010), seagrasses predominate on sandy shores from temperate to tropical regions (Short et al., 2007).

Seagrass beds and kelp forests are increasingly threatened by a variety of stressors (Orth et al., 2006; Waycott et al., 2009; Krumhansl et al., 2016). The combined effect of multiple climate-change related stressors on the extinction risk and productivity of macrophytes can be additive, synergistic, or antagonistic (Wahl

et al., 2011, 2015), and may not be predicted from the individual effect of each variable operating in isolation (Darling and Côté, 2008). Nevertheless, for many marine macrophytes, temperature is the most important range limiting factor, and ocean warming is considered the most severe threat among global climate change factors (Diaz-Almela et al., 2007; Moore et al., 2012; Jueterbock et al., 2013; Araújo et al., 2016; Assis et al., 2017a; Repolho et al., 2017). In contrast, the predicted rise in ocean CO₂ concentration is likely to have a positive effect on growth and photosynthesis because most macrophytes are carbon-limited at current ocean dissolved inorganic carbon (DIC) (Koch et al., 2013). However, the effect is unlikely to be big since the predicted long-term rise in CO₂ falls several orders of magnitude below current CO₂ and pH fluctuations within seagrass beds and kelp forests (Saderne et al., 2013; Wahl et al., 2017). Thus, in this review we mainly focus on ocean warming as the most important climate-change effect.

For macroalgae, the magnitude and direction of abundance changes vary strongly between geographic regions (Krumhansl et al., 2016), but macrophyte losses are concentrated in warm-temperate to tropical regions (Nicastro et al., 2013; Fraser et al., 2014). Physiological, genetic, and modeling data predict, and already document, that rising temperatures cause massive die-offs of genetically unique populations along warm-temperate distribution limits and open up new thermally suitable habitat in polar regions (Wernberg et al., 2011; Jueterbock et al., 2013, 2016; Brodie et al., 2014; Krause-Jensen and Duarte, 2014; Valle et al., 2014; Olesen et al., 2015; Assis et al., 2016a, 2017a; Hyndes et al., 2016). How fast and far warm-temperate range edges will retract toward higher latitudes largely depends on the macrophytes' ability to rapidly acclimatize or adapt to warm temperature extremes. In contrast, how fast and far poleward range-edges will extend into polar regions does not only depend on suitable temperatures for reproduction, but also on the macrophytes' ability to adapt to the extreme polar light conditions with month-long winters of constant darkness, and month-long summers of constant light (Krause-Jensen and Duarte, 2014; Berge et al., 2015).

The aim of the present paper is to review the potential of marine macrophytes to acclimatize and adapt to major climate change effects via three pillars of intraspecific variation (Figure 1). A holistic picture of ecologically and evolutionary relevant variation integrates genetic variation (A1) with non-genetic mechanisms, involving the functional composition of the epigenome (A2) and the microbiome (A3). All three levels create plasticity and adaptability via phenotypic variation. Most important in a climate change context is physiological variation (B1), variation in propagation success (B2), and in biotic interactions (B3). We do not aim to review ecological effects on macrophyte associated ecosystems, but on the macrophytes themselves. Our ultimate goal is to provide insight into recent and novel approaches that might be integrated in multidisciplinary studies and integrative niche modeling approaches (C) toward a better understanding of the future of these foundation species in a changing world (Figure 1).

A LEVELS OF INTRASPECIFIC VARIATION CREATING PLASTICITY AND ADAPTABILITY

A1 Genetic Variation and Structure—Explained by Biogeographic History

Geographic patterns of neutral genetic structure in macroalgae and temperate seagrass species frequently reveal the imprints of ancient, often multiple refugia that arose during past glacial cycles and persist to the present day, revealing distinct genetic or phylo-groups sharing limited gene flow. In the Mediterranean, ancient vicariance events, hypothetically attributed to the Messinian Salinity Crisis, were reported in the seagrasses *Posidonia oceanica* (Arnaud-Haond et al., 2007b; Serra et al., 2010) and *Ruppia* spp. (Triest and Sierens, 2014), although niche modeling indicated that the present phylogeography of *P. oceanica* is also shaped by more recent climate refugia (Chefaoui and Serrão, 2017). Mediterranean-Atlantic vicariance with two glacial refugia in West Africa and the Eastern Mediterranean was suggested in *Cymodocea nodosa* based on allelic distributions (Alberto et al., 2008), and niche models (Chefaoui et al., 2017). Across latitudinal gradients, a recurring theme is genetically unique and rich low latitude rear edge populations and low-diversity poleward along post-glacial expansion fronts (e.g., for *Zostera noltii*, Coyer et al., 2004; Diekmann et al., 2005), while central latitudes can be genetically rich (*Zostera marina*; Diekmann and Serrão, 2012). Some works point out to strong impacts of climate change on seagrasses (Valle et al., 2014) and macroalgae (Wernberg et al., 2011; Jueterbock et al., 2013; Assis et al., 2016a,b, 2017a; Neiva et al., 2016), with poleward shifts at low diversity expansion fronts, while significant diversity near the rear edge may be lost.

A range of life-history and oceanographic features can serve to maintain existing population or metapopulation structure. Seagrass meadows often spread via vegetative clonal expansion, with individual clones reaching extreme age and extent in long-lived species (e.g., *Posidonia oceanica*, Arnaud-Haond et al., 2012 or *Zostera marina* Reusch et al., 1999). Clonal propagation creates challenges for genetic and biogeographical studies (Arnaud-Haond et al., 2007a), such as requiring high resolution genetic markers for identifying individuals. Notwithstanding the importance of sexual propagation for seagrasses (Kendrick et al., 2012), its principal role may be recolonization after disturbance (Marba and Duarte, 1995).

Kelps disperse via haploid meiospores, subsequently followed by syngamy between closely spaced (ca. 1 mm) benthic dioicous male and female microgametophytes. As fertilization occurs after the planktonic phase, low dispersal distance and inbreeding may be the norm (Reed et al., 2004b; Raimondi et al., 2011; Johansson et al., 2013), although km-scale dispersal is possible given a suitably large source population (Reed et al., 2004a).

On biogeographic scales, dispersal of viable vegetative fragments, larger-scale rafting, or sexual propagules is dependent on surface currents transporting viable material (Alberto et al., 2011; Johansson et al., 2015; Assis et al., 2017a). However,

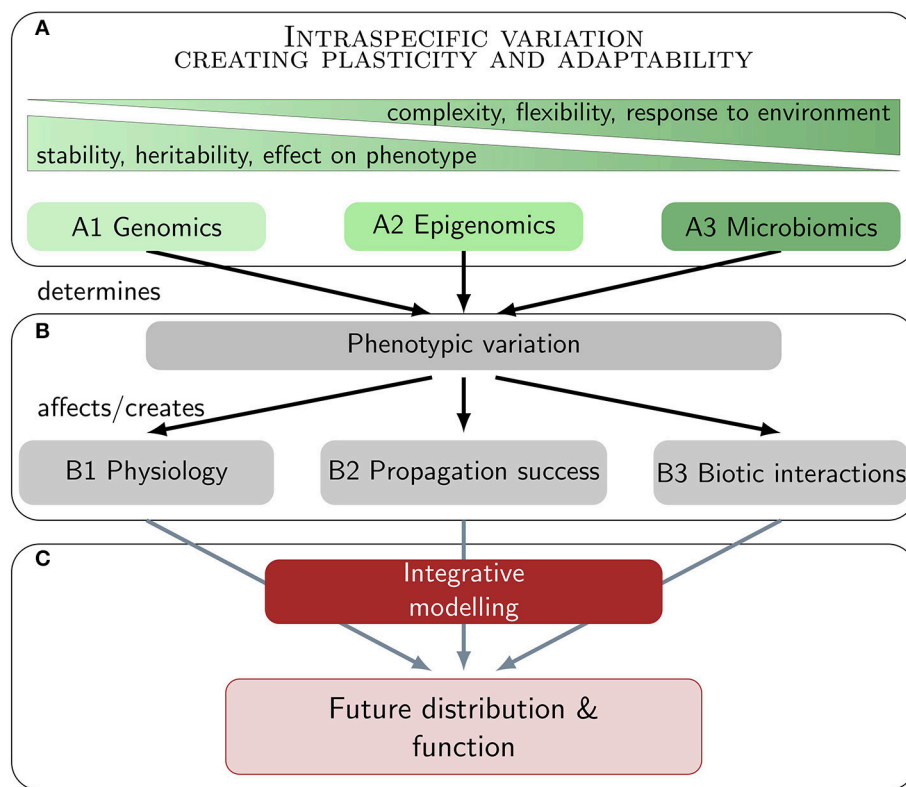


FIGURE 1 | Realistic predictions of future distributions and ecosystem functions of marine macrophytes under climate change rely on multi-disciplinary research. Climate change research should ideally integrate various levels of intraspecific variation and their effect on phenotypic and physiological variation. The ultimate goal is to widen the concept of niche stability in conventional modeling approaches with this multi-layered plasticity concept.

vicariance signatures suggest this type of dispersal is frequently unsuccessful in producing effective recruitment in seagrasses (Diekmann et al., 2005; Arnaud-Haond et al., 2007b; Alberto et al., 2008; Serra et al., 2010) but see Reusch et al. (2000) for *Z. marina* rafting success in the North Sea. A compelling hypothesis is that, even if oceanographic barriers are incomplete, dispersal into areas already colonized may be ineffective due to priority or density-barrier effects, in which incoming alleles are “swamped” by those already present at higher-frequency (De Meester et al., 2002; Neiva et al., 2012, 2016).

Populations differentiated along a latitudinal gradient experience climate change in different ways, due to their intrinsic genetic characteristics and population dynamics. A clearer picture of the biogeographic and metapopulation structure of macroalgae and seagrasses will be key to unravel variation in functional responses, adaptive potential, and likely resilience across species ranges. Much remains to be discovered, with the challenge to link genomic (Olsen et al., 2016) and functional trait variation (Jueterbock et al., 2016), and integrate this with projected threats arising from a rapidly changing climate. This is particularly urgent for rear-edge and marginal populations, many of which are under imminent threat.

Macrophytes can be locally adapted to their thermal regime (e.g., Zardi et al., 2013; Pereira et al., 2015; Saada et al., 2016; King et al., in press). This means that migrations are rather the

dislocation of those adapted subpopulations, and must also be investigated/ modeled as such (as in Assis et al., 2016b). Thus, below the surface of a species with an apparent broad tolerance, there may be more specialized sub-populations. However, the loss of genetic variability is likely to act against local adaptation of marginal populations (Pearson et al., 2009).

Genetic diversity is considered to be the key for future adaptation to environmental change, and the long-term survival of species (Bijlsma and Loeschcke, 2012). Genotypic diversity, as one subset of genetic diversity in clonally growing species, has been shown to increase productivity, and stress resilience in seagrasses and macroalgae (Hughes and Stachowicz, 2004; Reusch et al., 2005; Ehlers et al., 2008). Conservation management integrates the positive relation between genetic diversity and adaptive potential by focusing conservation efforts on populations with low genetic diversity, and by considering genetically diverse populations as source populations for restoration. However, evolutionary success of >1,000-years-old clonal seagrass beds with extremely low genetic diversity (Reusch et al., 1999) under substantial environmental change (Leipe et al., 2008), and the successful establishment of a putatively small North-European founder population of *Laminaria hyperborea* in Arctic Svalbard over the past few decades (Müller et al., 2009; Assis et al., 2016b) challenge the hypothesis of a straightforward relationship between genetic diversity and adaptive potential.

A2 Epigenetic Potential to Adapt to Climate Change

Epigenetic variation may contribute to rapid adaptation under climate change (Zhang et al., 2013; Schlichting and Wund, 2014; Prokopuk et al., 2015; Herman and Sultan, 2016; Rey et al., 2016), as adaptive evolution via DNA based polymorphisms is often considered too slow to keep pace with the increasing rate of anthropogenic environmental change (Quintero and Wiens, 2013). Epigenetic variations are molecular modifications that alter gene expression, but not the underlying DNA sequence, and occur in the form of histone modifications, non-coding RNAs, and DNA methylations (Bossdorf et al., 2008; Berger et al., 2009). Recent studies in the young research field of Ecological Epigenetics provide increasing evidence for the potential of epigenetic variation to increase plasticity, facilitate speciation and accelerate adaptation to new environments and stressful conditions (Schrey et al., 2013; Bonasio, 2015; Verhoeven et al., 2016; Kilvitis et al., 2017; Richards et al., 2017).

DNA-methylation variants (epialleles), epigenetic modifications that involve the addition of a methyl-group to cytosines (5-mC) in DNA sequence motifs, are currently the most popular epigenetic modification screened in evolutionary and ecological contexts (Schrey et al., 2013; Verhoeven et al., 2016; Richards et al., 2017). The possibility of methylation changes to respond directly to environmental change, and to trigger at least partly heritable changes in gene expression, resembles Lamarck's theory of the inheritance of acquired characteristics (Schmitz et al., 2013; Herman and Sultan, 2016) and ultimately challenges the classical theory of evolutionary adaptation.

The integration of epigenetic variation will certainly provide a more comprehensive understanding of the ecologically and evolutionary relevant variation of marine macrophytes, very much in the light of the recently suggested extended evolutionary synthesis (Pigliucci and Müller, 2010). This may enable for a more holistic prediction of the susceptibility of populations in terms of both genetic and epigenetic adaptive potential and, thus, for a more holistic conservation management under climate change. Due to their sessile nature, epigenetic variation is expected to be particularly relevant for rapid adaptation of marine macrophytes under climate change (Liu, 2013). Given the ecological key role of habitat-forming seagrass meadows, and macroalgal beds, epigenetic diversity in these systems is likely to secure the function of the entire associated coastal ecosystems. For example, DNA methylation enhanced the productivity, competitive advantage, and pathogen resistance of *Arabidopsis thaliana* plant populations (Latzel et al., 2013). Moreover, since the epigenome plays an essential role in plant development (Feng et al., 2010; Gutierrez-Marcos and Dickinson, 2012; Kawashima and Berger, 2014), its understanding is crucial to optimize seedling and gametophyte propagation for sustainable management, restoration, and cultivation of marine macrophytes.

Epigenetics research is growing particularly strong in terrestrial plants (Hirsch et al., 2013; Slotkin, 2016; Richards et al., 2017). A case in point within the context of climate change, is

thermal tolerance that may be partly ascribed to CG methylation-variants, which is supported by temperature-associated variation in gene-body methylation in natural populations of *A. thaliana* (Dubin et al., 2015; Keller et al., 2016) and the valley oak *Quercus lobata* (Gugger et al., 2016). Moreover, experimental warming increased CHH methylation in *A. thaliana* transposable elements (Dubin et al., 2015) and contributed to increased methylation variation and adaptive plasticity in seedlings of the alpine herb, *Wahlenbergia ceracea* (Nicotra et al., 2015). However, these studies could not resolve to what extent the temperature associated methylation variants provided an autonomous way of adaptation that cannot be simply explained by underlying genetic variation (Foust et al., 2016; Herrera and Bazaga, 2016).

Epigenetic responses to climate change related stresses have to date been understudied in marine organisms (reviewed in Hofmann, 2017). One pioneering study on an Antarctic polychaete showed that a net increase in DNA methylation contributed to acclimation to warmer temperatures (-1.5° vs. $+4^{\circ}$ C), by regulating energy metabolism (Marsh and Pasqualone, 2014). In the European sea bass, a temperature increase of 2° C was shown to change global DNA methylation in larval but not in juvenile stages (Anastasiadi et al., 2017). In the scleractinian coral *Pocillopora damicornis*, DNA methylation levels increased globally in response to increased pCO₂ levels (from ambient pH 7.9–7.65 to low pH 7.6–7.35) (Putnam et al., 2016). Accordingly, increasing DNA methylation likely contributed to phenotypic acclimation of the coral *Stylophora pistillata* under long-term exposure to reduced pH (Liew et al., 2017). These pioneering studies suggest that DNA methylation increases plasticity and adaptive potential in an ocean climate change context. While they focused on marine metazoans, the field is wide open in marine macrophytes.

Seagrasses likely show methylation in the same three sequence contexts as terrestrial plants, including CHG, CHH, and CG (Xie and Yu, 2015; Kilvitis et al., 2017; Richards et al., 2017). So-called CpG islands represent clusters of CG sites in gene promoter regions, and are commonly associated with gene expression regulation (Bossdorf et al., 2008; Illingworth and Bird, 2009; Zhang and Jeltsch, 2010). Transposable elements, generally silenced by DNA methylation, can be activated by stress-induced de-methylation processes and move to new genomic locations (Zhang et al., 2006; Slotkin and Martienssen, 2007; Biémont, 2010; Seymour et al., 2014). Such “jumping genes” can trigger changes in gene expression and genome structure, and may facilitate rapid species adaptation to new environmental conditions (González et al., 2010; Chénais et al., 2012; Casacuberta and González, 2013; Schrader et al., 2014; Stapley et al., 2015; Staton and Burke, 2015). Accordingly, a burst of transposable elements in the genome of the seagrass *Zostera marina* likely provided novel promoters and splicing sites, resulting in a gain of genes which may have facilitated its adaptation to the marine environment (Olsen et al., 2016). This suggests that DNA methylation changes and associated re-activation of transposable elements can additionally play an important role for rapid adaptation of seagrass under climate change.

Their partial clonal reproduction makes seagrass particularly well suited for epigenetic studies, as it allows to investigate epigenetic differentiation and change without the confounding factor of genetic variation. Vegetative reproduction entirely circumvents the meiotic resetting of epigenetic marks, thus enhancing the transgenerational epigenetic memory of clonal plants (Verhoeven and Preite, 2014; Latzel et al., 2016). Geographic variation in the degree of clonal reproduction allows to study the relevance of epigenetic variation under different reproduction modes. In a ~1,000-year old, predominantly clonal seagrass (*Z. marina*) meadow in the Baltic sea (Reusch et al., 1999), genetically identical shoots were recently shown to vary epigenetically in DNA methylation (Jueterbock et al., 2017). This variation may confer advantages that compensate evolutionary costs of clonal reproduction (Douhovnikoff and Dodd, 2014; Latzel et al., 2016), and may partly explain the evolutionary success of clonal seagrass meadows in the absence of genetic variation.

Another route to achieving genetic variation, despite clonal growth, may be somatic mutations, which have long been dismissed as route for adaptive mutational change. However, they do exist in long-lived seagrasses clones (Reusch and Boström, 2010) and may confer fitness advantages. Interestingly, in corals, genetic heterogeneity has also been observed within clones (Schweinsberg et al., 2015).

In contrast to seagrass DNA, it is still not clear which species of multicellular brown algae use DNA methylation as epigenetic mechanism. DNA methylation was found in the genomes of green and red algae, as well as in single-celled brown algae, and in diatoms (Maumus et al., 2011; Tirichine and Bowler, 2011; Veluchamy et al., 2013). MSAP analysis detected DNA methylation also in the kelp *Saccharina japonica*, with higher methylation-levels in sporophytes (ca. 25%) as compared with gametophytes (ca. 5%) (Qu et al., 2013). In contrast, undetectable 5-mC and C5-methyltransferase genes in the genome of *Ectocarpus siliculosus* (Cock et al., 2010) suggests a lack of DNA methylation as a derived feature in the brown algal order Ectocarpales. Sequence contexts and inheritance patterns of DNA-methylation variants are entirely unknown in brown macroalgae.

The first steps in marine macrophyte epigenetics can be taken with existing high-throughput techniques (Laird, 2010; Zhang and Jeltsch, 2010; Richards et al., 2017). Bisulfite sequencing is considered the 'gold-standard' to characterize DNA-methylation as the only method resolving nucleotide-level polymorphisms (Schrey et al., 2013; Adusumalli et al., 2014). While whole genome bisulfite sequencing is still expensive for large sample sizes, reduced representation techniques, such as RRBS (Gu et al., 2011), bsRADseq (Trucchi et al., 2016), and epiGBS (van Gurp et al., 2016) allow for cost-effective population epigenetic comparisons, partly without the need for a reference genome. Alternatively, DNA-methylation can be characterized with markers obtained via methylation-sensitive restriction enzymes, such as EpiRAD (Schield et al., 2016) and MethylRAD (Wang et al., 2015). While epigenetic population comparisons and stress responses can be studied for any species with DNA-methylation, an annotated reference genome is essential to infer

the functional relevance of epigenetic differences and stress responses.

As numerous temperate macrophytes are predicted to shift poleward under projected climate change (see Biogeographic history section or niche modeling section), rapid acclimation and adaptation potential will become particularly relevant along their equatorial and polar distribution edges. Initial research priorities in marine macrophytes with respect to the relevance of epigenetic variation under climate change, are: (1) to characterize the relation between epigenetic and genetic variation and structure along latitudinal temperature gradients, and (2) to identify induced epigenetic changes in response to climate change related stress, their effect on TE activity and gene expression, as well as their heritability, and thus adaptive potential.

A3 Marine Macrophyte Holobionts and Their Hologenomes

In addition to the above covered mechanisms for adaptation and acclimation of marine macrophytes, we highlight in this section that acclimation can also be mediated by changes in the structure of associated microbial communities. These fast dividing and evolving members of microbial communities can change orders of magnitude faster than their host. Future climate change conditions can shift host microbiome structure (microbial composition and abundances) and function. To what extent the host influences these shifts and whether these shifts increase the hosts' fitness under changed conditions is uncertain, but if so acclimation could be microbiome-mediated (Webster and Reusch, 2017). Over the last decade, it has become increasingly clear that the fitness of macro-organisms is at least partially determined by their associated microbiota, the microbiome, consisting of archaea, bacteria, fungi, viruses, protists, etc., all together with the host forming a holobiont. In the marine realm, microbiomes have been studied especially in corals and sponges (Bourne et al., 2016; Keller et al., 2016; Hernandez-Agreda et al., 2017). Although macroalgae and seagrasses form habitats worldwide known as hotspots of biodiversity and production, we know little about the microbes in these ecosystems (Bengtsson et al., 2012), but see Clasen and Shurin (2015) for an ecosystem approach. The relative few microbial studies performed have focused almost exclusively on (epi-)bacterial communities associated to seagrasses and macroalgae, neglecting most other microbes (Bengtsson et al., 2012; Bockelmann et al., 2012, 2013; Michelou et al., 2013; Brakel et al., 2014, 2017; Cúcio et al., 2016; Singh and Reddy, 2016). On top of that, particularly functional interactions between marine macrophytes and their microbiomes are poorly known. Molecular ecology of seagrass and macroalgae microbiomes is a young research field. With the progress in high throughput sequencing, it has the potential to radically influence our understanding of seagrass and macroalgae ecology.

Marine macrophytes associate with bacterial communities that differ strongly from those of their surrounding seawater, sediment or substrate (Bengtsson and Øvreås, 2010; Bengtsson et al., 2010; Aires et al., 2016; Cúcio et al., 2016). However, bacterial communities associated to marine macrophytes are not

fixed and can change temporally and spatially across seasons, lifespan, life stages and tissue types by biotic and abiotic factors (Staufenberger et al., 2008; Aires et al., 2016; Mancuso et al., 2016). While bacterial communities of some macroalgae appear species- or even lineage-specific (Aires et al., 2016; Vieira et al., 2016), this is yet unclear for kelps and seagrasses due to the low number of studies with inter-species comparisons. Recent results (Cúcio et al., 2016) suggest that sympatric seagrass species (in this case *Z. marina*, *Z. noltei*, and *Cymodocea nodosa*) might share largely the same rhizosphere community. Similar results were very recently obtained by (Crump et al., 2018) for a comparison between sympatric *Z. marina* and *Z. japonica* in Oregon, USA using metatranscriptomics and 16S amplicon sequencing. The co-occurring *Halophila ovalis*, *Halodule uninervis*, and *Cymodocea serrulata* each showed unique root microbiomes, as light was experimentally reduced their root exudation was altered which reduced the abundance of microorganisms that are potentially beneficial to the seagrasses, but not the predicted function (Martin et al., 2018).

Only few macroalgae have been the subject of microbiome studies. On *L. hyperborea*, one of Europe's most important marine forest former, epibacterial diversity increases with the age/successive colonization of the kelp surface (Bengtsson et al., 2012). Bacterial density and community composition follow the kelp seasonal growth cycle. As most of the biofilm seems to consist of bacteria utilizing carbon produced by the host (Bengtsson and Øvreås, 2010), microbiome dynamics are probably strongly linked to seasonal changes in the kelp metabolome and seawater temperature (Bengtsson et al., 2010). A recent study using shotgun metagenomics suggests a complementary and mutualistic relationship between the female gametophyte of the kelp *Saccharina japonica* and its microbiome, in which bacteria seem to benefit from kelp polysaccharides and the kelp profits from enhanced growth and nutrient uptake by bacterial bioactive compounds such as vitamins and hormones (Ji et al., 2017). Gene functions within this kelp epimicrobiome were mainly symbiosis-associated, indicating that selective pressures shape these microbiomes to sustain a mutual benefit for both kelp and bacteria (Ji et al., 2017).

Macroalgae associated bacteria can have a wide range of beneficial effects for their host. Already at a very early stage of development, macroalgae can depend on associated bacteria. Green algae of the genus *Ulva*, for example, depend on bacterial compounds for induction of cell divisions, differentiation, wall formation, and hence a normal morphogenesis (Provasoli and Pintner, 1980; Matsuo et al., 2003; Wichard, 2015; Grueneberg et al., 2016). We are not aware of similar findings reported for kelp or seagrasses. Kelp associated bacteria can have growth-promoting effects, like noted for *L. japonica* (Dimitrieva et al., 2006) and provide nutrients. In more than half of the algal kingdom bacteria provide vitamins to their hosts (Croft et al., 2005). *Azotobacter* bacteria associated with the green alga *Codium fragile*, for example, were shown to be involved in nitrogen fixation, and are thought to supply the alga with nitrogen compounds (Head, 1975). Diazotrophic heterotrophic bacteria in seagrasses rhizosphere are involved in nitrogen fixation (Welsh, 2000). Macrophyte associated bacteria are also

involved in the production of biologically active and defensive compounds, protecting the host from pathogens, herbivores, fouling, and chemical intrusion (Burgess et al., 1999; Rao et al., 2007; Penesyan et al., 2009; Egan et al., 2014; Saha et al., 2014). Bacterial antimicrobial metabolites negatively affect fouling organisms and control microbial communities on macroalgae surfaces (Egan et al., 2000; Joint et al., 2007; Romero et al., 2011). In *L. saccharina*, half of the bacterial strains isolated by Wiese et al. (2009) demonstrated antimicrobial activity, inhibiting the growth of at least one Gram-negative and Gram-positive bacterium.

In the light of rising seawater temperatures and consequent stress conditions for seagrasses and macroalgae resulting in northward shifts of their species distribution, it is important to assess the role associated microbiomes can perform for their macrophytic host. Increased physical disturbances and stress, resulting from changing environmental conditions, are known to affect the macroalgae-associated microbial composition (directly or via its physiological responses) and cause its structural, functional or behavioral changes (Goecke et al., 2010; Egan et al., 2013; Hollants et al., 2013; Dittami et al., 2016). Microorganisms seem to be able to play a pivoting role in enabling macrophytes to expand their physiological capacities, broadening their environmental tolerance (Goecke et al., 2010; Egan et al., 2013; Hollants et al., 2013). In a species of the genus *Ectocarpus* for example, specific bacteria are linked to low salinity tolerance in *Ectocarpus* cultures facilitating acclimation to environmental change (Dittami et al., 2016). To what extent the marine macrophyte microbiome could be involved in thermal acclimation and adaptation is not known. In terrestrial plants, fungal symbionts increased plant biomass under various global change scenarios, including warming (Kivlin et al., 2013). In their review, the authors conclude that it is critical to include plant-fungal symbioses in the prediction of ecosystem response to global change (Kivlin et al., 2013). In some cases, however thermal tolerance involves more partners. Marquez et al. (2007) showed elegantly that a virus of a fungal endophyte of a tropical grass confers heat tolerance to both organisms enabling them to grow at high soil temperatures. Experimental warming of *Cymodocea nodosa* and *Labyrinthula* spp. that cause seagrass wasting disease, showed that the seagrass was not more susceptible to infection at higher temperature. On the contrary, lesion size decreased with warming (Olsen et al., 2014). Based on these cases it seems likely that also the macrophyte microbiome is linked to environmental tolerance, including warming. The only study that combined elevated temperatures and ocean acidification showed that elevated temperatures alone drives dysbiosis in *Macrocystis pyrifera* under which kelp growth was also negatively affected (Minich et al., 2017). However, acidification counteracted the elevated temperature effects resulting in positive kelp growth and a commensal microbial community that increased mucus production (Minich et al., 2017). Although it is not clear whether the microbiome changes in reaction to a change in the health of the host or *vice versa* (probably a tight and complex interaction of the two), it is increasingly clear that the interaction of global change factors

on marine macrophytes and their microbiomes should be more investigated.

The association with microorganisms may allow marine macrophytes to acclimate/adapt to warming conditions by changing the composition of microbiota, a process that can be much faster than by genomic evolution. Therefore, the diverse microbiota can possibly assist the macrophyte holobionts functioning and survival under elevated temperatures. As the combination of host and microbiota genomes, i.e., the hologenome, might in some cases act as a unit of natural selection, the association with microbes might play a crucial role in the acclimation of marine macrophytes to warming. At this moment, few studies address this issue in seagrasses and macroalgae. However some evidences are already documented in filamentous algae (Dittami et al., 2016). Holobiont evolution requires strict partner fidelity and will only work under vertical transmission fidelity and can be evolutionary unstable due to microbial cheaters, or shifting cost:benefit ratios (Douglas and Werren, 2016). However, the persistence of co-introduced symbiont bacteria many decades after macroalgae invaded in the Mediterranean from Australia, and their correlation with the host ecology (Aires et al., 2013; Arnaud-Haond et al., 2017), suggests a tight inter-dependence in at least some invasive macroalgae lineages. Notwithstanding, positive functional roles of the host-associated microbiome are also possible if the microbiome and its host do not evolve as a strict unit. Thus, we propose that concepts of climate change effects on macroalgae and seagrasses require the inclusion of microbiome-mediated acclimation. In the coral world, the study of fitness effects of associated microbes is far more developed than in seagrasses and macroalgae. As some corals are functionally plants (i.e., in corals with photosynthetic symbionts photosynthesis mostly exceeds heterotrophic nutrition) it may be useful to actively search parallels among both functional groups of habitat forming species. For example, both somatic mutations and epigenetic changes owing to environmental conditions have recently been described, making corals a poster child for the adaptation of the holobiont (Webster and Reusch, 2017).

B FORMS AND EFFECTS OF PHENOTYPIC VARIATION

B1 Physiological Constrains Promoted by Climate Change

The direct link between epigenetic mechanisms and gene expression (Bossdorf et al., 2008; Berger et al., 2009), and the proven effect of the root microbiome on the leaf metabolome in a terrestrial plant (Badri et al., 2013), demonstrate the direct relation between epigenetic or microbiome variation and physiology. Despite the lack of research in marine macrophytes, it can be expected that rapid shifts in epigenetic marks or in the microbiome composition may contribute to acclimatization to climate-change related stressors.

Photosynthesis is one of the most essential physiological processes that will be affected by increasing ocean temperatures. From a physical point of view, increasing water temperatures

reduce oxygen solubility and CO₂ availability (Beardall et al., 1998). Photosynthetic efficiencies are severely impaired by low light and/or high temperature conditions (York et al., 2013). Kinetically, photosynthesis increases with increasing temperatures until an optimum temperature point or range of a few degrees, beyond which it declines rapidly (Davison, 1991). These physiological imbalances increase respiratory activity, and shift marine forests and seagrass beds from carbon sinks to carbon sources (York et al., 2013). Most photosynthetic changes are due to damage at the chloroplast level (Repolho et al., 2017). Thermal-stress induced structural alterations at the photosystem II (PS II) reaction centers can lead to photoinhibition over several days (Campbell et al., 2006), so that the affected macrophytes depend on the respiration of their storage compounds. Moreover, thermal stresses have a very typical signature at the PS II level (Srivastava et al., 1997; Strasser et al., 2000). Thermal stress impairs typically the donor side of the PS II reaction centers, which corresponds to the location of oxygen evolving complexes (OEC) (Strasser et al., 2000; Duarte et al., 2015a,b, 2016). This imposes serious physiological constrains to the chloroplastial electron transport and energy production. Therefore, only species with a high degree of physiological plasticity can cope with abrupt changes, such as heat waves (Duarte et al., 2015a,b, 2016). From an ecological point of view, rising temperatures affect the role of kelp forests and seagrass beds as primary oxygen producers and, thus, all the heterotrophic food chain. Zhang et al. (2017) suggest four possible mechanisms in macrophytes to balance the redox state of electron transport and regulate the energy distribution between the two photosystems, thereby protecting the photosynthetic tissues from thermal stress: (1) an enhancement in the active PS II reaction centers efficiency; (2) an increase in the activity of the PS II electron acceptor side; (3) an enhancement in the cyclic electron flow transport around photosystem (PS I), allowing this photosystem to absorb the excessive electron flow; (4) alternation between PS II and PS I.

The accumulation of reducing power inside the chloroplast (Duarte et al., 2015a) increases non-photochemical quenching and decreases the photochemical quenching in order to dissipate excessive energy (Repolho et al., 2017). This can be performed by quantum dissipation or by enzymatic means, through the de-epoxidation of the xanthophylls (Figure 2, DES). Due to the characteristics of any enzymatic reaction, also this enzymatic dissipation mechanisms can be impaired outside the thermal optimum of each species (Campbell et al., 2006; Repolho et al., 2017). Additionally, ocean warming can lower chlorophyll contents and, thus, lead to kelp bleaching and seagrass browning (Staehr and Wernberg, 2009; Figure 2).

Under stress, macrophytes can recycle the photosynthetic substrates using storage ATP and carbohydrates. Respiration is very sensitive to ocean warming. In *Ecklonia radiata*, respiration is more affected than photosynthesis, implying that increasing temperatures raise respiratory energy demands faster than the photosynthetic regeneration of new ATP and carbohydrates (Staehr and Wernberg, 2009). To prevent metabolic arrest under such conditions, the most direct means to maintain a positive carbon balance is to increase the light demands and the light harvesting capacity of the photosystems. In seagrasses,

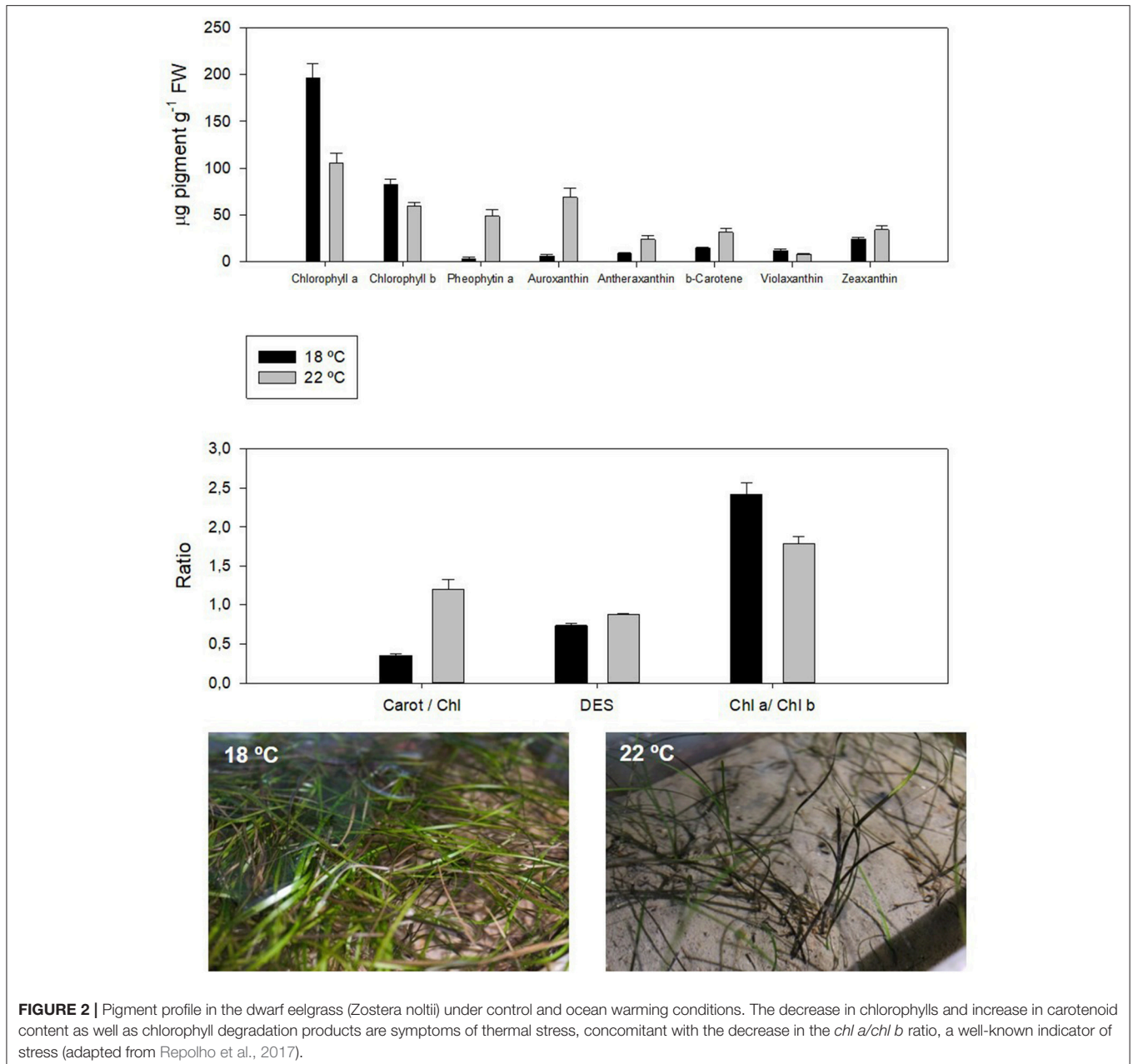


FIGURE 2 | Pigment profile in the dwarf eelgrass (*Zostera noltii*) under control and ocean warming conditions. The decrease in chlorophylls and increase in carotenoid content as well as chlorophyll degradation products are symptoms of thermal stress, concomitant with the decrease in the *chl a/chl b* ratio, a well-known indicator of stress (adapted from Repolho et al., 2017).

respiration mechanisms acquire a reinforced importance, due to the below-ground respiration of their root system. Leaf-based thermal optima may not represent thermal optima of the whole individual, since seagrasses have non-photosynthetic compartments (rhizome and roots), accounting for the majority of the total biomass (Collier et al., 2017). While respiratory activity under thermal stress can already surpass the plant photosynthetic capacity, this non-photosynthetic compartment imposes an additional respiratory burden (Fourqurean and Zieman, 1991).

The balance between photosynthesis and respiration will further determine whether macrophytes can extend poleward into regions that are predicted to become ice-free and thermally suitable. Survival of the light season in summer may depend

on the ability for increased light-respiration under constant light conditions. In contrast, survival of the dark winter season depends on the ability to store enough photosynthetates during the summer months to compensate for constant respiration in month-long darkness (Berge et al., 2015), especially when energy metabolism increases with rising temperatures (McMinn and Martin, 2013).

Low oxygenation levels imposed by global warming alter the sediment microbial community and biogeochemistry in sediments, favoring anaerobic organic carbon oxidation (Holmer and Bondgaard, 2001). Although this metabolic shift allows the system to recycle organic carbon, it comes at a high cost by generating high amounts of sulfide that is toxic for seagrasses (Koch and Erskine, 2001). Seagrasses are able to tolerate sulfide

intrusion by: (i) reoxidized sulfide by oxygen present in the aerenchyma (Pedersen et al., 2004) or in the rhizosphere (van der Heide et al., 2012) or (ii) organic sulfur conversion into thiols (Holmer and Hasler-Sheetal, 2014). If both mechanisms fail and sulfide intrudes into active tissues such as leaves and meristems, seagrasses suffer in performance (Garcias-Bonet et al., 2008; Pulido and Borum, 2010). Under increased anoxia, the already low levels of oxygen in the fine-grained soft sediments that seagrasses grow in, can increase sulfide production beyond optimal growth thresholds (Holmer and Bondgaard, 2001). Additionally, lower O₂ availabilities can impair the biological sulfide reoxidation (Pedersen et al., 2004; van der Heide et al., 2012), leading to increased sulfide accumulation. Moreover, sulfide impairs the sucrose transport from leaves, where it is photosynthetically generated, to the other non-photosynthetic organs where it is stored or consumed for active growing (Holmer and Bondgaard, 2001). If the plant cannot translocate sucrose efficiently to feed the underground organs, it will consume the storage sugars (underground starch) to maintain root growth and nutrient acquisition metabolisms. This re-mobilization of underground starch shifts the plant metabolism from an energy producer to an active consumer and, thus, impairs growth and primary productivity (Holmer and Bondgaard, 2001; Koch and Erskine, 2001; Holmer and Hasler-Sheetal, 2014).

Other climate-change associated stressors, such as hurricanes and excessive precipitation, can be equally disturbing for macrophytes. One of the direct consequences of these extreme events is the alteration of sedimentary budgets in transitional and coastal waters. During flood events the export of sediment from the river catchments to estuarine basins is substantially increased (Duarte and Caçador, 2012). Although both seagrasses and kelps depend on the sediment budget for their anchorage, they experience increased turbidity as additional stress as it reduces light availability (De Boer, 2007; Saunders et al., 2017). Light availability is a key factor that contributes to about 75% of the variation in the distribution of seagrass meadows and kelp forests (De Boer, 2007). However, seagrasses and kelps also influence sedimentation by trapping sediments from the water column, and thus actively decrease turbidity (De Boer, 2007). The sensible equilibrium between unproblematic and problematic levels of water-borne sediments can be disturbed by other climatic variables that act as multiple, synergistic stressors, which trigger more extreme ecological responses, particularly in ecosystems where foundation species exist near upper thermal tolerance limits (Fraser et al., 2014). While acidification can to some extent alleviate thermal stress due to higher CO₂ availability for photosynthesis (Repolho et al., 2017), exposure to multiple stresses may more often increase mortality and lead to carbon exportation.

Seagrass meadows and kelp forests can support high carbon uptake, depositing and preserving it as blue carbon over millennia in surrounding sediments (Duarte et al., 2013). The accelerated decline of macrophytes represents a loss of carbon sink capacity, and an increased risk for sedimentary carbon deposits to be lost through erosive and resuspension processes (Duarte et al., 2013). The loss of carbon stocks is not limited to carbon buried by erosion, but includes also the loss of

carbon sink capacity and a potential functional shift from carbon sinks to carbon sources via the re-mobilization of carbon stocks accumulated over millennia (Duarte et al., 2013).

Among other energy storage molecules, fatty acids play an important role not only for the physiology of the plant itself, but also in terms of macrophyte-based trophic chains, which are either directly based on macroalgae and seagrasses as food-source or on detritus exportation (Duarte et al., 2017b; Repolho et al., 2017). While animals can produce metabolically unsaturated and monosaturated fatty acids, they are able to synthesize polyunsaturated fatty acids (PUFAs), like linoleic acid (C18:2, n-6) and α -linolenic acid (C18:3, n-3) (van Ginneken et al., 2011). These are precursors of long chain PUFAs (LC-PUFAs) such as arachidonic acid (C20:4, n-6), eicosapentaenoic acid (EPA, C20:5, n-3) and docosahexaenoic acid (DHA, C22:6, n-3). Ocean warming is expected to have strong directional effects on the quantity and quality of fatty acids in marine macrophytes (Hixson and Arts, 2016), which will lead to modifications of the structure of their cellular membranes (Winter and Dzwolak, 2005), a mechanism of acclimatization known as homeoviscous adaptation (Sinensky, 1974). This adaptation involves remodeling of membrane lipids via the modification of fatty acid chain length and saturation, allowing to maintain a desired level of fluidity in cell membranes (Sinensky, 1974; Guschina and Harwood, 2006; Matos et al., 2007; Feijão et al., in press), and counteracting the increased fluidity promoted by higher temperatures. The decrease in the number of double bonds in PUFA and the increase of saturated fatty acids (SFA), enhances the ability of fatty acids to maintain structural rigidity of cell membranes in a less ordered environment (Fuschino et al., 2011). Global warming is expected to reduce the global production of PUFAs by marine macrophytes (Hixson and Arts, 2016). These biochemical and physiological cascades are predicted to affect also terrestrial animals because of the flux of aquatic biomass, containing n-3 LC-PUFA, which normally passes from aquatic to terrestrial ecosystems (Gladyshev et al., 2013). Marine ecosystems provide essential LC-PUFA for many omnivorous terrestrial animals, including humans. This transport of essential LC-PUFA from sea to land occurs through the trophic chain, as most terrestrial consumers are directly or indirectly fed by ocean products (Gladyshev et al., 2013). PUFAs were shown to enhance growth rates and reproductive capacities of aquatic animals (Von elert, 2004), as well as to be of great importance to the neural/cognitive, cardiovascular, and visual health of terrestrial vertebrates (Calder, 2015). Any stress like warming, that affects the fatty acid composition of membrane lipids, has inevitable impacts on the photosynthetic and respiratory pathways that are already under stress due to perturbations at the energy transduction level (Matos et al., 2007; Gameiro et al., 2016; Duarte et al., 2017a).

B2 Propagation Success: Climate Change Impacts on Early Life Stages

In plants, epigenome and microbiome shifts play an essential role during the development of early life stages (Feng et al., 2010; Chaparro et al., 2014), the life stages that are generally

most vulnerable to ocean warming in marine macrophytes (e.g., Brawley and Johnson, 1991; Schiel and Foster, 2006). Thus, propagation success of macroalgae and seagrass under climate change can be expected to at least partly depend on their epigenetic makeup or their microbiome composition.

Macroalgae, usually perceived as large canopy-forming beds or forests, all have microscopic phases that are generally highly susceptible to environmental stress (Roleda et al., 2007). The unicellular life stages of macroalgae, either spores or gametes, are released into the water column. These settle on the rocky coastline and give rise to the next macroscopic generation. Enormous numbers of these microscopic propagules are produced by macroalgae but only a small fraction survive to maturity. Physical stressors such as visible light, ultraviolet radiation (UVR), and temperature, account for much of the mortality among spores, embryos and juveniles (Schiel and Foster, 2006).

Macroalgae with complex life cycles have unicellular and microscopic cryptic stages that serve as seed banks for the next macroscopic generation. For example, the spores of some large macroalgae, such as kelps (i.e., *Laminariales*), germinate to produce a microscopic phase—a free-living generation with half the ploidy level of the macroscopic phase. Kelp sporophytes release spores that settle and germinate into free-living, haploid male and female microscopic filaments that grow on the seafloor. The gametophytes release sperm to fertilize eggs to form a zygote which develops into an embryonic sporophyte that matures into the morphologically complex macroscopic phase. Kelps are thus an example of a “heteromorphic alternation of generations” whereby two free-living phases are morphologically and ecologically distinct.

Stress physiological studies comparing the relative susceptibility of different life history stages showed that spores and gametes of brown, red and green macroalgae, are more susceptible to UVR compared to their corresponding juvenile and adult phases (Roleda et al., 2004, 2007, 2009). However, it seems that the microscopic kelp gametophytes are insensitive to anthropogenic CO₂ induced ocean acidification (Roleda et al., 2012; Leal et al., 2017b), and relatively tolerant to ocean warming (Leal et al., 2017a). Examples of thermal tolerances are specific to species and even to populations, suggesting local adaptation.

Arctic kelps' spore photosynthesis and gametophyte growth rate have a high temperature affinity between 12 and 13°C (Roleda, 2009, 2016); this temperature is 7–8°C higher than the *in situ* summer water temperature (5–6°C) in Kongsfjorden (Svalbard) (Hanelt et al., 2001; Svendsen et al., 2002). Moreover, the germination rate was also enhanced when summer mean temperature was increased by 4–5°C (Zacher et al., 2016). Among cold temperate populations, photosynthesis of *Laminaria digitata* gametophytes from Roscoff (France) was also not compromised when average summer temperature (17°C) was increased by 3°C (Delebecq et al., 2016). Among kelps in the Pacific, spore germination of *M. pyrifera* from New Zealand was not affected while germling growth rate was enhanced by a 4°C increase in summer water temperature (Leal et al., 2017a). On the other hand, spore germination of the same species from California

significantly decreased with a 5°C increase in temperature (Gaitán-Espitia et al., 2014).

Gametogenesis and fertilization are particularly sensitive to rising temperatures (Hooper, 1984; tom Dieck, 1989; Roleda, 2016). For example, the growth rate of *Laminaria digitata* gametophytes was highest at 10–18°C, while gametogenesis required lower temperatures (i.e., 10–15°C), and fertilization and recruitment of sporophytes was optimal at only 5°C (Martins et al., 2017).

Considering the worst-case scenario of a temperature increase by 4°C until 2100 (Reay et al., 2007), and predictions of more extreme warming in some areas in the northern hemisphere, photosynthesis and growth of different life history stages, e.g., the microscopic spores and gametophytes, and the canopy-forming sporophytes, are unlikely to be negatively compromised. However, ocean warming can negatively affect kelp's asexual (sporogenesis) and sexual (gametogenesis) reproduction (Viejo et al., 2011; Bartsch et al., 2013; Roleda, 2016; Martins et al., 2017). The impacts of climate change on the reproduction (both sporogenesis and gametogenesis) and embryogenesis among macroalgae with complex life cycles require further studies.

Cold temperatures currently prevent the dominant seagrass in the northern hemisphere, *Zostera marina*, to extend its range further poleward into Arctic regions, like Svalbard and northern Greenland. While this plant can flower at temperatures as cold as 0.5–3°C, the development of mature fruits requires 2 months at 14–15°C (Silberhorn et al., 1983). In contrast, extremely warm temperatures, like other stresses, commonly induce flowering in plants (Wada and Takeno, 2010). Accordingly, the Mediterranean seagrass *Posidonia oceanica* responded to an experimental heat wave (27°C for 6 weeks) with an up to 47% increase in flowering-rate (Ruiz et al., in press). While sexual reproduction certainly provides the potential to escape from too warm regions, and to increase genetic and phenotypic diversity in this highly clonal plant, this potential can only be realized if the produced early life stages can successfully establish a new generation.

Early life stages of seagrass are comprised by seeds and seedlings, which can be defined as the single shoot germinated from seed prior to initiation of clonal growth. Evidence for temperature effects on seagrass germination is equivocal, as some authors report enhanced germination rates with increasing temperature (e.g., Hootsmans et al., 1987; Jinhua et al., 2011; Kaldy et al., 2015), whereas others report no effects of temperature within the ranges explored (e.g., Phillips et al., 1983; Loques et al., 1990), even if some of these contrasting results refer to germination experiments conducted with the same species. These contrasting results reflect either local adaptation to particular spring regimes or the fact that the response of seagrass seed germination to temperature is likely to be best represented by a Gaussian distribution, with minimal and maximum thermal tolerances and an optimum temperature for germination. Abe et al. (2009) determined that optimal water temperature for seed germination of a Japanese *Z. marina* stand was in the range from 10 to 15°C, with optimal temperature for seedling growth ranging from 20 to 25°C; and seedling mortality observed at water temperatures exceeding 28°C. Based on these results,

they predicted that *Z. marina* stands would be lost from areas exceeding maximum temperatures of 28°C (Abe et al., 2009), thereby leading to the expectation of losses with warming in the lower latitudinal limit of the species in Japan (Abe et al., 2009). Seed abortion following marine heat waves has been documented in *Posidonia* species, both in the Mediterranean (*P. oceanica*, Balestri and Cinelli, 2003) and Australia (*P. australis*, Shark Bay, Thomson et al., 2015).

Seedling performance is also negatively affected by extreme temperatures expected with further warming. Experimental simulated heat waves and warming at projected levels in the NW Mediterranean led to reduced growth, increased mortality, leaf necrosis, and respiration in *Posidonia oceanica* seedlings (Herman and Sultan, 2016; Guerrero-Meseguer et al., 2017), and also increased their susceptibility to consumption by grazers (Hernán et al., 2016). Likewise, experiments with *Z. japonica* seedlings showed a thermal limit of 29°C above which seedlings die (Abe et al., 2009), similar to the thermal limit for *P. oceanica* seedlings. Seagrass seedling mortality at temperatures around 30°C are likely to constrain the extant distribution of seagrasses (e.g., Abe et al., 2009), and their capacity to accommodate to future, warmer regimes.

Elevated CO₂ is believed to positively influence seagrasses, which are often CO₂ limited (Koch et al., 2013). This also applies to seedlings, as *P. oceanica* seedlings grown under elevated CO₂ improved photosynthetic performance, and developed larger carbon storage in belowground tissues, having thus more resources to tolerate and recover from stressors. However, elevated CO₂ also favors filamentous algae, which can overgrow seagrass seedlings, leading to reduced growth (Burnell et al., 2014). Moreover, lower N content and increased sucrose levels in seedlings growing under high pCO₂ lead to higher herbivory pressure (Hernán et al., 2016).

B3 Biotic Interactions—Increased Grazing Pressure

Indirect effects of rising temperatures are often mediated by biotic interactions. For macrophytes, increased grazing pressure is likely the most important indirect effect of the tropicalization of temperate seas as herbivores are progressively moving poleward (Vergés et al., 2014; Hyndes et al., 2016). Herbivore-induced shifts from productive kelp forests to turf substrate or barren grounds are already documented in the Mediterranean, Japan, and Australia (Vergés et al., 2014). For example, in a tropical-temperate transition zone in Eastern Australia, tropical herbivorous fishes contributed to the deforestation of kelp communities within ten years as sea surface temperature increased by 0.6°C (Vergés et al., 2016).

With rising temperatures, detrital-based food webs, supported by temperate seagrass ecosystems, are likely to turn into ones that are based on the direct consumption of seagrass (Lal et al., 2010; Kelkar et al., 2013; Hyndes et al., 2016). While few temperate species use seagrass as primary food source (Heck and Valentine, 2006), poleward-extending herbivorous fishes and macrograzers such as dugongs and marine turtles will likely have highest impact

on temperate seagrass meadows in the winter months, when low light levels limit growth (Hyndes et al., 2016).

In addition to the northward shift of tropical herbivores, temperate calcified herbivores are becoming more abundant with rising temperatures (Harley et al., 2012), and further increase grazing pressure on temperate macroalgae. For example, the loss in cover of the fucoid macroalga *Ascophyllum nodosum* in regions of Northern Ireland was accompanied by increases in limpet densities due to a series of mild winters since the 1980s (Davies et al., 2007). While even small herbivores, such as limpets, can graze down mature *A. nodosum* monocultures (Lorenzen, 2007), the species that are most susceptible to increased grazing are those with small generation times, as herbivores can prevent the nearly annual germling recruitment that these macroalgae depend on (Jenkins et al., 2005; Coleman et al., 2006; Hawkins et al., 2008; Bennett et al., 2015; Franco et al., 2015). However, how the contrasting effect of rising temperatures and ocean acidification on calcified herbivores will affect canopy-forming macroalgae, is yet poorly understood (reviewed in Harley et al., 2012).

While the impact of increased herbivory on temperate macrophytes will certainly be strong, it may be mitigated by epigenetic or microbiome shifts that affect defense mechanisms. Initial studies in terrestrial plants demonstrate that epigenetic variation can influence plant-herbivore interactions across generations (Herrera and Bazaga, 2011; Holeski et al., 2012; Latzel et al., 2012; Rasmann et al., 2012). Moreover, beneficial microbes have been shown to enhance defense against insect herbivores (Pangesti et al., 2013; Pieterse et al., 2014). In marine macrophytes, the potential for non-genetic rapid adaptation to increased herbivory is entirely unknown. Initial studies may focus on the correlation between epigenetic or microbiome variation and variation in compensatory growth (Vergés et al., 2008) or in defense chemicals, such as phlorotannins and phenolic compounds (Hay and Fenical, 1988; Arnold and Targett, 2002; Vergés et al., 2007).

C INTEGRATIVE MODELING—UNDERSTANDING THE PAST AND MODELING THE FUTURE

These plastic and evolutionary dimensions of seagrass and macroalgae performance under climate change are difficult to synthesize into a unifying concept/vision. The development of modeling tools able to incorporate relevant processes and parameters appears as a powerful tool to provide a holistic scenario and, thus, project climate change effects accounting for the diverse dimensions involved in seagrass and macroalgae production.

Nonetheless, numerical models of marine primary producers are still scarce in the scientific literature. Some of the first published models targeted phytoplankton productivity (Falkowski and Wirick, 1981); during the 90's with the global onset of coastal eutrophication, models of opportunistic macroalgal species growth (mostly *Ulva* spp.) became rather popular (Bendoricchio et al., 1993; Fong et al., 1997; Solidoro

et al., 1997; Martins and Marques, 2002). More recently, seagrass and kelp models are getting prominent due to the growing recognition of their important ecosystem services and the increasing need to preserve them (Elkalay et al., 2003; Plus et al., 2003; Koch et al., 2007; Ortiz, 2008; Downie et al., 2013; Young et al., 2015; Franco et al., 2018). Thus, from the analysis of published literature, it is possible to identify two fundamentally different but complementary modeling approaches that have been applied to study primary producers: species distribution models (SDMs) and productivity models.

Species distribution models, also called “Ecological Niche Models” (ENMs) (Guisan and Zimmermann, 2000; Kelly et al., 2001; Murphy and Lovett-Doust, 2007; Elith and Leathwick, 2009; Kearney et al., 2009), have been applied to seagrasses and macroalgae, aiming to predict species distribution and habitat suitability (Downie et al., 2013; Jueterbock et al., 2013; Assis et al., 2016b, 2017a,b; Neiva et al., 2016) or to unveil past species range shifts (Assis et al., 2016a,b; Neiva et al., 2016; Chefaoui and Serrão, 2017; Chefaoui et al., 2017). In general, results from SDM’s of temperate marine macroalgae predict that rising temperatures will cause massive die-offs along warm-temperate distribution limits and disclose new thermally suitable habitat in the Arctic (Müller et al., 2009; Jueterbock et al., 2013; Assis et al., 2017a). Besides projecting the distribution of species abundance, SDM’s can also identify the main drivers associated with the presence/absence of seagrasses and macroalgae across coastal and marine areas (Chefaoui and Serrão, 2017), genetic diversity hotspots of long-term persistence, adaptive potential for several species (Bellard et al., 2012; Beaumont et al., 2016; Chefaoui and Serrão, 2017; Chefaoui et al., 2017), estimate seagrass colonization area or the probability of successful restoration (Kelly et al., 2001).

For marine macrophytes, both kelp and seagrasses, temperature was generally identified as the most important range-limiting factor and, consequently, ocean warming as the most severe threat among other global climate drivers (Downie et al., 2013; Jueterbock et al., 2013; Assis et al., 2016b, 2017a,b; Neiva et al., 2016; Chefaoui et al., 2017). Nevertheless, macrophytes can be exposed to extreme temperatures along their distribution ranges, especially in the intertidal zone where desiccation can prevent cellular stress and allow persistence under temperatures beyond their thermal tolerances (Mota et al., 2015). Thus, site-specific and species-specific relevant processes must be accounted for in order to build accurate SDM’s of marine macrophytes and macroalgae (Assis et al., 2016b; Neiva et al., 2016). These models can give a first rough approximation of future distributions but they often do not take biological aspects or the eco-evolutionary responding potential of the focal species into account (but see Assis et al., 2016b).

Productivity models aim at describing the growth of algae and plants in a specific system, either through static (Eilers and Peeters, 1988) or dynamic (time-dependent) (Duarte and Ferreira, 1997) approaches, whereby the underlying mathematics is either empirical (Adams et al., 2017) or mechanistic (for a review see Macedo and Duarte, 2006). A major complication of the mechanistic approach is that its implementation requires extensive knowledge on the physiology and life history of the

modeled species. Indeed, these models can even account for different size-classes or population groups (Duarte and Ferreira, 1997; Martins et al., 2007), which will add realism to the model, though it can also increase model instability due to the high number of variables (Duarte and Ferreira, 1997). Dealing with this requires application of the parsimony rule to model complexity vs. data quality throughout the entire modeling process (Jørgensen, 1994).

Productivity models have provided sensible descriptions of standing stock variations of marine primary producers, assessed the sensitivity of parameters and projected variations for scenarios of climatic changes and other stressors (Duarte and Ferreira, 1997; Fong et al., 1997; Elkalay et al., 2003; Lirman and Cropper, 2003; Biber et al., 2004; Martins et al., 2007; Couto et al., 2014). Nonetheless, there is a generalized consensus that marine primary production models should aim for increasing accuracy of parameters, spatial discrimination and uncertainty quantification (Coffaro et al., 1997; Lirman and Cropper, 2003; Biber et al., 2004; Laufkötter et al., 2015).

Multi-model approaches have the potential to compensate the weaknesses and bias associated to a single type of model and can provide richer information regarding the system. The ultimate goal is to integrate information on species’ plasticity, adaptability, dispersal potential, and biotic interactions into a single forecasting approach (Moore et al., 2007; Lavergne et al., 2010). Although the need for an integrative approach is well recognized (Guisan and Thuiller, 2005; Guisan et al., 2006; Lavergne et al., 2010; Sinclair et al., 2010; Franco et al., 2018), implementation is largely unexplored and lacks consensus. Based on high-quality data retrieved from comprehensive environmental datasets (van Vuuren et al., 2011; Taylor et al., 2012; Tyberghein et al., 2012; Assis et al., 2017a) and empirical approaches (Franco et al., 2018), we propose a stepwise multi-model strategy that combines correlative SDMs with mechanistic productivity models into an integrative forecasting tool aimed at understanding changes at the ecosystem level. This multi-model approach comprises:

- Building SDMs to identify key environmental drivers for the distribution of seagrass/macroalgae, to predict sensitive areas where the species are threatened with extinction and robust areas for restoration;
- Developing productivity models for the dominant species incorporating species- and site-specific parameters identified in the previous step; these models should account for the spatial variability of the modeled area (e.g., depth, type of sediment, wave exposure) and the ecotypic differentiation of the focal species in terms of plastic and adaptive potential.

This stepwise modeling approach would provide dynamic and spatial explicit simulations of seagrass and macroalgal ecosystems coupled to an accurate evaluation of uncertainty at each stage of the modeling process (Larson et al., 2004). Implementing such a modeling framework is a challenging task that, nonetheless, is worthwhile trying as it will improve the power to predict range shifts and assessing species extinction risks under climate change. This is of paramount importance for an effective management of

marine primary producer habitats and derived ecosystem services.

Final Remarks

Seagrasses and macroalgae are in multiple ways at stake under the ongoing climatic changes. Physiological responses and the survivability of early life stages (both seeds and spores) are intrinsically connected to their genetic and epigenetic characteristics. Additionally, environmental changes affect the symbiotic relation between microbiome communities and their hosts. Biochemical changes in macrophytes can have severe impacts on trophic levels feeding on seagrass derived organic matter, including reduced energy transfer due to reduced carbon fixation, but also severe reduction of essential fatty acid production. In order to predict with a more holistic understanding the constraints to which these important foundation species will be subjected in the near future, the concept of niche stability in conventional modeling approaches should be widened by coupling physiological and ecological insights in primary productivity models and ecological niche models. Ideally, research on seagrasses and macroalgae should be multi-disciplinary, integrating genetic, epigenetic, and microbiome levels of intra-specific variation and ecotypic differentiation for a comprehensive understanding of phenotypic variation and more realistic scenarios of change that are essential for mitigation and conservation purposes (**Figure 1**).

AUTHOR CONTRIBUTIONS

IM and AJ wrote the section focusing modeling approaches. RR, AM, and BD prepared the section regarding the physiological impacts of climate change. MR and CD worked on the section

regarding the early life stages. The biogeographical gradients section was prepared GP and AJ. The epigenetics section was developed by TR and AJ. ES and AE focused on the microbiome section. BD gathered all the sections into this unified manuscript, supervised by all authors and specially by IC, JM, AJ, ES, and CD.

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