1

Seagrasses in an era of ocean warming: a review

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ABSTRACT

Seagrasses are valuable sources of food and habitat for marine life and are one of Earth's most efficient carbon sinks. However, they are facing a global decline due to ocean warming and eutrophication. In the last decade, with the advent of new technology and molecular advances, there has been a dramatic increase in the number of studies focusing on the effects of ocean warming on seagrasses. Here, we provide a comprehensive review of the future of seagrasses in an era of ocean warming. We have gathered information from published studies to identify potential commonalities in the effects of warming and the responses of seagrasses across four distinct levels: molecular, biochemical/physiological, morphological/population, and ecosystem/planetary. To date, we know that although warming strongly affects seagrasses at all four levels, seagrass responses diverge amongst species, populations, and over depths. Furthermore, warming alters seagrass distribution causing massive die-offs in some seagrass populations, whilst also causing tropicalization and migration of temperate species. In this review, we evaluate the combined effects of ocean warming with other environmental stressors and emphasize the need for multiple-stressor studies to provide a deeper understanding of seagrass resilience. We conclude by discussing the most significant knowledge gaps and future directions for seagrass research.

Key words: seagrasses, ocean warming, climate change, multiple-stressor studies, seagrass die-off, tropicalization, ocean solution, conservation, restoration

CONTENTS

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I. INTRODUCTION

(1) Global warming is happening at an alarming rate

Since the beginning of the industrial revolution in the mid-18th century, human activities have been continuously releasing billions of tons of CO_2 into the atmosphere (e.g. 10.4 billion tons in 2011). This has resulted in a massive increase in atmospheric CO_2 concentration from ∼280 ppm in the 1700s (Monastersky, 2013) to over 419 ppm at the beginning of 2021 (https://www.co2.earth/) contributing to the greenhouse effect (Anderson, Hawkins & Jones, 2016). This human-induced phenomenon has led to irreversible changes to the Earth's climate, with global warming the strongest consequence (Solomon et al., 2009; Shakun et al., 2012): the temperature of the Earth's surface increased by $0.61°C \pm 0.16°C$ between 1861 and 2000 (Keller, 2009). Exceeding the tipping point of $1.5°C$ above pre-industrial global temperature level is predicted to cause irreversible global-ecosystem shifts that will challenge the existence of millions of species, including humans (Masson-Delmotte et al., 2018; Lenton et al., 2019). Global warming is not only reflected by a pronounced upward trend in the average global temperature, but also by an increased frequency of extreme thermal events (i.e. heatwaves) (Meehl & Tebaldi, 2004; Christidis, Jones & Stott, 2015). For instance, the European heatwave of 2003 was one of the most significant examples of such abnormal climatic events with extremely hot and dry weather causing widespread environmental, economic, and social consequences (Schär & Jendritzky, 2004).

Covering over 70% of the Earth's surface, the ocean plays a fundamental role in the Earth's climate, and is a habitat for an estimated 50–80% of all life on Earth. Global warming is also affecting the ocean, which is warming at an alarming rate, especially in coastal areas, where the temperature increase has been reported as $0.17°C \pm 0.11°C$/decade (Liao et al., 2015). In semi-closed seas (e.g. the Red Sea and the Mediterranean Sea), the rate is even faster (Nguyen et al., 2020b).

In the sea, thermal conditions are more stable than on land (except for the intertidal zone). Recent studies have documented a rapid rise in the occurrence of extreme climatic events in the ocean, known as marine heatwaves (MHWs) (Oliver et al., 2018). MHWs are extreme warm periods that last for at least 5 days with a temperature level exceeding the 90th percentile, based on three-decade historical baseline temperature values (Hobday et al., 2016). Ocean warming, and especially MHWs, is already having catastrophic consequences in coastal benthic communities worldwide (Coma et al., 2009; Harley et al., 2012; Wernberg et al., 2016). Indeed, the impact of MHWs is of more concern than the increase in average seawater temperature, because organisms are generally more vulnerable to sudden temperature changes than to progressive ones (Smale et al., 2019). Thus, MHWs may trigger destructive chronic impacts on marine creatures that can result in shifts in species distributions and even local extinctions (Easterling et al., 2000).

(2) Seagrasses are being impacted by ocean warming

Seagrasses are a unique group of angiosperms that recolonized the marine realm 60–90 million years ago on at least three occasions (Les, Cleland & Waycott, 1997). To overcome the numerous challenges presented by a submerged

lifestyle in the marine environment, seagrasses have developed a range of specialized adaptive characteristics (Invers, Perez & Romero, 1999; Borum *et al.*, 2007; Wissler *et al.*, 2011; Hogarth, 2015; Olsen *et al.*, 2016). Consisting of a surprisingly small number of species (∼60–70 species in total), seagrasses are distributed across thousands of kilometres of sedimentary shorelines from sub-Artic to tropical regions (Short *et al.*, 2007). They provide highly valuable socio-economic services, including primary productivity, organic carbon sequestration and burial, as well as sediment stabilization (Orth *et al.*, 2006; Fourqurean *et al.*, 2012; Bertelli & Unsworth, 2014; Unsworth, Nordlund & Cullen-Unsworth, 2019). They also provide nursery habitats for fish and a diversity of marine organisms (e.g. invertebrates). Seagrasses represent one of the most valuable ecosystems on Earth with an estimated value of $1.9 trillion per annum (Waycott *et al.*, 2009; Costanza *et al.*, 2014). Furthermore, they have been acknowledged as one of Earth's most efficient carbon sinks, and are listed as one of the potential solutions to mitigate CO_2 emissions and ultimately to address the threat of global warming (Gattuso *et al.*, 2018).

Despite their critical value, they are suffering a global decline, driven mainly by the growing number of pressures linked directly to human activities (e.g. ocean warming, coastal modification, water quality degradation) (Orth *et al.*, 2006; Waycott *et al.*, 2009). Globally, seagrasses are disappearing at an alarming rate of 110 km^2 per annum, resulting in a cumulative loss of 29% of the total world seagrass population by the end of 2006 (Waycott *et al.*, 2009). The total population of *Posidonia oceanica*, for example, a seagrass species endemic to the Mediterranean Sea, has decreased by 13–50% since the mid-nineteenth century (Telesca *et al.*, 2015). However, the rate of seagrass loss, at least at a regional scale, seems to have been reduced as a result of the implementation of management plans, such as European environmental protection measures (de los Santos *et al.*, 2019).

A recent study listed seagrasses as one of the habitat-forming species that are likely to disappear as a consequence of climate change (Trisos, Merow & Pigot, 2020). Seagrass die-offs, as a consequence of MHWs, have been reported for different species, including *P. oceanica* (Marbà & Duarte, 2010), *Zostera marina* (Reusch *et al.*, 2005; Jarvis, Brush & Moore, 2014), and *Amphibolis antarctica* (Seddon, Connolly & Edyvane, 2000; Arias-Ortiz *et al.*, 2018; Strydom *et al.*, 2020). The observed mass mortality of several seagrass populations after extreme MHWs (Arias-Ortiz *et al.*, 2018; Strydom *et al.*, 2020) and the projected warming trend for the next decades has motivated the prediction of a functional extinction of seagrass meadows in the near future (Marbà & Duarte, 2010; Jordà, Marbà & Duarte, 2012; Chefaoui, Duarte & Serrão, 2018). Interestingly, while MHWs have already caused extensive local extinction of seaweed species across hundreds of kilometres (Smale, 2020), the comparative effects on seagrasses might appear to be smaller. This suggests that further research investigating the mechanisms driving potential differences in the resilience between seagrasses and other marine macrophytes is clearly needed.

(3) Why is this review timely?

The recent application of advanced molecular technologies in seagrass research (see review by Davey *et al.*, 2016) together with the implementation of controlled laboratory manipulations have enabled rapid progress in the understanding of seagrass responses to changing environments (Egea *et al.*, 2019; Saha *et al.*, 2019). Moreover, the availability of the first two sequenced seagrass genomes, for *Z. marina* (Olsen *et al.*, 2016) and *Zostera muelleri* (Lee *et al.*, 2016), has enhanced seagrass molecular research.

Over the last decade, there has been a rapid increase in the number of studies documenting the impact of warming on seagrasses as well as the responses of seagrasses to this environmental challenge (Fig. 1). These studies have investigated the response of seagrasses to warming at the biological level (i.e. biochemical, physiological and morphological), and also at the molecular, population and even ecosystem/planetary level (Fig. 1). A review on the effects of warming on seagrasses is timely since: (*i*) ocean warming is occurring at an alarming rate and will continue to have strong impacts on seagrasses in the future; (*ii*) a substantial amount of information on the effects of warming on seagrasses has become available recently; and (*iii*) there is no comprehensive review on the effects of ocean warming on seagrasses [but see Bulthuis, 1987; Lee, Park & Kim, 2007a; Koch *et al.*, 2013; Duarte *et al.*, 2018]. This review focuses on the effects of warming on seagrasses across different functional levels (molecular, biochemical/physiological, morphological/population and ecosystem/planetary), describes the effects of warming on seagrasses in combination with other stressors (e.g. salinity, light, etc.), and suggests future research directions to close knowledge gaps in our understanding of seagrass resilience in a changing climate.

II. EFFECTS OF WARMING ON SEAGRASSES

(1) Effects of warming and seagrass responses at the molecular level

In the face of rapid ocean warming, it is critically important to predict the future responses of seagrasses in order to develop mitigation strategies to prevent their loss through effective management, conservation, and restoration. The molecular basis of seagrass responses to a warming ocean can uncover seagrass traits that can be correlated to the persistence of that species under changing climatic conditions (Procaccini, Olsen & Reusch, 2007; Reusch & Wood, 2007). Innovative molecular experiments in parallel with routine physiological/morphological measurements can provide early warning measures to detect changes in the ecological status of seagrass meadows well before any
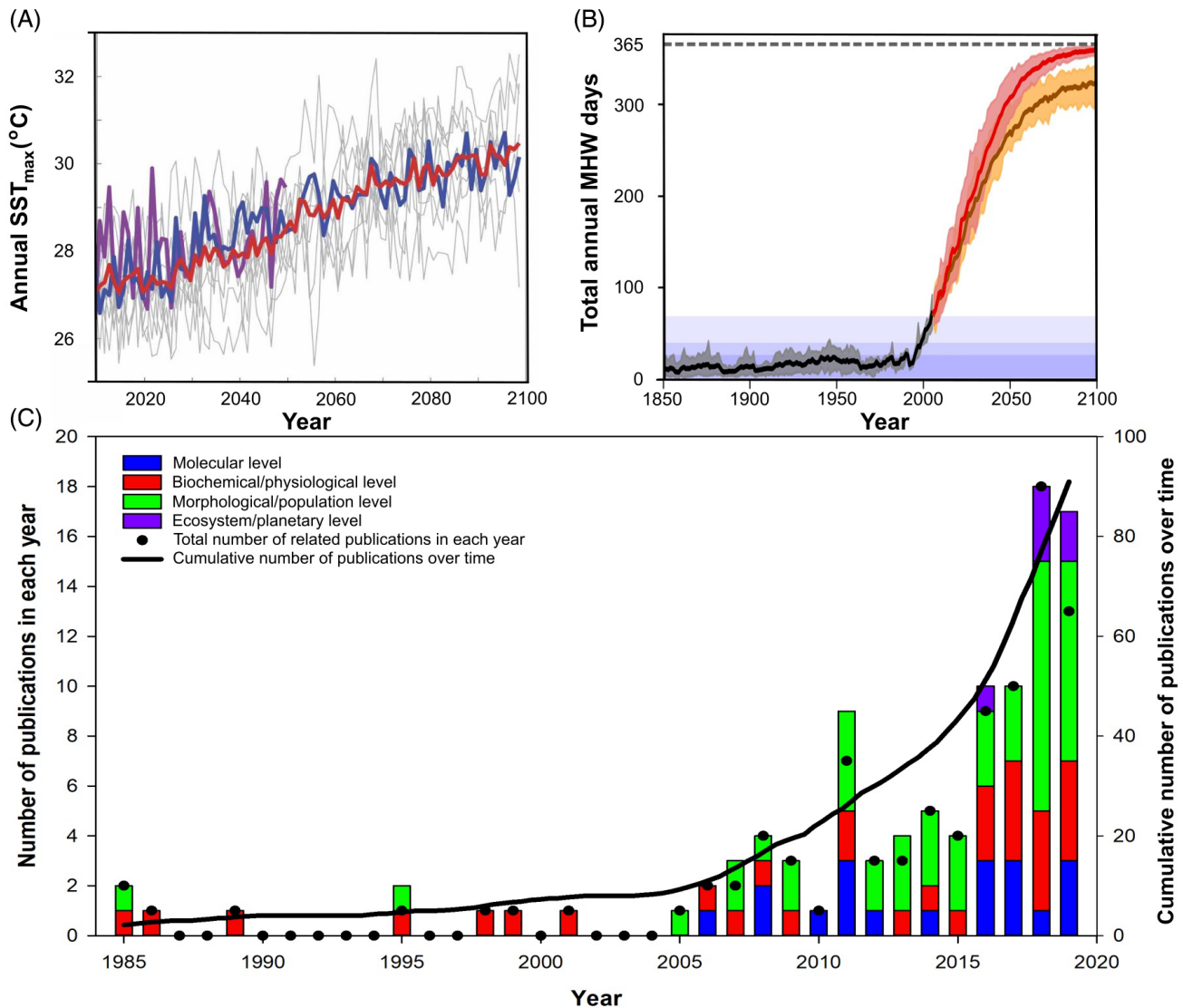
Fig 1. Ocean warming and thermal-related studies in seagrasses. (A) Increase in sea surface temperature (SST_{max}) over this century adapted from Jordà *et al.* (2012). Grey lines show the outputs of single general (atmospheric-ocean general circulation models) models; purple and blue lines show the outputs of PROTHEUS and VANIMEDAT2 (regional) models, respectively; the red line is the ensemble average (Jordà *et al.*, 2012). (B) Increase in the number of annual marine heatwave (MHW) days from 1950 to present, and predicted values to 2100, adapted from Oliver *et al.* (2019). Annual time series for historical (black), RCP4.5 (brown; which assumes anthropogenic greenhouse gas emissions peak in the year 2040 and then stabilize at a radiative forcing of 4.5 W m^{-2}), and RCP8.5 (red; which assumes these emissions continue to rise throughout the 21st century with radiative forcing reaching 8.5 W m^{-2} by the end of the century) runs. The grey, red, and brown shaded regions indicate the maximum range between individual model runs. The blue shaded areas present the expected range of natural variability based on a 66% confidence interval (darkest blue), 95% confidence interval (medium blue), and full min-to-max range (lightest blue) of the historicalNat (which represents historical conditions without anthropogenic influence where models are forced by natural volcanic and solar forcing only, with greenhouse gases and aerosols held at pre-industrial levels, spanning 1850–2005) runs (Oliver *et al.*, 2019). (C) Number of publications related to thermal stress studies in seagrasses from 1985 to 2020 across four different levels: molecular (blue), biochemical/physiological (red), morphological/population (green), and ecosystem/planetary (purple). Data were collected from *Google Scholar* using the key words "seagrass thermal stress", "seagrass heat stress", "seagrass temperature" and "seagrass warming" together with personal knowledge from the authors.

signs of mortality appear (Procaccini *et al.*, 2007; Pernice *et al.*, 2015; Schliep *et al.*, 2015; Ceccherelli *et al.*, 2018). The extensive application of gene expression studies (transcriptomics) over the last decade (Davey *et al.*, 2016) and the

availability of two seagrass genomes, *Z. marina* (Olsen *et al.*, 2016) and *Z. muelleri* (Lee *et al.*, 2016), have greatly fostered our understanding of seagrass responses to environmental changes at the molecular level (see Fig. 1C). We are

now much closer to integrating the fields of seagrass ecophysiology and ecological genomics, as anticipated almost a decade ago (Procaccini *et al.*, 2012).

To date, gene expression studies (quantitative reverse transcription polymerase chain reaction and RNA sequencing) have been conducted for only a handful of seagrass species. Large transcriptomic differences observed in seagrasses that had recovered from long-term acute temperature stress (3 weeks at 26°C) identified transcriptomic resilience as a predictor of thermal adaptation (Franssen *et al.*, 2011; Jueterbock *et al.*, 2016). Other studies found different transcriptomic responses to short-term acute stress (5 days, 32°C), leading to the identification of molecular mechanisms involved in maintaining photosynthetic stability and respiratory acclimation of seagrasses under heat stress (Marín-Guirao *et al.*, 2017). Investigations of the responses of seagrasses to thermal stress have revealed some interspecific similarities (see Fig. 2), comparable to those observed in the heat response of terrestrial plants, including refolding of proteins, activation of oxidative-stress defence, and cell wall fortification (Franssen *et al.*, 2011, 2014; Gu *et al.*, 2012; Jueterbock *et al.*, 2016; Marín-Guirao *et al.*, 2016, 2017).

(a) Heat shock proteins

Seagrasses have developed several sophisticated molecular mechanisms to respond to environmental triggers. Among these mechanisms, the production of chaperones, especially heat shock proteins (HSPs) are among the most important. HSPs are common proteins found in both plants and animals. They play fundamental roles in cells under normal and stressed conditions, including roles in protein folding, assembly, translocation, and protein degradation (Vierling, 1991; Kiang & Tsokos, 1998; Park & Seo, 2015). Under stressful conditions, HSPs can either help to fix non-functional/partly denatured proteins or remove degraded/damaged proteins (Sørensen, Kristensen & Loeschcke, 2003).

Multiple studies have highlighted the role of molecular chaperones (especially HSPs) in seagrass responses to warming (Reusch *et al.*, 2008; Bergmann *et al.*, 2010; Franssen
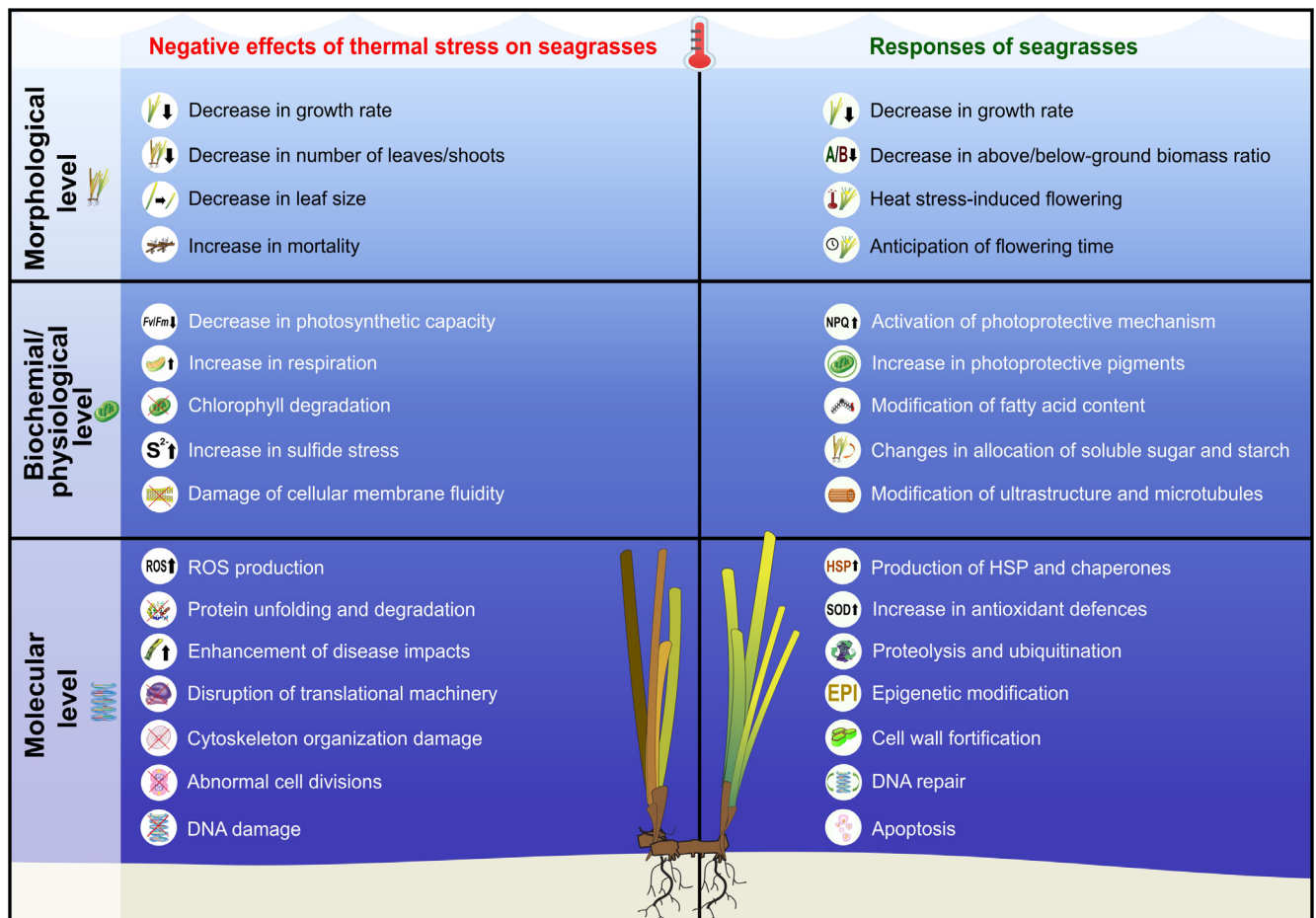

Fig 2. Common effects and responses of thermal stress on seagrasses at the molecular, biochemical/physiological and morphological level. HSP, heat shock protein; ROS, reactive oxygen species.

et al., 2011, 2014; Massa et al., 2011; Gu et al., 2012; Marín-Guirao et al., 2016, 2017; Malandrakis et al., 2017; Tutar et al., 2017; Traboni et al., 2018; Purnama et al., 2019; Nguyen et al., 2020b). HSP70 and HSP90 are the best studied chaperones in seagrasses. In terrestrial plants, heat shock factors (HSFs) act as transcriptional activators of HSPs and some have a critical role in plant thermal tolerance (Qu et al., 2013). It remains mostly unclear whether HSFs have the same role in seagrasses compared with terrestrial plants, although some of these genes have been shown to be responsive in at least two seagrass species (Zostera noltii and P. oceanica) when exposed to rapid and severe heat stress (Massa et al., 2011; Marín-Guirao et al., 2016).

(b) Oxidative stress

Oxidative stress, generated by the enhanced production of reactive oxygen species (ROS) under increased temperatures, is a common secondary stress response in plants (Hasanuzzaman, Nahar & Fujita, 2013). Gene expression studies in different seagrass species strongly support the involvement of genes encoding ROS-scavengers, indicating the production of ROS in seagrasses during thermal stress (Reusch et al., 2008; Winters et al., 2011; Gu et al., 2012; Liu et al., 2016; Marín-Guirao et al., 2017; Tutar et al., 2017; Purnama et al., 2019). In seagrasses, superoxide dismutase (SOD) and ascorbate peroxidase (APX) appear to be among the most active ROS-scavenging enzymes under heat stress (Reusch et al., 2008; Winters et al., 2011; Liu et al., 2016; Marín-Guirao et al., 2017; Purnama et al., 2019). These enzymes have been shown to inhibit free radicals and ROS (Teotia & Singh, 2014).

Using a metabolomics approach, Gu et al. (2012) detected myo-inositol among the three most responsive metabolites to oxidative stress in two seagrass species (Z. marina and Z. noltii) subjected to heat stress. In terrestrial plants, myo-inositol is important in the galactinol and raffinose biosynthetic pathways that have been characterized as osmoprotectants. These osmoprotectants can function as scavengers of ROS (Nishizawa, Yabuta & Shigeoka, 2008) whereas myo-inositol alone has been found to increase the midpoint denaturation temperature of proteins (Ortbauer & Popp, 2008).

(c) Other molecular responses

Apart from HSPs and ROS-scavenging proteins, other mechanisms by which seagrasses respond to warming have been discovered in recent molecular studies. Gu et al. (2012) on Z. marina and Traboni et al. (2018) on P. oceanica revealed the involvement of ubiquitination and proteolysis in response to thermal stress, indicative of severe protein damage as a consequence of elevated temperature. In terrestrial plants, ubiquitin-mediated proteolysis is a multi-step process that identifies, labels, and destroys damaged proteins. It is the principal mechanism of protein catabolism to facilitate plant proteostasis when

exposed to stressful conditions (reviewed by Stone, 2014). The cell wall is fundamentally important for the survival and development of plants as it provides a structural framework and is the first line of defence against pathogens. Moreover, cell wall modification can enhance plant responses to many environmental stressors (reviewed by Houston et al., 2016). In seagrasses, transcriptomic studies revealed higher expression of cell wall-related genes in plants exposed to thermal stress, suggesting the potential involvement of cell wall fortification in the thermal stress response as in terrestrial plants (Gu et al., 2012; Franssen et al., 2014; Jueterbock et al., 2016; Marín-Guirao et al., 2017, 2019).

Warming can have detrimental effects on the translational machinery of seagrasses, by limiting the availability of associated molecular components (Malandrakis et al., 2017) with destructive consequences on the organization of the cytoskeleton (Massa et al., 2011; Malandrakis et al., 2017; Tutar et al., 2017) which can in turn damage cell division processes (Malandrakis et al., 2017; Marín-Guirao et al., 2017). Furthermore, warming can diminish the expression of pathogen defence genes, thereby potentially enhancing susceptibility to disease (Jueterbock et al., 2016) although experimental evidence to date suggests the contrary (see Section II.5f). Given the past massive die-off of seagrass meadows due to 'wasting disease' (Orth et al., 2006), the combined effects of warming and disease deserve further investigation.

Warming causes damage to DNA and protein structure (e.g. protein unfolding, protein degradation) in seagrasses, resulting in homeostatic cell imbalance and cell death (Franssen et al., 2011; Tutar et al., 2017). Under severe conditions, seagrasses activate apoptotic pathways by upregulating expression levels of genes involved in the programmed cell death process aimed at eliminating irreparably damaged cells (Massa et al., 2011; Tutar et al., 2017; Traboni et al., 2018). This apoptotic mechanism is also connected with the production of HSPs (Beere, 2005).

(d) Intraspecific differences in molecular responses to warming amongst seagrass populations from different thermal origins

Seagrass populations from different thermal origins respond differently to warming. Plants living in more fluctuating and/or warmer environments are more resilient to warming than those from colder and/or more stable thermal environments. Examples include Z. marina from different latitudes (Bergmann et al., 2010; Franssen et al., 2011; Winters et al., 2011; Jueterbock et al., 2016; Jahnke et al., 2019), P. oceanica from different depths (Marín-Guirao et al., 2016, 2017; Procaccini et al., 2017; Tutar et al., 2017) and latitudes (Marín-Guirao et al., 2019), and Halophila stipulacea from the Red Sea and Mediterranean Sea (Nguyen et al., 2020b). Plants from warm environments (i.e. Z. marina from southern populations and P. oceanica from shallow meadow stands) activate a more complete (i.e. higher number of up-regulated genes) and intense (i.e. stronger activation of heat-responsive genes) transcriptomic response than plants from cold

environments (*Z. marina* from northern populations, *P. oceanica* from deep-water populations) (Franssen *et al.*, 2014; Marín-Guirao *et al.*, 2017). Plants with a 'warmer thermal history' also showed higher constitutive levels of heat-responsive genes, likely reflecting their local (pre-)adaptation to warmer and more stressful thermal conditions. Higher constitutive expression levels of heat-responsive genes have been associated with a pre-adaptive defence strategy that confers higher thermal tolerance to cope with frequent heat stress in several marine organisms, including corals and marine gastropods (Barshis *et al.*, 2013; Gleason & Burton, 2015). While plants from southern and northern European populations of *Z. marina* reacted similarly to acute heat stress (Franssen *et al.*, 2011), they differed in their global transcriptome recovery after the temperature returned to 'normal'. This phenomenon is known as transcriptomic resilience and may be part of a more universal indicator of whether or not plants can endure critical temperatures or other stressor levels.

(e) Epigenetic modification

Studies regarding epigenetic modifications are now emerging in the field of seagrass molecular biology (Jueterbock *et al.*, 2020; Nguyen *et al.*, 2020a). Epigenetic modifications are molecular modifications that alter gene expression in response to internal (e.g. ontogenetic processes) or external (e.g. environmental changes) triggers, without changes in the underlying DNA sequence (Bossdorf, Richards & Pigliucci, 2008). Epigenetic modifications are inherited through mitosis in most cases, but are also transmittable to the next generation. While epigenetic modifications have been widely studied in terrestrial plants (Chinnusamy & Zhu, 2009; Kinoshita & Seki, 2014; Liu *et al.*, 2015), only a few studies have investigated epigenetic responses to warming in seagrasses (Ruocco *et al.*, 2019a,b; Jueterbock *et al.*, 2020; Nguyen *et al.*, 2020a; L. Entrambasaguas, M. Ruocco, K.J.F. Verhoeven, G. Procaccini & L. Marín-Guirao, in preparation). Some transcriptomic data sets suggest the involvement of epigenetic modification in the responses of seagrasses to thermal stress (Marín-Guirao *et al.*, 2017; Marín-Guirao *et al.*, 2019; Jueterbock *et al.*, 2020). For example, in *P. oceanica*, heat-tolerant plants showed higher expression of epigenetic-related genes (Marín-Guirao *et al.*, 2017, 2019). Stress-induced epigenetic mechanisms are crucial in the activation of the immediate stress response and favour both short- and long-term adaptation, due to their important role in regulating the expression of stress-related genes (Liu *et al.*, 2015). Increased knowledge on the epigenetic responses of plants to environmental changes in terrestrial systems (Molinier *et al.*, 2006; Feng & Jacobsen, 2011; Kinoshita & Seki, 2014; Wang *et al.*, 2016), and the possible application of more advanced molecular technologies (Kurdyukov & Bullock, 2016; Van Wesenbeeck *et al.*, 2018) may stimulate further study of epigenetic modification in seagrasses.

(2) Effects of warming and seagrass responses at the physiological/biochemical level

Biochemical and physiological response to thermal stress in seagrasses have been studied extensively since the 1990s (Fig. 1C), with earlier studies summarized in previous reviews (Bulthuis, 1987; Lee *et al.*, 2007a; Koch *et al.*, 2013). Thermal stress tends to inhibit photosynthetic activity while simultaneously enhancing respiration. Recent findings suggest that extreme temperature changes could cause the degradation of chlorophyll as well as affecting the fluidity of the cellular membrane, among other impacts. In response to thermal stress, seagrasses tend to activate protective mechanisms such as the accumulation of photo-protective pigments and modification of fatty acid contents (see Fig. 2).

(a) Physiological responses

Warming affects seagrass physiological and metabolic processes including photosynthesis and respiration (Bulthuis, 1987; Lee *et al.*, 2007a). Under mild temperature increments, photosynthetic rate increases, likely due to an increase in membrane fluidity that improves the mobility of photosynthetic proteins embedded within the thylakoid membrane (e.g. the plastoquinone pool). Other factors, such as temperature-enhanced enzyme activity, may also play a role. Further temperature increases, however, reduce photosynthetic rate due to factors such as the detachment of functional proteins from the thylakoid membrane (e.g. PSII antenna, oxygen-evolving complex) and the inactivation of Rubisco (Sharkey, 2005; Allakhverdiev *et al.*, 2008).

The optimal temperature for photosynthesis differs between tropical (27–33°C) and temperate (21–32°C) seagrasses (Lee *et al.*, 2007a). Beyond this optimal window, warming negatively alters the functioning of the photosynthetic apparatus. The reaction centre of photosystem II (PSII) is one of the most thermally sensitive components together with processes driving the electron transport chain, stromal enzymes, PSI activity, and chloroplast envelopes. Damage to PSII due to thermal stress can cause a reduction of effective quantum yield and maximum quantum yield, due to a significant increase in minimum fluorescence level (F_0) (Marín-Guirao *et al.*, 2016, 2017, 2018; Nguyen *et al.*, 2020a,b). In terrestrial plants, an increase in F_0 is one of the clearest indications of PSII inactivation due to thermal stress (Allakhverdiev *et al.*, 2008). The key enzymes of the carbon fixation cycle (Rubisco and Rubisco activase) are also highly sensitive to heat stress, as a secondary consequence of disruptions in the thylakoid membrane (Salvucci & Crafts-Brandner, 2004), thereby disturbing carbon fixation (Marín-Guirao *et al.*, 2016). Extreme thermal stress can result in degradation of photosynthetic pigments (Chl *a* and Chl *b*) together with the accumulation of chlorophyll degradation products (pheophytin *a* and pheophytin *b*), further reducing photosynthetic capacity (Repolho *et al.*, 2017; Beca-Carretero *et al.*, 2018b; Nguyen *et al.*, 2020a,b). Seagrasses commonly activate a photo-protective mechanism associated

with xanthophyll cycle pigments to deal with excess energy in the photosynthetic apparatus resulting from heat-stress-associated photosynthetic inhibition (Marín-Guirao *et al.*, 2016; Ontoria *et al.*, 2019*a*). This mechanism is linked with increased concentrations of the photo-protective pigments zeaxanthin, antheraxanthin, and violaxanthin (York *et al.*, 2013).

Plants with a history of high thermal fluctuation, or grown in warmer waters show less photosynthetic thermal-induced damage than those from colder origins or more stable temperature regimes [e.g. *P. oceanica* (Marín-Guirao *et al.*, 2016, 2017, 2018); *Cymodocea nodosa* (Marín-Guirao *et al.*, 2018); *H. stipulacea* (Nguyen *et al.*, 2020*b*); *Cymodocea serrulata*, *Halodule uninervis* and *Z. muelleri* (Collier *et al.*, 2017)]. Additionally, it has recently become evident that leaf tissues of different age exhibit variable thermal plasticity and activate different strategies to withstand heat stress (Ruocco *et al.*, 2019*a*).

In *P. oceanica*, the strong induction of a complete set of genes encoding functional and structural proteins of the thylakoid electron transport chain may be part of the molecular mechanisms underlying the enhanced photosynthetic stability of seagrasses in response to heat stress (Marín-Guirao *et al.*, 2017). This strong transcriptomic reprogramming could favour the turnover of relevant parts of the photosynthetic apparatus, enabling correct electron flow and thus protecting the thylakoid membranes from heat impairment.

Together with impacts on photosynthesis, warming enhances respiration rates in seagrasses resulting in a carbon imbalance (Lee *et al.*, 2007*a*; Marín-Guirao *et al.*, 2016, 2018; Yaping *et al.*, 2019). In most cases, the respiration rate of the above-ground part of the plant is higher in comparison to the below-ground parts (Collier *et al.*, 2017). The increase in above- to below-ground biomass ratio during thermal stress seen in many seagrass species may represent a defensive mechanism to lower the impact of thermal-induced elevated respiration (Collier, Uthicke & Waycott, 2011; Olsen *et al.*, 2012; Marín-Guirao *et al.*, 2018).

(b) Biochemical responses

Modification of cell membrane fluidity is a common response of plants under stressful conditions including thermal stress. When exposed to increased temperatures, the viscosity of the lipid bilayer of cell membranes changes, leading to increased membrane fluidity, which can potentially affect the function of molecules embedded in or attached to the membrane (e.g. the water-splitting complex bonded to the thylakoid membrane). The ability to adjust the fatty acid content and composition of cell membranes plays a central role in the modification of membrane fluidity to cope with temperature changes. An increase in saturated fatty acid content makes the membrane less fluid and more stable under increased temperatures (Gaur & Sharma, 2014). Seagrasses can increase the amount of saturated fatty acid and decrease the number of unsaturated fatty acids, thus maintaining membrane fluidity in response to thermal stress (Beca-Carretero *et al.*, 2018*a*). Beca-Carretero *et al.* (2018*a*) showed

that (*i*) seagrasses from a warm climate (southwest Mediterranean) were able to adjust their lipid components rapidly in response to rising temperatures compared with their counterparts from the colder northwest Mediterranean, and (*ii*) the fast-growing *C. nodosa* had a greater capacity to manipulate its lipid components compared with the slow-growing *P. oceanica*. Furthermore, modification of lipid content, ultrastructure, and microtubule organization all play an important role in stabilizing cell membrane fluidity under thermal stress conditions (Koutalianou, Orfanidis & Katsaros, 2016).

In thermal stress conditions, most terrestrial plants increase the storage of soluble and insoluble (starch) sugars to maintain a stable energy supply, membrane function, and to reduce the impact of increased respiration rates (Guy *et al.*, 2007). Similarly, both tropical (*Halodule wrightii* and *Thalassia testudinum*; Koch *et al.*, 2007) and temperate seagrasses (*P. oceanica* and *C. nodosa*; Marín-Guirao *et al.*, 2018) significantly increased their sugar content in response to increased water temperature. Only the plants from warm regions were able to re-allocate additional carbohydrate content from leaves (higher respiration rate) to rhizomes (lower respiration rate). This mechanism reduces the negative impact of thermal-enhanced respiration, allowing the plants to survive better under elevated thermal stress (Marín-Guirao *et al.*, 2018). A comparison of the results from Koch *et al.* (2007) and Marín-Guirao *et al.* (2018) show that the tropical seagrasses *H. wrightii* and *T. testudinum* were better able to manage respiration stress through manipulation of carbohydrate content compared with the temperate species *C. nodosa* and *P. oceanica*.

(3) Effects of warming and seagrass responses at the morphological/population level

(a) Morphological responses

Warming has a strong effect on seagrass growth rates (Collier *et al.*, 2011; Olsen *et al.*, 2012; Collier & Waycott, 2014; Hammer *et al.*, 2018; Marín-Guirao *et al.*, 2018; Kim *et al.*, 2019; Nguyen *et al.*, 2020*a*,*b*), leaf traits (York *et al.*, 2013; Nguyen *et al.*, 2020*b*), and leaf/shoot number (Mayot, Boudouresque & Leriche, 2005; Nejrup & Pedersen, 2008; Beca-Carretero *et al.*, 2018*b*; Nguyen *et al.*, 2020*b*). While modification of the above-ground part can result in a reduction of above- to below-ground biomass ratio (York *et al.*, 2013; Collier *et al.*, 2017; Marín-Guirao *et al.*, 2018), warming can also increase the above- to below-ground biomass ratio in fast-growing seagrass species (see Collier *et al.*, 2011; Marín-Guirao *et al.*, 2018), reducing the biomass of non-photosynthetic (below-ground) tissues and increasing photosynthetic biomass to offset the negative impacts of heat stress-enhanced respiration (see also Fig. 2).

(b) Population responses

In response to ocean warming, seagrass meadows can acclimatize or adapt to environmental changes (i.e. acclimation/
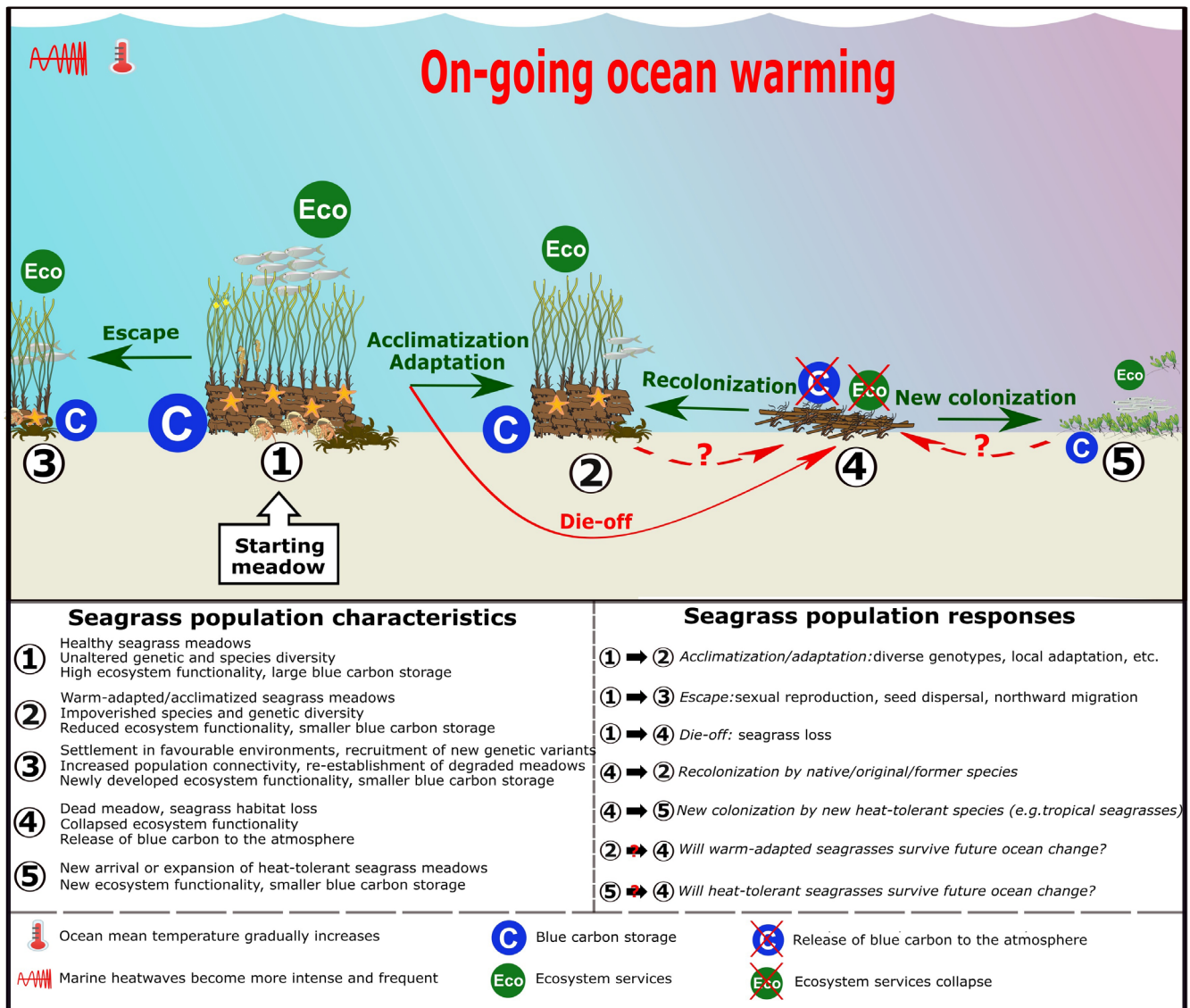
Fig 3. Conceptual diagram summarizing the fate of seagrass populations under conditions of ocean warming as illustrated by *Posidonia oceanica* in the Mediterranean Sea. Blue carbon is the carbon stored in coastal and marine ecosystems.

adaptation: 1 → 2 in Fig. 3). Seagrass meadows that normally experience large fluctuations in environmental parameters such as temperature, light, etc. are more likely to be able to survive ocean warming (Massa *et al.*, 2009; Collier *et al.*, 2011; Marín-Guirao *et al.*, 2018; Soissons *et al.*, 2018). In addition, the resilience of seagrass meadows depends on the genetic diversity of the population (Williams, 2001; Hughes & Stachowicz, 2004; Ehlers, Worm & Reusch, 2008). There is some evidence of local adaptation both in adjacent and distant meadows, and therefore it is difficult to generalize the effects observed in specific populations (Jueterbock *et al.*, 2016; Marín-Guirao *et al.*, 2016, 2018).

In monospecific populations, plant responses to warming can be delayed and can be genotype specific (Reynolds *et al.*, 2016a). During this recovery phase, the genotypic

diversity of natural populations determines their resilience to MHWs in term of both the immediate response and recovery (Reusch *et al.*, 2005; Ehlers *et al.*, 2008). In meadows composed of different species, co-occurring species can change in relative abundance due to different heat sensitivities (Richardson, Lefcheck & Orth, 2018) or differ in their ability to recover and recolonize after the perturbation (Nowicki *et al.*, 2017). These changes can affect the structure and function of seagrass ecosystems and their resilience. Ocean warming usually favours small- and medium-sized species at the expense of larger species, reduces meadows structure, and decreases function and resilience as seen in the case of the small seagrass *H. stipulacea* (Winters *et al.*, 2020).

Warming can also alter flowering in seagrasses, thus providing an escape mechanism through sexual reproduction

and seed dispersal (escape in space and time: 1➔3 in Fig. 3). Warming induces flowering in some species (Diaz-Almela, Marbà & Duarte, 2007; Ruiz *et al.*, 2018) and advances the onset of flowering in other cases (Blok, Olesen & Krause-Jensen, 2018; Marín-Guirao *et al.*, 2019). In the case of the clonal and long-lived *P. oceanica*, flowering has been linked to a heat stress response with potential adaptive consequences (Marín-Guirao *et al.*, 2019). Through sexual reproduction, warming induces an increase in genetic diversity of seagrass populations, thus potentially sustaining the resilience of that seagrass meadow (Massa *et al.*, 2009; Collier *et al.*, 2011; Marín-Guirao *et al.*, 2018; Soissons *et al.*, 2018). Sexual reproduction provides seagrasses with an escape mechanism not only in space, but also in time. In some seagrass species, their seeds have a resting stage, which can last up to 2 years (e.g. *Zostera*, *Halodule* and *Syringodium*; reviewed by Orth *et al.*, 2000). In other species, seagrass seeds can be dispersed over long distances by floating fruits (e.g. up to 55 km for for *P. australis*; Ruiz-Montoya *et al.*, 2012) or by mega-herbivores like dugongs (*Dugong dugon*) and green sea turtles (*Chelonia mydas*) which can help to spread seagrass seeds as far as 650 km away from the parental plants (Tol *et al.*, 2017). These dormancy and dispersal mechanisms can potentially provide an avenue of escape for seagrasses from other environmental stressors.

In some cases, when the environmental temperatures are too extreme, they can be deleterious (i.e. die-off: 1 ➔ 4 in Fig. 3). Massive die-offs of seagrasses due to ocean warming, especially after MHWs, have been reported recently (Marbà & Duarte, 2010; Arias-Ortiz *et al.*, 2018; Strydom *et al.*, 2020). Increased mortality due to warming has been observed in adult plants and also in seedlings (Olsen *et al.*, 2012; Guerrero-Meseguer, Marín & Sanz-Lázaro, 2017; Hernán *et al.*, 2017; Pereda-Briones, Terrados & Tomas, 2019). After such massive mortality, in some cases seagrass meadows can recover naturally, although such recovery can take decades, especially for slow-growing species (O'Brien *et al.*, 2018). For example, after the acute MHW that affected the coastline of Western Australia in the austral summer of 2010/2011, recovery of the seagrass *Amphibolis antarctica* was still partial 5 years post-MHW (Strydom *et al.*, 2020) while no seed production was recorded in the disturbed *P. australis* meadow until 2016–2017 (Kendrick *et al.*, 2019). Recurrent MHWs can further increase plant mortality in already impacted populations, hampering their recovery and jeopardizing their survival (Marbà & Duarte, 2010).

After a local extinction, the same seagrass population can potentially recolonize its former space by asexual reproduction (i.e. vegetative recruitment) of acclimatized/adapted plants, and/or by sexual reproduction through seed dispersal and seed dormancy (i.e. re-colonization: 4➔2 in Fig. 3) (Diaz-Almela *et al.*, 2007; Blok *et al.*, 2018; Ruiz *et al.*, 2018; Marín-Guirao *et al.*, 2019). This phenomenon has been documented following physical disturbance (Olesen *et al.*, 2004), warm-induced anoxia events (Plus, Deslous-Paoli & Dagault, 2003), or microalgal blooms (Lee *et al.*, 2007b). Importantly, while relatively slow-growing

seagrasses [e.g. *Thalassia hemprichii* and *Enhalus acoroides* (Olesen *et al.*, 2004) and *Z. marina* (Plus *et al.*, 2003; Lee *et al.*, 2007b)] tend to recolonize through sexual reproduction, faster-growing seagrasses [e.g. *Cymodocea rotundata* and *H. uninervis* (Olesen *et al.*, 2004)] tend to undergo vegetative recolonization. Small- and medium-sized species often grow rapidly and can quickly re-occupy an area after heat stress.

On the other hand, the disappearance of local populations of seagrasses due to ocean warming can create an empty niche for colonization by new thermally tolerant species (new colonization: 4➔5 in Fig. 3). The rapid expansion of the tropical seagrass *H. stipulacea* in the Mediterranean is an example of this phenomenon (Lipkin, 1975; Gambi, Barbieri & Bianchi, 2009). Given that the invasive *H. stipulacea* has expanded rapidly throughout coastal areas of the Caribbean Sea within less than 20 years (Willette & Ambrose, 2012; Steiner & Willette, 2015), the distribution of this species in the Mediterranean has been predicted to accelerate in future (Georgiou *et al.*, 2016; Beca-Carretero *et al.*, 2020; Nguyen *et al.*, 2020b). Optimistically, new colonizations by thermally tolerant species could provide alternative ecosystem services, including carbon sinks (even if less successfully; e.g. *H. stipulacea*, see Fig. 3) potentially counterbalancing service loss due to the extinction of the local temperate seagrasses (Apostolaki *et al.*, 2019).

Finally, in an era of rapid ocean change, the future of seagrasses is, indeed, difficult to forecast (i.e. 2➔4 & 5➔4 in Fig. 3). Although some thermal-adapted/thermal-tolerant seagrasses could potentially survive and even benefit from ocean warming in the near future (Saha *et al.*, 2019; Nguyen *et al.*, 2020b), the existence of these species/populations may be challenged due to the on-going increased frequency of extreme climatic events and human-induced impacts on the marine environment (Ralph *et al.*, 2007; Oliver *et al.*, 2019). However, seagrass management and restoration could effectively contribute to sustaining these seagrasses and their services into the future (Ramesh *et al.*, 2019; Valdez *et al.*, 2020). Will warm-adapted/thermal-tolerant seagrasses survive future ocean change? To the best of our knowledge, an answer to this question remains open.

(4) Effects of warming and seagrass responses at the ecosystem/planetary level

Warming can switch seagrass ecosystems from autotrophic to heterotrophic (Burkholz, Duarte & Garcias-Bonet, 2019) and enhance CO_2 together with methane fluxes from meadows into the atmosphere (Burkholz, Garcias-Bonet & Duarte, 2020), not only reducing the ability of this ecosystem to buffer climate warming, but also contributing to it (see Fig. 3). After the massive mortality of seagrasses in Shark Bay (Australia), substantial quantities of CO_2 were released to the atmosphere, contributing to the greenhouse effect (Arias-Ortiz *et al.*, 2018). A trophic transformation is not always the result of ocean warming, but will depend on seagrass species, co-occurring stressors (Macreadie & Hardy, 2018), and sometimes the diversity of seagrass

meadows (Burkholz *et al.*, 2019). Warming threatens the distribution of large and long-lived species of seagrass [e.g. *P. oceanica* (Marbà & Duarte, 2010; Jordà *et al.*, 2012)], favouring the expansion of some small rapid-growing species [e.g. *H. stipulacea* (Georgiou *et al.*, 2016; Nguyen *et al.*, 2020*b*)]. Thus, warming is accelerating the tropicalization of temperate meadows (Hyndes *et al.*, 2016). When the ecosystem functions of seagrasses depend strongly on their primary production (i.e. their biomass), a switch from large species to small species due to warming could significantly reduce their value in terms of ecosystem services as well as blue carbon storage (i.e. the carbon stored in coastal and marine ecosystems).

Globally, seagrass meadows represent over 20% of nursery habitats for the 25 most important fishery species (Unsworth *et al.*, 2019). Therefore, loss of seagrass meadows negatively impacts global fisheries, the economy, and coastal communities that rely on fishing for food and employment (Tuya, Haroun & Espino, 2014; Unsworth *et al.*, 2019).

Worldwide, seagrasses protect coastlines from the impact of waves and storms (Guannel *et al.*, 2016). Nevertheless, it is important to note that the coastal defence service of seagrasses mostly depends on some large, long-lived species (e.g. *Z. marina* and *P. oceanica*). Warming threatens the existence of these species and enhances tropicalization with their replacement by small, seasonal species, which have a much lower capacity for coastal protection.

Warming-induced seagrass declines can potentially alter neighbouring habitat-formers, such as corals (Bulleri *et al.*, 2018). Where seagrasses grow alongside corals (e.g. Gulf of Aqaba, Israel; Winters *et al.*, 2017), the disappearance of seagrasses has led to: (*i*) incremented sediment re-suspension and nutrients in the water column resulting in algal blooms (Genin, Lazar & Brenner, 1995); (*ii*) enhanced decalcification of corals as a consequence of increased ocean acidification (Hoegh-Guldberg *et al.*, 2007); (*iii*) a reduction in biodiversity as some reef fish feed in nearby seagrass meadows (Beck *et al.*, 2001); and (*iv*) increased prevalence of pathogens (Lamb *et al.*, 2017). Warming, therefore, will not only affect seagrass habitats but also other nearby habitat-former species such as coral reefs.

(5) Combined effects of warming and other stressors

Under natural conditions, environmental stressors do not occur individually, but concurrently and synergistically (Sandifer & Sutton-Grier, 2014). Hence, studying the interaction of ocean warming with other stressors is crucial for the comprehensive and precise understanding of seagrass responses to their changing environment (Gunderson, Armstrong & Stillman, 2016).

(a) Warming and salinity changes

Changes in salinity are recognized as a major factor forcing the evolutionary trajectory of seagrasses, conditioning their distribution, ecology, and biology (Kuo & Den Hartog, 2000). It is among the most challenging factors for seagrasses to tolerate (Olsen *et al.*, 2016), as is also the case for terrestrial plants. Global warming causes ice melting and sea-level rise, and an increase in watershed runoff, reducing salinity in some areas (Nicholls & Cazenave, 2010), but warmer temperatures are also increasing salinity in semi-isolated oceans such as the Mediterranean Sea (Borghini *et al.*, 2014). Increased salinity in seagrass habitats can also occur as a consequence of brine discharge into coastal waters from desalination plants (Touchette, 2007). Seawater desalination is a growing industry in several regions that are now experiencing water scarcity (Lattemann & Höpner, 2008); brine discharge can have a negative impact on seagrass populations (Ruíz, Marín-Guirao & Sandoval-Gil, 2009; Sandoval-Gil *et al.*, 2014). Generally, seagrasses are tolerant to a range of salinities. Nonetheless, increased seagrass mortality in response to warming is greater at low salinity levels (i.e. below 15 PSU) (Nejrup & Pedersen, 2008; Kaldy & Shafer, 2013; Collier *et al.*, 2014; Salo & Pedersen, 2014). Thus, the combined effects of ocean warming and salinity changes (especially lower salinity levels) is a concern.

The synergistic effects of salinity and temperature cannot be generalized among different species or populations. In fact, seagrass responses to stressors such as salinity changes depend on plasticity and local adaptation (Pazzaglia *et al.*, 2021). Kaldy & Shafer (2013) showed, for example, intraspecific differences between populations: northern *Zostera japonica* plants, which experienced a higher salinity range at Padilla Bay, were less resilient to heat stress than their counterparts growing at the southern limit of the species range (Coos Bay) that experienced a lower salinity range. Interspecific differences related to divergent responses to warming and salinity have been identified in the seagrass species *Halophila ovalis*, *H. uninervis*, and *Z. muelleri* (Collier *et al.*, 2014). Moreover, the combined effects of temperature and salinity not only affects adult plants, but also induces mortality in seagrass seedlings, which can greatly influence the adaptation and resilience of seagrass meadows (Salo & Pedersen, 2014).

(b) Warming and light limitation

One of the most widespread threats to seagrasses is light limitation due to anthropogenic activities. Changes in sedimentation regime, nutrient loading with subsequent algal blooms, and dredging all cause water turbidity (e.g. De Boer, 2007). Widespread seagrass die-off has been attributed to reduced water clarity (Walker & McComb, 1992; Ralph *et al.*, 2007).

Seagrasses can be distributed along wide depth gradients with different light regimes (in quality and quantity). The impact of thermal stress is likely to be more severe in plants under conditions in which there is light limitation (Collier *et al.*, 2011; York *et al.*, 2013; Kim *et al.*, 2019). Having enough light for photosynthesis enables plants to maintain a positive energy/carbon balance when increased temperature enhances respiration. Thus under conditions of reduced light availability, seagrasses show reduced thermal tolerance and

are more prone to suffer from heat stress during MHWs. For example, the Australian species *H. uninervis* and *Z. muelleri* require saturating light levels to respond positively to increasing temperatures (Collier *et al.*, 2011). This highlights the importance of maintaining and improving water quality to enhance the resilience of seagrass to climate warming. The interactive effects of light and temperature have been shown to be weaker than for each factor separately, and temperature seems to play a dominant role in this combination (York *et al.*, 2013; Kim *et al.*, 2019). For *P. oceanica*, Hendriks, Olesen & Duarte (2017) identified the roles of light and temperature to be far more critical to seagrass health than CO_2 levels. In fact, the negative effects of ocean warming are forecast to outweigh any potentially positive effect of ocean acidification on some seagrass species (Zimmerman, Hill & Gallegos, 2015; Repolho *et al.*, 2017; Collier *et al.*, 2018).

(c) Warming and sulphide stress

Sulphate reduction is a fundamental process that occurs in terrestrial water-saturated soils as well as marine sediments, where gas exchanges are very limited, resulting in the natural accumulation of sediment sulphide (Holmer & Hasler-Sheetal, 2014). Generally, sulphide is toxic to living organisms including seagrasses, as it can strongly impact cellular enzymatic processes (Raven & Scrimgeour, 1997). To survive in the highly toxic sulphide environment of marine sediments, seagrasses have developed sophisticated mechanisms to transport oxygen from the leaves into the rhizosphere to maintain an aerobic environment, protecting their tissues from the intrusion of sulphide (Borum *et al.*, 2007). Warming can accelerate microbial activities, in turn increasing sulphate reduction, and consequently, sulphide concentration in the sediments (Frederiksen *et al.*, 2007; Marbà *et al.*, 2007). This phenomenon, when accompanied by warming, can enhance sulphide intrusion into seagrass tissue with the potential further to disrupt carbon metabolism and result in plant starvation and mortality (Robblee *et al.*, 1991; Koch *et al.*, 2007; Holmer & Hasler-Sheetal, 2014). There is evidence that warming can enhance sulphide stress in seagrasses (Garcias-Bonet *et al.*, 2008; García *et al.*, 2012, 2013). Importantly, the sensitivity of seagrasses to the combined effects of warming and sulphide will be species specific (Koch *et al.*, 2007) and depth specific (García *et al.*, 2013). However, with on-going ocean warming, even deep seagrasses are likely to be negatively impacted by sulphide stress in the future (García *et al.*, 2013).

(d) Warming and eutrophication

The rapid development of agricultural activities across the globe has released huge nutrient loads into rivers and coastal waters triggering eutrophication that leads to catastrophic consequences for sessile marine organisms (Rabalais, Harper & Turner, 2001; Diaz & Rosenberg, 2008; Rabalais *et al.*, 2009). Nutrient enrichment also induces overgrowth of macroalgae, phytoplankton, and seagrass epiphytes, leading to light reduction and impacting seagrass growth and survival. Indeed, together with ocean warming, eutrophication is recognized as one of the main stressors to seagrasses globally [see reviews by Burkholder *et al.* (2007) and Lee *et al.* (2007a)]. Previous studies have demonstrated that the combined effect of warming and nutrient enrichment can vary. For instance, nutrient enrichment can accelerate the negative impact of warming on some seagrass species, such as *Zostera capensis*, *C. nodosa* and *P. oceanica* (Mvungi & Pillay, 2019; Ontoria *et al.*, 2019a,b). Pazzaglia *et al.* (2020) investigated the combined effects of warming and nutrient enrichment on different *P. oceanica* populations with different nutrient load histories. Plants growing in chronically eutrophic conditions were more prone to suffer from thermal stress than plants from populations living under oligotrophic/pristine conditions. Additionally, the accumulation of drift algae following an increase in seawater temperature and eutrophication may also affect seagrasses negatively. Drift algae are shallow-water unattached macroalgae that often bloom massively in eutrophication conditions and can deleteriously impact seagrass meadows (McGlathery, 2001). Holmer, Wirachwong & Thomsen (2011) investigated the combined effects of drift algae and warming, showing that warming/nutrient-induced higher densities of drifting algae can additively and synergistically extend the negative impacts of warming on the seagrass species *H. ovalis* and suggesting that drift algae should be removed to protect seagrass meadows. By contrast, Egea *et al.* (2018) showed that the combination of warming, nutrient enrichment, and acidification could have positive effects on the seagrass *C. nodosa*, and thus predicted that this species could benefit from future ocean change. Interestingly, warming and nutrient enrichment could also reduce grazing pressure on seagrasses, as in the case of the sea urchin *Amblypneustes pallidus* on the seagrass *A. antarctica* (Burnell *et al.*, 2013).

(e) Warming and herbicides

The increase in coastal agriculture activities has led to the runoff of large quantities of agricultural herbicides (e.g. diuron, atrazine, hexazinone, tebuthiuron and ametryn) into coastal marine environments (Smith *et al.*, 2012). These herbicides can have a strong impact on PSII of seagrasses, not only damaging seagrass performance but also increasing their susceptibility to other stressors (Flores *et al.*, 2013; Negri *et al.*, 2015; Wilkinson *et al.*, 2015). To date, only one study has investigated the combined effects of warming and a herbicide (diuron), which showed strong antagonistic effects of combined stressors on the tropical seagrass species *H. ovalis* (Wilkinson *et al.*, 2017).

The impact of herbicides on seagrasses thus will become a greater concern with ocean warming. Additionally, we note that most studies investigating the effects of herbicides on seagrass species targeted the Great Barrier Reef area (Lewis *et al.*, 2009; Flores *et al.*, 2013; Negri *et al.*, 2015; Wilkinson *et al.*, 2015, 2017). Globally, the use of herbicide-resistant genetically modified (GM) crops is still controversial, thus

conventional agricultural production remains dependent on herbicides to control weeds (Green, 2014). Consequently, herbicides still pose a great potential risk for seagrasses across the globe, and future studies to understand the effects of herbicides on seagrasses from other regions of the world are highly encouraged.

(f) Warming and pathogens

Massive losses of seagrass meadows have been documented across the globe after outbreaks of seagrass diseases (see review by Sullivan *et al.*, 2018). Human-induced environmental changes, especially ocean warming, can enhance the susceptibility of seagrasses to these biotic threats by promoting the development of seagrass diseases and reducing their resilience (Sullivan *et al.*, 2018; Burge & Hershberger, 2020). 'Wasting disease', caused by the protist *Labyrinthula* sp., is the best studied example in seagrasses [e.g. *Phytophthora gemini* and *Halophytophthora zostera* (reviewed by Sullivan *et al.*, 2018)]. There was a wasting disease epidemic in the seagrass *Z. marina* along the Atlantic coasts of North America and Europe during the 1930s, causing the extinction of as much as 90% of the total *Z. marina* population, and leading to profound ecological impacts within the coastal ecosystem (Renn, 1936). Nevertheless, experimental studies have also shown that an increase in ocean temperature may limit infections of seagrass diseases. For example, recent studies on two Mediterranean seagrass species, *P. oceanica* and *C. nodosa*, suggested that temperatures above 28°C inhibit the growth of *Labyrinthula* sp., thus reducing the pathogenic pressure on this seagrass (Olsen *et al.*, 2014; Olsen & Duarte, 2015). In addition, Brakel *et al.* (2019) tested the effect of this protist on *Z. marina* in a predicted scenario with a combination of heat stress, light limitation, and different salinity levels, confirming the predicted reduction in pathogen pressure on seagrasses in response to predicted future warming. These results provide a more optimistic view about the future of seagrasses, particularly in the context of seagrass–pathogen dynamics. However, note that ocean warming may facilitate the presence and virulence of other marine diseases (both viruses and bacteria) (Burge & Hershberger, 2020). Given that there remain few studies on this topic and that seagrass diseases remain virtually unexplored [see review by Sullivan *et al.* (2018) for examples of other diseases in seagrasses], we recommend that future studies should attempt to broaden our understanding of the relationship between warming and pathogens in seagrasses.

(g) Warming and herbivores

The plant–herbivore interaction is fundamental for both parties not only from an evolutionary point of view (Fritz & Simms, 1992), but also from its role in sustaining ecosystem dynamics (Bakker *et al.*, 2016). In the presence of ocean warming, increases in seawater temperature will affect seagrasses and their herbivores not only individually, but also interactively. In general, warming increases the metabolic rate of herbivores, consequently enhancing grazing pressure (Hillebrand

et al., 2009). Nevertheless, studies on the interactions of seagrasses with herbivores in response to temperature changes revealed a complex situation (Burnell *et al.*, 2013; Garthwin, Poore & Vergés, 2014; Pagès *et al.*, 2018; Guerrero-Meseguer, Marín & Sanz-Lázaro, 2020; Buñuel *et al.*, 2021). Pagès *et al.* (2018) studied the sea urchin *Paracentrotus lividus* that, in some cases [e.g. *P. oceanica* beds on the northeast Spanish.

coast and in the south of France (Prado *et al.*, 2007)], consumes about 17% of seagrass production annually, showing that warming could weaken herbivore pressure on two Mediterranean seagrass species, *P. oceanica* and *C. nodosa* (Pagès *et al.*, 2018). By contrast, Burnell *et al.* (2013) showed that a temperature increase could enhance grazing pressure of *Amblypneustes pallidus* on the seagrass *A. antarctica*; however, nutrient enrichment was shown to reduce grazing pressure in combination with ocean warming and acidification. Similarly, a recent study on *P. oceanica* and its main fish herbivore *Sarpa salpa* demonstrated that warming can make the seagrass more palatable, increasing the growth rate of the fish (especially in the larval stage), and thus potentially intensifying herbivory pressure (Buñuel *et al.*, 2021). The combined effects of warming and herbivores also affect seagrass seedlings: Guerrero-Meseguer *et al.* (2020) found that the combined effects of MHWs and overgrazing led to a greater reduction in leaf growth and increased leaf senescence of *P. oceanica* seedlings in comparison with the effects of each factor alone. The authors suggested that the combined effects of ocean warming and other stressors are likely to threaten the survival of *P. oceanica* seedlings, and consequently sexual recruitment (Guerrero-Meseguer *et al.*, 2020). By contrast, Garthwin *et al.* (2014) conducted a simulated herbivory experiment on a *Zostera muelleri* meadow warmed by the thermal plume from a power station for 30 years and three nearby control meadows. Their results demonstrated that the ability of *Z. muelleri* to tolerate herbivory is not strongly affected by warming. The future of seagrass–herbivore interactions in an era of ocean warming still remains unclear and deserves additional attention in future studies.

III. FUTURE PERSPECTIVES

Seagrasses are facing a critical time in their evolutionary history in which their continued existence will depend on our actions, including research, restoration, and management activities. Below, we discuss some significant gaps in knowledge and recommend future directions for seagrass studies.

(1) Enlarging the number of species and populations studied

Previous studies have shown that the effects of ocean warming are not the same for all seagrass species and populations. Therefore, it remains difficult to predict the future of seagrasses accurately. Most seagrass studies in the context of ocean warming come from three regions: the

Mediterranean Sea, USA, and Australia (Fig. 4, see online Supporting Information Table S1). Most of these studies have focused on only a few seagrass species: *Z. marina*, *P. oceanica* and *C. nodosa* (Table S2). This highlights a significant gap in our understanding of how warming affects seagrasses; the vast majority of the world's seagrass species have not been studied in this context to date. Future studies should focus not only on additional species but also on more populations within each species to deliver a more comprehensive picture of how seagrasses will respond to a future changing climate.

Since warming potentially interacts with many other stress factors, seagrass meadows are currently under multiple anthropogenic pressures. Populations that are chronically stressed (e.g. under eutrophic conditions) might have a different tolerance or ability to respond to warming compared to healthy populations. There is an urgent need to explore how responses to warming differ between healthy and chronically stressed populations. This knowledge will be critical for improving the management and protection of valuable seagrass ecosystems by managing local factors that directly affect seagrass health, potentially enhancing their resilience to warming.

(2) Developing more precise and detailed seagrass distribution maps

Some seagrass species are losing habitat at a rapid rate (Robblee *et al.*, 1991; Seddon *et al.*, 2000; Jordà *et al.*, 2012; Marbà, Díaz-Almela & Duarte, 2014) or are being replaced by the rapid expansion of other species (Gambi *et al.*, 2009; Scheibling, Patriquin & Filbee-Dexter, 2018; Nguyen *et al.*, 2020*b*). Studies (Short *et al.*, 2007; Jayathilake & Costello, 2018) have provided general information regarding seagrass distribution, but there are many regions that remain unmapped (Assis *et al.*, 2020; McKenzie *et al.*, 2020). Building seagrass distribution maps can be challenging, especially for species that have a wide distribution range with different depths or inhabit mixed-species meadows. Effective methods have been developed to map seagrasses (see review by McKenzie, Finkbeiner & Kirkman, 2001) and more recently, a low-cost field-survey method using snorkelling and
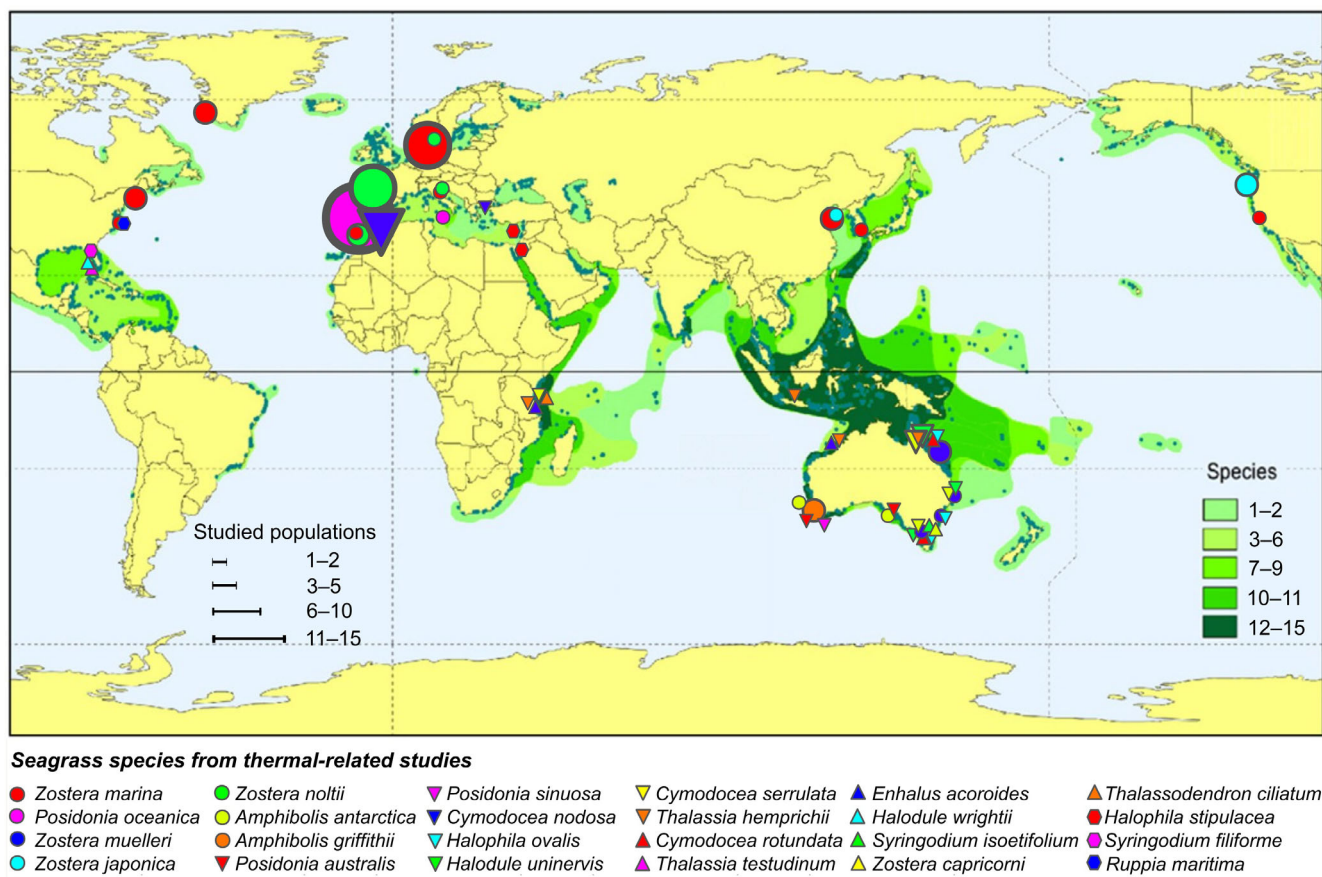
Fig 4. World map of seagrass populations used for thermal-related studies from 1985 to 2020. Coloured symbols indicate study populations, with symbol sizes scaled according to the key on the left. World distributions of species are shown by background green shading, with species numbers indicated according to the key on the right. Data were collected from *Google Scholar* as indicated in the legend to Fig. 1. Figure created by adapting Fig. 3 of Short *et al.* (2007). Details of locations and related publications are provided in Table S1.

perpendicular transects (Winters *et al.*, 2017) was developed at a small regional scale. Advanced technologies [e.g. satellite remote sensing, Geographic Information System (GIS) technologies, camera-equipped drones] have also been employed in seagrass mapping research (Barrell *et al.*, 2015; Phinn *et al.*, 2018). Future work is encouraged both in developing advanced technologies and in building more detailed seagrass maps across different regions of the world.

(3) Long-term monitoring programs

Many countries across the globe have implemented seagrass long-term monitoring networks appropriate to their local species and habitats. Since the end of the 20th century, many monitoring programs have been aggregating data to create regional and/or global monitoring networks with the aim to preserve seagrass meadows and to increase scientific knowledge and public awareness about these threatened and valuable ecosystems. At the global level, Seagrass-Watch (http://www.seagrasswatch.org/) and SeagrassNet (http://www.seagrassnet.org/) integrate hundreds of sites distributed along the coasts of dozens of countries for the long-term ecological monitoring of seagrasses. In the Mediterranean, the regional integration of existing networks is lacking, but initiatives are currently ongoing, for instance the POSIMED project (http://posimed.org/).

Data from long-term seagrass monitoring programs are not only providing valuable information to unravel the status and trends of natural populations at the global, regional, and local scales (e.g. Thomas, Unsworth & Rasheed, 2010; Rasheed & Unsworth, 2011; de los Santos *et al.*, 2019), but they are also helping in the development and execution of international environmental protection policies (e.g. the Marine Strategy European Directive). Seagrass monitoring programs are also recording environmental data, including water temperature, to correlate seagrass decline with warming trends or extreme warming events (Marbà & Duarte, 2010; Richardson *et al.*, 2018; Shields, Parrish & Moore, 2019). However, ecosystem modelling and forecasting activities for seagrasses are still needed. This could be facilitated by bridging global and local observations, and by linking long-term data series from seagrass monitoring programs to the continuous recording of coastal environmental conditions. Currently, platforms and sensor systems to measure physical, chemical, geological, and biological properties are increasingly being installed in coastal areas and oceanic regions worldwide [e.g. GOOS (https://www.goosocean.org/) and OOI (https://oceanobservatories.org/)]. The production of high-throughput data from multidisciplinary studies is a promising advance towards improving all aspects of seagrass conservation, from dynamic model development to forecast validation. These are powerful holistic approaches to monitoring seagrass ecosystems and their evolution in a rapidly changing ocean, as well as to contribute to their effective conservation and to the management of human activities in coastal areas (Capotondi *et al.*, 2019). The integration of time-series data through multivariate statistics and/or machine-learning algorithms could also provide promising tools to monitor coastal ecosystems in a changing climate (Danovaro *et al.*, 2016; Crise *et al.*, 2018).

(4) More realistic experiments in controlled conditions

Many past studies suffered from experimental constraints/limitations such as using unrealistic temperature levels, warming rates, experimental duration, small water volumes, or even single seagrass shoots that prevented clonal integration (Bulthuis, 1987; Lee *et al.*, 2007*a*). By contrast, recent experiments have become more realistic due to the development of sophisticated mesocosm systems for the culture of seagrasses in optimal conditions, and their use to conduct finely tuned and highly controlled experiments (Bergmann *et al.*, 2010; Marín-Guirao *et al.*, 2011; Georgiou *et al.*, 2016; Cambridge *et al.*, 2017; Oscar, Barak & Winters, 2018; Ruocco *et al.*, 2019*b*). These new systems have enabled more robust experiments to obtain not only a significant amount of knowledge in a short period but also novel results (Bulthuis, 1987; Lee *et al.*, 2007*a*). In the near future, the application of more advanced technologies are expected to push the boundary of seagrass research even further by enabling *in situ* experiments (e.g. Egea *et al.*, 2019) and near-natural simulated environment experiments (e.g. Saha *et al.*, 2019).

(5) The study of the holobiont

There is now an increasing recognition of the fundamental interactions between symbiotic microorganisms (bacteria, fungi, and archaea) and their host organisms. From both an ecological and evolutionary point of view, we should perhaps consider the organisms and their symbiotic microorganisms not separately but together. The term 'holobiont' has been used to describe this combination of the host organism and its microbiome (Vandenkoornhuyse *et al.*, 2015). In terrestrial plants, the number of studies considering the holobiont has increased, uncovering important functions of the microbiome in plant nutrition, resistance to biotic and abiotic stresses, and evolution (Vandenkoornhuyse *et al.*, 2015). In marine environments, interactions across holobionts are expected to be more flexible, with faster microbial community shifts, and greater phylogenetic diversity compared to terrestrial ecosystems (Dittami *et al.*, 2021). Compared with terrestrial plants, the importance of the holobionts in marine ecosystems is understudied. Some pivotal investigations of seagrass–bacteria interactions have suggested many important roles in providing nutrients, sustaining fitness, enhancing growth, and protecting seagrasses from toxic compounds and pathogens [see reviews by Ugarelli *et al.* (2017), Tarquinio *et al.* (2019) and Conte *et al.* (2021)]. In the face of ocean warming, the activity of the seagrass–bacterial community in relation to carbon remineralization is expected to increase, consequently reducing carbon accumulation rates in seagrass meadows (Trevathan-Tackett *et al.*, 2017). Future studies of

the seagrass holobiont should focus on a better understanding of (*i*) the components of the seagrass microbiome, (*ii*) seagrass–microbiome interactions in an ecological context, and especially (*iii*) how the seagrass microbiome can help seagrasses to be more resilient to environmental changes. Such studies will not only broaden our understanding of this important aspect of seagrass ecology but will also be extremely useful for seagrass restoration activities, as symbiotic microorganisms could potentially be used to enhance the survival of transplanted seagrasses (both seedlings and adult plants).

(6) Seagrasses as a solution to mitigate climate change

Adopting the concept of Gattuso *et al.* (2018) that ocean solutions may allow us to address climate change, it is essential to restore and conserve healthy seagrass meadows worldwide in order to preserve the ecosystem services that they provide in mitigating climate change and its associated effects. In the agriculture and food industries, the application of genetic engineering has significantly improved the productivity and quality of crops and commercial species (see review by Janni *et al.*, 2020). To the best of our knowledge, such approaches [e.g. clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR/Cas9)] have never been applied in seagrass research. This novel approach provides a promising way to select, breed, or produce genotypes that can survive future harsh environmental conditions (i.e. assisted evolution; see also Bulleri *et al.*, 2018). Such potential super-seagrasses could help us to re-establish ecosystems in areas where seagrasses have been completely destroyed due to natural and/or human-induced catastrophic events. Additionally, as seagrasses growing in extreme environments (e.g. under anthropogenic pressures, frequent MHWs, etc.) are expected to be more resilient to ocean warming, transplantations performed using such selected plants could be extremely useful in seagrass restoration (see review by Tan *et al.*, 2020). Moreover, emerging knowledge in the field of thermal stress memory and epigenetic memory in seagrasses (Jueterbock *et al.*, 2020; Nguyen *et al.*, 2020a) could yield in many potential applications in seagrass restoration. Together, the application of such new approaches could support attempts to restore degraded seagrass meadows effectively and sustainably at a global scale and consequently protect their ecosystem services (Reynolds *et al.*, 2016b), thus ultimately mitigating the negative impacts of climate change.

IV. CONCLUSIONS

(1) Warming strongly affects seagrasses at all levels from molecular, physiological, biochemical, morphological, and population to planetary level.

(2) Seagrass responses to warming vary amongst species, populations, and depths.

(3) Warming causes massive die-offs, tropicalization, and migration in seagrasses.

(4) Multiple-stressor studies in seagrasses are much needed to provide deeper insights into seagrass resilience, especially in an era of ocean warming.

(5) Significant knowledge gaps and future directions for seagrass research include: (*i*) studies involving additional species and populations; (*ii*) development of more precise and detailed seagrass distribution maps; (*iii*) more long-term monitoring programs; (*iv*) more realistic experiments in controlled conditions; (*v*) investigation of the seagrass holobiont; and (*vi*) seagrasses as a solution to mitigate climate change.

V. ACKNOWLEDGEMENTS

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VII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Table S1. List of thermal-related studies on seagrasses from 1985 to 2020.
Table S2. Number of studied populations from each seagrass species used for thermal-related studies from 1985 to 2020.