

Mediterranean seagrass vulnerable to regional climate warming

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The Mediterranean Sea, one of the regions warming fastest under climate change^{1,2}, harbours lush seagrass (*Posidonia oceanica*) meadows that form the basis for a key ecosystem in the region³. Recent field results have shown that increased maximum annual seawater temperature in the Mediterranean has already led to increased seagrass mortality⁴. Here we project the trajectory of *P. oceanica* meadows under the warming expected in the western Mediterranean through the twenty-first century to conclude that warming will lead to the functional extinction of *P. oceanica* meadows by the middle of this century (year 2049 ± 10) even under a relatively mild greenhouse-gas emissions scenario. Efforts to alleviate local stresses adding to the loss of *P. oceanica* meadows will have a limited effect in conserving the meadows under climate change. Efforts to mitigate climate change are urgently needed to preserve this key ecosystem.

P. oceanica, a Mediterranean endemic seagrass (marine clonal angiosperm), forms lush meadows across about 50,000 km² (ref. 5) providing important ecosystem services including carbon burial, nutrient cycling, coastal protection from erosion, and enhanced biodiversity⁶. Seagrass meadows rank among the most valuable biomes on Earth on the basis of the important ecosystem services they provide⁷. *P. oceanica* is one of the longest-lived, with shoots living up to 50 years and clones for several millennia^{8,9}, and slowest-growing (1 cm yr⁻¹) plant species in the biosphere¹⁰. Accordingly, *Posidonia* meadows are highly vulnerable to even small increases in mortality rate, which lead to rapid vegetation loss, as observed throughout the Mediterranean owing to excess nutrient and organic inputs and mechanical impacts^{11,12}.

P. oceanica is highly sensitive to seawater warming, with mortality rates in natural populations increasing threefold with a 3 °C increase in maximum annual seawater temperature⁴. The mean maximum summer seawater temperature between 2002 and 2010 around the Balearic Islands (western Mediterranean) has already increased by 1.05 ± 0.37 °C relative to 1980–2000 (ref. 4), and model projections predict that the temperature in the Mediterranean region will continue to rise. However, no predictions have yet been formulated to derive expectation on the future trajectories of the key ecosystem this species forms.

Here we examine the future trajectories of *P. oceanica* meadows under climate warming and assess whether seagrass resistance to climate warming increases by alleviating other local pressures also contributing to mortality. First, we estimate the temporal evolution of annual maximum seawater surface temperature (SST_{max}) from calibrated time series of a multi-model ensemble formed by ten coupled atmospheric–ocean general circulation models (AOGCMs), one coupled atmospheric–ocean regional

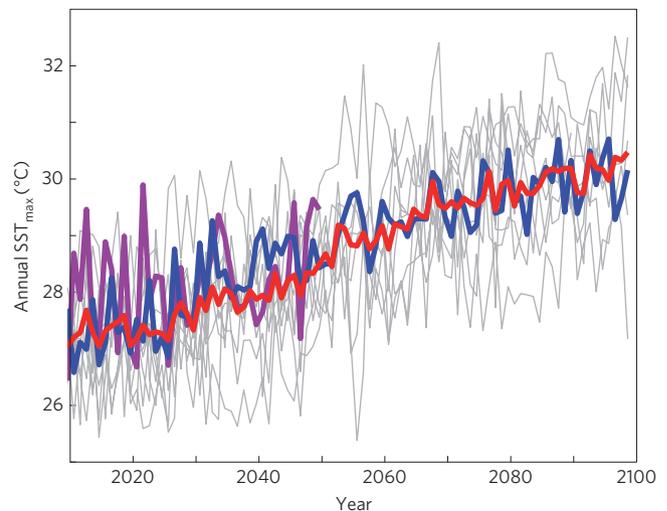


Figure 1 | Annual SST_{max} in the Balearic Islands region projected for the twenty-first century. Grey lines: the outputs of single general (AOGCMs) models; purple and blue lines, respectively: the outputs of PROTHEUS and VANIMEDAT2 (regional) models; red line: the ensemble average.

circulation model and one forced ocean regional model (see Supplementary Methods). These models run for the twenty-first century under the *Special Report on Emissions Scenarios* (SRES) A1B scenario of greenhouse-gas (GHG) emissions¹³, a moderately optimistic scenario assuming a balance between fossil and non-fossil energy sources conducive to stabilized GHG concentrations after 2050 (ref. 13). We then use the empirically derived functional relationship between annual SST_{max} and *P. oceanica* shoot mortality⁴ (Supplementary Fig. S1) to predict the trajectory of *P. oceanica* meadows under the expected seawater warming.

All models project a rapid warming of surface waters around the Balearic Islands during the twenty-first century for the scenario SRES A1B (Fig. 1). On average, the models project an increase in summer SST_{max} of 3.4 ± 1.3 °C by the end of this century. This increase is due to two factors. First, an increase in annual mean temperature (2.8 ± 1.1 °C, Supplementary Table S1) due to the combined effect of reduced heat loss across the sea surface and warming of the water flowing from the Atlantic Ocean through the Gibraltar Strait. Second, the amplitude of the seasonal cycle increases by 0.6 ± 0.5 °C (Supplementary Table S1), so summers would be warmer relative to the annual mean at the end of the century when compared with the present.

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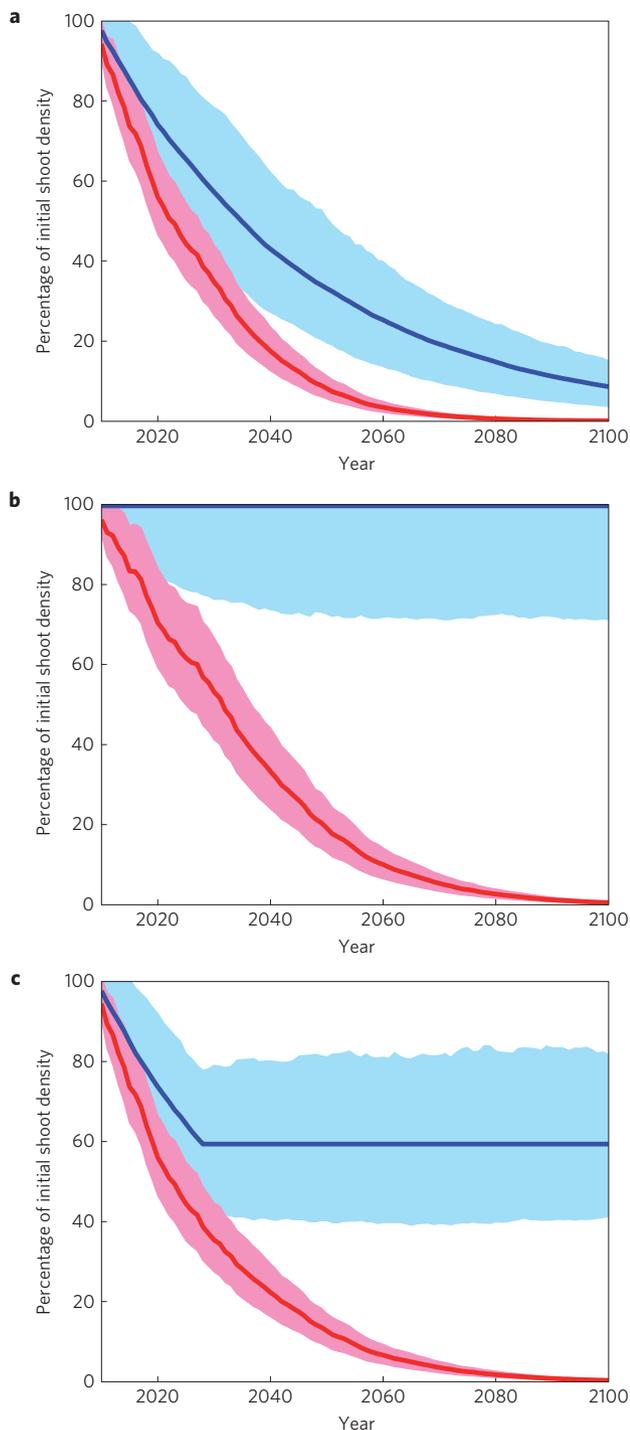


Figure 2 | Percentage of *P. oceanica* shoot density in the twenty-first century. a–c. Pink line: considering warming and local impacts (a), warming but local impacts removed by 2010 (b) and warming but local impacts removed by 2030 (c). Blue lines: the projected percentage of shoot density in the absence of warming. The shadowed areas show the uncertainty ranges (estimated as the 90% of the Monte Carlo distribution).

All models indicate an increase in the number of extreme warm events during this century (Supplementary Table S2). Models project, on average, 0.78 ± 0.27 extreme warm events per year (that is, three events every four years) for the period 2025–2050, which is three times the present frequency (0.22 ± 0.15 events per year; that is, one event every four years; Supplementary Table S2). Moreover, the average intensity of heatwaves is expected to increase

from the present 19.15 ± 16.10 degree-days ($^{\circ}\text{C}$) to 513.20 ± 324.20 degree-days ($^{\circ}\text{C}$) by year 2050 (Supplementary Table S2). The frequency and intensity of heatwaves is likely to continue to increase along the second half of the twenty-first century (that is, on average, 1 ± 0.01 event per year of $3,425.4 \pm 1,202.9$ degree-days ($^{\circ}\text{C}$) intensity; Supplementary Table S2). The duration of warm periods is projected to be longer.

Annual SST_{max} in the region would consistently exceed 28°C , the critical seawater temperature above which *P. oceanica* mortality accelerates⁴, after year $2,047 \pm 19$ (Fig. 1). Thus, seawater warming forecasted for the Balearic Islands region under the A1B scenario would seriously compromise the persistence of *P. oceanica* meadows. Examination of predicted trajectories of *P. oceanica* density under projected SST warming reveals that seagrass density would rapidly decrease during the first 30 years (Fig. 2a) to reach the threshold of shoot density below which meadow functionality is lost (that is, the 10% of the present density) by year 2049 (Fig. 2a and Table 1). The uncertainty associated with the time of functional extinction of *P. oceanica* meadows is one decade (± 10 years), owing the combined uncertainties in temperature projections and the variability in the temperature dependence of the mortality and recruitment parameters (Supplementary Methods).

P. oceanica meadows are already declining in the Balearic Islands owing to local disturbances (for example, water and sediment deterioration and physical anthropogenic disturbances), resulting in a mortality rate of 0.07 yr^{-1} in the region before year 2000, when SST_{max} did not exceed 25.7°C and no evidence of warming-driven mortality was available¹³. At this rate, *P. oceanica* would reach 10% of the present density by year 2093 ± 12 (Fig. 2a, Table 1). Hence, warming compounds with local disturbances may advance by 44 years the functional loss of *P. oceanica* meadows.

The benefits of adopting mitigation measures of coastal deterioration in increasing the resistance of *P. oceanica* to warming were examined by comparing *P. oceanica* density under two further scenarios: complete mitigation of local disturbances effective since year 2010 with further seagrass mortality due exclusively to warming; and complete mitigation of local coastal deterioration effective after year 2030 and subsequent seagrass mortality due exclusively to warming. As *P. oceanica* meadows achieve demographic balance (that is, mortality \approx recruitment) at a mortality rate of 0.05 yr^{-1} , the excess mortality due to local anthropogenic pressure in the region can be estimated as the difference between *P. oceanica* mortality rates observed in the absence of excess SST warming of 0.07 yr^{-1} (ref. 13) and the equilibrium mortality rate of 0.05 yr^{-1} , yielding an excess seagrass mortality due to local disturbances of 0.02 yr^{-1} . If local anthropogenic pressures were completely removed in year 2010, *P. oceanica* meadows are expected to lose their functionality (that is, reach 10% of the present density) owing to warming by year 2061 ± 13 (Fig. 2b, Table 1). Hence, implementation of measures to remove local pressures on *P. oceanica* meadows at the beginning of the present decade would delay the functional loss of the meadow by about one decade. If local anthropogenic pressures were removed only by year 2030, *P. oceanica* meadows would reach 10% of the present density by year 2053 ± 14 (Fig. 2c, Table 1), hence delaying their functional loss by only a few years. These model calculations consider that local anthropogenic impacts and warming impacts are additive, whereas the magnitude of local anthropogenic impacts on *P. oceanica* may be amplified with increasing seawater temperature. For instance, the vulnerability of *P. oceanica* to nutrient and organic coastal inputs may increase with increasing seawater temperature, because warming enhances sediment microbial activity. Warming in areas with excessive nutrient and organic inputs, therefore, may increase the risk for sediment anoxia and production of metabolites as sulphides, both detrimental for seagrass survival¹⁴.

Anthropogenic GHG emissions trigger impacts beyond warming, including for instance ocean acidification¹⁵. Ocean

Table 1 | Estimated average (\pm s.e.m.) year when *P. oceanica* meadows would reach 10% of their density in 2100 under different combinations of forecasted warming under scenario SRES A1B, no warming (that is, seawater temperature remaining similar to that observed for the period 1980–2000), persistence of local anthropogenic pressures at the year 2000 level, and complete mitigation of local anthropogenic pressures by year 2010 and year 2030.

Simulation	Year when meadow density reaches 10% of the present density
No warming but local anthropogenic pressures	2093 \pm 12
Warming and local anthropogenic pressures	2049 \pm 10
Warming but complete mitigation of local anthropogenic pressures by year 2010	2061 \pm 13
Warming but complete mitigation of local anthropogenic pressures by year 2030	2053 \pm 14

acidification may enhance seagrass productivity^{16–18}, because seagrass photosynthesis is often CO₂ limited¹⁹. However, the lack of experimental analyses addressing synergetic effects of seawater warming and acidification precludes the assessment of whether increased CO₂ availability may possibly enhance seagrass resistance to thermal stress. Field observations, however, suggest that it is unlikely that enhanced CO₂ may increase seagrass resistance to disturbances such as warming. Retrospective examination of *P. oceanica* growth nearby thermal vents in the region of Sicily (Italy) reveals a decrease of plant growth, indicative of plant stress, after an explosive episode, which dropped pH to 4.7–5.4, with the associated increase in CO₂, and increased turbidity and seawater temperature above the upper thermal tolerance limit of the species (28 °C–30 °C; refs 4,20) for some months²¹. Seagrass was reported to remain stressed 3 years after the disturbing event²¹. This suggests that even greatly increased CO₂ does not confer resistance to thermal stress. In addition, the global rate of seagrass loss has accelerated since 1990 (ref. 22) in spite of the increase of CO₂ atmospheric concentrations²³, further indicating a limited capacity of ocean acidification to buffer seagrass vulnerability to disturbances.

Organisms typically respond to climate change by shifting their biogeographic ranges to maintain their thermal regime²⁴. However, recent analysis of the velocity of climate change, as the rate of poleward migration of isotherms with climate change, identified the Mediterranean Sea as a region of concern because the northward displacement of the biogeographic ranges of endemic species, such as *P. oceanica*, is bound by the presence of the European continent². Hence, *P. oceanica* must either adapt to changing climate or face extinction. The slow growth and sparse sexual reproduction of *P. oceanica*^{10,25}, together with its reported low evolutionary and mutation rates^{9,26}, suggest little resilience and limited capacity for adaptation of this species to the rapid warming projected for the Mediterranean Sea. Moreover, examination of the link between genetic diversity and the resistance to perturbations for *P. oceanica* delivered no evidence that the limited genetic diversity present in their populations adds resistance to perturbations⁹. Mediterranean warming also stimulates the proliferation of competing macrophytes, in particular invasive macroalgae from tropical and subtropical origin²⁷, which are already impacting on *P. oceanica* meadows²⁸ and are expected to gain greater competitive advantage with further warming. Our understanding of competitive interactions with invasive species is still insufficient for this process to be incorporated in models of *P. oceanica* trajectories with warming. The contrasting effects of warming on *P. oceanica* and invasive macroalgal communities may accelerate *Posidonia* decline further, resulting in a steeper decline in *P. oceanica* meadows with warming than predicted here. Hence, the trajectories of *P. oceanica* with warming projected here should be considered to be conservative ones.

The results presented show that SST_{max} is likely to rapidly increase in the Balearic Archipelago region, accelerating the functional loss of already impacted *P. oceanica* meadows. Modelled scenarios show that actions to mitigate other local impacts,

although beneficial, will have a modest effect in the seagrass resistance to warming events, with the likely functional loss of this seagrass by the middle of this century. This finding shows that there is no alternative to rapid and substantial international action to reduce GHG emissions, well below those considered in the relatively conservative emission scenario used here, to guarantee that this key millenary ecosystem will continue to deliver services beyond year 2100.

Methods

Projections of summer SST_{max} in the Balearic Archipelago region (Spain, western Mediterranean) for years 2010–2100 were obtained from the daily outputs of 12 climate models (10 AOGCMs, 1 atmosphere–ocean regional climate model and 1 ocean regional climate model). These models were run for the period 1950–2100. During the control period (1950–2000), the models were forced with observed GHG concentrations. During the scenario period (2001–2100), GHG concentrations increased in agreement with the SRES A1B scenario of GHG emissions (http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php). Temperature time series from the models were scaled to remove eventual biases and to adjust the amplitude of the seasonal cycle and the intraseasonal variability to observed values. The scaling was carried out for the control period and then applied to the scenario period (Supplementary Methods).

The trajectories of *P. oceanica* density over time (N) were modelled using an exponential function:

$$N = N_0 \cdot \exp[-t \cdot (M - R)] \quad (1)$$

where N_0 is the initial density, t (in years) is the time elapsed between density observations, R is the shoot recruitment rate and M is the shoot mortality rate. We estimated M using the empirical linear relationship fitted between observed *P. oceanica* shoot mortality reported by ref. 4 and summer SST_{max} averaged over the Balearic Islands region:

$$M = a \cdot \text{SST}_{\text{max}} + b$$

The fitted parameters ($a = 0.021 \pm 0.002$, $b = -0.471 \pm 0.065$, Supplementary Fig. S1) were not significantly different from those fitted using *in situ* maximum summer seawater temperature⁴. Because *P. oceanica* recruitment rate is independent of seawater warming⁴, we used the average (\pm standard error) shoot recruitment rate observed in the Balearic Islands between years 2001 and 2007 ($0.05 \pm 0.01 \text{ yr}^{-1}$, ref. 4) to model future recruitment. Uncertainty in *P. oceanica* density projections was estimated using a Monte Carlo method considering an ensemble of realizations including both the variability in SST projections and that of the parameters of equation (1) (Supplementary Methods).

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Author contributions

G.J., N.M. and C.M.D. conceived and designed the study, discussed the results and wrote the manuscript and Supplementary Information. G.J. wrote the code, ran the model and analysed output data.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to N.M.