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

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 $0.61 \pm 0.16\,°C$ 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 $0.17 \pm 0.11\,°C$/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.*, 2020*a*).

26   In the sea, thermal conditions are more stable than on land (except for the intertidal zone).

27   Recent studies have documented a rapid rise in the occurrence of extreme climatic events in

28   the ocean, known as marine heatwaves (MHWs) (Oliver *et al.*, 2018). MHWs are extreme

29   warm periods that last for at least five days with a temperature level exceeding the 90th

30   percentile, based on three-decade historical baseline temperature values (Hobday *et al.*,

31   2016). Ocean warming, and especially MHWs, is already having catastrophic consequences

32   in coastal benthic communities worldwide (Coma *et al.*, 2009; Harley *et al.*, 2012; Wernberg

33   *et al.*, 2016). Indeed, the impact of MHWs is of more concern than the increase in average

34   seawater temperature, because organisms are generally more vulnerable to sudden

35   temperature changes than to progressive ones (Smale *et al.*, 2019). Thus, MHWs may trigger

36   destructive chronic impacts on marine creatures that can result in shifts in species

37   distributions and even local extinctions (Easterling *et al.*, 2000).

38

39   **(2) Seagrasses are being impacted by ocean warming**

40   Seagrasses are a unique group of angiosperms that recolonized the marine realm 60–90

41   million years ago on at least three occasions (Les, Cleland & Waycott, 1997). To overcome

42   the numerous challenges presented by a submerged lifestyle in the marine environment,

43   seagrasses have developed a range of specialized adaptive characteristics (Invers, Perez &

44   Romero, 1999; Borum *et al.*, 2007; Wissler *et al.*, 2011; Hogarth, 2015; Olsen *et al.*, 2016).

45   Consisting of a surprisingly small number of species (∼60–70 species in total), seagrasses are

46   distributed across thousands of kilometres of sedimentary shorelines from sub-Artic to

47   tropical regions (Short *et al.*, 2007). They provide highly valuable socio-economic services,

48   including primary productivity, organic carbon sequestration and burial, as well as sediment

49   stabilization (Orth *et al.*, 2006; Fourqurean *et al.*, 2012; Bertelli & Unsworth, 2014;

50   Unsworth, Nordlund & Cullen-Unsworth, 2019). They also provide nursery habitats for fish

51 and a diversity of marine organisms (e.g. invertebrates). Seagrasses represent one of the most

52 valuable ecosystems on Earth with an estimated value of $1.9 trillion per annum (Waycott *et*

53 *al.*, 2009; Costanza *et al.*, 2014). Furthermore, they have been acknowledged as one of

54 Earth's most efficient carbon sinks, and are listed as one of the potential solutions to mitigate

55 CO_2 emissions and ultimately to address the threat of global warming (Gattuso *et al.*, 2018).

56 Despite their critical value, they are suffering a global decline, driven mainly by the growing

57 number of pressures linked directly to human activities (e.g. ocean warming, coastal

58 modification, water quality degradation) (Orth *et al.*, 2006; Waycott *et al.*, 2009). Globally,

59 seagrasses are disappearing at an alarming rate of 110 km^2 per annum, resulting in a

60 cumulative loss of 29% of the total world seagrass population by the end of 2006 (Waycott *et*

61 *al.*, 2009). The total population of *Posidonia oceanica*, for example, a seagrass species

62 endemic to the Mediterranean Sea, has decreased by 13–50% since the mid-nineteenth

63 century (Telesca *et al.*, 2015). However, the rate of seagrass loss, at least at a regional scale,

64 seems to have been reduced as a result of the implementation of management plans, such as

65 European environmental protection measures (de los Santos *et al.*, 2019).

66 A recent study listed seagrasses as one of the habitat-forming species that are likely to

67 disappear as a consequence of climate change (Trisos, Merow & Pigot, 2020). Seagrass die-

68 offs, as a consequence of MHWs, have been reported for different species, including *P.*

69 *oceanica* (Marbà & Duarte, 2010), *Zostera marina* (Reusch *et al.*, 2005; Jarvis, Brush &

70 Moore, 2014), and *Amphibolis antarctica* (Seddon, Connolly & Edyvane, 2000; Arias-Ortiz

71 *et al.*, 2018; Strydom *et al.*, 2020). The observed mass mortality of several seagrass

72 populations after extreme MHWs (Arias-Ortiz *et al.*, 2018; Strydom *et al.*, 2020) and the

73 projected warming trend for the next decades has motivated the prediction of a functional

74 extinction of seagrass meadows in the near future (Marbà & Duarte, 2010; Jordà, Marbà, &

75 Duarte, 2012; Chefaoui, Duarte & Serrão, 2018). Interestingly, while MHWs have already

76 caused extensive local extinction of seaweed species across hundreds of kilometres (Smale,

77 2020), the comparative effects on seagrasses might appear to be smaller. This suggests that

78 further research investigating the mechanisms driving potential differences in the resilience

79 between seagrasses and other marine macrophytes is clearly needed.

80

81 **(3) Why is this review timely?**

82 The recent application of advanced molecular technologies in seagrass research (see review

83 by Davey *et al.*, 2016) together with the implementation of controlled laboratory

84 manipulations have enabled rapid progress in the understanding of seagrass responses to

85 changing environments (Egea *et al.*, 2019; Saha *et al.*, 2019). Moreover, the availability of

86 the first two sequenced seagrass genomes, for *Z. marina* (Olsen *et al.*, 2016) and *Zostera*

87 *muelleri* (Lee *et al.*, 2016), has enhanced seagrass molecular research.

88 Over the last decade, there has been a rapid increase in the number of studies documenting

89 the impact of warming on seagrasses as well as the responses of seagrasses to this

90 environmental challenge (Fig. 1). These studies have investigated the response of seagrasses

91 to warming at the biological level (i.e. biochemical, physiological and morphological), and

92 also at the molecular, population and even ecosystem/planetary level (Fig. 1). A review on

93 the effects of warming on seagrasses is timely since: (1) ocean warming is occurring at an

94 alarming rate and will continue to have strong impacts on seagrasses in the future; (2) a

95 substantial amount of information on the effects of warming on seagrasses has become

96 available recently; and (3) there is no comprehensive review on the effects of ocean warming

97 on seagrasses [but see Bulthuis, 1987; Lee, Park & Kim, 2007*a*; Koch *et al.*, 2013; Duarte *et*

98 *al.*, 2018]. This review focuses on the effects of warming on seagrasses across different

99 functional levels (molecular, biochemical/physiological, morphological/population and

100 ecosystem/planetary), describes the effects of warming on seagrasses in combination with

101   other stressors (e.g. salinity, light, etc.), and suggests future research directions to close

102   knowledge gaps in our understanding of seagrass resilience in a changing climate.

103

104   **II. EFFECTS OF WARMING ON SEAGRASSES**

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

106   In the face of rapid ocean warming, it is critically important to predict the future responses of

107   seagrasses in order to develop mitigation strategies to prevent their loss through effective

108   management, conservation, and restoration. The molecular basis of seagrass responses to a

109   warming ocean can uncover seagrass traits that can be correlated to the persistence of that

110   species under changing climatic conditions (Procaccini, Olsen & Reusch, 2007; Reusch &

111   Wood, 2007). Innovative molecular experiments in parallel with routine

112   physiological/morphological measurements can provide early warning measures to detect

113   changes in the ecological status of seagrass meadows well before any signs of mortality

114   appear (Procaccini *et al*., 2007; Pernice *et al*., 2015; Schliep *et al*., 2015; Ceccherelli *et al*.,

115   2018). The extensive application of gene expression studies (transcriptomics) over the last

116   decade (Davey *et al*., 2016) and the availability of two seagrass genomes, *Z. marina* (Olsen *et*

117   *al*., 2016) and *Z. muelleri* (Lee *et al*., 2016), have greatly fostered our understanding of

118   seagrass responses to environmental changes at the molecular level (see Fig. 1C). We are

119   now much closer to integrating the fields of seagrass ecophysiology and ecological genomics,

120   as anticipated almost a decade ago (Procaccini *et al*., 2012).

121   To date, gene expression studies (quantitative reverse transcription polymerase chain reaction

122   and RNA sequencing) have been conducted for only a handful of seagrass species. Large

123   transcriptomic differences observed in seagrasses that had recovered from long-term acute

124   temperature stress (3 weeks at 26 ºC) identified transcriptomic resilience as a predictor of

125   thermal adaptation (Franssen *et al*., 2011; Jueterbock *et al*., 2016). Other studies found

126 different transcriptomic responses to short-term acute stress (5 days, 32 ºC), leading to the

127 identification of molecular mechanisms involved in maintaining photosynthetic stability and

128 respiratory acclimation of seagrasses under heat stress (Marín-Guirao *et al.*, 2017).

129 Investigations of the responses of seagrasses to thermal stress have revealed some

130 interspecific similarities (see Fig. 2), comparable to those observed in the heat response of

131 terrestrial plants, including refolding of proteins, activation of oxidative-stress defence, and

132 cell wall fortification (Franssen *et al.*, 2011, 2014; Gu *et al.*, 2012; Jueterbock *et al.*, 2016;

133 Marín-Guirao *et al.*, 2016, 2017).

134

135 (*a*) *Heat shock proteins*

136 Seagrasses have developed several sophisticated molecular mechanisms to respond to

137 environmental triggers. Among these mechanisms, the production of chaperones, especially

138 heat shock proteins (HSPs) are among the most important. HSPs are common proteins found

139 in both plants and animals. They play fundamental roles in cells under normal and stressed

140 conditions, including roles in protein folding, assembly, translocation, and protein

141 degradation (Vierling, 1991; Kiang & Tsokos, 1998; Park & Seo, 2015). Under stressful

142 conditions, HSPs can either help to fix non-functional/partly denatured proteins or remove

143 degraded/damaged proteins (Sørensen, Kristensen & Loeschcke, 2003).

144 Multiple studies have highlighted the role of molecular chaperones (especially HSPs) in

145 seagrass responses to warming (Reusch *et al.*, 2008; Bergmann *et al.*, 2010; Franssen *et al.*,

146 2011, 2014; Massa *et al.*, 2011; Gu *et al.*, 2012; Marín-Guirao *et al.*, 2016, 2017; Tutar *et al.*,

147 2017; Malandrakis *et al.*, 2017; Traboni *et al.*, 2018; Purnama *et al.*, 2019; Nguyen *et al.*,

148 2020*a*). HSP70 and HSP90 are the best studied chaperones in seagrasses. In terrestrial plants,

149 heat shock factors (HSFs) act as transcriptional activators of HSPs and some have a critical

150 role in plant thermal tolerance (Qu *et al.*, 2013). It remains mostly unclear whether HSFs

151   have the same role in seagrasses compared with terrestrial plants, although some of these

152   genes have been shown to be responsive in at least two seagrass species (*Zostera noltii* and *P.*

153   *oceanica*) when exposed to rapid and severe heat stress (Massa *et al*., 2011; Marín-Guirao *et*

154   *al*., 2016).

155

156   (*b*) *Oxidative stress*

157   Oxidative stress, generated by the enhanced production of reactive oxygen species (ROS)

158   under increased temperatures, is a common secondary stress response in plants

159   (Hasanuzzaman, Nahar & Fujita, 2013). Gene expression studies in different seagrass species

160   strongly support the involvement of genes encoding ROS-scavengers, indicating the

161   production of ROS in seagrasses during thermal stress (Reusch *et al*., 2008; Winters *et al*.,

162   2011; Gu *et al*., 2012; Liu *et al*., 2016; Marín-Guirao *et al*., 2017; Tutar *et al*., 2017; Purnama

163   *et al*., 2019). In seagrasses, superoxide dismutase (SOD) and ascorbate peroxidase (APX)

164   appear to be among the most active ROS-scavenging enzymes under heat stress (Reusch *et*

165   *al*., 2008; Winters *et al*., 2011; Liu *et al*., 2016; Marín-Guirao *et al*., 2017; Purnama *et al*.,

166   2019). These enzymes have been shown to inhibit free radicals and ROS (Teotia & Singh,

167   2014).

168   Using a metabolomics approach, Gu *et al*. (2012) detected myo-inositol among the three most

169   responsive metabolites to oxidative stress in two seagrass species (*Z. marina* and *Z. noltii*)

170   subjected to heat stress. In terrestrial plants, myo-inositol is important in the galactinol and

171   raffinose biosynthetic pathways that have been characterized as osmoprotectants. These

172   osmoprotectants can function as scavengers of ROS (Nishizawa, Yabuta, & Shigeoka, 2008)

173   whereas myo-inositol alone has been found to increase the midpoint denaturation temperature

174   of proteins (Ortbauer & Popp, 2008).

175

176   (*c*) *Other molecular responses*

177   Apart from HSPs and ROS-scavenging proteins, other mechanisms by which seagrasses

178   respond to warming have been discovered in recent molecular studies. Gu *et al*. (2012) on *Z.*

179   *marina* and Traboni *et al*. (2018) on *P. oceanica* revealed the involvement of ubiquitination

180   and proteolysis in response to thermal stress, indicative of severe protein damage as a

181   consequence of elevated temperature. In terrestrial plants, ubiquitin-mediated proteolysis is a

182   multi-step process that identifies, labels, and destroys damaged proteins. It is the principal

183   mechanism of protein catabolism to facilitate plant proteostasis when exposed to stressful

184   conditions (reviewed by Stone, 2014). The cell wall is fundamentally important for the

185   survival and development of plants as it provides a structural framework and is the first line

186   of defence against pathogens. Moreover, cell wall modification can enhance plant responses

187   to many environmental stressors (reviewed by Houston *et al*., 2016). In seagrasses,

188   transcriptomic studies revealed higher expression of cell wall-related genes in plants exposed

189   to thermal stress, suggesting the potential involvement of cell wall fortification in the thermal

190   stress response as in terrestrial plants (Gu *et al*., 2012; Franssen *et al*., 2014; Jueterbock *et al*.,

191   2016; Marín-Guirao *et al*., 2017, 2019).

192   Warming can have detrimental effects on the translational machinery of seagrasses, by

193   limiting the availability of associated molecular components (Malandrakis *et al*., 2017) with

194   destructive consequences on the organization of the cytoskeleton (Massa *et al*., 2011;

195   Malandrakis *et al*., 2017; Tutar *et al*., 2017) which can in turn damage cell division processes

196   (Malandrakis *et al*., 2017; Marín-Guirao *et al*., 2017). Furthermore, warming can diminish

197   the expression of pathogen defence genes, thereby potentially enhancing susceptibility to

198   disease (Jueterbock *et al*., 2016) although experimental evidence to date suggests the contrary

199   (see Section II.5*f*). Given the past massive die-off of seagrass meadows due to 'wasting

200 disease' (Orth *et al*., 2006), the combined effects of warming and disease deserve further

201 investigation.

202 Warming causes damage to DNA and protein structure (e.g. protein unfolding, protein

203 degradation) in seagrasses, resulting in homeostatic cell imbalance and cell death (Franssen *et*

204 *al*., 2011; Tutar *et al*., 2017). Under severe conditions, seagrasses activate apoptotic pathways

205 by upregulating expression levels of genes involved in the programmed cell death process

206 aimed at eliminating irreparably damaged cells (Massa *et al*., 2011; Tutar *et al*., 2017;

207 Traboni *et al*., 2018). This apoptotic mechanism is also connected with the production of

208 HSPs (Beere, 2005).

209

210 (*d*) *Intraspecific differences in molecular responses to warming amongst seagrass*

211 *populations from different thermal origins*

212 Seagrass populations from different thermal origins respond differently to warming. Plants

213 living in more fluctuating and/or warmer environments are more resilient to warming than

214 those from colder and/or more stable thermal environments. Examples include *Z. marina*

215 from different latitudes (Bergmann *et al*., 2010; Franssen *et al*., 2011; Winters *et al*., 2011;

216 Jueterbock *et al*., 2016; Jahnke *et al*., 2019), *P. oceanica* from different depths (Marín-Guirao

217 *et al*., 2016, 2017; Tutar *et al*., 2017; Procaccini *et al*., 2017) and latitudes (Marín-Guirao *et*

218 *al*., 2019), and *Halophila stipulacea* from the Red Sea and Mediterranean Sea (Nguyen *et al*.,

219 2020*a*). Plants from warm environments (i.e. *Z. marina* from southern populations and *P.*

220 *oceanica* from shallow meadow stands) activate a more complete (i.e. higher number of up-

221 regulated genes) and intense (i.e. stronger activation of heat-responsive genes) transcriptomic

222 response than plants from cold environments (*Z. marina* from northern populations, *P.*

223 *oceanica* from deep-water populations) (Franssen *et al*., 2014; Marín-Guirao *et al*., 2017).

224 Plants with a 'warmer thermal history' also showed higher constitutive levels of heat-

225 responsive genes, likely reflecting their local (pre-)adaptation to warmer and more stressful

226 thermal conditions. Higher constitutive expression levels of heat-responsive genes have been

227 associated with a pre-adaptive defence strategy that confers higher thermal tolerance to cope

228 with frequent heat stress in several marine organisms, including corals and marine gastropods

229 (Barshis *et al.*, 2013; Gleason & Burton, 2015). While plants from southern and northern

230 European populations of *Z. marina* reacted similarly to acute heat stress (Franssen *et al.*,

231 2011), they differed in their global transcriptome recovery after the temperature returned to

232 'normal'. This phenomenon is known as transcriptomic resilience and may be part of a more

233 universal indicator of whether or not plants can endure critical temperatures or other stressor

234 levels.

235

236 (*e*) *Epigenetic modification*

237 Studies regarding epigenetic modifications are now emerging in the field of seagrass

238 molecular biology (Jueterbock *et al.*, 2020; Nguyen *et al.*, 2020*b*). Epigenetic modifications

239 are molecular modifications that alter gene expression in response to internal (e.g.

240 ontogenetic processes) or external (e.g. environmental changes) triggers, without changes in

241 the underlying DNA sequence (Bossdorf, Richards & Pigliucci, 2008). Epigenetic

242 modifications are inherited through mitosis in most cases, but are also transmittable to the

243 next generation. While epigenetic modifications have been widely studied in terrestrial plants

244 (Chinnusamy & Zhu, 2009; Kinoshita & Seki, 2014; Liu *et al.*, 2015), only a few studies

245 have investigated epigenetic responses to warming in seagrasses (Ruocco *et al.*, 2019*a*,*b*;

246 Jueterbock *et al.*, 2020; Nguyen *et al.*, 2020*b*; Entrambasaguas, L., Ruocco, M., Verhoeven,

247 K.J.F., Procaccini, G. & Marín-Guirao, L., in preparation). Some transcriptomic data sets

248 suggest the involvement of epigenetic modification in the responses of seagrasses to thermal

249 stress (Marín-Guirao *et al.*, 2017; Marín-Guirao *et al.*, 2019; Jueterbock *et al.*, 2020). For

250   example, in *P. oceanica*, heat-tolerant plants showed higher expression of epigenetic-related

251   genes (Marín-Guirao *et al.*, 2017; Marín-Guirao *et al.*, 2019). Stress-induced epigenetic

252   mechanisms are crucial in the activation of the immediate stress response and favour both

253   short- and long-term adaptation, due to their important role in regulating the expression of

254   stress-related genes (Liu *et al.*, 2015). Increased knowledge on the epigenetic responses of

255   plants to environmental changes in terrestrial systems (Molinier *et al.*, 2006; Feng &

256   Jacobsen, 2011; Kinoshita & Seki, 2014; Wang *et al.*, 2016), and the possible application of

257   more advanced molecular technologies (Kurdyukov & Bullock, 2016; Van Wesenbeeck *et

258   al.*, 2018) may stimulate further study of epigenetic modification in seagrasses.

259

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

261   Biochemical and physiological response to thermal stress in seagrasses have been studied

262   extensively since the 1990s (Fig. 1C), with earlier studies summarized in previous reviews

263   (Bulthuis, 1987; Lee *et al.*, 2007*a*; Koch *et al.*, 2013). Thermal stress tends to inhibit

264   photosynthetic activity while simultaneously enhancing respiration. Recent findings suggest

265   that extreme temperature changes could cause the degradation of chlorophyll as well as

266   affecting the fluidity of the cellular membrane, among other impacts. In response to thermal

267   stress, seagrasses tend to activate protective mechanisms such as the accumulation of photo-

268   protective pigments and modification of fatty acid contents (see Fig. 2).

269

270   (*a*) *Physiological responses*

271   Warming affects seagrass physiological and metabolic processes including photosynthesis

272   and respiration (Bulthuis, 1987; Lee *et al.*, 2007*a*). Under mild temperature increments,

273   photosynthetic rate increases, likely due to an increase in membrane fluidity that improves

274   the mobility of photosynthetic proteins embedded within the thylakoid membrane (e.g. the

275   plastoquinone pool). Other factors, such as temperature-enhanced enzyme activity, may also

276   play a role. Further temperature increases, however, reduce photosynthetic rate due to factors

277   such as the detachment of functional proteins from the thylakoid membrane (e.g. PSII

278   antenna, oxygen-evolving complex) and the inactivation of Rubisco (Sharkey, 2005;

279   Allakhverdiev *et al.*, 2008).

280   The optimal temperature for photosynthesis differs between tropical (27–33 ºC) and

281   temperate (21–32 ºC) seagrasses (Lee *et al.*, 2007*a*). Beyond this optimal window, warming

282   negatively alters the functioning of the photosynthetic apparatus. The reaction centre of

283   photosystem II (PSII) is one of the most thermally sensitive components together with

284   processes driving the electron transport chain, stromal enzymes, PSI activity, and chloroplast

285   envelopes. Damage to PSII due to thermal stress can cause a reduction of effective quantum

286   yield and maximum quantum yield, due to a significant increase in minimum fluorescence

287   level (F_0) (Marín-Guirao *et al.*, 2016, 2017, 2018; Nguyen *et al.*, 2020*a,b*). In terrestrial

288   plants, an increase in F_0 is one of the clearest indications of PSII inactivation due to thermal

289   stress (Allakhverdiev *et al.*, 2008). The key enzymes of the carbon fixation cycle (Rubisco

290   and Rubisco activase) are also highly sensitive to heat stress, as a secondary consequence of

291   disruptions in the thylakoid membrane (Salvucci & Crafts-Brandner, 2004), thereby

292   disturbing carbon fixation (Marín-Guirao *et al.*, 2016). Extreme thermal stress can result in

293   degradation of photosynthetic pigments (Chl *a* and Chl *b*) together with the accumulation of

294   chlorophyll degradation products (pheophytin *a* and pheophytin *b*), further reducing

295   photosynthetic capacity (Repolho *et al.*, 2017; Beca-Carretero *et al.*, 2018*a*; Nguyen *et al.*,

296   2020*a,b*). Seagrasses commonly activate a photo-protective mechanism associated with

297   xanthophyll cycle pigments to deal with excess energy in the photosynthetic apparatus

298   resulting from heat-stress-associated photosynthetic inhibition (Marín-Guirao *et al.*, 2016;

299 Ontoria *et al*., 2019*a*). This mechanism is linked with increased concentrations of the photo-

300 protective pigments zeaxanthin, antheraxanthin, and violaxanthin (York *et al*., 2013).

301 Plants with a history of high thermal fluctuation, or grown in warmer waters show less

302 photosynthetic thermal-induced damage than those from colder origins or more stable

303 temperature regimes [e.g. *P. oceanica* (Marín-Guirao *et al*., 2016, 2017, 2018); *Cymodocea*

304 *nodosa* (Marín-Guirao *et al*., 2018); *H. stipulacea* (Nguyen *et al*., 2020*a*); *Cymodocea*

305 *serrulata*, *Halodule uninervis* and *Z. muelleri* (Collier *et al*., 2017)]. Additionally, it has

306 recently become evident that leaf tissues of different age exhibit variable thermal plasticity

307 and activate different strategies to withstand heat stress (Ruocco *et al*., 2019*a*).

308 In *P. oceanica*, the strong induction of a complete set of genes encoding functional and

309 structural proteins of the thylakoid electron transport chain may be part of the molecular

310 mechanisms underlying the enhanced photosynthetic stability of seagrasses in response to

311 heat stress (Marín-Guirao *et al*., 2017). This strong transcriptomic reprogramming could

312 favour the turnover of relevant parts of the photosynthetic apparatus, enabling correct

313 electron flow and thus protecting the thylakoid membranes from heat impairment.

314 Together with impacts on photosynthesis, warming enhances respiration rates in seagrasses

315 resulting in a carbon imbalance (Lee *et al*., 2007*a*; Marín-Guirao *et al*., 2016, 2018; Yaping

316 *et al*., 2019). In most cases, the respiration rate of the above-ground part of the plant is higher

317 in comparison to the below-ground parts (Collier *et al*., 2017). The increase in above- to

318 below-ground biomass ratio during thermal stress seen in many seagrass species may

319 represent a defensive mechanism to lower the impact of thermal-induced elevated respiration

320 (Collier, Uthicke & Waycott, 2011; Olsen *et al*., 2012; Marín-Guirao *et al*., 2018).

321

322 (*b*) *Biochemical responses*

323   Modification of cell membrane fluidity is a common response of plants under stressful

324   conditions including thermal stress. When exposed to increased temperatures, the viscosity of

325   the lipid bilayer of cell membranes changes, leading to increased membrane fluidity, which

326   can potentially affect the function of molecules embedded in or attached to the membrane

327   (e.g. the water-splitting complex bonded to the thylakoid membrane). The ability to adjust the

328   fatty acid content and composition of cell membranes plays a central role in the modification

329   of membrane fluidity to cope with temperature changes. An increase in saturated fatty acid

330   content makes the membrane less fluid and more stable under increased temperatures (Gaur

331   & Sharma, 2014). Seagrasses can increase the amount of saturated fatty acid and decrease the

332   number of unsaturated fatty acids, thus maintaining membrane fluidity in response to thermal

333   stress (Beca-Carretero *et al.*, 2018*b*). Beca-Carretero *et al.* (2018*b*) showed that (1)

334   seagrasses from a warm climate (southwest Mediterranean) were able to adjust their lipid

335   components rapidly in response to rising temperatures compared with their counterparts from

336   the colder northwest Mediterranean, and (2) the fast-growing *C. nodosa* had a greater

337   capacity to manipulate its lipid components compared with the slow-growing *P. oceanica*.

338   Furthermore, modification of lipid content, ultrastructure, and microtubule organization all

339   play an important role in stabilizing cell membrane fluidity under thermal stress conditions

340   (Koutalianou, Orfanidis, & Katsaros, 2016).

341   In thermal stress conditions, most terrestrial plants increase the storage of soluble and

342   insoluble (starch) sugars to maintain a stable energy supply, membrane function, and to

343   reduce the impact of increased respiration rates (Guy *et al.*, 2007). Similarly, both tropical

344   (*Halodule wrightii* and *Thalassia testudinum*; Koch *et al.*, 2007) and temperate seagrasses (*P.*

345   *oceanica* and *C. nodosa*; Marín-Guirao *et al.*, 2018) significantly increased their sugar

346   content in response to increased water temperature. Only the plants from warm regions were

347   able to re-allocate additional carbohydrate content from leaves (higher respiration rate) to

348 rhizomes (lower respiration rate). This mechanism reduces the negative impact of thermal-

349 enhanced respiration, allowing the plants to survive better under elevated thermal stress

350 (Marín-Guirao *et al.*, 2018). A comparison of the results from Koch *et al.* (2007) and Marín-

351 Guirao *et al.* (2018) show that the tropical seagrasses *H. wrightii* and *T. testudinum* were

352 better able to manage respiration stress through manipulation of carbohydrate content

353 compared with the temperate species *C. nodosa* and *P. oceanica*.

354

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

356 (*a*) *Morphological responses*

357 Warming has a strong effect on seagrass growth rates (Collier *et al.*, 2011; Olsen *et al.*, 2012;

358 Collier & Waycott, 2014; Hammer *et al.*, 2018; Kim *et al.*, 2019; Marín-Guirao *et al.*, 2018;

359 Nguyen *et al.*, 2020*a,b*), leaf traits (York *et al.*, 2013; Nguyen *et al.*, 2020*a*), and leaf/shoot

360 number (Mayot, Boudouresque & Leriche, 2005; Nejrup & Pedersen, 2008; Beca-Carretero

361 *et al.*, 2018*a*; Nguyen *et al.*, 2020*a*). While modification of the above-ground part can result

362 in a reduction of above- to below-ground biomass ratio (York *et al.*, 2013; Collier *et al.*,

363 2017; Marín-Guirao *et al.*, 2018), warming can also increase the above- to below-ground

364 biomass ratio in rapid-growing seagrass species (see Collier *et al.*, 2011; Marín-Guirao *et al.*,

365 2018), reducing the biomass of non-photosynthetic (below-ground) tissues and increasing

366 photosynthetic biomass to offset the negative impacts of heat stress-enhanced respiration (see

367 also Fig. 2).

368

369 (*b*) *Population responses*

370 In response to ocean warming, seagrass meadows can acclimatize or adapt to environmental

371 changes (i.e. acclimation/adaptation: 1 → 2 in Fig. 3). Seagrass meadows that normally

372 experience large fluctuations in environmental parameters such as temperature, light, etc. are

373   more likely to be able to survive ocean warming (Massa *et al.*, 2009; Collier *et al.*, 2011;

374   Marín-Guirao *et al.*, 2018; Soissons *et al.*, 2018). In addition, the resilience of seagrass

375   meadows depends on the genetic diversity of the population (Williams, 2001; Hughes &

376   Stachowicz, 2004; Ehlers, Worm & Reusch, 2008). There is some evidence of local

377   adaptation both in adjacent and distant meadows, and therefore it is difficult to generalize the

378   effects observed in specific populations (Jueterbock *et al.*, 2016; Marín-Guirao *et al.*, 2016,

379   2018).

380   In monospecific populations, plant responses to warming can be delayed and can be genotype

381   specific (Reynolds *et al.*, 2016*a*). During this recovery phase, the genotypic diversity of

382   natural populations determines their resilience to MHWs in term of both the immediate

383   response and recovery (Ehlers *et al.*, 2008; Reusch *et al.*, 2005). In meadows composed of

384   different species, co-occurring species can change in relative abundance due to different heat

385   sensitivities (Richardson, Lefcheck & Orth, 2018) or differ in their ability to recover and

386   recolonize after the perturbation (Nowicki *et al.*, 2017). These changes can affect the

387   structure and function of seagrass ecosystems and their resilience. Ocean warming usually

388   favours small- and medium-sized species at the expense of larger species, reduces meadows

389   structure, and decreases function and resilience as seen in the case of the small seagrass *H.*

390   *stipulacea* (Winters *et al.*, 2020).

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

392   sexual reproduction and seed dispersal (escape in space and time: 1➔3 in Fig. 3). Warming

393   induces flowering in some species (Diaz-Almela, Marbà & Duarte, 2007; Ruiz *et al.*, 2018)

394   and advances the onset of flowering in other cases (Blok, Olesen & Krause-Jensen, 2018;

395   Marín-Guirao *et al.*, 2019). In the case of the clonal and long-lived *P. oceanica*, flowering

396   has been linked to a heat stress response with potential adaptive consequences (Marín-Guirao

397   *et al.*, 2019). Through sexual reproduction, warming induces an increase in genetic diversity

398 of seagrass populations, thus potentially sustaining the resilience of that seagrass meadow

399 (Massa *et al.*, 2009; Collier *et al.*, 2011; Marín-Guirao *et al.*, 2018; Soissons *et al.*, 2018).

400 Sexual reproduction provides seagrasses with an escape mechanism not only in space, but

401 also in time. In some seagrass species, their seeds have a resting stage, which can last up to

402 two years (e.g. *Zostera*, *Halodule* and *Syringodium*; reviewed by Orth *et al.*, 2000). In other

403 species, seagrass seeds can be dispersed over long distances by floating fruits (e.g. up to 55

404 km for for *P. australis*; Ruiz-Montoya *et al.*, 2012) or by mega-herbivores like dugongs

405 (*Dugong dugon*) and green sea turtles (*Chelonia mydas*) which can help to spread seagrass

406 seeds as far as 650 km away from the parental plants (Tol *et al.*, 2017). These dormancy and

407 dispersal mechanisms can potentially provide an avenue of escape for seagrasses from other

408 environmental stressors.

409 In some cases, when the environmental temperatures are too extreme, they can be deleterious

410 (i.e. die-off: 1 → 4 in Fig. 3). Massive die-offs of seagrasses due to ocean warming,

411 especially after MHWs, have been reported recently (Marbà & Duarte, 2010; Arias-Ortiz *et*

412 *al.*, 2018; Strydom *et al.*, 2020). Increased mortality due to warming has been observed in

413 adult plants and also in seedlings (Olsen *et al.*, 2012; Guerrero-Meseguer, Marín & Sanz-

414 Lázaro, 2017; Hernán *et al.*, 2017; Pereda-Briones, Terrados & Tomas, 2019). After such

415 massive mortality, in some cases seagrass meadows can recover naturally, although such

416 recovery can take decades, especially for slow-growing species (O'Brien *et al.*, 2018). For

417 example, after the acute MHW that affected the coastline of Western Australia in the austral

418 summer of 2010/2011, recovery of the seagrass *Amphibolis antarctica* was still partial 5

419 years post-MHW (Strydom *et al.*, 2020) while no seed production was recorded in the

420 disturbed *P. australis* meadow until 2016–2017 (Kendrick *et al.*, 2019). Recurrent MHWs

421 can further increase plant mortality in already impacted populations, hampering their

422 recovery and jeopardizing their survival (Marbà & Duarte, 2010).

423   After a local extinction, the same seagrass population can potentially recolonize its former

424   space by asexual reproduction (i.e. vegetative recruitment) of acclimatized/adapted plants,

425   and/or by sexual reproduction through seed dispersal and seed dormancy (i.e. re-colonization:

426   4→2 in Fig. 3) (Diaz-Almela *et al*., 2007; Blok *et al*., 2018; Ruiz *et al*., 2018; Marín-Guirao

427   *et al*., 2019). This phenomenon has been documented following physical disturbance (Olesen

428   *et al*., 2004), warm-induced anoxia events (Plus, Deslous-Paoli & Dagault, 2003), or

429   microalgal blooms (Lee *et al*., 2007*b*). Importantly, while relatively slow-growing seagrasses

430   [e.g. *Thalassia hemprichii* and *Enhalus acoroides* (Olesen *et al*., 2004) and *Z. marina* (Lee *et*

431   *al*., 2007*b*; Plus *et al*., 2003)] tend to recolonize through sexual reproduction, faster-growing

432   seagrasses [e.g. *Cymodocea rotundata* and *H. uninervis* (Olesen *et al*., 2004)], tend to

433   undergo vegetative recolonization. Small- and medium-sized species often grow rapidly and

434   can quickly re-occupy an area after heat stress.

435   On the other hand, the disappearance of local populations of seagrasses due to ocean

436   warming can create an empty niche for colonization by new thermally tolerant species (new

437   colonization: 4→5 in Fig. 3). The rapid expansion of the tropical seagrass *H. stipulacea* in the

438   Mediterranean is an example of this phenomenon (Lipkin, 1975; Gambi, Barbieri & Bianchi,

439   2009). Given that the invasive *H. stipulacea* has expanded rapidly throughout coastal areas of

440   the Caribbean Sea within less than 20 years (Willette & Ambrose, 2012; Steiner & Willette,

441   2015), the distribution of this species in the Mediterranean has been predicted to accelerate in

442   future (Georgiou *et al*., 2016; Beca-Carretero *et al*., 2020; Nguyen *et al*., 2020*a*).

443   Optimistically, new colonizations by thermally tolerant species could provide alternative

444   ecosystem services, including carbon sinks (even if less successfully; e.g. *H. stipulacea*, see

445   Fig. 3) potentially counterbalancing service loss due to the extinction of the local temperate

446   seagrasses (Apostolaki *et al*., 2019).

447 Finally, in an era of rapid ocean change, the future of seagrasses is, indeed, difficult to

448 forecast (i.e. 2→4 & 5→4 in Fig. 3). Although some thermal-adapted/thermal-tolerant

449 seagrasses could potentially survive and even benefit from ocean warming in the near future

450 (Saha *et al.*, 2019; Nguyen *et al.*, 2020*a*), the existence of these species/populations may be

451 challenged due to the on-going increased frequency of extreme climatic events and human-

452 induced impacts on the marine environment (Ralph *et al.*, 2007; Oliver *et al.*, 2019).

453 However, seagrass management and restoration could effectively contribute to sustaining

454 these seagrasses and their services into the future (Ramesh *et al.*, 2019; Valdez *et al.*, 2020).

455 Will warm-adapted/thermal-tolerant seagrasses survive future ocean change? To the best of

456 our knowledge, an answer to this question remains open.

457

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

459 Warming can switch seagrass ecosystems from autotrophic to heterotrophic (Burkholz,

460 Duarte & Garcias-Bonet, 2019) and enhance CO_2 together with methane fluxes from

461 meadows into the atmosphere (Burkholz, Garcias-Bonet & Duarte, 2020), not only reducing

462 the ability of this ecosystem to buffer climate warming, but also contributing to it (see Fig. 3).

463 After the massive mortality of seagrasses in Shark Bay (Australia), substantial quantities of

464 CO_2 were released to the atmosphere, contributing to the greenhouse effect (Arias-Ortiz *et*

465 *al.*, 2018). A trophic transformation is not always the result of ocean warming, but will

466 depend on seagrass species, co-occurring stressors (Macreadie & Hardy, 2018), and

467 sometimes the diversity of seagrass meadows (Burkholz *et al.*, 2019). Warming threatens the

468 distribution of large and long-lived species of seagrass [e.g. *P. oceanica* (Marbà & Duarte,

469 2010; Jordà *et al.*, 2012)], favouring the expansion of some small rapid-growing species [e.g.

470 *H. stipulacea* (Georgiou *et al.*, 2016; Nguyen *et al.*, 2020*a*)]. Thus, warming is accelerating

471 the tropicalization of temperate meadows (Hyndes *et al.*, 2016). When the ecosystem

472 functions of seagrasses depend strongly on their primary production (i.e. their biomass), a

473 switch from large species to small species due to warming could significantly reduce their

474 value in terms of ecosystem services as well as blue carbon storage (blue carbon is the carbon

475 stored in coastal and marine ecosystems).

476 Globally, seagrass meadows represent over 20% of nursery habitats for the 25 most important

477 fishery species (Unsworth *et al.*, 2019). Therefore, loss of seagrass meadows negatively

478 impacts global fisheries, the economy, and coastal communities that rely on fishing for food

479 and employment (Tuya, Haroun & Espino, 2014; Unsworth *et al.*, 2019).

480 Worldwide, seagrasses protect coastlines from the impact of waves and storms (Guannel *et*

481 *al.*, 2016). Nevertheless, it is important to note that the coastal defence service of seagrasses

482 mostly depends on some large, long-lived species (e.g. *Z. marina* and *P. oceanica*). Warming

483 threatens the existence of these species and enhances tropicalization with their replacement

484 by small, seasonal species, which have a much lower capacity for coastal protection.

485 Warming-induced seagrass declines can potentially alter neighbouring habitat-formers, such

486 as corals (Bulleri *et al.*, 2018). Where seagrasses grow alongside corals (e.g. Gulf of Aqaba,

487 Israel; Winters *et al.*, 2017), the disappearance of seagrasses has led to: (1) incremented

488 sediment re-suspension and nutrients in the water column resulting in algal blooms (Genin,

489 Lazar & Brenner, 1995); (2) enhanced decalcification of corals as a consequence of increased

490 ocean acidification (Hoegh-Guldberg *et al.*, 2007); (3) a reduction in biodiversity as some

491 reef fish feed in nearby seagrass meadows (Beck *et al.*, 2001); and (4) increased prevalence

492 of pathogens (Lamb *et al.*, 2017). Warming, therefore, will not only affect seagrass habitats

493 but also other nearby habitat-former species such as coral reefs.

494

495 **(5) Combined effects of warming and other stressors**

496 Under natural conditions, environmental stressors do not occur individually, but concurrently

497 and synergistically (Sandifer & Sutton-Grier, 2014). Hence, studying the interaction of ocean

498 warming with other stressors is crucial for the comprehensive and precise understanding of

499 seagrass responses to their changing environment (Gunderson, Armstrong & Stillman, 2016).

500

501 (*a*) *Warming and salinity changes*

502 Changes in salinity are recognized as a major factor forcing the evolutionary trajectory of

503 seagrasses, conditioning their distribution, ecology, and biology (Kuo & Den Hartog, 2000).

504 It is among the most challenging factors for seagrasses to tolerate (Olsen *et al.*, 2016), as is

505 also the case for terrestrial plants. Global warming causes ice melting and sea-level rise, and

506 an increase in watershed runoff, reducing salinity in some areas (Nicholls & Cazenave,

507 2010), but warmer temperatures are also increasing salinity in semi-isolated oceans such as

508 the Mediterranean Sea (Borghini *et al.*, 2014). Increased salinity in seagrass habitats can also

509 occur as a consequence of brine discharge into coastal waters from desalination plants

510 (Touchette, 2007). Seawater desalination is a growing industry in several regions that are

511 now experiencing water scarcity (Lattemann & Höpner, 2008); brine discharge can have a

512 negative impact on seagrass populations (Ruíz, Marín-Guirao & Sandoval-Gil, 2009;

513 Sandoval-Gil *et al.*, 2014). Generally, seagrasses are tolerant to a range of salinities.

514 Nonetheless, increased seagrass mortality in response to warming is greater at low salinity

515 levels (i.e. below 15 PSU) (Nejrup & Pedersen, 2008; Kaldy & Shafer, 2013; Collier *et al.*,

516 2014; Salo & Pedersen, 2014). Thus, the combined effects of ocean warming and salinity

517 changes (especially lower salinity levels) is a concern.

518 The synergistic effects of salinity and temperature cannot be generalized among different

519 species or populations. In fact, seagrass responses to stressors such as salinity changes

520 depend on plasticity and local adaptation (Pazzaglia *et al.*, 2021). Kaldy & Shafer (2013)

521 showed, for example, intraspecific differences between populations: northern *Zostera*

522 *japonica* plants, which experienced a higher salinity range at Padilla Bay, were less resilient

523 to heat stress than their counterparts growing at the southern limit of the species range (Coos

524 Bay) that experienced a lower salinity range. Interspecific differences related to divergent

525 responses to warming and salinity have been identified in the seagrass species *Halophila*

526 *ovalis*, *H. uninervis*, and *Z. muelleri* (Collier *et al.*, 2014). Moreover, the combined effects of

527 temperature and salinity not only affects adult plants, but also induces mortality in seagrass

528 seedlings, which can greatly influence the adaptation and resilience of seagrass meadows

529 (Salo & Pedersen, 2014).

530

531 (*b*) *Warming and light limitation*

532 One of the most widespread threats to seagrasses is light limitation due to anthropogenic

533 activities. Changes in sedimentation regime, nutrient loading with subsequent algal blooms,

534 and dredging all cause water turbidity (e.g. De Boer, 2007). Widespread seagrass die-off has

535 been attributed to reduced water clarity (Walker & McComb, 1992; Ralph *et al.*, 2007).

536 Seagrasses can be distributed along wide depth gradients with different light regimes (in

537 quality and quantity). The impact of thermal stress is likely to be more severe in plants under

538 conditions in which there is light limitation (Collier *et al.*, 2011; York *et al.*, 2013; Kim *et al.*,

539 2019). Having enough light for photosynthesis enables plants to maintain a positive

540 energy/carbon balance when increased temperature enhances respiration. Thus under

541 conditions of reduced light availability, seagrasses show reduced thermal tolerance and are

542 more prone to suffer from heat stress during MHWs. For example, the Australian species *H.*

543 *uninervis* and *Z. muelleri* require saturating light levels to respond positively to increasing

544 temperatures (Collier *et al.*, 2011). This highlights the importance of maintaining and

545 improving water quality to enhance the resilience of seagrass to climate warming. The

546 interactive effects of light and temperature have been shown to be weaker than for each factor

547 separately, and temperature seems to play a dominant role in this combination (York *et al.*,

548 2013; Kim *et al.*, 2019). For *P. oceanica*, Hendriks *et al.* (2017) identified the roles of light

549 and temperature to be far more critical to seagrass health than CO_2 levels. In fact, the

550 negative effects of ocean warming are forecast to outweigh any potentially positive effect of

551 ocean acidification on some seagrass species (Zimmerman, Hill & Gallegos, 2015; Repolho

552 *et al.*, 2017; Collier *et al.*, 2018).

553

554 (*c*) *Warming and sulphide stress*

555 Sulphate reduction is a fundamental process that occurs in terrestrial water-saturated soils as

556 well as marine sediments, where gas exchanges are very limited, resulting in the natural

557 accumulation of sediment sulphide (Holmer & Hasler-Sheetal, 2014). Generally, sulphide is

558 toxic to living organisms including seagrasses, as it can strongly impact cellular enzymatic

559 processes (Raven & Scrimgeour, 1997). To survive in the highly toxic sulphide environment

560 of marine sediments, seagrasses have developed sophisticated mechanisms to transport

561 oxygen from the leaves into the rhizosphere to maintain an aerobic environment, protecting

562 their tissues from the intrusion of sulphide (Borum *et al.*, 2007). Warming can accelerate

563 microbial activities, in turn increasing sulphate reduction, and consequently, sulphide

564 concentration in the sediments (Frederiksen *et al.*, 2007; Marbà *et al.*, 2007). This

565 phenomenon, when accompanied by warming, can enhance sulphide intrusion into seagrass

566 tissue with the potential further to disrupt carbon metabolism and result in plant starvation

567 and mortality (Robblee *et al.*, 1991; Koch *et al.*, 2007; Holmer & Hasler-Sheetal, 2014).

568 There is evidence that warming can enhance sulphide stress in seagrasses (Garcias-Bonet *et*

569 *al.*, 2008; García *et al.*, 2012, 2013). Importantly, the sensitivity of seagrasses to the

570 combined effects of warming and sulphide will be species specific (Koch *et al.*, 2007) and

571   depth specific (García *et al.*, 2013). However, with on-going ocean warming, even deep

572   seagrasses are likely to be negatively impacted by sulphide stress in the future (García *et al.*,

573   2013).

574

575   (*d*) *Warming and eutrophication*

576   The rapid development of agricultural activities across the globe has released huge nutrient

577   loads into rivers and coastal waters triggering eutrophication that leads to catastrophic

578   consequences for sessile marine organisms (Rabalais, Harper & Turner, 2001; Rabalais *et al.*,

579   2009; Diaz & Rosenberg, 2008). Nutrient enrichment also induces overgrowth of

580   macroalgae, phytoplankton, and seagrass epiphytes, leading to light reduction and impacting

581   seagrass growth and survival. Indeed, together with ocean warming, eutrophication is

582   recognized as one of the main stressors to seagrasses globally [see reviews by Burkholder *et*

583   *al.* (2007) and Lee *et al.* (2007*a*)]. Previous studies have demonstrated that the combined

584   effect of warming and nutrient enrichment can vary. For instance, nutrient enrichment can

585   accelerate the negative impact of warming on some seagrass species, such as *Zostera*

586   *capensis*, *C. nodosa* and *P. oceanica* (Mvungi & Pillay, 2019; Ontoria *et al.*, 2019*a,b*).

587   Pazzaglia *et al.* (2020) investigated the combined effects of warming and nutrient enrichment

588   on different *P. oceanica* populations with different nutrient load histories. Plants growing in

589   chronically eutrophic conditions were more prone to suffer from thermal stress than plants

590   from populations living under oligotrophic/pristine conditions. Additionally, the

591   accumulation of drift algae following an increase in seawater temperature and eutrophication

592   may also affect seagrasses negatively. Drift algae are shallow-water unattached macroalgae

593   that often bloom massively in eutrophication conditions and can deleteriously impact

594   seagrass meadows (McGlathery, 2001). Holmer, Wirachwong & Thomsen (2011)

595   investigated the combined effects of drift algae and warming, showing that warming/nutrient-

596   induced higher densities of drifting algae can additively and synergistically extend the

597   negative impacts of warming on the seagrass species *H. ovalis* and suggesting that drift algae

598   should be removed to protect seagrass meadows. By contrast, Egea *et al.* (2018) showed that

599   the combination of warming, nutrient enrichment, and acidification could have positive

600   effects on the seagrass *C. nodosa*, and thus predicted that this species could benefit from

601   future ocean change. Interestingly, warming and nutrient enrichment could also reduce

602   grazing pressure on seagrasses, as in the case of the sea urchin *Amblypneustes pallidus* on the

603   seagrass *A. antarctica* (Burnell *et al.*, 2013).

604

605   (*e*) *Warming and herbicides*

606   The increase in coastal agriculture activities has led to the runoff of large quantities of

607   agricultural herbicides (e.g. diuron, atrazine, hexazinone, tebuthiuron and ametryn) into

608   coastal marine environments (Smith *et al.*, 2012). These herbicides can have a strong impact

609   on PSII of seagrasses, not only damaging seagrass performance but also increasing their

610   susceptibility to other stressors (Flores *et al.*, 2013; Negri *et al.*, 2015; Wilkinson *et al.*,

611   2015). To date, only one study has investigated the combined effects of warming and a

612   herbicides (diuron), which showed strong antagonistic effects of combined stressors on the

613   tropical seagrass species *H. ovalis* (Wilkinson *et al.*, 2017).

614   The impact of herbicides on seagrasses thus will become a greater concern with ocean

615   warming. Additionally, we note that most studies investigating the effects of herbicides on

616   seagrass species targeted the Great Barrier Reef area (Lewis *et al.*, 2009; Flores *et al.*, 2013;

617   Negri *et al.*, 2015; Wilkinson *et al.*, 2015, 2017). Globally, the use of herbicide-resistant

618   genetically modified (GM) crops is still controversial, thus conventional agricultural

619   production remains dependent on herbicides to control weeds (Green, 2014). Consequently,

620   herbicides still pose a great potential risk for seagrasses across the globe, and future studies to

621 understand the effects of herbicides on seagrasses from other regions of the world are highly

622 encouraged.

623

624 (*f*) *Warming and pathogens*

625 Massive losses of seagrass meadows have been documented across the globe after outbreaks

626 of seagrass diseases (see review by Sullivan *et al.*, 2018). Human-induced environmental

627 changes, especially ocean warming, can enhance the susceptibility of seagrasses to these

628 biotic threats by promoting the development of seagrass diseases and reducing their resilience

629 (Burge & Hershberger, 2020; Sullivan *et al.*, 2018). 'Wasting disease', caused by the protist

630 *Labyrinthula* sp., is the best studied example in seagrasses [e.g. *Phytophthora gemini* and

631 *Halophytophthora zostera* (reviewed by Sullivan *et al.*, 2018)]. There was a wasting disease

632 epidemic in the seagrass *Z. marina* along the Atlantic coasts of North America and Europe

633 during the 1930s, causing the extinction of as much as 90% of the total *Z. marina* population,

634 and leading to profound ecological impacts within the coastal ecosystem (Renn, 1936).

635 Nevertheless, experimental studies have also shown that an increase in ocean temperature

636 may limit infections of seagrass diseases. For example, recent studies on two Mediterranean

637 seagrass species, *P. oceanica* and *C. nodosa*, suggested that temperatures above 28 ºC inhibit

638 the growth of *Labyrinthula* sp., thus reducing the pathogenic pressure on this seagrass (Olsen

639 *et al.*, 2014; Olsen & Duarte, 2015). In addition, Brakel *et al.* (2019) tested the effect of this

640 protist on *Z. marina* in a predicted scenario with a combination of heat stress, light limitation,

641 and different salinity levels, confirming the predicted reduction in pathogen pressure on

642 seagrasses in response to predicted future warming. These results provide a more optimistic

643 view about the future of seagrasses, particularly in the context of seagrass–pathogen

644 dynamics. However, note that ocean warming may facilitate the presence and virulence of

645 other marine diseases (both viruses and bacteria) (Burge & Hershberger, 2020). Given that

646 there remain few studies on this topic and that seagrass diseases remain virtually unexplored

647 [see review by Sullivan *et al.* (2018) for examples of other diseases in seagrasses], we

648 recommend that future studies should attempt to broaden our understanding of the

649 relationship between warming and pathogens in seagrasses.

650

651 (*g*) *Warming and herbivores*

652 The plant-herbivore interaction is fundamental for both parties not only from an evolutionary

653 point of view (Fritz & Simms, 1992), but also from its role in sustaining ecosystem dynamics

654 (Bakker *et al.*, 2016). In the presence of ocean warming, increases in seawater temperature

655 will affect seagrasses and their herbivores not only individually, but also interactively. In

656 general, warming increases the metabolic rate of herbivores, consequently enhancing grazing

657 pressure (Hillebrand *et al.*, 2009). Nevertheless, studies on the interactions of seagrasses with

658 herbivores in response to temperature changes revealed a complex situation (Burnell *et al.*,

659 2013; Garthwin, Poore & Vergés, 2014; Pagès *et al.*, 2018; Buñuel *et al.*, 2021; Guerrero-

660 Meseguer, Marín & Sanz-Lázaro, 2020). Pagès *et al.* (2018) studied the sea urchin

661 *Paracentrotus lividus* that, in some cases [e.g. *P. oceanica* beds on the northeast Spanish

662 coast and in the south of France (Prado *et al.*, 2007)], consumes about 17% of seagrass

663 production annually, showing that warming could weaken herbivore pressure on two

664 Mediterranean seagrass species, *P. oceanica* and *C. nodosa* (Pagès *et al.*, 2018). By contrast,

665 Burnell *et al.* (2013) showed that a temperature increase could enhance grazing pressure of

666 *Amblypneustes pallidus* on the seagrass *A. antarctica*; however, nutrient enrichment was

667 shown to reduce grazing pressure in combination with ocean warming and acidification.

668 Similarly, a recent study on *P. oceanica* and its main fish herbivore *Sarpa salpa*

669 demonstrated that warming can make the seagrass more palatable, increasing the growth rate

670 of the fish (especially in the larval stage), and thus potentially intensifying herbivory pressure

671   (Buñuel *et al*., 2021). The combined effects of warming and herbivores also affect seagrass

672   seedlings: Guerrero-Meseguer *et al*. (2020) found that the combined effects of MHWs and

673   overgrazing led to a greater reduction in leaf growth and increased leaf senescence of *P.*

674   *oceanica* seedlings in comparison with the effects of each factor alone. The authors suggested

675   that the combined effects of ocean warming and other stressors are likely to threaten the

676   survival of *P. oceanica* seedlings, and consequently sexual recruitment (Guerrero-Meseguer

677   *et al*., 2020). By contrast, Garthwin *et al*. (2014) conducted a simulated herbivory experiment

678   on a *Zostera muelleri* meadow warmed by the thermal plume from a power station for 30

679   years and three nearby control meadows. Their results demonstrated that the ability of *Z.*

680   *muelleri* to tolerate herbivory is not strongly affected by warming. The future of seagrass-

681   herbivore interactions in an era of ocean warming still remains unclear and deserves

682   additional attention in future studies.

683

684   **III. FUTURE PERSPECTIVES**

685   Seagrasses are facing a critical time in their evolutionary history in which their continued

686   existence will depend on our actions, including research, restoration, and management

687   activities. Below, we discuss some significant gaps in knowledge and recommend future

688   directions for seagrass studies.

689

690   **(1) Enlarging the number of species and populations studied**

691   Previous studies have shown that the effects of ocean warming are not the same for all

692   seagrass species and populations. Therefore, it remains difficult to predict the future of

693   seagrasses accurately. Most seagrass studies in the context of ocean warming come from

694   three regions: the Mediterranean Sea, USA, and Australia (Fig. 4, see online Supporting

695   Information Table S1). Most of these studies have focused on only a few seagrass species: *Z.*

696 *marina*, *P. oceanica* and *C. nodosa* (Table S2). This highlights a significant gap in our

697 understanding of how warming affects seagrasses; the vast majority of the world's seagrass

698 species have not been studied in this context to date. Future studies should focus not only on

699 additional species but also on more populations within each species to deliver a more

700 comprehensive picture of how seagrasses will respond to a future changing climate.

701 Since warming potentially interacts with many other stress factors, seagrass meadows are

702 currently under multiple anthropogenic pressures. Populations that are chronically stressed

703 (e.g. under eutrophic conditions) might have a different tolerance or ability to respond to

704 warming compared to healthy populations. There is an urgent need to explore how responses

705 to warming differ between healthy and chronically stressed populations. This knowledge will

706 be critical for improving the management and protection of valuable seagrass ecosystems by

707 managing local factors that directly affect seagrass health, potentially enhancing their

708 resilience to warming.

709

710 **(2) Developing more precise and detailed seagrass distribution maps**

711 Some seagrass species are losing habitat at a rapid rate (Robblee *et al.*, 1991; Seddon *et al.*,

712 2000; Jordà *et al.*, 2012; Marbà, Díaz-Almela & Duarte, 2014) or are being replaced by the

713 rapid expansion of other species (Gambi *et al.*, 2009; Scheibling, Patriquin, & Filbee-Dexter,

714 2018; Nguyen *et al.*, 2020*a*). Studies (Short *et al.*, 2007; Jayathilake & Costello, 2018) have

715 provided general information regarding seagrass distribution, but there are many regions that

716 remain unmapped (Assis *et al.*, 2020; McKenzie *et al.*, 2020). Building seagrass distribution

717 maps can be challenging, especially for species that have a wide distribution range with

718 different depths or inhabit mixed-species meadows. Effective methods have been developed

719 to map seagrasses (see review by McKenzie, Finkbeiner & Kirkman, 2001) and more

720 recently, a low-cost field-survey method using snorkelling and perpendicular transects

721   (Winters *et al.*, 2017) was developed at a small regional scale. Advanced technologies [e.g.

722   satellite remote sensing, Geographic Information System (GIS) technologies, camera-

723   equipped drones] have also been employed in seagrass mapping research (Barrell *et al.*, 2015;

724   Phinn *et al.*, 2018). Future work is encouraged both in developing advanced technologies and

725   in building more detailed seagrass maps across different regions of the world.

726

727   **(3) Long-term monitoring programs**

728   Many countries across the globe have implemented seagrass long-term monitoring networks

729   appropriate to their local species and habitats. Since the end of the 20th century, many

730   monitoring programs have been aggregating data to create regional and/or global monitoring

731   networks with the aim to preserve seagrass meadows and to increase scientific knowledge

732   and public awareness about these threatened and valuable ecosystems. At the global level,

733   Seagrass-Watch (http://www.seagrasswatch.org/) and SeagrassNet

734   (http://www.seagrassnet.org/) integrate hundreds of sites distributed along the coasts of

735   dozens of countries for the long-term ecological monitoring of seagrasses. In the

736   Mediterranean, the regional integration of existing networks is lacking, but initiatives are

737   currently ongoing, for instance the POSIMED project (http://posimed.org/).

738   Data from long-term seagrass monitoring programs are not only providing valuable

739   information to unravel the status and trends of natural populations at the global, regional, and

740   local scales (e.g. Thomas, Unsworth & Rasheed, 2010; Rasheed & Unsworth, 2011; de los

741   Santos *et al.*, 2019), but they are also helping in the development and execution of

742   international environmental protection policies (e.g. the Marine Strategy European

743   Directive). Seagrass monitoring programs are also recording environmental data, including

744   water temperature, to correlate seagrass decline with warming trends or extreme warming

745   events (Marbà & Duarte, 2010; Richardson *et al.*, 2018; Shields, Parrish & Moore, 2019).

746   However, ecosystem modelling and forecasting activities for seagrasses are still needed. This

747   could be facilitated by bridging global and local observations, and by linking long-term data

748   series from seagrass monitoring programs to the continuous recording of coastal

749   environmental conditions. Currently, platforms and sensor systems to measure physical,

750   chemical, geological, and biological properties are increasingly being installed in coastal

751   areas and oceanic regions worldwide [e.g. GOOS (https://www.goosocean.org/) and OOI

752   (https://oceanobservatories.org/)]. The production of high-throughput data from

753   multidisciplinary studies is a promising advance towards improving all aspects of seagrass

754   conservation, from dynamic model development to forecast validation. These are powerful

755   holistic approaches to monitoring seagrass ecosystems and their evolution in a rapidly

756   changing ocean, as well as to contribute to their effective conservation and to the

757   management of human activities in coastal areas (Capotondi *et al.*, 2019). The integration of

758   time-series data through multivariate statistics and/or machine-learning algorithms could also

759   provide promising tools to monitor coastal ecosystems in a changing climate (Danovaro *et*

760   *al.*, 2016; Crise *et al.*, 2018).

761

762   **(4) More realistic experiments in controlled conditions**

763   Many past studies suffered from experimental constraints/limitations such as using unrealistic

764   temperature levels, warming rates, experimental duration, small water volumes, or even

765   single seagrass shoots that prevented clonal integration (Bulthuis, 1987; Lee *et al.*, 2007*a*).

766   By contrast, recent experiments have become more realistic due to the development of

767   sophisticated mesocosm systems for the culture of seagrasses in optimal conditions, and their

768   use to conduct finely tuned and highly controlled experiments (Bergmann *et al.*, 2010; Marín-

769   Guirao *et al.*, 2011; Georgiou *et al.*, 2016; Cambridge *et al.*, 2017; Oscar, Barak & Winters,

770   2018; Ruocco *et al.*, 2019*b*). These new systems have enabled more robust experiments to

771 obtain not only a significant amount of knowledge in a short period but also novel results

772 (Bulthuis, 1987; Lee *et al.*, 2007*a*). In the near future, the application of more advanced

773 technologies are expected to push the boundary of seagrass research even further by enabling

774 *in situ* experiments (e.g. Egea *et al.*, 2019) and near-natural simulated environment

775 experiments (e.g. Saha *et al.*, 2019).

776

777 **(5) The study of the holobiont**

778 There is now an increasing recognition of the fundamental interactions between symbiotic

779 microorganisms (bacteria, fungi, and archaea) and their host organisms. From both an

780 ecological and evolutionary point of view, we should perhaps consider the organisms and

781 their symbiotic microorganisms not separately but together. The term 'holobiont' has been

782 used to describe this combination of the host organism and its microbiome

783 (Vandenkoornhuyse *et al.*, 2015). In terrestrial plants, the number of studies considering the

784 holobiont has increased, uncovering important functions of the microbiome in plant nutrition,

785 resistance to biotic and abiotic stresses, and evolution (Vandenkoornhuyse *et al.*, 2015). In

786 marine environments, interactions across holobionts are expected to be more flexible, with

787 faster microbial community shifts, and greater phylogenetic diversity compared to terrestrial

788 ecosystems (Dittami *et al.*, 2021). Compared with terrestrial plants, the importance of the

789 holobionts in marine ecosystems is understudied. Some pivotal investigations of seagrass–

790 bacteria interactions have suggested many important roles in providing nutrients, sustaining

791 fitness, enhancing growth, and protecting seagrasses from toxic compounds and pathogens

792 [see reviews by Ugarelli *et al.* (2017), Tarquinio *et al.* (2019) and Conte *et al.* (2021)]. In the

793 face of ocean warming, the activity of the seagrass–bacterial community in relation to carbon

794 remineralization is expected to increase, consequently reducing carbon accumulation rates in

795 seagrass meadows (Trevathan-Tackett *et al.*, 2017). Future studies of the seagrass holobiont

796   should focus on a better understanding of (1) the components of the seagrass microbiome, (2)

797   seagrass–microbiome interactions in an ecological context, and especially (3) how the

798   seagrass microbiome can help seagrasses to be more resilient to environmental changes. Such

799   studies will not only broaden our understanding of this important aspect of seagrass ecology

800   but will also be extremely useful for seagrass restoration activities, as symbiotic

801   microorganisms could potentially be used to enhance the survival of transplanted seagrasses

802   (both seedlings and adult plants).

803

804   **(6) Seagrasses as a solution to mitigate climate change**

805   Adopting the concept of Gattuso *et al.* (2018) that ocean solutions may allow us to address

806   climate change, it is essential to restore and conserve healthy seagrass meadows worldwide in

807   order to preserve the ecosystem services that they provide in mitigating climate change and

808   its associated effects. In the agriculture and food industries, the application of genetic

809   engineering has significantly improved the productivity and quality of crops and commercial

810   species (see review by Janni *et al.*, 2020). To the best of our knowledge, such approaches

811   (e.g. CRISPR/Cas9 which is short for clustered regularly interspaced short palindromic

812   repeats and CRISPR-associated protein 9) have never been applied in seagrass research. This

813   novel approach provides a promising way to select, breed, or produce genotypes that can

814   survive future harsh environmental conditions (i.e. assisted evolution; see also Bulleri *et al.*,

815   2018). Such potential super-seagrasses could help us to re-establish ecosystems in areas

816   where seagrasses have been completely destroyed due to natural and/or human-induced

817   catastrophic events. Additionally, as seagrasses growing in extreme environments (e.g. under

818   anthropogenic pressures, frequent MHWs, etc.) are expected to be more resilient to ocean

819   warming, transplantations performed using such selected plants could be extremely useful in

820   seagrass restoration (see review by Tan *et al.*, 2020). Moreover, emerging knowledge in the

821 field of thermal stress memory and epigenetic memory in seagrasses (Jueterbock *et al.*, 2020;

822 Nguyen *et al.*, 2020*b*) could yield in many potential applications in seagrass restoration.

823 Together, the application of such new approaches could support attempts to restore degraded

824 seagrass meadows effectively and sustainably at a global scale and consequently protect their

825 ecosystem services (Reynolds *et al.*, 2016*b*), thus ultimately mitigating the negative impacts

826 of climate change.

827

828 **IV. CONCLUSIONS**

829 (1) Warming strongly affects seagrasses at all levels from molecular, physiological,

830 biochemical, morphological, and population to planetary level.

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

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

833 (4) Multiple-stressor studies in seagrasses are much needed to provide deeper insights into

834 seagrass resilience, especially in an era of ocean warming.

835 (5) Significant knowledge gaps and future directions for seagrass research include: (*i*) studies

836 involving additional species and populations; (*ii*) development of more precise and detailed

837 seagrass distribution maps; (*iii*) more long-term monitoring programs; (*iv*) more realistic

838 experiments in controlled conditions; (*v*) investigation of the seagrass holobiont; and (*vi*)

839 seagrasses as a solution to mitigate climate change.

840

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847

848   **VI. REFERENCES**

849   ALLAKHVERDIEV, S.I., KRESLAVSKI, V.D., KLIMOV, V. V., LOS, D.A., CARPENTIER, R. &

850   MOHANTY, P. (2008). Heat stress: an overview of molecular responses in

851   photosynthesis. *Photosynthesis Research* **98**, *541*–550.

852   ANDERSON, T.R., HAWKINS, E. & JONES, P.D. (2016). CO_2, the greenhouse effect and global

853   warming: from the pioneering work of Arrhenius and Callendar to today's Earth System

854   Models. *Endeavour* **40**, 178–187.

855   APOSTOLAKI, E.T., VIZZINI, S., SANTINELLI, V., KABERI, H., ANDOLINA, C. &

856   PAPATHANASSIOU, E. (2019). Exotic *Halophila stipulacea* is an introduced carbon sink

857   for the Eastern Mediterranean Sea. *Scientific Reports* **9**, 9643.

858   ARIAS-ORTIZ, A., SERRANO, O., MASQUÉ, P., LAVERY, P.S., MUELLER, U., KENDRICK, G.A.,

859   ROZAIMI, M., ESTEBAN, A., FOURQUREAN, J.W., MARBÀ, N., MATEO, M.A., MURRAY,

860   K., RULE, M.J. & DUARTE, C.M. (2018). A marine heatwave drives massive losses from

861   the world's largest seagrass carbon stocks. *Nature Climate Change* **8**, 1–7.

862   DITTAMI, S.M., ARBOLEDA, E., AUGUET, J., BIGALKE, A., BRIAND, E., CARDENAS, P.,

863   CARDINI, U., DECELLE, J., ENGELEN, A.H., EVEILLARD, D., GACHON, C.M.M.,

864   GRIFFITHS, S.M., HARDER, T., KAYAL, E., KAZAMIA, E., *ET AL.* (2021). A community

865   perspective on the concept of marine holobionts: current status, challenges, and future

866   directions. *PeerJ* **9**, e10911.

867   ASSIS, J., FRAGKOPOULOU, E., FRADE, D., NEIVA, J., OLIVEIRA, A., ABECASIS, D., FAUGERON,

868   S. & SERRÃO, E.A. (2020). A fine-tuned global distribution dataset of marine forests.

869   *Scientific Data* **7**, 119.

870   BAKKER, E.S., WOOD, K.A., PAGÈS, J.F., VEEN, G.F.C., CHRISTIANEN, M.J.A., SANTAMARÍA,

871   L., NOLET, B.A. & HILT, S. (2016). Herbivory on freshwater and marine macrophytes: a

872   review and perspective. *Aquatic Botany* **135**, 18–36.

873   BARBER, B.J. & BEHRENS, P.J. (1985). Effects of elevated temperature on seasonal *in situ* leaf

874   productivity of *Thalassia testudinum* Banks ex König and *Syringodium filiforme*

875   Kützing. *Aquatic Botany* **22**, 61–69.

876   BARRELL, J., GRANT, J., HANSON, A. & MAHONEY, M. (2015). Evaluating the

877   complementarity of acoustic and satellite remote sensing for seagrass landscape

878   mapping. *International Journal of Remote Sensing* **36**, 4069–4094.

879   BARSHIS, D.J., LADNER, J.T., OLIVER, T.A., SENECA, F.O., TRAYLOR-KNOWLES, N. &

880   PALUMBI, S.R. (2013). Genomic basis for coral resilience to climate change.

881   *Proceedings of the National Academy of Sciences of the United States of America* **110**,

882   1387–1392.

883   BECA-CARRETERO, P., OLESEN, B., MARBÀ, N. & KRAUSE-JENSEN, D. (2018*a*). Response to

884   experimental warming in northern eelgrass populations: comparison across a range of

885   temperature adaptations. *Marine Ecology Progress Series* **589**, 59–72.

886   BECA-CARRETERO, P., GUIHÉNEUF, F., MARÍN-GUIRAO, L., BERNARDEAU-ESTELLER, J.,

887   GARCÍA-MUÑOZ, R., STENGEL, D.B. & RUIZ, J.M. (2018*b*). Effects of an experimental

888   heat wave on fatty acid composition in two Mediterranean seagrass species. *Marine*

889   *Pollution Bulletin* **134**, 27–37.

890   BECA-CARRETERO, P., TEICHBERG, M., WINTERS, G., PROCACCINI, G. & REUTER, H. (2020).

891   Projected rapid habitat expansion of tropical seagrass species in the mediterranean sea as

892   climate change progresses. *Frontiers in Plant Science* **11**, 1762.

893   BECK, M.W., HECK, K.L., ABLE, K.W., CHILDERS, D.L., EGGLESTON, D.B., GILLANDERS,

894   B.M., HALPERN, B., HAYS, C.G., HOSHINO, K., MINELLO, T.J., ORTH, R.J., SHEDIRAN,

895   P.F. & WEINSTEIN, M.P. (2001). The Identification, Conservation, and Management of

896   Estuarine and Marine Nurseries for Fish and Invertebrates: A better understanding of the

897   habitats that serve as nurseries for marine species and the factors that create site-specific

898   variability in nursery quality will improve conservation and management of these areas.

899   *BioScience* **51**, 633–641.

900 BEERE, H.M. (2005). Death versus survival: Functional interaction between the apoptotic and

901   stress-inducible heat shock protein pathways. *Journal of Clinical Investigation* **115**,

902   *2633*–2639.

903 BERGMANN, N., WINTERS, G., RAUCH, G., EIZAGUIRRE, C., GU, J., NELLE, P., FRICKE, B. &

904   REUSCH, T.B.H. (2010). Population-specificity of heat stress gene induction in northern

905   and southern eelgrass *Zostera marina* populations under simulated global warming.

906   *Molecular Ecology* **19**, 2870–2883.

907 BERTELLI, C.M. & UNSWORTH, R.K.F. (2014). Protecting the hand that feeds us: Seagrass

908   (*Zostera marina*) serves as commercial juvenile fish habitat. *Marine Pollution Bulletin*

909   **83**, 425–429.

910 BLOK, S.E., OLESEN, B. & KRAUSE-JENSEN, D. (2018). Life history events of eelgrass *Zostera*

911   *marina* L. populations across gradients of latitude and temperature. *Marine Ecology*

912   *Progress Series* **590**, 79–93.

913 BORGHINI, M., BRYDEN, H., SCHROEDER, K., SPARNOCCHIA, S. & VETRANO, A. (2014). The

914   Mediterranean is getting saltier. *Ocean Science Discussions* **11**, 735–752.

915 BORUM, J., SAND-JENSEN, K., BINZER, T., PEDERSEN, O. & GREVE, T.M. (2007). Oxygen

916   movement in seagrasses. In *Seagrasses: biology, ecologyand conservation,* pp. 255–270.

917   Springer.

918 BOSSDORF, O., RICHARDS, C.L. & PIGLIUCCI, M. (2008). Epigenetics for ecologists. *Ecology*

919   *Letters* **11***, 106*–115.

920 BRAKEL, J., JAKOBSSON-THOR, S., BOCKELMANN, A.C. & REUSCH, T.B.H. (2019).

Modulation of the Eelgrass – *Labyrinthula zosterae* Interaction Under Predicted Ocean Warming, Salinity Change and Light Limitation. *Frontiers in Marine Science* **6**, 268.

BULLERI, F., ERIKSSON, B.K., QUEIRÓS, A., AIROLDI, L., ARENAS, F., ARVANITIDIS, C., BOUMA, T.J., CROWE, T.P., DAVOULT, D., GUIZIEN, K., IVEŠA, L., JENKINS, S.R., MICHALET, R., OLABARRIA, C., PROCACCINI, G., *ET AL*. (2018). Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. *PLoS Biology* **16**, e2006852.

BULTHUIS, D.A. (1987). Effects of temperature on photosynthesis and growth of seagrasses. *Aquatic Botany* **27**, 27–40.

BUÑUEL, X., ALCOVERRO, T., ROMERO, J., ARTHUR, R., RUIZ, J.M., PÉREZ, M., ONTORIA, Y., RAVENTÓS, N., MACPHERSON, E. & TORRADO, H. (2021). Warming intensifies the interaction between the temperate seagrass *Posidonia oceanica* and its dominant fish herbivore *Sarpa salpa*. *Marine Environmental Research* **165**, 105237.

BURGE, C.A. & HERSHBERGER, P.K. (2020). Climate change can drive marine diseases. In *Marine Disease Ecology*, pp. 83. Oxford University Press, USA.

BURKHOLDER, J.M., TOMASKO, D.A. & TOUCHETTE, B.W. (2007). Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology* **350**, 46–72.

BURKHOLZ, C., DUARTE, C.M. & GARCIAS-BONET, N. (2019). Thermal dependence of seagrass ecosystem metabolism in the Red Sea. *Marine Ecology Progress Series* **614**, 79–90.

BURKHOLZ, C., GARCIAS-BONET, N. & DUARTE, C.M. (2020). Warming enhances carbon dioxide and methane fluxes from Red Sea seagrass (*Halophila stipulacea*) sediments. *Biogeosciences* **17**, 1717–1730.

BURNELL, O.W., RUSSELL, B.D., IRVING, A.D. & CONNELL, S.D. (2013). Eutrophication offsets increased sea urchin grazing on seagrass caused by ocean warming and

946   acidification. *Marine Ecology Progress Series* **485**, 37–46.

947   CAMBRIDGE, M.L., ZAVALA-PEREZ, A., CAWTHRAY, G.R., MONDON, J. & KENDRICK, G.A.

948   (2017). Effects of high salinity from desalination brine on growth, photosynthesis, water

949   relations and osmolyte concentrations of seagrass *Posidonia australis*. *Marine Pollution*

950   *Bulletin* **115**, 252–260.

951   CAMPBELL, S.J., MCKENZIE, L.J. & KERVILLE, S.P. (2006). Photosynthetic responses of seven

952   tropical seagrasses to elevated seawater temperature. *Journal of Experimental Marine*

953   *Biology and Ecology* **330**, 455–468.

954   CAPOTONDI, A., JACOX, M., BOWLER, C., KAVANAUGH, M., LEHODEY, P., BARRIE, D.,

955   BRODIE, S., CHAFFRON, S., CHENG, W. & DIAS, D.F. (2019). Observational Needs

956   Supporting Marine Ecosystems Modeling and Forecasting: From the Global Ocean to

957   Regional and Coastal Systems. *Frontiers in Marine Science* **6**, 623.

958   CECCHERELLI, G., OLIVA, S., PINNA, S., PIAZZI, L., PROCACCINI, G., MARÍN-GUIRAO, L.,

959   DATTOLO, E., GALLIA, R., LA MANNA, G., GENNARO, P., COSTA, M.M., BARROTE, I.,

960   SILVA, J. & BULLERI, F. (2018). Seagrass collapse due to synergistic stressors is not

961   anticipated by phenological changes. *Oecologia* **186**, 1137–1152.

962   CHEFAOUI, R.M., DUARTE, C.M. & SERRÃO, E.A. (2018). Dramatic loss of seagrass habitat

963   under projected climate change in the Mediterranean Sea. *Global Change Biology* **24**,

964   4919–4928.

965   CHINNUSAMY, V. & ZHU, J.-K. (2009). Epigenetic regulation of stress responses in plants.

966   *Current Opinion in Plant Biology* **12**, 133–139.

967   CHRISTIDIS, N., JONES, G.S. & STOTT, P.A. (2015). Dramatically increasing chance of

968   extremely hot summers since the 2003 European heatwave. *Nature Climate Change* **5**,

969   46–50.

970   COLLIER, C.J., LANGLOIS, L., OW, Y., JOHANSSON, C., GIAMMUSSO, M., ADAMS, M.P.,

971   O'BRIEN, K.R. & UTHICKE, S. (2018). Losing a winner: thermal stress and local

972   pressures outweigh the positive effects of ocean acidification for tropical seagrasses.

973   *New Phytologist* **219,**1005–1017.

974   COLLIER, C.J., OW, Y.X., LANGLOIS, L., UTHICKE, S., JOHANSSON, C.L., O'BRIEN, K.R.,

975   HREBIEN, V. & ADAMS, M.P. (2017). Optimum temperatures for net primary

976   productivity of three tropical seagrass species. *Frontiers in plant science* **8**, 1446.

977   COLLIER, C.J., UTHICKE, S. & WAYCOTT, M. (2011). Thermal tolerance of two seagrass

978   species at contrasting light levels: Implications for future distribution in the Great

979   Barrier Reef. *Limnology and Oceanography* **56**, 2200–2210.

980   COLLIER, C.J., VILLACORTA-RATH, C., TAKAHASHI, M. & WAYCOTT, M. (2014). Seagrass

981   proliferation precedes mortality during hypo-salinity events: a stress-induced

982   morphometric response. *PLoS One* **9**, e94014.

983   COLLIER, C.J. & WAYCOTT, M. (2014). Temperature extremes reduce seagrass growth and

984   induce mortality. *Marine Pollution Bulletin* **83**, 483–490.

985   COMA, R., RIBES, M., SERRANO, E., JIMÉ NEZ, E., SALAT, J. & PASCUAL, J. (2009). Global

986   warming-enhanced stratification and mass mortality events in the Mediterranean.

987   *Proceedings of the National Academy of Sciences of the United States of America* **106**,

988   6176–6181.

989   CONTE, C., ROTINI, A., MANFRA, L., D'ANDREA, M.M., WINTERS, G. & MIGLIORE, L. (2021).

990   The seagrass holobiont: what we know and what we still need to disclose for its possible

991   use as an ecological indicator. *Water* **13**, 406.

992   COSTANZA, R., DE GROOT, R., SUTTON, P., VAN DER PLOEG, S., ANDERSON, S.J.,

993   KUBISZEWSKI, I., FARBER, S. & TURNER, R.K. (2014). Changes in the global value of

994   ecosystem services. *Global Environmental Change* **26**, 152–158.

995   CRISE, A., RIBERA D'ALCALÀ, M., MARIANI, P., PETIHAKIS, G., ROBIDART, J., IUDICONE, D.,

996   BACHMAYER, R. & MALFATTI, F. (2018). A conceptual framework for developing the

997   next generation of Marine OBservatories (MOBs) for science and society. *Frontiers in*

998   *Marine Science* **5**, 318.

999   DANOVARO, R., CARUGATI, L., BERZANO, M., CAHILL, A.E., CARVALHO, S., CHENUIL, A.,

1000   CORINALDESI, C., CRISTINA, S., DAVID, R. & DELL'ANNO, A. (2016). Implementing and

1001   innovating marine monitoring approaches for assessing marine environmental status.

1002   *Frontiers in Marine Science* **3**, 213.

1003 DAVEY, P.A., PERNICE, M., SABLOK, G., LARKUM, A., LEE, H.T., GOLICZ, A., EDWARDS, D.,

1004   DOLFERUS, R. & RALPH, P. (2016). The emergence of molecular profiling and omics

1005   techniques in seagrass biology; furthering our understanding of seagrasses. *Functional*

1006   *and Integrative Genomics* **16**, 465–480.

1007 DE BOER, W.F. (2007). Seagrass–sediment interactions, positive feedbacks and critical

1008   thresholds for occurrence: a review. *Hydrobiologia* **591**, 5–24.

1009 DE LOS SANTOS, C.B., KRAUSE-JENSEN, D., ALCOVERRO, T., MARBÀ, N., DUARTE, C.M., VAN

1010   KATWIJK, M.M., PÉREZ, M., ROMERO, J., SÁNCHEZ-LIZASO, J.L., ROCA, G., JANKOWSKA,

1011   E., PÉREZ-LLORÉNS, J.L., FOURNIER, J., MONTEFALCONE, M., PERGENT, G., *ET AL.* (2019).

1012   Recent trend reversal for declining European seagrass meadows. *Nature*

1013   *Communications* **10**, 3356.

1014 DIAZ-ALMELA, E., MARBÀ, N. & DUARTE, C.M. (2007). Consequences of Mediterranean

1015   warming events in seagrass (*Posidonia oceanica*) flowering records. *Global Change*

1016   *Biology* **13**, 224–235.

1017 DIAZ, R.J. & ROSENBERG, R. (2008). Spreading dead zones and consequences for marine

1018   ecosystems. *Science* **321**, 926–929.

1019 DUARTE, B., MARTINS, I., ROSA, R., MATOS, A.R., ROLEDA, M.Y., REUSCH, T., ENGELEN,

1020   A.H., SERRAO, E.A., PEARSON, G.A. & MARQUES, J.C.J.C.M. (2018). Climate change

1021   impacts on seagrass meadows and macroalgal forests: an integrative perspective on

1022   acclimation and adaptation potential. *Frontiers in Marine Science* **5**, 190.

1023   EASTERLING, D.R., MEEHL, G.A., PARMESAN, C., CHANGNON, S.A., KARL, T.R. & MEARNS,

1024   L.O. (2000). Climate extremes: Observations, modeling, and impacts. *Science* **289**,

1025   2068–2074.

1026   EGEA, L.G., JIMÉNEZ-RAMOS, R., VERGARA, J.J., HERNÁNDEZ, I. & BRUN, F.G. (2018).

1027   Interactive effect of temperature, acidification and ammonium enrichment on the

1028   seagrass *Cymodocea nodosa*. *Marine Pollution Bulletin* **134**, 14–26.

1029   EGEA, L.G., JIMÉNEZ–RAMOS, R., HERNÁNDEZ, I. & BRUN, F.G. (2019). Effect of *in situ*

1030   short-term temperature increase on carbon metabolism and dissolved organic carbon

1031   (DOC) fluxes in a community dominated by the seagrass *Cymodocea nodosa*. *PLoS One*

1032   **14**, e0210386.

1033   EHLERS, A., WORM, B. & REUSCH, T.B.H. (2008). Importance of genetic diversity in eelgrass

1034   *Zostera marina* for its resilience to global warming. *Marine Ecology Progress Series*

1035   **355**, 1–7.

1036   EVANS, A.S., WEBB, K.L. & PENHALE, P.A. (1986). Photosynthetic temperature acclimation

1037   in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. *Aquatic Botany*

1038   **24**, 185–197.

1039   FENG, S. & JACOBSEN, S.E. (2011). Epigenetic modifications in plants: An evolutionary

1040   perspective. *Current Opinion in Plant Biology* **14**, 179–186.

1041   FLORES, F., COLLIER, C.J., MERCURIO, P. & NEGRI, A.P. (2013). Phytotoxicity of four

1042   photosystem II herbicides to tropical seagrasses. *PloS One* **8**, e75798.

1043   FOURQUREAN, J.W., DUARTE, C.M., KENNEDY, H., MARBÀ, N., HOLMER, M., MATEO, M.A.,

1044   APOSTOLAKI, E.T., KENDRICK, G.A., KRAUSE-JENSEN, D. & MCGLATHERY, K.J. (2012).

1045   Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* **5**, 505–

509.

FRANSSEN, S.U., GU, J., BERGMANN, N., WINTERS, G., KLOSTERMEIER, U.C., ROSENSTIEL, P., BORNBERG-BAUER, E. & REUSCH, T.B.H. (2011). Transcriptomic resilience to global warming in the seagrass *Zostera marina*, a marine foundation species. *Proceedings of the National Academy of Sciences* **108**, 19276–19281.

FRANSSEN, S.U., GU, J., WINTERS, G., HUYLMANS, A.-K., WIENPAHL, I., SPARWEL, M., COYER, J.A., OLSEN, J.L., REUSCH, T.B.H. & BORNBERG-BAUER, E. (2014). Genome-wide transcriptomic responses of the seagrasses *Zostera marina* and *Nanozostera noltii* under a simulated heatwave confirm functional types. *Marine Genomics* **15**, 65–73.

FREDERIKSEN, M.S., HOLMER, M., DÍAZ-ALMELA, E., MARBA, N. & DUARTE, C.M. (2007). Sulfide invasion in the seagrass *Posidonia oceanica* at Mediterranean fish farms: assessment using stable sulfur isotopes. *Marine Ecology Progress Series* **345**, 93–104.

FRITZ, R.S. & SIMMS, E.L. (1992). *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press.

GAMBI, M.C., BARBIERI, F. & BIANCHI, C.N. (2009). New record of the alien seagrass *Halophila stipulacea* (Hydrocharitaceae) in the western Mediterranean: a further clue to changing Mediterranean Sea biogeography. *Marine Biodiversity Records* **2**, e84.

GARCÍA, R., HOLMER, M., DUARTE, C.M. & MARBÀ, N. (2013). Global warming enhances sulphide stress in a key seagrass species (NW Mediterranean). *Global Change Biology* **19**, 3629–3639.

GARCÍA, R., SÁNCHEZ-CAMACHO, M., DUARTE, C.M. & MARBÀ, N. (2012). Warming enhances sulphide stress of Mediterranean seagrass (*Posidonia oceanica*). *Estuarine, Coastal and Shelf Science* **113**, 240–247.

GARCIAS-BONET, N., MARBÀ, N., HOLMER, M. & DUARTE, C.M. (2008). Effects of sediment sulfides on seagrass *Posidonia oceanica* meristematic activity. *Marine Ecology*

Progress Series **372**, 1–6.

GARTHWIN, R.G., POORE, A.G.B. & VERGÉS, A. (2014). Seagrass tolerance to herbivory under increased ocean temperatures. *Marine Pollution Bulletin* **83**, 475–482.

GATTUSO, J.-P., MAGNAN, A.K., BOPP, L., CHEUNG, W.W.L., DUARTE, C.M., HINKEL, J., MCLEOD, E., MICHELI, F., OSCHLIES, A., WILLIAMSON, P., BILLÉ, R., CHALASTANI, V.I., GATES, R.D., IRISSON, J.-O., MIDDELBURG, J.J., *ET AL.* (2018). Ocean Solutions to Address Climate Change and Its Effects on Marine Ecosystems. *Frontiers in Marine Science* **5**, 337.

GAUR, R.K. & SHARMA, P. (2014). *Approaches to plant stress and their management*. Springer.

GENIN, A., LAZAR, B. & BRENNER, S. (1995). Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature* **377**, 507-510.

GEORGE, R., GULLSTROM, M., MANGORA, M.M., MTOLERA, M.S. & BJORK, M. (2018). High midday temperature stress has stronger effects on biomass than on photosynthesis: a mesocosm experiment on four tropical seagrass species. *Ecology and Evolution* **8**, 4508–4517.

GEORGIOU, D., ALEXANDRE, A., LUIS, J. & SANTOS, R. (2016). Temperature is not a limiting factor for the expansion of *Halophila stipulacea* throughout the Mediterranean Sea. *Marine Ecology Progress Series* **544**, 159–167.

GLEASON, L.U. & BURTON, R.S. (2015). RNA-seq reveals regional differences in transcriptome response to heat stress in the marine snail *Chlorostoma funebralis*. *Molecular Ecology* **24**, 610–627.

GREEN, J.M. (2014). Current state of herbicides in herbicide-resistant crops. *Pest Management Science* **70**, 1351–1357.

GU, J., WEBER, K., KLEMP, E., WINTERS, G., FRANSSEN, S.U., WIENPAHL, I., HUYLMANS,

1096 A.K., ZECHER, K., REUSCH, T.B.H., BORNBERG-BAUER, E. & WEBER, A.P.M. (2012).

1097 Identifying core features of adaptive metabolic mechanisms for chronic heat stress

1098 attenuation contributing to systems robustness. *Integrative Biology* **4**, 480–493.

1099 GUANNEL, G., ARKEMA, K., RUGGIERO, P. & VERUTES, G. (2016). The power of three: coral

1100 reefs, seagrasses and mangroves protect coastal regions and increase their resilience.

1101 *PLoS One* **11**, e0158094.

1102 GUERRERO-MESEGUER, L., MARÍN, A. & SANZ-LÁZARO, C. (2017). Future heat waves due to

1103 climate change threaten the survival of *P. oceanica* seedlings. *Environmental Pollution*

1104 **230**, 40–45.

1105 GUERRERO-MESEGUER, L., MARÍN, A. & SANZ-LÁZARO, C. (2020). Heat wave intensity can

1106 vary the cumulative effects of multiple environmental stressors on *Posidonia oceanica*

1107 seedlings. *Marine Environmental Research* **159**, 105001.

1108 GUNDERSON, A.R., ARMSTRONG, E.J. & STILLMAN, J.H. (2016). Multiple stressors in a

1109 changing world: the need for an improved perspective on physiological responses to the

1110 dynamic marine environment. *Annual Review of Marine Science* **8**, 357–378.

1111 GUY, C., KAPLAN, F., KOPKA, J., SELBIG, J. & HINCHA, D.K. (2007). Metabolomics of

1112 temperature stress. *Physiologia Plantarum* **132**, 220–235.

1113 HAMMER, K.J., BORUM, J., HASLER-SHEETAL, H., SHIELDS, E.C., SAND-JENSEN, K. &

1114 MOORE, K.A. (2018). High temperatures cause reduced growth, plant death and

1115 metabolic changes in eelgrass *Zostera marina*. *Marine Ecology Progress Series* **604**,

1116 121–132.

1117 HARLEY, C.D.G., ANDERSON, K.M., DEMES, K.W., JORVE, J.P., KORDAS, R.L., COYLE, T.A.

1118 & GRAHAM, M.H. (2012). Effects of climate change on global seaweed communities.

1119 *Journal of Phycology* **48**, 1064–1078.

1120 HASANUZZAMAN, M., NAHAR, K. & FUJITA, M. (2013). Extreme temperature responses,

1121   oxidative stress and antioxidant defense in plants. In *Abiotic stress-Plant responses and*

1122   *applications in agriculture,* pp.169–205. IntechOpen.

1123 HENDRIKS, I.E., OLSEN, Y.S. & DUARTE, C.M. (2017). Light availability and temperature, not

1124   increased CO_2, will structure future meadows of *Posidonia oceanica*. *Aquatic Botany*

1125   **139**, 32–36.

1126 HERNÁN, G., ORTEGA, M.J., GÁNDARA, A.M., CASTEJÓN, I., TERRADOS, J. & TOMAS, F.

1127   (2017). Future warmer seas: increased stress and susceptibility to grazing in seedlings of

1128   a marine habitat-forming species. *Global Change Biology* **23**, 4530–4543.

1129 HILLEBRAND, H., BORER, E.T., BRACKEN, M.E.S., CARDINALE, B.J., CEBRIAN, J., CLELAND,

1130   E.E., ELSER, J.J., GRUNER, D.S., STANLEY HARPOLE, W. & NGAI, J.T. (2009). Herbivore

1131   metabolism and stoichiometry each constrain herbivory at different organizational scales

1132   across ecosystems. *Ecology Letters* **12**, 516–527.

1133 HOBDAY, A.J., ALEXANDER, L. V, PERKINS, S.E., SMALE, D.A., STRAUB, S.C., OLIVER,

1134   E.C.J., BENTHUYSEN, J.A., BURROWS, M.T., DONAT, M.G. & FENG, M. (2016). A

1135   hierarchical approach to defining marine heatwaves. *Progress in Oceanography* **141**,

1136   227–238.

1137 HOEGH-GULDBERG, O., MUMBY, P.J., HOOTEN, A.J., STENECK, R.S., GREENFIELD, P., GOMEZ,

1138   E., HARVELL, C.D., SALE, P.F., EDWARDS, A.J., CALDEIRA, K., KNOWLTON, N., EAKIN,

1139   C.M., IGLESIAS-PRIETO, R., MUTHIGA, N., BRADBURY, R.H., *ET AL.* (2007). Coral reefs

1140   under rapid climate change and ocean acidification. *Science* **318**, 1737–1742.

1141 HOGARTH, P.J. (2015). *The biology of mangroves and seagrasses*. Oxford University Press.

1142 HOLMER, M. & HASLER-SHEETAL, H. (2014). Sulfide intrusion in seagrasses assessed by

1143   stable sulfur isotopes—a synthesis of current results. *Frontiers in Marine Science* **1**, 64.

1144 HOLMER, M., WIRACHWONG, P. & THOMSEN, M.S. (2011). Negative effects of stress-resistant

1145   drift algae and high temperature on a small ephemeral seagrass species. *Marine Biology*

158, 297–309.

HOUSTON, K., TUCKER, M.R., CHOWDHURY, J., SHIRLEY, N. & LITTLE, A. (2016). The plant cell wall: A complex and dynamic structure as revealed by the responses of genes under stress conditions. *Frontiers in Plant Science* **7**, 984.

HUGHES, A.R. & STACHOWICZ, J.J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 8998–9002.

HYNDES, G.A., HECK, K.L., VERGÉS, A., HARVEY, E.S., KENDRICK, G.A., LAVERY, P.S., MCMAHON, K., ORTH, R.J., PEARCE, A., VANDERKLIFT, M., WERNBERG, T., WHITING, S. & WILSON, S. (2016). Accelerating tropicalization and the transformation of temperate seagrass meadows. *BioScience* **66**, 938–945.

INVERS, O., PEREZ, M. & ROMERO, J. (1999). Bicarbonate utilization in seagrass photosynthesis: role of carbonic anhydrase in *Posidonia oceanica* (L.) Delile and *Cymodocea nodosa* (Ucria) Ascherson. *Journal of Experimental Marine Biology and Ecology* **235**, 125–133.

JAHNKE, M., D'ESPOSITO, D., ORRÙ, L., LAMONTANARA, A., DATTOLO, E., BADALAMENTI, F., MAZZUCA, S., PROCACCINI, G. & ORSINI, L. (2019). Adaptive responses along a depth and a latitudinal gradient in the endemic seagrass *Posidonia oceanica*. *Heredity* **122**, 233–243.

JANNI, M., GULLÌ, M., MAESTRI, E., MARMIROLI, M., VALLIYODAN, B., NGUYEN, H.T. & MARMIROLI, N. (2020). Molecular and genetic bases of heat stress responses in crop plants and breeding for increased resilience and productivity. *Journal of Experimental Botany* **71**, 3780-3802.

JARVIS, J.C., BRUSH, M.J. & MOORE, K.A. (2014). Modeling loss and recovery of *Zostera marina* beds in the Chesapeake Bay: The role of seedlings and seed-bank viability.

1171   *Aquatic Botany* **113**, 32–45.

1172 JAYATHILAKE, D.R.M. & COSTELLO, M.J. (2018). A modelled global distribution of the

1173   seagrass biome. *Biological Conservation* **226**, 120–126.

1174 JORDÀ, G., MARBÀ, N. & DUARTE, C.M. (2012). Mediterranean seagrass vulnerable to

1175   regional climate warming. *Nature Climate Change* **2**, 821–824.

1176 JUETERBOCK, A., BOSTRÖM, C., COYER, J.A., OLSEN, J.L., KOPP, M., DHANASIRI, A.K.S.,

1177   SMOLINA, I., ARNAUD-HAOND, S., VAN DE PEER, Y. & HOARAU, G. (2020). The seagrass

1178   methylome is associated with variation in photosynthetic performance among clonal

1179   shoots. *Frontiers in Plant Science* **11**, 1387.

1180 JUETERBOCK, A., FRANSSEN, S.U., BERGMANN, N., GU, J., COYER, J.A., REUSCH, T.B.H.,

1181   BORNBERG-BAUER, E. & OLSEN, J.L. (2016). Phylogeographic differentiation versus

1182   transcriptomic adaptation to warm temperatures in *Zostera marina*, a globally important

1183   seagrass. *Molecular Ecology* **25**, 5396–5411.

1184 KALDY, J.E. & SHAFER, D.J. (2013). Effects of salinity on survival of the exotic seagrass

1185   *Zostera japonica* subjected to extreme high temperature stress. *Botanica Marina* **56**, 75–

1186   82.

1187 KALDY, J.E., SHAFER, D.J. & MAGOUN, A.D. (2015). Duration of temperature exposure

1188   controls growth of *Zostera japonica*: implications for zonation and colonization. *Journal*

1189   *of Experimental Marine Biology and Ecology* **464**, 68–74.

1190 KELLER, C.F. (2009). Global warming: A review of this mostly settled issue. *Stochastic*

1191   *Environmental Research and Risk Assessment* **23**, 643–676.

1192 KENDRICK, G.A., NOWICKI, R., OLSEN, Y.S., STRYDOM, S., FRASER, M.W., SINCLAIR, E.A.,

1193   STATTON, J., HOVEY, R.K., THOMSON, J.A., BURKHOLDER, D., MCMAHON, K.M.,

1194   KILMINSTER, K., HETZEL, Y., FOURQUREAN, J.W., HEITHAUS, M.R., *ET AL.* (2019). A

1195   systematic review of how multiple stressors from an extreme event drove ecosystem-

wide loss of resilience in an iconic seagrass community. *Frontiers in Marine Science* **6**, 455.

KERR, E.A. & STROTHER, S. (1985). Effects of irradiance, temperature and salinity on photosynthesis of *Zostera muelleri*. *Aquatic Botany* **23**, 177–183.

KIANG, J.G. & TSOKOS, G.C. (1998). Heat shock protein 70 kDa: molecular biology, biochemistry, and physiology. *Pharmacology & Therapeutics* **80**, 183–201.

KIM, M., QIN, L.Z., KIM, S.H., SONG, H.J., KIM, Y.K. & LEE, K.S. (2019). Influence of water temperature anomalies on the growth of *Zostera marina* plants held under high and low irradiance levels. *Estuaries and Coasts* **43**, 463–476.

KINOSHITA, T. & SEKI, M. (2014). Epigenetic memory for stress response and adaptation in plants. *Plant and Cell Physiology* **55**, 1859–1863.

KOCH, M., BOWES, G., ROSS, C. & ZHANG, X.H. (2013). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology* **19**, 103–132.

KOCH, M.S., SCHOPMEYER, S., KYHN-HANSEN, C. & MADDEN, C.J. (2007). Synergistic effects of high temperature and sulfide on tropical seagrass. *Journal of Experimental Marine Biology and Ecology* **341**, 91–101.

KONG, F., LI, H., SUN, P., ZHOU, Y. & MAO, Y. (2014). *De Novo* Assembly and Characterization of the Transcriptome of Seagrass *Zostera marina* Using Illumina Paired-End Sequencing. *PLoS One* **9,** e112245.

KOUTALIANOU, M., ORFANIDIS, S. & KATSAROS, C. (2016). Effects of high temperature on the ultrastructure and microtubule organization of interphase and dividing cells of the seagrass *Cymodocea nodosa*. *Protoplasma* **253**, 299–310.

KUO, J. & DEN HARTOG, C. (2000). Seagrasses: A profile of an ecological group. *Biologia Marina Mediterranea* **7**, 3–17.

1221   KURDYUKOV, S. & BULLOCK, M. (2016). DNA Methylation Analysis: Choosing the Right

1222   Method. *Biology* **5**, 3.

1223   LAMB, J.B., VAN DE WATER, J.A.J.M.J.M., BOURNE, D.G., ALTIER, C., HEIN, M.Y.,

1224   FIORENZA, E.A., ABU, N., JOMPA, J. & HARVELL, C.D. (2017). Seagrass ecosystems

1225   reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. *Science*

1226   **355**, 731–733.

1227   LATTEMANN, S. & HÖPNER, T. (2008). Environmental impact and impact assessment of

1228   seawater desalination. *Desalination* **220**, 1–15.

1229   LEE, H., GOLICZ, A.A., BAYER, P.E., JIAO, Y., TANG, H., PATERSON, A.H., SABLOK, G.,

1230   KRISHNARAJ, R.R., CHAN, C.-K.K., BATLEY, J., KENDRICK, G.A., LARKUM, A.W.D.,

1231   RALPH, P.J. & EDWARDS, D. (2016). The genome of a Southern Hemisphere seagrass

1232   species (*Zostera muelleri*). *Plant Physiology* **172**, 272–283.

1233   LEE, K.-S., PARK, S.R. & KIM, Y.K. (2007*a*). Effects of irradiance, temperature, and nutrients

1234   on growth dynamics of seagrasses: a review. *Journal of Experimental Marine Biology*

1235   *and Ecology* **350**, 144–175.

1236   LEE, K.-S., PARK, J.-I., KIM, Y.K., PARK, S.R. & KIM, J.-H. (2007*b*). Recolonization of

1237   *Zostera marina* following destruction caused by a red tide algal bloom: the role of new

1238   shoot recruitment from seed banks. *Marine Ecology Progress Series* **342**, 105–115.

1239   LENTON, T.M., ROCKSTRÖM, J., GAFFNEY, O., RAHMSTORF, S., RICHARDSON, K., STEFFEN,

1240   W. & SCHELLNHUBER, H.J. (2019). Climate tipping points — too risky to bet against.

1241   *Nature* **575**, 592–595.

1242   LES, D.H., CLELAND, M.A. & WAYCOTT, M. (1997). Phylogenetic studies in Alismatidae, II:

1243   Evolution of marine angiosperms (seagrasses) and hydrophily. *Systematic Botany* **22**,

1244   443–463.

1245   LEWIS, S.E., BRODIE, J.E., BAINBRIDGE, Z.T., ROHDE, K.W., DAVIS, A.M., MASTERS, B.L.,

1246 MAUGHAN, M., DEVLIN, M.J., MUELLER, J.F. & SCHAFFELKE, B. (2009). Herbicides: a
1247   new threat to the Great Barrier Reef. *Environmental Pollution* **157**, 2470–2484.

1248 LIAO, E., LU, W., YAN, X.H., JIANG, Y. & KIDWELL, A. (2015). The coastal ocean response to
1249   the global warming acceleration and hiatus. *Scientific Reports* **5**, 1–10.

1250 LIPKIN, Y. (1975). *Halophila stipulacea*, a review of a successful immigration. *Aquatic*
1251   *Botany* **1**, 203–215.

1252 LIU, J., FENG, L., LI, J. & HE, Z. (2015). Genetic and epigenetic control of plant heat
1253   responses. *Frontiers in Plant Science* **06**, 267.

1254 LIU, J., TANG, X., WANG, Y., ZANG, Y. & ZHOU, B. (2016). A *Zostera marina* manganese
1255   superoxide dismutase gene involved in the responses to temperature stress. *Gene* **575**,
1256   718–724.

1257 MACREADIE, P.I. & HARDY, S.S.S. (2018). Response of seagrass 'Blue Carbon' stocks to
1258   increased water temperatures. *Diversity* **10**, 115.

1259 MALANDRAKIS, E., DADALI, O., KAVOURAS, M., DANIS, T., PANAGIOTAKI, P., MILIOU, H.,
1260   TSIOLI, S., ORFANIDIS, S., KÜPPER, F.C. & EXADACTYLOS, A. (2017). Identification of
1261   the abiotic stress-related transcription in little Neptune grass *Cymodocea nodosa* with
1262   RNA-seq. *Marine Genomics* **34**, 47–56.

1263 MARBÀ, N., CALLEJA, M.L., DUARTE, C.M., ÁLVAREZ, E., DÍAZ-ALMELA, E. & HOLMER, M.
1264   (2007). Iron additions reduce sulfide intrusion and reverse seagrass (*Posidonia*
1265   *oceanica*) decline in carbonate sediments. *Ecosystems* **10**, 745–756.

1266 MARBÀ, N., DÍAZ-ALMELA, E. & DUARTE, C.M. (2014). Mediterranean seagrass (*Posidonia*
1267   *oceanica*) loss between 1842 and 2009. *Biological Conservation* **176**, 183–190.

1268 MARBÀ, N. & DUARTE, C.M. (2010). Mediterranean warming triggers seagrass (*Posidonia*
1269   *oceanica*) shoot mortality. *Global Change Biology* **16**, 2366–2375.

1270 MARÍN-GUIRAO, L., BERNARDEAU-ESTELLER, J., GARCÍA-MUÑOZ, R., RAMOS, A., ONTORIA,

1271   Y., ROMERO, J., PÉREZ, M., RUIZ, J.M. & PROCACCINI, G. (2018). Carbon economy of

1272   Mediterranean seagrasses in response to thermal stress. *Marine Pollution Bulletin* **135**,

1273   617–629.

1274 MARÍN-GUIRAO, L., ENTRAMBASAGUAS, L., DATTOLO, E., RUIZ, J.M. & PROCACCINI, G.

1275   (2017). Molecular mechanisms behind the physiological resistance to intense transient

1276   warming in an iconic marine plant. *Frontiers in Plant Science* **8**, 1142.

1277 MARÍN-GUIRAO, L., RUIZ, J.M., DATTOLO, E., GARCIA-MUNOZ, R. & PROCACCINI, G. (2016).

1278   Physiological and molecular evidence of differential short-term heat tolerance in

1279   Mediterranean seagrasses. *Scientific Reports* **6**, 28615.

1280 MARÍN-GUIRAO, L., SANDOVAL-GIL, J.M., RUÍZ, J.M. & SÁNCHEZ-LIZASO, J.L. (2011).

1281   Photosynthesis, growth and survival of the Mediterranean seagrass *Posidonia oceanica*

1282   in response to simulated salinity increases in a laboratory mesocosm system. *Estuarine,*

1283   *Coastal and Shelf Science* **92**, 286–296.

1284 MARÍN-GUIRAO, L., ENTRAMBASAGUAS, L., RUIZ, J.M. & PROCACCINI, G. (2019). Heat-stress

1285   induced flowering can be a potential adaptive response to ocean warming for the iconic

1286   seagrass *Posidonia oceanica*. *Molecular Ecology* **28**, 2486–2501.

1287 MARSH JR, J.A., DENNISON, W.C. & ALBERTE, R.S. (1986). Effects of temperature on

1288   photosynthesis and respiration in eelgrass (*Zostera marina* L.). *Journal of Experimental*

1289   *Marine Biology and Ecology* **101**, 257–267.

1290 MASINI, R.J., CARY, J.L., SIMPSON, C.J. & MCCOMB, A.J. (1995). Effects of light and

1291   temperature on the photosynthesis of temperate meadow-forming seagrasses in Western

1292   Australia. *Aquatic Botany* **49**, 239–254.

1293 MASINI, R.J. & MANNING, C.R. (1997). The photosynthetic responses to irradiance and

1294   temperature of four meadow-forming seagrasses. *Aquatic Botany* **58**, 21–36.

1295 MASSA, S.I., ARNAUD-HAOND, S., PEARSON, G.A. & SERRÃO, E.A. (2009). Temperature

1296   tolerance and survival of intertidal populations of the seagrass *Zostera noltii*

1297   (Hornemann) in Southern Europe (Ria Formosa, Portugal). *Hydrobiologia* **619**, 195–

1298   201.

1299   MASSA, S.I., PEARSON, G.A., AIRES, T., KUBE, M., OLSEN, J.L., REINHARDT, R., SERRÃO,

1300   E.A. & ARNAUD-HAOND, S. (2011). Expressed sequence tags from heat-shocked

1301   seagrass *Zostera noltii* (Hornemann) from its southern distribution range. *Marine*

1302   *Genomics* **4**, 181–188.

1303   MASSON-DELMOTTE, V., ZHAI, P., PÖRTNER, H.-O., ROBERTS, D., SKEA, J., SHUKLA, P.R.,

1304   PIRANI, A., MOUFOUMA-OKIA, W., PÉAN, C. & PIDCOCK, R. (2018). *Global Warming of*

1305   *1.5°C: An IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-*

1306   *industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the*

1307   *Context of Strengthening the Global Response to the Threat of Climate Change*. World

1308   Meteorological Organization Geneva, Switzerland.

1309   MAYOT, N., BOUDOURESQUE, C.F. & LERICHE, A. (2005). Unexpected response of the

1310   seagrass *Posidonia oceanica* to a warm-water episode in the North Western

1311   Mediterranean Sea. *Comptes Rendus Biologies* **328**, 291–296.

1312   MCGLATHERY, K.J. (2001). Macroalgal blooms contribute to the decline of seagrass in

1313   nutrient-enriched coastal waters. *Journal of Phycology* **37**, 453–456.

1314   MCKENZIE, L., NORDLUND, L.M., JONES, B.L., CULLEN-UNSWORTH, L.C., ROELFSEMA, C.M.

1315   & UNSWORTH, R. (2020). The global distribution of seagrass meadows. *Environmental*

1316   *Research Letters* **15**, 074041.

1317   MCKENZIE, L.J., FINKBEINER, M.A. & KIRKMAN, H. (2001). Methods for mapping seagrass

1318   distribution. In *Global seagrass research methods*, pp. 101–121. Elsevier.

1319   MEEHL, G.A. & TEBALDI, C. (2004). More intense, more frequent, and longer lasting heat

1320   waves in the 21st century. *Science* **305**, 994–997.

1321 MOLINIER, J., RIES, G., ZIPFEL, C. & HOHN, B. (2006). Transgeneration memory of stress in

1322   plants. *Nature* **442**, 1046–1049.

1323 MONASTERSKY, R. (2013). Global carbon dioxide levels near worrisome milestone. *Nature*

1324   **497**, 13–14.

1325 MOTA, C.F., ENGELEN, A.H., SERRAO, E.A., COELHO, M.A.G., MARBÀ, N. & KRAUSE-JENSEN,

1326   D. (2018). Differentiation in fitness-related traits in response to elevated temperatures

1327   between leading and trailing edge populations of marine macrophytes. *PLoS One* **13**,

1328   e0203666.

1329 MVUNGI, E.F. & PILLAY, D. (2019). Eutrophication overrides warming as a stressor for a

1330   temperate African seagrass (*Zostera capensis*). *PLoS One* **14**, e0215129.

1331 NEGRI, A.P., FLORES, F., MERCURIO, P., MUELLER, J.F. & COLLIER, C.J. (2015). Lethal and

1332   sub-lethal chronic effects of the herbicide diuron on seagrass. *Aquatic Toxicology* **165**,

1333   73–83.

1334 NEJRUP, L.B. & PEDERSEN, M.F. (2008). Effects of salinity and water temperature on the

1335   ecological performance of *Zostera marina*. *Aquatic Botany* **88**, 239–246.

1336 NGUYEN, H.M., YADAV, N.S., BARAK, S., LIMA, F.P., SAPIR, Y. & WINTERS, G. (2020*a*).

1337   Responses of invasive and native populations of the seagrass *Halophila stipulacea* to

1338   simulated climate change. *Frontiers in Marine Science* **6**, 812.

1339 NGUYEN, H.M., KIM, M., RALPH, P.J., MARÍN-GUIRAO, L., PERNICE, M. & PROCACCINI, G.

1340   (2020*b*). Stress memory in seagrasses: first insight into the effects of thermal priming

1341   and the role of epigenetic modifications. *Frontiers in Plant Science* **11**, 494.

1342 NICHOLLS, R.J. & CAZENAVE, A. (2010). Sea-level rise and its impact on coastal zones.

1343   *Science* **328**, 1517–1520.

1344 NISHIZAWA, A., YABUTA, Y. & SHIGEOKA, S. (2008). Galactinol and raffinose constitute a

1345   novel function to protect plants from oxidative damage. *Plant Physiology* **147**, 1251–

1346   1263.

NOWICKI, R.J., THOMSON, J.A., BURKHOLDER, D.A., FOURQUREAN, J.W. & HEITHAUS, M.R.

1348   (2017). Predicting seagrass recovery times and their implications following an extreme

1349   climate event. *Marine Ecology Progress Series* **567**, 79–93.

O'BRIEN, K.R., WAYCOTT, M., MAXWELL, P., KENDRICK, G.A., UDY, J.W., FERGUSON, A.J.P.,

1351   KILMINSTER, K., SCANES, P., MCKENZIE, L.J., MCMAHON, K., ADAMS, M.P., SAMPER-

1352   VILLARREAL, J., COLLIER, C., LYONS, M., MUMBY, P.J., *ET AL.* (2018). Seagrass

1353   ecosystem trajectory depends on the relative timescales of resistance, recovery and

1354   disturbance. *Marine Pollution Bulletin* **134**, 166–176.

OLESEN, B., MARBA, N., DUARTE, C.M., SAVELA, R.S. & FORTES, M.D. (2004).

1356   Recolonization dynamics in a mixed seagrass meadow: the role of clonal versus sexual

1357   processes. *Estuaries* **27**, 770–780.

OLIVER, E.C.J., BURROWS, M.T., DONAT, M.G., SEN GUPTA, A., ALEXANDER, L. V.,

1359   PERKINS-KIRKPATRICK, S.E., BENTHUYSEN, J.A., HOBDAY, A.J., HOLBROOK, N.J.,

1360   MOORE, P.J., THOMSEN, M.S., WERNBERG, T. & SMALE, D.A. (2019). Projected Marine

1361   Heatwaves in the 21st Century and the Potential for Ecological Impact. *Frontiers in*

1362   *Marine Science* **6**, 734.

OLIVER, E.C.J., DONAT, M.G., BURROWS, M.T., MOORE, P.J., SMALE, D.A., ALEXANDER, L.

1364   V., BENTHUYSEN, J.A., FENG, M., SEN GUPTA, A., HOBDAY, A.J., HOLBROOK, N.J.,

1365   PERKINS-KIRKPATRICK, S.E., SCANNELL, H.A., STRAUB, S.C. & WERNBERG, T. (2018).

1366   Longer and more frequent marine heatwaves over the past century. *Nature*

1367   *Communications* **9**, 1–12.

OLSEN, J.L., ROUZÉ, P., VERHELST, B., LIN, Y.C., BAYER, T., COLLEN, J., DATTOLO, E., DE

1369   PAOLI, E., DITTAMI, S., MAUMUS, F., MICHEL, G., KERSTING, A., LAURITANO, C.,

1370   LOHAUS, R., TÖPEL, M., *ET AL.* (2016). The genome of the seagrass *Zostera marina*

reveals angiosperm adaptation to the sea. *Nature* **530**, 331–335.

OLSEN, Y.S. & DUARTE, C.M. (2015). Combined effect of warming and infection by *Labyrinthula* sp. on the Mediterranean seagrass *Cymodocea nodosa*. *Marine Ecology Progress Series* **532**, 101–109.

OLSEN, Y.S., POTOUROGLOU, M., GARCIAS-BONET, N. & DUARTE, C.M. (2014). Warming reduces pathogen pressure on a climate-vulnerable seagrass species. *Estuaries and Coasts* **38**, 659–667.

OLSEN, Y.S., SÁNCHEZ-CAMACHO, M., MARBÀ, N. & DUARTE, C.M. (2012). Mediterranean seagrass growth and demography responses to experimental warming. *Estuaries and Coasts* **35**, 1205–1213.

ONTORIA, Y., CUESTA-GRACIA, A., RUIZ, J.M., ROMERO, J. & PÉREZ, M. (2019*a*). The negative effects of short-term extreme thermal events on the seagrass *Posidonia oceanica* are exacerbated by ammonium additions. *PLoS One* **14**, e0222798.

ONTORIA, Y., GONZALEZ-GUEDES, E., SANMARTÍ, N., BERNARDEAU-ESTELLER, J., RUIZ, J.M., ROMERO, J. & PÉREZ, M. (2019*b*). Interactive effects of global warming and eutrophication on a fast-growing Mediterranean seagrass. *Marine Environmental Research* **145**, 27–38.

ORTBAUER, M. & POPP, M. (2008). Functional role of polyhydroxy compounds on protein structure and thermal stability studied by circular dichroism spectroscopy. *Plant Physiology and Biochemistry* **46**, 428–434.

ORTH, R.J., CARRUTHERS, T.J.B., DENNISON, W.C., DUARTE, C.M., FOURQUREAN, J.W., HECK, K.L., HUGHES, A.R., KENDRICK, G.A., KENWORTHY, W.J. & OLYARNIK, S. (2006). A global crisis for seagrass ecosystems. *AIBS Bulletin* **56**, 987–996.

ORTH, R.J., HARWELL, M.C., BAILEY, E.M., BARTHOLOMEW, A., JAWAD, J.T., LOMBANA, A.V, MOORE, K.A., RHODE, J.M. & WOODS, H.E. (2000). A review of issues in seagrass

1396   seed dormancy and germination: implications for conservation and restoration. *Marine*

1397   *Ecology Progress Series* **200**, 277–288.

1398   OSCAR, M.A., BARAK, S. & WINTERS, G. (2018). The tropical invasive seagrass, *Halophila*

1399   *stipulacea* has a superior ability to tolerate dynamic changes in salinity levels compared

1400   to its freshwater relative, Vallisneria americana. *Frontiers in Plant Science* **9**, 950.

1401   PAGÈS, J.F., SMITH, T.M., TOMAS, F., SANMARTÍ, N., BOADA, J., DE BARI, H., PÉREZ, M.,

1402   ROMERO, J., ARTHUR, R. & ALCOVERRO, T. (2018). Contrasting effects of ocean

1403   warming on different components of plant-herbivore interactions. *Marine Pollution*

1404   *Bulletin* **134**, 55–65.

1405   PARK, C.-J. & SEO, Y.-S. (2015). Heat shock proteins: a review of the molecular chaperones

1406   for plant immunity. *The Plant Pathology Journal* **31**, 323–333.

1407   PAZZAGLIA, J., REUSCH, T.B.H., TERLIZZI, A., MARÍN-GUIRAO, L. & PROCACCINI, G. (2021).

1408   Prompt phenotypic plasticity under rapid global changes: the intrinsic force for future

1409   seagrasses survival. *Evolutionary Applications* **00**, 1–21.

1410   PAZZAGLIA, J., SANTILLÁN-SARMIENTO, A., HELBER, S.B., RUOCCO, M., TERLIZZI, A.,

1411   MARÍN-GUIRAO, L. & PROCACCINI, G. (2020). Does warming enhance the effects of

1412   eutrophication in the seagrass *Posidonia oceanica*? *Frontiers in Marine Science* **7**, 1067.

1413   PEDERSEN, O., COLMER, T.D., BORUM, J., ZAVALA-PEREZ, A. & KENDRICK, G.A. (2016). Heat

1414   stress of two tropical seagrass species during low tides–impact on underwater net

1415   photosynthesis, dark respiration and diel *in situ* internal aeration. *New Phytologist* **210**,

1416   1207–1218.

1417   PEREDA-BRIONES, L., TERRADOS, J. & TOMAS, F. (2019). Negative effects of warming on

1418   seagrass seedlings are not exacerbated by invasive algae. *Marine Pollution Bulletin* **141**,

1419   36–45.

1420   PEREZ, M. & ROMERO, J. (1992). Photosynthetic response to light and temperature of the

seagrass *Cymodocea nodosa* and the prediction of its seasonality. *Aquatic Botany* **43**, 51–62.

PERNICE, M., SCHLIEP, M., SZABO, M., RASHEED, M., BRYANT, C., YORK, P., CHARTRAND, K., PETROU, K. & RALPH, P. (2015). Development of a molecular biology tool kit to monitor dredging-related light stress in the seagrass *Zostera muelleri* ssp. capricorni in Port Curtis. A Report for Gladstone Ports Corporation Limited. Report No. 15/08. TropWATER, Cairns, QLD, Australia.

PHINN, S., ROELFSEMA, C., KOVACS, E., CANTO, R., LYONS, M., SAUNDERS, M. & MAXWELL, P. (2018). Mapping, monitoring and modelling seagrass using remote sensing techniques. In *Seagrasses of Australia,* pp. 445–487. Springer.

PLUS, M., DESLOUS-PAOLI, J.-M. & DAGAULT, F. (2003). Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquatic Botany* **77**, 121–134.

PRADO, P., TOMAS, F., ALCOVERRO, T. & ROMERO, J. (2007). Extensive direct measurements of *Posidonia oceanica* defoliation confirm the importance of herbivory in temperate seagrass meadows. *Marine Ecology Progress Series* **340**, 63–71.

PROCACCINI, G., BEER, S., BJÖRK, M., OLSEN, J., MAZZUCA, S. & SANTOS, R. (2012). Seagrass ecophysiology meets ecological genomics: are we ready? *Marine Ecology* **33**, 522–527.

PROCACCINI, G., OLSEN, J.L. & REUSCH, T.B.H. (2007). Contribution of genetics and genomics to seagrass biology and conservation. *Journal of Experimental Marine Biology and Ecology* **350**, 234–259.

PROCACCINI, G., RUOCCO, M., MARÍN-GUIRAO, L., DATTOLO, E., BRUNET, C., D'ESPOSITO, D., LAURITANO, C., MAZZUCA, S., SERRA, I.A., BERNARDO, L., PIRO, A., BEER, S., BJÖRK, M., GULLSTRÖM, M., BUAPET, P., *ET AL.* (2017). Depth-specific fluctuations of gene expression and protein abundance modulate the photophysiology in the seagrass

Posidonia oceanica. *Scientific Reports* **7**, 42890.

PURNAMA, P.R., HARIYANTO, S., SRI, Y., MANUHARA, W. & PURNOBASUKI, H. (2019). Gene expression of antioxidant enzymes and heat shock proteins in tropical seagrass *Thalassia hemprichii* under heat Stress. *Taiwania* **64**, 117–123.

QU, A.L., DING, Y.F., JIANG, Q. & ZHU, C. (2013). Molecular mechanisms of the plant heat stress response. *Biochemical and Biophysical Research Communications* **432**, 203–207.

RABALAIS, N.N., HARPER, D.E. & TURNER, R.E. (2001). Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. In *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*, pp. 115–128. American Geophysical Union.

RABALAIS, N.N., TURNER, R.E., DIAZ, R.J. & JUSTIĆ, D. (2009). Global change and eutrophication of coastal waters. *Journal of Marine Science* **66**, 1528–1537.

RALPH, P.J. (1998). Photosynthetic response of laboratory-cultured *Halophila ovalis* to thermal stress. *Marine Ecology Progress Series* **171**, 123–130.

RALPH, P.J. (1999). Photosynthetic response of *Halophila ovalis* (R. Br.) Hook. f. to combined environmental stress. *Aquatic Botany* **65**, 83–96.

RALPH, P.J., TOMASKO, D., MOORE, K., SEDDON, S. & MACINNIS-NG, C.M.O. (2007). Human impacts on seagrasses: eutrophication, sedimentation, and contamination. In *Seagrasses: Biology, Ecology and Conservation,* pp. 567–593. Springer.

RAMESH, R., BANERJEE, K., PANEERSELVAM, A., RAGHURAMAN, R., PURVAJA, R. & LAKSHMI, A. (2019). Importance of seagrass management for effective mitigation of climate change. In *Coastal Management,* pp. 283–299. Elsevier.

RANSBOTYL, V. & REUSCH, T.B. (2006). Housekeeping gene selection for quantitative real-time PCR assays in the seagrass *Zostera marina* subjected to heat stress. *Limnology and Oceanography: Methods* **4**, 367–373.

1471   RASHEED, M.A. & UNSWORTH, R.K.F.F. (2011). Long-term climate-associated dynamics of a

1472   tropical seagrass meadow: implications for the future. *Marine Ecology Progress Series*

1473   **422**, 93–103.

1474   RAVEN, J.A. & SCRIMGEOUR, C.M. (1997). The influence of anoxia on plants of saline

1475   habitats with special reference to the sulphur cycle. *Annals of Botany* **79**, 79–86.

1476   RENN, C.E. (1936). The wasting disease of *Zostera marina*: I. A phytological investigation of

1477   the diseased plant. *The Biological Bulletin* **70**, 148–158.

1478   REPOLHO, T., DUARTE, B., DIONÍSIO, G., PAULA, J.R., LOPES, A.R., ROSA, I.C., GRILO, T.F.,

1479   CAÇADOR, I., CALADO, R. & ROSA, R. (2017). Seagrass ecophysiological performance

1480   under ocean warming and acidification. *Scientific Reports* **7**, 41443.

1481   REUSCH, T.B.H., EHLERS, A., HÄMMERLI, A. & WORM, B. (2005). Ecosystem recovery after

1482   climatic extremes enhanced by genotypic diversity. *Proceedings of the National*

1483   *Academy of Sciences of the United States of America* **102**, 2826–2831.

1484   REUSCH, T.B.H., VERON, A.S., PREUSS, C., WEINER, J., WISSLER, L., BECK, A., KLAGES, S.,

1485   KUBE, M., REINHARDT, R. & BORNBERG-BAUER, E. (2008). Comparative analysis of

1486   expressed sequence tag (EST) libraries in the seagrass *Zostera marina* subjected to

1487   temperature stress. *Marine Biotechnology* **10**, 297–309.

1488   REUSCH, T.B.H. & WOOD, T.E. (2007). Molecular ecology of global change. *Molecular*

1489   *Ecology* **16**, 3973–3992.

1490   REYNOLDS, L.K., DUBOIS, K., ABBOTT, J.M., WILLIAMS, S.L. & STACHOWICZ, J.J. (2016*a*).

1491   Response of a habitat-forming marine plant to a simulated warming event is delayed,

1492   genotype specific, and varies with phenology. *PloS One* **11**, e0154532.

1493   REYNOLDS, L.K., WAYCOTT, M., MCGLATHERY, K.J. & ORTH, R.J. (2016*b*). Ecosystem

1494   services returned through seagrass restoration. *Restoration Ecology* **24**, 583–588.

1495   RICHARDSON, P.J., LEFCHECK, J.S. & ORTH, R.J. (2018). Warming temperatures alter the

relative abundance and distribution of two co-occurring foundational seagrasses in

chesapeake bay, USA. *Marine Ecology Progress Series* **599**, 65–74.

ROBBLEE, M., BARBER, T., CARLSON, P., DURAKO, M., FOURQUREAN, J., MUEHLSTEIN, L.,

PORTER, D., YARBRO, L., ZIEMAN, R. & ZIEMAN, J. (1991). Mass mortality of the

tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress*

Series **71**, 297–299.

RUIZ, J.M., MARÍN-GUIRAO, L., GARCÍA-MUÑOZ, R., RAMOS-SEGURA, A., BERNARDEAU-

ESTELLER, J., PÉREZ, M., SANMARTÍ, N., ONTORIA, Y., ROMERO, J., ARTHUR, R.,

ALCOVERRO, T. & PROCACCINI, G. (2018). Experimental evidence of warming-induced

flowering in the Mediterranean seagrass *Posidonia oceanica*. *Marine Pollution Bulletin*

134, 49–54.

RUÍZ, J.M., MARÍN-GUIRAO, L. & SANDOVAL-GIL, J.M. (2009). Responses of the

Mediterranean seagrass *Posidonia oceanica* to *in situ* simulated salinity increase.

Botanica Marina **52**, 459–470.

RUIZ-MONTOYA, L., LOWE, R.J., VAN NIEL, K.P. & KENDRICK, G.A. (2012). The role of

hydrodynamics on seed dispersal in seagrasses. *Limnology and Oceanography* **57**,

1257–1265.

RUOCCO, M., DE LUCA, P., MARÍN-GUIRAO, L. & PROCACCINI, G. (2019*a*). Differential Leaf

Age-Dependent Thermal Plasticity in the Keystone Seagrass *Posidonia oceanica*.

Frontiers in Plant Science **10**, 1556.

RUOCCO, M., MARÍN-GUIRAO, L. & PROCACCINI, G. (2019*b*). Within- and among-leaf

variations in photo-physiological functions, gene expression and DNA methylation

patterns in the large-sized seagrass *Posidonia oceanica*. *Marine Biology* **166**, 24.

SAHA, M., BARBOZA, F.R., SOMERFIELD, P.J., AL-JANABI, B., BECK, M., BRAKEL, J., ITO, M.,

PANSCH, C., NASCIMENTO-SCHULZE, J.C., JAKOBSSON THOR, S., WEINBERGER, F. &

1521   SAWALL, Y. (2019). Response of foundation macrophytes to near-natural simulated

1522   marine heatwaves. *Global Change Biology* **26**, 417-430.

1523   SALO, T. & PEDERSEN, M.F. (2014). Synergistic effects of altered salinity and temperature on

1524   estuarine eelgrass (*Zostera marina*) seedlings and clonal shoots. *Journal of*

1525   *Experimental Marine Biology and Ecology* **457**, 143–150.

1526   SALVUCCI, M.E. & CRAFTS-BRANDNER, S.J. (2004). Mechanism for deactivation of Rubisco

1527   under moderate heat stress. *Physiologia Plantarum* **122**, 513–519.

1528   SANDIFER, P.A. & SUTTON-GRIER, A.E. (2014). Connecting stressors, ocean ecosystem

1529   services, and human health. *Natural Resources Forum* **38**, 157–167.

1530   SANDOVAL-GIL, J.M., RUIZ, J.M., MARÍN-GUIRAO, L., BERNARDEAU-ESTELLER, J. &

1531   SÁNCHEZ-LIZASO, J.L. (2014). Ecophysiological plasticity of shallow and deep

1532   populations of the Mediterranean seagrasses *Posidonia oceanica* and *Cymodocea*

1533   *nodosa* in response to hypersaline stress. *Marine Environmental Research* **95**, 39–61.

1534   SAVVA, I., BENNETT, S., ROCA, G., JORDÀ, G & MARBÀ, N. (2018). Thermal tolerance of

1535   Mediterranean marine macrophytes: Vulnerability to global warming. *Ecology and*

1536   *Evolution* **8**, 12032–12043.

1537   SCHÄR, C. & JENDRITZKY, G. (2004). Hot news from summer 2003. *Nature* **432**, 559–560.

1538   SCHEIBLING, R.E., PATRIQUIN, D.G. & FILBEE-DEXTER, K. (2018). Distribution and

1539   abundance of the invasive seagrass *Halophila stipulacea* and associated benthic

1540   macrofauna in Carriacou, Grenadines, Eastern Caribbean. *Aquatic Botany* **144**, 1–8.

1541   SCHLIEP, M., PERNICE, M., SINUTOK, S., BRYANT, C. V, YORK, P.H., RASHEED, M.A. &

1542   RALPH, P.J. (2015). Evaluation of reference genes for RT-qPCR studies in the seagrass

1543   *Zostera muelleri* exposed to light limitation. *Scientific Reports* **5**, 17051.

1544   SEDDON, S. & CHESHIRE, A.C. (2001). Photosynthetic response of *Amphibolis antarctica* and

1545   *Posidonia australis* to temperature and desiccation using chlorophyll fluorescence.

1546   *Marine Ecology Progress Series* **220**, 119–130.

1547   SEDDON, S., CONNOLLY, R.M. & EDYVANE, K.S. (2000). Large-scale seagrass dieback in

1548   northern Spencer Gulf, South Australia. *Aquatic Botany* **66**, 297–310.

1549   SHAKUN, J.D., CLARK, P.U., HE, F., MARCOTT, S.A., MIX, A.C., LIU, Z., OTTO-BLIESNER, B.,

1550   SCHMITTNER, A. & BARD, E. (2012). Global warming preceded by increasing carbon

1551   dioxide concentrations during the last deglaciation. *Nature* **484**, 49–54.

1552   SHARKEY, T.D. (2005). Effects of moderate heat stress on photosynthesis: importance of

1553   thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance

1554   provided by isoprene. *Plant, Cell & Environment* **28**, 269–277.

1555   SHIELDS, E.C., PARRISH, D. & MOORE, K. (2019). Short-Term Temperature Stress Results in

1556   Seagrass Community Shift in a Temperate Estuary. *Estuaries and Coasts* **42**, 755–764.

1557   SHORT, F.T., CARRUTHERS, T., DENNISON, W. & WAYCOTT, M. (2007). Global seagrass

1558   distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology*

1559   *and Ecology* **350**, 3–20.

1560   SMALE, D.A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytologist*

1561   **225**, 1447–1454.

1562   SMALE, D.A., WERNBERG, T., OLIVER, E.C.J., THOMSEN, M., HARVEY, B.P., STRAUB, S.C.,

1563   BURROWS, M.T., ALEXANDER, L. V, BENTHUYSEN, J.A. & DONAT, M.G. (2019). Marine

1564   heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature*

1565   *Climate Change* **9**, 306–312.

1566   SMITH, R., MIDDLEBROOK, R., TURNER, R., HUGGINS, R., VARDY, S. & WARNE, M. (2012)

1567   Large-scale pesticide monitoring across Great Barrier Reef catchments–paddock to reef

1568   integrated monitoring, modelling and reporting program. *Marine Pollution Bulletin* **65**,

1569   117–127.

1570   SOISSONS, L.M., HAANSTRA, E.P., VAN KATWIJK, M.M., ASMUS, R., AUBY, I., BARILLÉ, L.,

BRUN, F.G., CARDOSO, P.G., DESROY, N., FOURNIER, J., GANTHY, F., GARMENDIA, J.-M., GODET, L., GRILO, T.F., KADEL, P., *ET AL.* (2018). Latitudinal patterns in european seagrass carbon reserves: influence of seasonal fluctuations versus short-term stress and disturbance events. *Frontiers in Plant Science* **9**, 88.

SOLOMON, S., PLATTNER, G.-K., KNUTTI, R. & FRIEDLINGSTEIN, P. (2009). Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences* **106**, 1704–1709.

SØRENSEN, J.G., KRISTENSEN, T.N. & LOESCHCKE, V. (2003). The evolutionary and ecological role of heat shock proteins. *Ecology Letters* **6**, 1025–1037.

STEINER, S.C.C. & WILLETTE, D.A. (2015). The Expansion of *Halophila Stipulacea* (Hydrocharitaceae, Angiospermae) is Changing the Seagrass Landscape in the Commonwealth of Dominica Lesser Antiles. *Caribbean Naturalist* **22**, 1–19.

STONE, S.L. (2014). The role of ubiquitin and the 26S proteasome in plant abiotic stress signaling. *Frontiers in Plant Science* **5**, 135.

STRYDOM, S., MURRAY, K., WILSON, S., HUNTLEY, B., RULE, M., HEITHAUS, M., BESSEY, C., KENDRICK, G.A., BURKHOLDER, D., HOLMES, T., FRASER, M.W. & ZDUNIC, K. (2020). Too hot to handle: unprecedented seagrass death driven by marine heatwave in a World Heritage Area. *Global Change Biology* **26**, 3525–3538.

SULLIVAN, B.K., TREVATHAN-TACKETT, S.M., NEUHAUSER, S. & GOVERS, L.L. (2018). Host-pathogen dynamics of seagrass diseases under future global change. *Marine Pollution Bulletin* **134**, 75–88.

TAN, Y.M., DALBY, O., KENDRICK, G.A., STATTON, J., SINCLAIR, E.A., FRASER, M.W., MACREADIE, P.I., GILLIES, C.L., COLEMAN, R.A. & WAYCOTT, M. (2020). Seagrass restoration is possible: Insights and lessons from Australia and New Zealand. *Frontiers in Marine Science* **7**, 617.

1596   TARQUINIO, F., HYNDES, G.A., LAVEROCK, B., KOENDERS, A. & SÄWSTRÖM, C. (2019). The

1597   seagrass holobiont: Understanding seagrass-bacteria interactions and their role in

1598   seagrass ecosystem functioning. *FEMS Microbiology Letters* **366**, fnz057.

1599   TELESCA, L., BELLUSCIO, A., CRISCOLI, A., ARDIZZONE, G., APOSTOLAKI, E.T., FRASCHETTI,

1600   S., GRISTINA, M., KNITTWEIS, L., MARTIN, C.S. & PERGENT, G. (2015). Seagrass

1601   meadows (*Posidonia oceanica*) distribution and trajectories of change. *Scientific*

1602   *Reports* **5**, 12505.

1603   TEOTIA, S. & SINGH, D. (2014). Oxidative stress in plants and its management. In *Approaches*

1604   *to Plant Stress and their Management,* pp. 227–253. Springer India.

1605   THOMAS, R., UNSWORTH, R.K.F. & RASHEED, M. (2010). *Seagrasses of Port Curtis and*

1606   *Rodds Bay and long term seagrass monitoring, November 2009*. Department of

1607   Employment, Economic Development and Innovation, Cairns, Australia.

1608   TOL, S.J., JARVIS, J.C., YORK, P.H., GRECH, A., CONGDON, B.C. & COLES, R.G. (2017). Long

1609   distance biotic dispersal of tropical seagrass seeds by marine mega-herbivores. *Scientific*

1610   *Reports* **7**, 4458.

1611   TOMASELLO, A., DI MAIDA, G., CALVO, S., PIRROTTA, M., BORRA, M. & PROCACCINI, G.

1612   (2009). Seagrass meadows at the extreme of environmental tolerance: the case of

1613   *Posidonia oceanica* in a semi-enclosed coastal lagoon. *Marine Ecology* **30**, 288–300.

1614   TOUCHETTE, B.W. (2007). Seagrass-salinity interactions: Physiological mechanisms used by

1615   submersed marine angiosperms for a life at sea. *Journal of Experimental Marine*

1616   *Biology and Ecology* **350**, 194–215.

1617   TRABONI, C., MAMMOLA, S.D., RUOCCO, M., ONTORIA, Y., RUIZ, J.M., PROCACCINI, G. &

1618   MARÍN-GUIRAO, L. (2018). Investigating cellular stress response to heat stress in the

1619   seagrass *Posidonia oceanica* in a global change scenario. *Marine Environmental*

1620   *Research* **141**, 12–23.

1621 TREVATHAN-TACKETT, S.M., SEYMOUR, J.R., NIELSEN, D.A., MACREADIE, P.I., JEFFRIES,

1622   T.C., SANDERMAN, J., BALDOCK, J., HOWES, J.M., STEVEN, A.D.L. & RALPH, P.J.

1623   (2017). Sediment anoxia limits microbial-driven seagrass carbon remineralization under

1624   warming conditions. *FEMS Microbiology Ecology* **93**, fix033.

1625 TRISOS, C.H., MEROW, C. & PIGOT, A.L. (2020). The projected timing of abrupt ecological

1626   disruption from climate change. *Nature* **580**, 496–501.

1627 TUTAR, O., MARÍN-GUIRAO, L., RUIZ, J.M. & PROCACCINI, G. (2017). Antioxidant response

1628   to heat stress in seagrasses. A gene expression study. *Marine Environmental Research*

1629   **132**, 94–102.

1630 TUYA, F., HAROUN, R. & ESPINO, F. (2014). Economic assessment of ecosystem services:

1631   monetary value of seagrass meadows for coastal fisheries. *Ocean & Coastal*

1632   *Management* **96**, 181–187.

1633 UGARELLI, K., CHAKRABARTI, S., LAAS, P. & STINGL, U. (2017). The seagrass holobiont and

1634   its microbiome. *Microorganisms* **5**, 81.

1635 UNSWORTH, R.K.F., NORDLUND, L.M. & CULLEN-UNSWORTH, L.C. (2019). Seagrass

1636   meadows support global fisheries production. *Conservation Letters* **12**, e12566.

1637 VALDEZ, S.R., ZHANG, Y.S., VAN DER HEIDE, T., VANDERKLIFT, M.A., TARQUINIO, F., ORTH,

1638   R.J. & SILLIMAN, B.R. (2020). Positive Ecological Interactions and the Success of

1639   Seagrass Restoration. *Frontiers in Marine Science* **7**, 91.

1640 VAN WESENBEECK, L., JANSSENS, L., MEEUWS, H., LAGATIE, O. & STUYVER, L. (2018).

1641   Droplet digital PCR is an accurate method to assess methylation status on FFPE

1642   samples. *Epigenetics* **13**, 207–213.

1643 VANDENKOORNHUYSE, P., QUAISER, A., DUHAMEL, M., LE VAN, A. & DUFRESNE, A. (2015).

1644   The importance of the microbiome of the plant holobiont. *New Phytologist* **206**, 1196-

1645   1206.

VIERLING, E. (1991). The roles of heat shock proteins in plants. *Annual Review of Plant Biology* **42**, 579–620.

WALKER, D.I. & CAMBRIDGE, M.L. (1995). An experimental assessment of the temperature responses of two sympatric seagrasses, *Amphibolis antarctica* and *Amphibolis griffithii*, in relation to their biogeography. *Hydrobiologia* **302**, 63–70.

WALKER, D.I. & McCOMB, A.J. (1992). Seagrass degradation in Australian coastal waters. *Marine Pollution Bulletin* **25**, 191–195.

WANG, X., XIN, C., CAI, J., ZHOU, Q., DAI, T., CAO, W. & JIANG, D. (2016). Heat priming induces trans-generational tolerance to high temperature stress in wheat. *Frontiers in Plant Science* **7**, 501.

WAYCOTT, M., DUARTE, C.M., CARRUTHERS, T.J.B., ORTH, R.J., DENNISON, W.C., OLYARNIK, S., CALLADINE, A., FOURQUREAN, J.W., HECK, K.L. & HUGHES, A.R. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* **106**, 12377–12381.

WERNBERG, T., BENNETT, S., BABCOCK, R.C., DE BETTIGNIES, T., CURE, K., DEPCZYNSKI, M., DUFOIS, F., FROMONT, J., FULTON, C.J., HOVEY, R.K., HARVEY, E.S., HOLMES, T.H., KENDRICK, G.A., RADFORD, B., SANTANA-GARCON, J., *ET AL.* (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science* **353**, 169–172.

WILKINSON, A.D., COLLIER, C.J., FLORES, F., LANGLOIS, L., RALPH, P.J. & NEGRI, A.P. (2017). Combined effects of temperature and the herbicide diuron on Photosystem II activity of the tropical seagrass *Halophila ovalis*. *Scientific Reports* **7**, 45404.

WILKINSON, A.D., COLLIER, C.J., FLORES, F. & NEGRI, A.P. (2015). Acute and additive toxicity of ten photosystem-II herbicides to seagrass. *Scientific Reports* **5**, 17443.

WILLETTE, D.A. & AMBROSE, R.F. (2012). Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and

1671   epibiota communities in the Eastern Caribbean. *Aquatic Botany* **103**, 74–82.

1672   WILLIAMS, S.L. (2001). Reduced genetic diversity in eelgrass transplantations affects both

1673   population growth and individual fitness. *Ecological Applications* **11**, 1472–1488.

1674   WINTERS, G., BEER, S., WILLETTE, D.A., VIANA, I., CHIQUILLO, K.L., BECA-CARRETERO, P.,

1675   BETTY VILLAMAYOR, B., AZCÁRATE-GARCÍA, T., SHEM-TOV, R. & MWABVU, B. (2020).

1676   The tropical seagrass *Halophila stipulacea*: reviewing what we know from its native and

1677   invasive habitats, alongside identifying knowledge gaps. *Frontiers in Marine Science* **7**,

1678   300.

1679   WINTERS, G., EDELIST, D., SHEM-TOV, R., BEER, S. & RILOV, G. (2017). A low cost field-

1680   survey method for mapping seagrasses and their potential threats: an example from the

1681   northern Gulf of Aqaba, Red Sea. *Aquatic Conservation: Marine and Freshwater*

1682   *Ecosystems* **27**, 324–339.

1683   WINTERS, G., NELLE, P., FRICKE, B., RAUCH, G. & REUSCH, T.B.H. (2011). Effects of a

1684   simulated heat wave on photophysiology and gene expression of high-and low-latitude

1685   populations of *Zostera marina*. *Marine Ecology Progress Series* **435**, 83–95.

1686   WISSLER, L., CODÕER, F.M., GU, J., REUSCH, T.B., OLSEN, J.L., PROCACCINI, G. &

1687   BORNBERG-BAUER, E. (2011). Back to the sea twice: Identifying candidate plant genes

1688   for molecular evolution to marine life. *BMC Evolutionary Biology* **11**, 8.

1689   YAPING, G., ZENGJIE, J., MEIRONG, D., JINGHUI, F., WEIWEI, J. & JIANGUANG, F. (2019).

1690   Photosynthetic and metabolic responses of eelgrass *Zostera marina* L. to short-term

1691   high-temperature exposure. *Journal of Oceanology and Limnology* **37**, 199–209.

1692   YORK, P.H., GRUBER, R.K., HILL, R., RALPH, P.J., BOOTH, D.J. & MACREADIE, P.I. (2013).

1693   Physiological and morphological responses of the temperate seagrass *Zostera muelleri*

1694   to multiple stressors: investigating the interactive effects of light and temperature. *PloS*

1695   *One* **8**, e76377.

1696   ZHANG, D., ZHANG, Q.S. & YANG, X.Q. (2017). Adaptive strategies of *Zostera japonica*

1697   photosynthetic electron transport in response to thermal stress. *Marine Biology* **164**, 35.

1698   ZIMMERMAN, R.C., HILL, V.J. & GALLEGOS, C.L. (2015). Predicting effects of ocean

1699   warming, acidification, and water quality on Chesapeake region eelgrass. *Limnology and*

1700   *Oceanography* **60**, 1781–1804.

1701   ZIMMERMAN, R.C., SMITH, R.D. & ALBERTE, R.S. (1989). Thermal acclimation and whole-

1702   plant carbon balance in *Zostera marina* L.(eelgrass). *Journal of Experimental Marine*

1703   *Biology and Ecology* **130**, 93–109.

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VIII. SUPPORTING INFORMATION

1706   Additional supporting information may be found online in the Supporting Information section

1707   at the end of the article.

1708   Table S1. List of thermal-related studies on seagrasses from 1985 to 2020. Data were

1709   collected from *Google Scholar* as indicated in the legend to Fig.1.

1710   Table S2. Number of studied populations from each seagrass species used for thermal-related

1711   studies from 1985 to 2020. Data were collected from *Google Scholar* as indicated in the

1712   legend to Fig.1.

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Figure legends

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: the

outputs of single general (atmospheric-ocean general circulation models) models; purple and

blue lines, respectively: the outputs of PROTHEUS and VANIMEDAT2 (regional) models;

red line: 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 gray, 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.

1745 **Fig. 2.** Common effects and responses of thermal stress on seagrasses at the molecular,

1746 biochemical/physiological and morphological level. HSP, heat shock protein; ROS, reactive

1747 oxygen species.

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1749 **Fig. 3.** Conceptual diagram summarizing the fate of seagrass populations under conditions of

1750 ocean warming as illustrated by *Posidonia oceanica* in the Mediterranean Sea. Blue carbon is

1751 the carbon stored in coastal and marine ecosystems.

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1753 **Fig. 4.** World map of seagrass populations used for thermal-related studies from 1985 to

1754 2020. Coloured symbols indicate study populations, with symbols sizes scaled according to

1755 the key on the left. World distributions of species are shown by background green shading,

1756 with species numbers indicated according to the key on the right. Data were collected from

1757 *Google Scholar* as indicated in the legend to Fig.1. Figure created by adapting Fig. 3 in Short

1758 *et al*. (2007). Details of locations and related publications are provided in Table S1.

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1771   Figure 1

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Negative effects of thermal stress on seagrasses	Responses of seagrasses
Morphological level	
Decrease in growth rate	Decrease in growth rate
Decrease in number of leaves/shoots	Decrease in above/below-ground biomass ratio
Decrease in leaf size	Heat stress-induced flowering
Increase in mortality	Anticipation of flowering time
Biochemial/physiological level	
Decrease in photosynthetic capacity	Activation of photoprotective mechanism
Increase in respiration	Increase in photoprotective pigments
Chlorophyll degradation	Modification of fatty acid content
Increase in sulfide stress	Changes in allocation of soluble sugar and starch
Damage of cellular membrane fluidity	Modification of ultrastructure and microtubules
Molecular level	
ROS production	Production of HSP and chaperones
Protein unfolding and degradation	Increase in antioxidant defences
Enhancement of disease impacts	Proteolysis and ubiquitination
Disruption of translational machinery	Epigenetic modification
Cytoskeleton organization damage	Cell wall fortification
Abnormal cell divisions	DNA repair
DNA damage	Apoptosis

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1786   Figure 2

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On-going ocean warming

Escape

Acclimatization Adaptation

Recolonization — New colonization

Die-off

Starting meadow

Eco

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Seagrass population characteristics

① Healthy seagrass meadows
Unaltered genetic and species diversity
High ecosystem functionality, large blue carbon storage

② Warm-adapted/acclimatized seagrass meadows
Impoverished species and genetic diversity
Reduced ecosystem functionality, smaller blue carbon storage

③ Settlement in favourable environments, recruitment of new genetic variants
Increased population connectivity, re-establishment of degraded meadows
Newly developed ecosystem functionality, smaller blue carbon storage

④ Dead meadow, seagrass habitat loss
Collapsed ecosystem functionality
Release of blue carbon to the atmosphere

⑤ New arrival or expansion of heat-tolerant seagrass meadows
New ecosystem functionality, smaller blue carbon storage

Seagrass population responses

① ➡ ② *Acclimatization/adaptation:* diverse genotypes, local adaptation, etc.

① ➡ ③ *Escape:* sexual reproduction, seed dispersal, northward migration

① ➡ ④ *Die-off:* seagrass loss

④ ➡ ② *Recolonization by native/original/former species*

④ ➡ ⑤ *New colonization by new heat-tolerant species (e.g.tropical seagrasses)*

② ➡ ④ *Will warm-adapted seagrasses survive future ocean change?*

⑤ ➡ ④ *Will heat-tolerant seagrasses survive future ocean change?*

🌡 Ocean mean temperature gradually increases

〜 Marine heatwaves become more intense and frequent

C Blue carbon storage

C Release of blue carbon to the atmosphere

Eco Ecosystem services

Eco Ecosystem services collapse
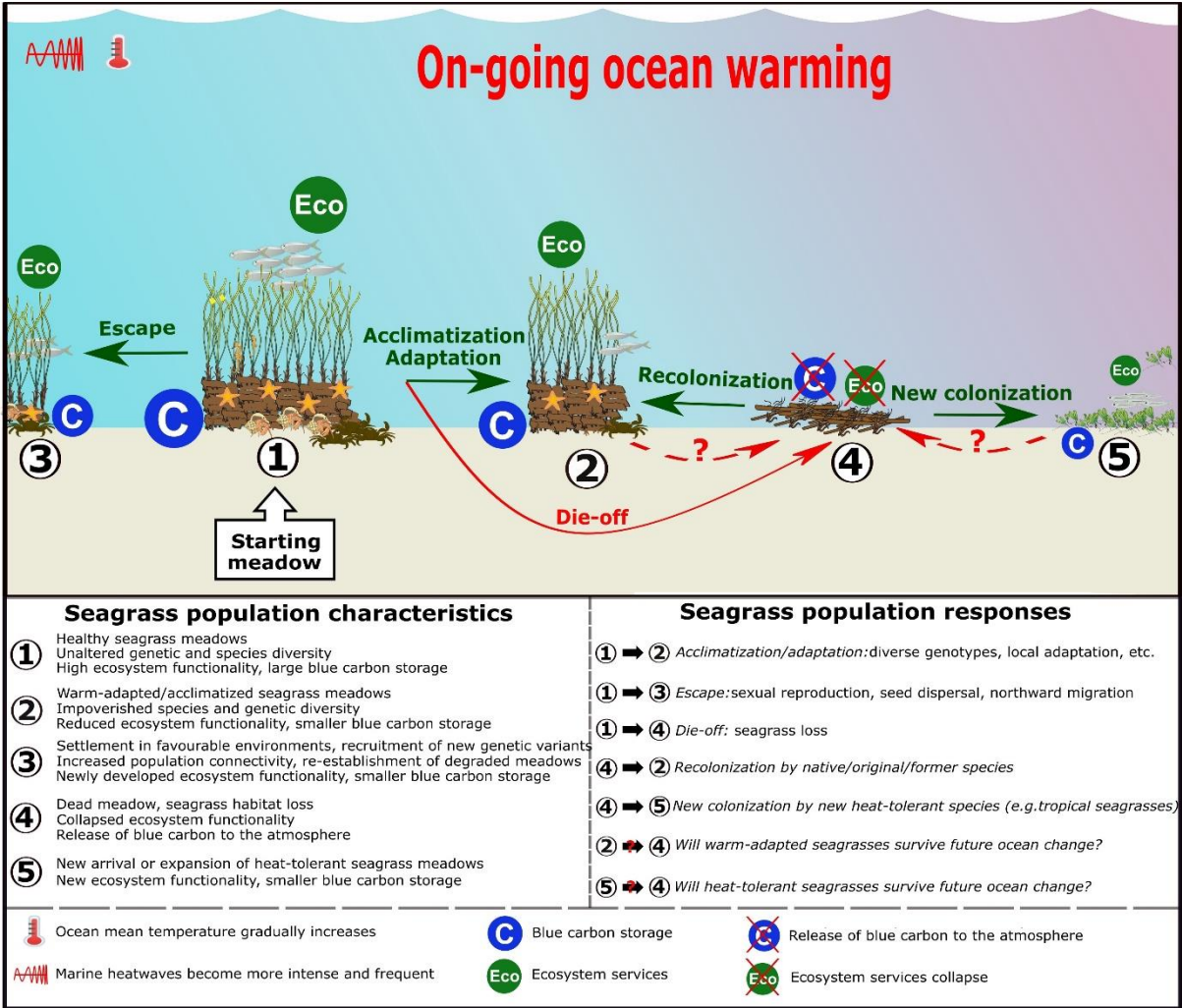
1802

1803 Figure 3

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Seagrass species from thermal-related studies

- ● *Zostera marina*
- ● *Posidonia oceanica*
- ● *Zostera muelleri*
- ● *Zostera japonica*
- ● *Zostera noltii*
- ○ *Amphibolis antarctica*
- ● *Amphibolis griffithii*
- ▼ *Posidonia australis*
- ▼ *Posidonia sinuosa*
- ▼ *Cymodocea nodosa*
- ▼ *Halophila ovalis*
- ▼ *Halodule uninervis*
- ▽ *Cymodocea serrulata*
- ▽ *Thalassia hemprichii*
- ▲ *Cymodocea rotundata*
- ▲ *Thalassia testudinum*
- ▲ *Enhalus acoroides*
- △ *Halodule wrightii*
- △ *Syringodium isoetifolium*
- △ *Zostera capricorni*
- ▲ *Thalassodendron ciliatum*
- ● *Halophila stipulacea*
- ● *Syringodium filiforme*
- ● *Ruppia maritima*

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1817   Figure 4