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Decline of seagrass (*Posidonia oceanica*) production over two decades in the face of warming of the Eastern Mediterranean Sea

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Summary

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- The response of *Posidonia oceanica* meadows to global warming of the Eastern Mediterranean Sea, where the increase in sea surface temperature (SST) is particularly severe, is poorly investigated.
- Here, we reconstructed the long-term *P. oceanica* production in 60 meadows along the Greek Seas over two decades (1997–2018), using lepidochronology. We determined the effect of warming on production by reconstructing the annual and maximum (i.e. August) SST, considering the role of other production drivers related to water quality (i.e. Chla, suspended particulate matter, Secchi depth).
- Grand mean (\pm SE) production across all sites and the study period was 48 ± 1.1 mg DW per shoot yr^{-1} . Production over the last two decades followed a trajectory of decrease, which was related to the concurrent increase in annual SST and SST_{aug}. Annual SST $> 20^\circ\text{C}$ and SST_{aug} $> 26.5^\circ\text{C}$ was related to production decline (GAMM, $P < 0.05$), while the rest of the tested factors did not help explain the production pattern.
- Our results indicate a persistent and increasing threat for Eastern Mediterranean meadows, drawing attention to management authorities, highlighting the necessity of reducing local impacts to enhance the resilience of seagrass meadows to global change threats.

Introduction

The unprecedented rise in sea surface temperature (SST) and the increasing frequency and intensity of marine heat waves (MHWs) over the past four decades (Frölicher *et al.*, 2018) pose an imminent threat to biodiversity across the globe (Smale *et al.*, 2019; Trisos *et al.*, 2020). Seagrasses rank among the marine habitats most affected by warming (Perry *et al.*, 2019; Garrabou *et al.*, 2022). Their performance is hampered at multiple levels (Hendriks *et al.*, 2017; Marín-Guirao *et al.*, 2019; Kim *et al.*, 2020; Nguyen *et al.*, 2021), resulting in shoot mortality and cover loss (Kendrick *et al.*, 2019; Strydom *et al.*, 2020) with cascading effects on the ecosystem services provided by them (Arias-Ortiz *et al.*, 2018; Aoki *et al.*, 2020). Understanding the response of benthic foundation species like seagrass to global warming is essential for implementing appropriate restoration schemes to enhance the resilience of our coasts (Unsworth *et al.*, 2019).

The iconic endemic seagrass of the Mediterranean Sea, *Posidonia oceanica* (L.) Delile, is particularly vulnerable to thermal stress, showing extensive damage (Ontoria *et al.*, 2019a; Pansini

et al., 2021; Stipcich *et al.*, 2022a) or even massive mortality (Díaz-Almela *et al.*, 2009; Marbà & Duarte, 2010). The Mediterranean Sea is warming on average 20% faster than the global ocean (Lionello & Scarascia, 2018), with a cumulative increase in mean SST of 1.3°C over the last 40 yr (Pastor *et al.*, 2020), and an increase of $0.056^\circ\text{C yr}^{-1}$ in maximum (i.e. summer) surface temperature (Pisano *et al.*, 2020). In addition, over the past decades, MHWs have become increasingly common, and a fourfold increase in their intensity is projected by the end of this century for the basin (Darmaraki *et al.*, 2019). Nevertheless, information on the regression of *P. oceanica* due to warming is strongly biased towards the Western Mediterranean subregion, while very limited data exists for the Eastern Mediterranean (Bennett *et al.*, 2022a; Stipcich *et al.*, 2022a), where warming is particularly intense, likely underestimating the magnitude of impact across the Mediterranean Sea. The increase in SST has been sharper in the eastern basin with a rate of $0.048^\circ\text{C yr}^{-1}$ compared with $0.036^\circ\text{C yr}^{-1}$ in the western part (Pisano *et al.*, 2020), which together with the forecasted intensity and frequency of MHWs in the former (Soto-Navarro *et al.*, 2020; Garrabou

et al., 2022) poses relatively higher risks to marine habitats in the eastern basin. Along the Greek Seas, in particular, increasing SST trends have been identified ranging from 0.045 to 0.069°C yr⁻¹, while at the same time, the number and duration of MHWs have significantly increased during the last years (i.e. 2008–2021; Androulidakis & Krestenitis, 2022). A deeper understanding of the impact of warming on *P. oceanica* meadows extending along the Greek Seas is crucial, given that their extent represents 71% of the total extent estimated for the *P. oceanica* meadows of the Eastern Mediterranean Sea (Pergent-Martini *et al.*, 2021). However, the lack of historical baselines of seagrass dynamics in Greece (Gerakaris *et al.*, 2021) and the scarce and rather localized information on the potential response of these meadows to warming (Bennett *et al.*, 2022b; Stipcich *et al.*, 2022a,b) limits our comprehension on the impact of warming in this region and, thus, our capacity to design specialized mitigation measures.

Even though the Eastern Mediterranean seagrass populations are subjected to higher sea temperatures than in the western basin, occasionally above the upper thermal limit for survival previously reported for the latter (i.e. 28.9°C; Chefaoui *et al.*, 2017; Savva *et al.*, 2018), predicting their vulnerability to global warming can be challenging. Experimental studies suggest intraspecific variability in thermal tolerance depending on the thermal geography of the species, with warm-edge populations showing higher tolerance to warming (Bennett *et al.*, 2019, 2022b). However, a recent translocation experiment showed that shoots collected from the cool (i.e. Catalunya, Spain) and warm (i.e. Cyprus) edges of the species distribution performed equally well under common warming scenarios, but both did better than those from the central (i.e. Mallorca, Spain) edge, implying that species performance under thermal stress does not necessarily reflect the geographical (i.e. thermal) origin of the species (Bennett *et al.*, 2022a). Moreover, those studies underpin the difficulty in predicting the thermal resilience of the species from single populations. To gain a deeper understanding of *P. oceanica* response to warming, it is important to study the other environmental factors that drive seagrass response, apart from the thermal origin of the population. In natural environments, local drivers of seagrass production, such as light and nutrient availability, shape seagrass traits (Alcoverro *et al.*, 1995), introducing complex relationships of the environmental regime with warming (Moreno-Marín *et al.*, 2018). Local environmental stressors, like eutrophication and light deprivation (York *et al.*, 2013; Pansini *et al.*, 2021), can act synergically to the warming effect (Moreno-Marín *et al.*, 2018), and could render seagrass meadows more vulnerable to temperature rise (Egea *et al.*, 2018; Ontoria *et al.*, 2019b; Pansini *et al.*, 2021). Thus, the study of multiple populations along environmental gradients is necessary to disentangle the response of *P. oceanica* populations to warming at larger spatial scales.

Furthermore, although information derived from field and/or laboratory experiments at small temporal scales is crucial for deciphering the physiological response of *P. oceanica* to warming, it may prove less efficient in providing insights into the long-term vulnerability of the species. The study of proxies encompassing seagrass variability at longer temporal scales could be important in understanding the response to warming. This is possible based

on the analyses of *P. oceanica* shoots, which offer the opportunity to reconstruct past changes in production at annual resolution using the lepidochronology method (Pergent, 1990). Previous studies showed that rhizome elongation and leaf production responded to temporal cycles linked to natural variability (Pergent-Martini *et al.*, 1994; González-Correa *et al.*, 2007; di Maida *et al.*, 2013), as well as to human impacts (Guidetti, 2001; Gonzalez- *et al.*, 2008; Manzanera *et al.*, 2014) including MHWs (Stipcich *et al.*, 2022a).

Here, we studied the long-term variability of *P. oceanica* production in the Eastern Mediterranean Sea (Greek Seas). To do so, we reconstructed the annual rhizome growth over two decades (1997–2018) using lepidochronology in 60 meadows encompassing different environmental conditions along the Greek Seas. To determine the spatiotemporal effect of warming, seagrass production was related to satellite time-series data of annual and maximum (i.e. August) SST, taking into consideration the effects of local environmental factors related to water quality, namely nutrients, water transparency and turbidity, across the country.

Materials and Methods

Study area and sampling procedures

The Greek Seas encompass natural and anthropogenic gradients in environmental conditions that allowed us to study the potential response of *Posidonia oceanica* (L.) Delile to warming, taking into consideration the water quality. The Ionian and South Aegean Seas are formed by cold modified Atlantic water and ultraoligotrophic warm Levantine water, while the North Aegean Sea originates from colder and nutrient-rich water masses entering from the Black Sea through the Dardanelles Strait. As a result, there is a clear gradient of SST and primary production from the North towards the South–East of the country (Fig. 1a–e; see relative section in the Materials and Methods). At the same time, the pattern of SST warming but also localized phenomena of eutrophication are spatially diversified, with stronger warming in the Ionian and North Aegean Seas (Androulidakis & Krestenitis, 2022), whereas the degree of human pressure is higher close to major cities (e.g. Athens, Attica) (Pavlidou *et al.*, 2015) and towards the continent as opposed to insular areas (e.g. Cyclades) (Gerakaris *et al.*, 2021).

Sixty monospecific *P. oceanica* meadows were studied covering the whole species distribution in the Greek Seas (South Aegean, North Aegean and Ionian Seas) (Panayotidis *et al.*, 2022) and encompassing both continental and insular (e.g. Cyclades Islands, Dodecanese Islands, Crete, Ionian Islands and North Aegean Islands) meadows in diverse environmental regimes (Supporting Information Fig. S1; Fig. 1a–e). Multiple meadows were sampled inside the Saronikos Gulf to allow the detection of possible meadow degradation due to the proximity of the Athens metropolitan area (Attica). The studied meadows extended from 3 to 30 m water depth. The substrate was sand (fine to coarse). At each sampling site, orthotropic shoots were randomly collected by hand by carefully detaching the vertical rhizome with the living foliar shoot from the horizontal rhizome to determine

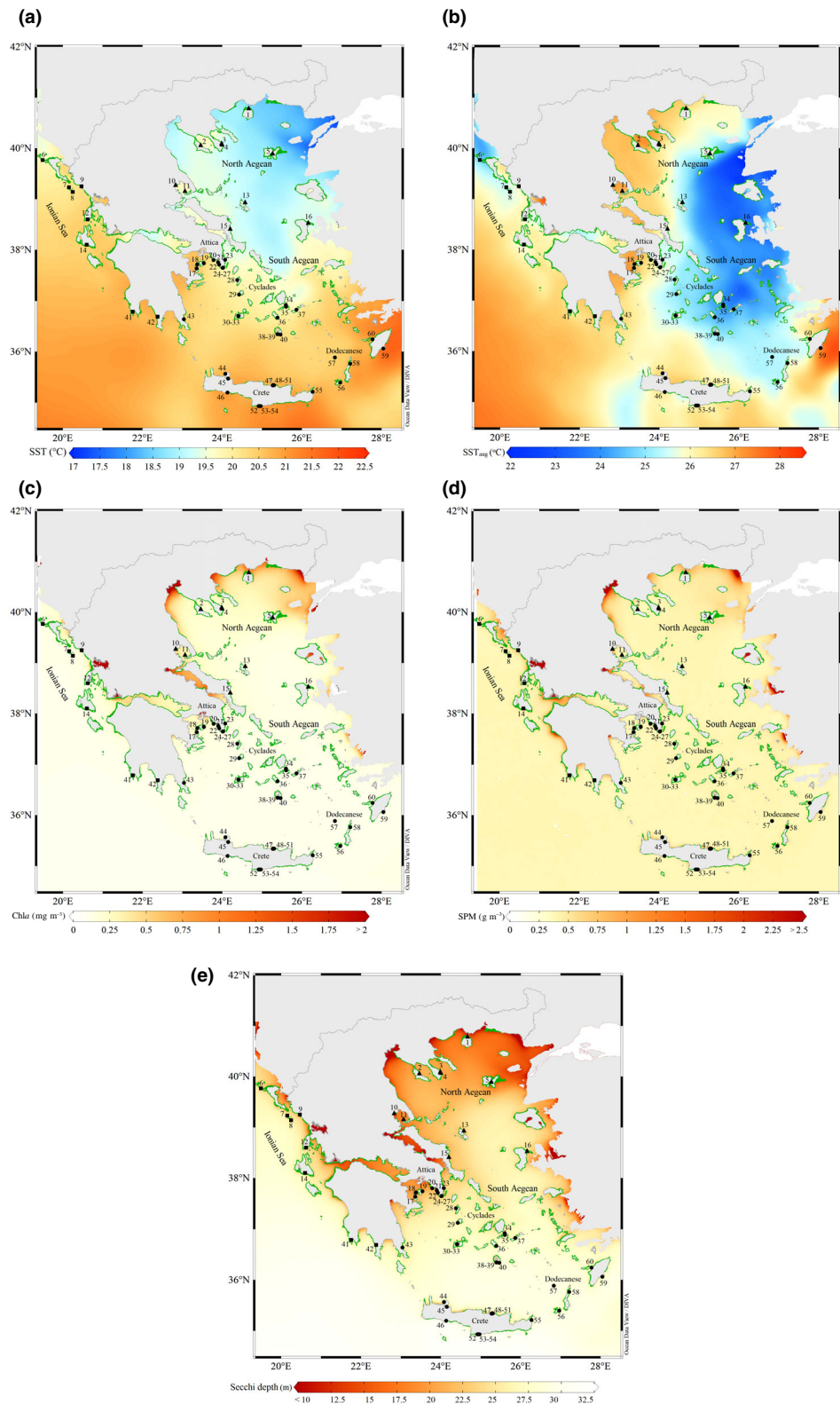


Fig. 1 Heatmaps of mean values (i.e. for the whole period of study (1997–2018)) of annual (a) sea surface temperature (SST, °C), (b) maximum sea surface temperature (SST_{max} , °C), (c) Chl a ($mg\ m^{-3}$), (d) suspended particulate matter (SPM, $g\ m^{-3}$) and (e) Secchi depth (m) along the Greek Seas. Sampling sites are shown. *Posidonia oceanica* distribution (from Panayotidis *et al.*, 2022) is indicated in green. Sites corresponding to different regions are represented by the applicable shape: triangles, North Aegean; circles, South Aegean; squares, Ionian Sea.

shoot age. On average, nine orthotropic shoots (ranging from 3 to 16 shoots per site) were randomly collected by hand during the period 2013–2020.

Environmental regime

The environmental regime, that is annual SST (SST), SST of August (SST_{aug}), Chl_a, suspended particulate matter (SPM) and Secchi depth, along all the Greek Seas, including our sampling sites, was reconstructed using daily or monthly (i.e. depending on their availability) satellite data from Copernicus Marine Database (<https://marine.copernicus.eu/>). Level-4 (L4) reprocessed and interpolated daily estimates of foundation SST data, which is free (or nearly free) of any diurnal cycle (SST MED SST L4 REP OBSERVATIONS 010 021), were downloaded at 5.5 × 5.5 km resolution. The daily data of SST_{aug} were also considered given that August corresponds to the warmest month of the Mediterranean Sea when major impacts are expected to occur (Marbà *et al.*, 2015). Level-4 (L4) reprocessed interpolated daily Chl_a, and monthly SPM and Secchi depth data were downloaded at 4 × 4 km resolution (OCEANCOLOUR GLO BGC L4 MY 009 104). Annual mean values per site were calculated by averaging the daily data in the case of SST, SST_{aug} and Chl_a and by averaging the monthly data in the case of SPM and Secchi depth.

We acknowledge that satellite-based estimates refer to the top 10 m of water depth (Beggs, 2021). Nevertheless, since the mean sampling depth across our sites was 12.4 m and the median was 15 m, and only five sites were found at water deeper than 15 m, we assumed that the satellite estimates were representative of the environmental profile at the given sampling depth of each site. Besides, in cases of coastal ecosystems where real-time *in situ* observations (e.g. buoys) are limited (<https://marine.copernicus.eu/>), the use of satellite-based estimates is a widely used and largely accepted methodology to relate the dynamics and response of marine biota, including seagrass meadows, to the environmental regime (Marbà *et al.*, 2015; Gerakaris *et al.*, 2021; Garrabou *et al.*, 2022).

For each site, the ‘nearest neighbour’ with available satellite data was carefully selected in MATLAB v.R2018a software. Satellite data were retrieved for the 1997–2018 period to match the period reconstructed for *P. oceanica* production (to be described later).

Laboratory and numerical procedures

A total of 540 *P. oceanica* shoots were analysed using the reconstructive technique of lepidochronology (Pergent, 1990). This method allows the identification of the different lepidochronological years based on the annual cyclic variation of sheath thickness. One lepidochronological year was identified between two consecutive minima in sheath thickness starting from the rhizome apex (sampling year). By convention, each lepidochronological year was assigned one calendar year. The thickness of each sheath per shoot was measured using a calliper. Shoot age was considered to equal the maximum age measured for the given shoot. Following the year assignment, the rhizome of each shoot was cut into separate segments, each of which corresponded to a different

year. The rhizome segments were dried at 60°C until constant weight to obtain their dry weight. Rhizome segments corresponding to the last 2 years of each shoot were excluded from the analysis, as the lepidochronological cycles may have not been complete at the time of sampling (Peirano, 2002). The dataset obtained covered the period from 1997 to 2018.

Production (mg DW per shoot yr⁻¹) was estimated as the dry weight of the rhizome segment per shoot and year for each site. The mean production for each study site was estimated as the average of production data for the whole reconstructed period for the given site. The annual mean production was estimated as the average of production data across all sites for each year. The grand mean production for our study was estimated as the average of production data across all sites and the whole reconstructed period.

Data analysis

One-way analysis of variance (ANOVA) was used to test for significant differences in mean production between regions (North Aegean, South Aegean and Ionian Sea). Normality and homogeneity of variance were checked before analysis using the Shapiro–Wilk test and Levene’s test, respectively. When these assumptions were not met, data were log₁₀ transformed. If significant differences occurred ($P < 0.05$), a Tukey’s *post hoc* test was used to identify significant differences among levels. Simple linear regressions were used to assess the temporal trend of SST, SST_{aug}, Chl_a, SPM and Secchi depth over the reconstructed period (1997–2018).

A generalized additive model (GAM) was used to assess the temporal trend of annual mean production through the years 1997–2018, using production data and a thin plate regression spline applied in the covariate ‘Year’. Despite the low number of measurements in the first 3 yr examined (1997–1999), the corresponding values did not deviate from the rest of the measurements. We tested the sensitivity of the model by excluding those values, and the statistical power of the model remained. Therefore, those values were included in the final analysis. Outliers represented a small percentage (4%) of total measurements that were within the range of natural variability; thus, they were also considered in the model.

Generalized additive mixed models (GAMMs) were used to determine the spatiotemporal effect of warming on seagrass production. Production data at each site and year were related to the annual mean of the thermal (SST, SST_{aug}) and the other environmental variables (Chl_a, SPM and Secchi depth) at the given site and year. This approach allowed the determination of the effect of warming on seagrass production, taking into consideration the role of local environmental drivers shaping the variability of production across the country. The GAMMs were examined by forward selection (Zuur *et al.*, 2009), starting with the effect of temperature (SST or SST_{aug}) and gradually adding the other environmental variables (i.e. Chl_a, SPM and Secchi depth). Following exploratory analysis, thin plate regression splines were added in the covariates SST, SST_{aug}, Chl_a, SPM and Secchi depth. Highly correlated variables (Pearson’s coefficient > 0.7)

were not included in the same model (i.e. SST–SST_{aug}, Chl_a–Secchi depth). Given the strong relationship of production with water depth (Tomasello *et al.*, 2016; Madonia *et al.*, 2021) and the confounding effect of shoot age in analyses of impacts on rhizome production of *P. oceanica* (Tomasello *et al.*, 2007, 2016), sampling depth and shoot age were taken into account in the data analysis to ensure that possible effects of temperature and the rest of the environmental variables would have been properly assessed and not masked. Therefore, sampling depth and shoot age were included in the models, as thin plate regression spline and linear covariates respectively, and indeed increased the robustness of the model (Table S1). Intercepts of each shoot were assumed to be random factors, accounting for the temporal autocorrelation of the measurements within the shoot. Spatial autocorrelation was also examined by including ‘Site’ as an additional random factor. However, its inclusion did not modify the autocorrelation pattern. As a result, the most parsimonious model, consisting of one random factor, was selected. The degree of smoothness was determined by the degrees of freedom (df) in each model, and equilibrium between the total number of df and the total number of observations was kept, avoiding overfitting the model. The degrees of freedom were selected by cross-validation. Gamma distribution with a logarithmic link was used.

All the models had the following form:

$$\text{Log}_e(\text{Production}) = a + f(\text{SST or SST}_{\text{aug}}) + f(\text{covariate}_{i\dots n}) \\ + f(\text{sampling depth}) + \text{shoot age} \\ + f(\text{Shoot}) + \varepsilon_{\tau}, \varepsilon_{\tau} \sim N(0, \sigma^2)$$

where $f(\text{covariate}_{i\dots n})$ was a thin plate spline applied to each covariate (Chl_a, SPM and Secchi depth) and $f(\text{Shoot})$ was the random intercept term for each shoot.

During the model selection process, variables that were not significant ($P > 0.05$) were excluded from further analysis. Finally, the best model was selected based on the lower Akaike information criterion (AIC; Akaike, 1973). A relative difference in the AIC (ΔAIC) > 2 units indicated a significant difference between two models (Burnham & Anderson, 2002). In the case ΔAIC between two models was equal or lower than 2, the most parsimonious model was selected. Model smoothers were fit in the ‘MGCV’ R package (Wood, 2011). All analyses were performed in R v.4.0.5 (R Core Team, 2021).

Results

The environmental regime (i.e. mean values of annual SST, SST_{aug}, Chl_a, SPM and Secchi depth) for the whole period of study (1997–2018) along the Greek Seas is shown in Fig. 1(a–e). The mean values of annual SST, SST_{aug}, Chl_a, SPM and Secchi depth for each sampling site for the whole period of study (1997–2018) are given in Table S2 and summarized across our sites in Table 1. Mean ($\pm\text{SD}$) annual SST was $19.8 \pm 0.7^\circ\text{C}$, with differences up to almost 3°C from the sites located in the northern (18.0 – 19.5°C) towards those located in the southern part of the country (20.0 – 21.2°C ; Tables 1, S2). Mean SST_{aug}

Table 1 Mean ($\pm\text{SD}$), minimum (Min), maximum (Max) and median values of annual sea surface temperature (SST, $^\circ\text{C}$), maximum sea surface temperature (SST_{aug}, $^\circ\text{C}$), Chl_a (mg m^{-3}), suspended particulate matter (SPM, g m^{-3}) and Secchi depth (m) across all sampling sites for the whole period of study (1997–2018).

	Mean ($\pm\text{SD}$)	Min	Max	Median
SST ($^\circ\text{C}$)	19.8 ± 0.7	18.0	21.2	19.8
SST _{aug} ($^\circ\text{C}$)	25.6 ± 0.8	23.2	27.3	25.7
Chl _a (mg m^{-3})	0.19 ± 0.10	0.10	0.68	0.16
SPM (g m^{-3})	0.53 ± 0.14	0.37	1.10	0.49
Secchi depth (m)	23.1 ± 3.7	13.0	30.4	23.7

($\pm\text{SD}$) was $25.6 \pm 0.8^\circ\text{C}$, with the lowest values found in Cyclades Islands (23.9 – 25.2°C) and the higher ones ($> 26.5^\circ\text{C}$) towards the continental coasts and some sites of Crete and Dodecanese Islands (Tables 1, S2). Mean annual ($\pm\text{SD}$) Chl_a was $0.19 \pm 0.10 \text{ mg m}^{-3}$, with most of the sites having low concentrations (ranging from 0.10 to 0.20 mg m^{-3}), apart from a few sites in the northern part of the country and closer to the continental coasts (0.22 – 0.68 mg m^{-3} ; Tables 1, S2). Mean annual SPM followed a similar pattern to Chl_a, with a mean value of $0.53 \pm 0.14 \text{ g m}^{-3}$ and higher values (0.57 – 1.10 g m^{-3}) towards the continental sites (Tables 1, S2). Mean annual Secchi depth ($\pm\text{SD}$) was generally high with a mean of $23.1 \pm 3.7 \text{ m}$ and 13.0 – 30.4 m range among sites (Tables 1, S2). SST and SST_{aug} along the Greek Seas increased over the period of study, following a linear warming rate of 0.045 and $0.044^\circ\text{C yr}^{-1}$, respectively (Fig. 2a,b). Chl_a showed a significant linear increase too ($P < 0.05$), while SPM and Secchi depth did not show a significant change during the reconstructed period ($P > 0.05$) (Table S3).

The lepidochronological dating resulted in the analysis of 534 *P. oceanica* shoots and 4347 rhizome segments. The mean production ($\pm\text{SE}$) differed significantly between the regions (ANOVA, $\text{MS} = 0.81$, $F = 16.61$, $P < 0.05$) due to the higher mean of the South Aegean meadows ($52.0 \pm 1.5 \text{ mg DW per shoot yr}^{-1}$) than those of the North Aegean ($39.2 \pm 2.3 \text{ mg DW per shoot yr}^{-1}$) and the Ionian ($41.9 \pm 2.2 \text{ mg DW per shoot yr}^{-1}$; Tukey’s *post hoc* test, $P < 0.05$; Fig. 3; Table S2). The significant differentiation within South Aegean (Tukey’s *post hoc* test, $P < 0.05$) was attributed to the difference between the mean values of insular meadows of Cyclades Islands ($58.2 \pm 3.1 \text{ SE mg DW per shoot yr}^{-1}$) and continental meadows extending inside Saronikos Gulf (Attica), although the latter had a relatively high production ($49.0 \pm 1.8 \text{ mg DW per shoot yr}^{-1}$). The other insular meadows of the region (Dodecanese, Crete) did not differ from those in the Cyclades or Saronikos Gulf. Overall, the range of production was similar between regions (19.5 ± 0.8 to $86.4 \pm 4.5 \text{ mg DW per shoot yr}^{-1}$ at the South Aegean, 21.3 ± 0.7 to $71.8 \pm 2.8 \text{ mg DW per shoot yr}^{-1}$ at the North Aegean and 18.5 ± 1.1 to $60.5 \pm 5 \text{ mg DW per shoot yr}^{-1}$ at the Ionian), suggesting that the observed spatial differences in production based on the ANOVA results should be attributed to the production of a few sites that yielded a higher mean per region. Differences in production were more pronounced between sites, which

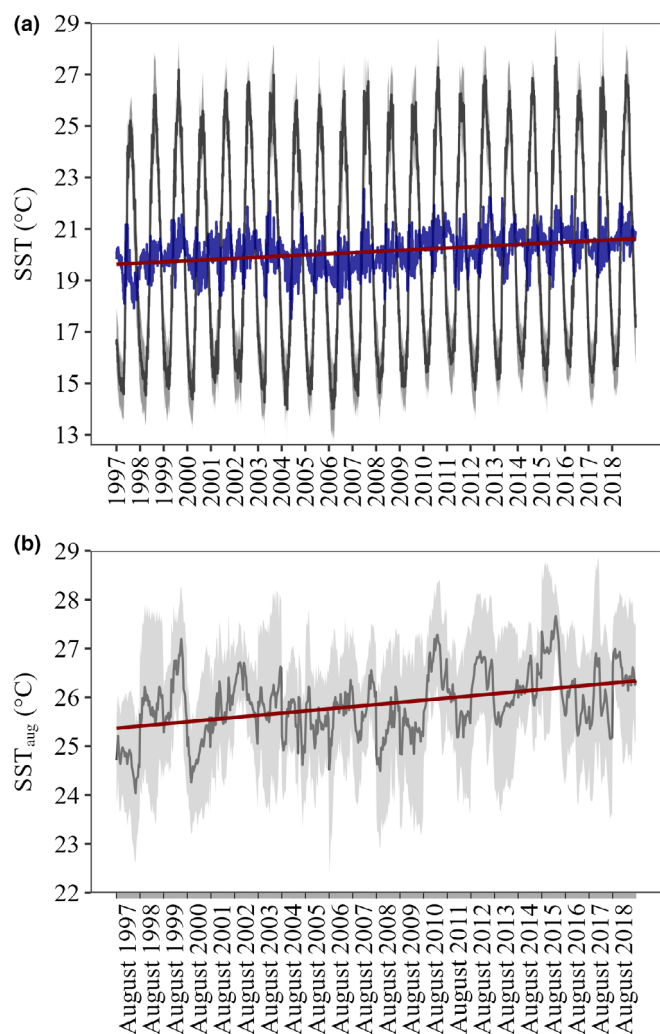


Fig. 2 Time series of (a) daily sea surface temperature (SST, 1 January–31 December) and (b) daily maximum sea surface temperature (SST_{aug} , 1–31 August) during the reconstructed period (1997–2018) along the Greek Seas. The blue line represents the de-seasoned SST trend component. The red line designates a linear fit (at 95% confidence interval). The grey-shaded area represents the standard deviation from the mean of each daily measurement based on the total number of available grid points.

supported production ranging from 18.5 ± 1.1 mg DW per shoot yr^{-1} at Oitylo (Ionian Sea) to 86.4 ± 4.5 mg DW per shoot yr^{-1} at Keros (Cyclades; Fig. 3; Table S2), suggesting that local conditions drove the differences between sites rather than geographic discontinuities.

During the period 1997–2018, the annual mean (\pm SE) production across all sites ranged from 33.9 ± 0.4 mg DW per shoot yr^{-1} to 69.0 ± 0.9 mg DW per shoot yr^{-1} (Fig. 4). Annual mean production across all sites followed a declining trend (GAM model $P < 0.05$, Fig. 4) with a 51% decline from the year of highest production (i.e. 1999) to the last investigated one (i.e. 2018). Especially after 2011, annual mean production across all sites remained consistently below the grand mean production (i.e. across all sites and the study period) (48 ± 1.1 mg DW per shoot yr^{-1}), ranging from 34 to 46 mg DW per shoot yr^{-1} (Fig. 4).

According to the selected GAMM models, annual SST and SST_{aug} had a significant effect on the production pattern (GAMM, $P < 0.05$; Table S4), while the effect of Chl a , SPM or Secchi depth did not contribute towards a more robust explanation of that pattern (Table S1). The range of 17–20°C for annual SST and 24–26.5°C for SST_{aug} had a positive effect on seagrass production (Fig. 5a,b). Values of annual SST $> 20^\circ\text{C}$ and $SST_{aug} > 26.5^\circ\text{C}$ had a negative effect on production, leading to an 8 and 17% decline in production, respectively, compared with the grand mean of our study.

Discussion

Our analysis showed that *P. oceanica* production followed a trajectory of decline along the Greek Seas over two decades (1997–2018), which was mainly related to the increase in the thermal regime during the study period. The data presented in this study contribute to bridging the big imbalance in the research effort regarding the spatial and temporal dynamics of *P. oceanica* across the Mediterranean Sea. Most studies so far have focused on the Western Mediterranean (mostly in Italy) and covered earlier periods (1960–2010). The grand mean production across all sites during the reconstructed period (48 ± 1.1 mg DW per shoot yr^{-1}) fell within the range previously reported for *P. oceanica* in the Mediterranean (20–220 mg DW per shoot yr^{-1}) (Pergent & Pergent-Martini, 1990; Pergent-Martini *et al.*, 1994; Calvo *et al.*, 2006, 2021; González-Correa *et al.*, 2007; Montefalcone *et al.*, 2008; Tomasello *et al.*, 2016; Pansini *et al.*, 2021; Stipcich *et al.*, 2022a). The range of our estimates is similar to that of the few studies that reconstructed *P. oceanica* production over the last decade (i.e. after 2010, 29–112 mg DW per shoot yr^{-1} ; Calvo *et al.*, 2021; Pansini *et al.*, 2021; Stipcich *et al.*, 2022a). However, those studies did not explore the temporal trend in production, which precludes a thorough comparison of *P. oceanica* dynamics across the basin, especially during the last decade when warming has been particularly intense in the region (Androulidakis & Krestenitis, 2022).

Annual SST surpassed the 20°C in 36% of the measurements, leading to a decline in mean production of 1.2-fold compared with the mean production when SST was within the range of 17–20°C. SST_{aug} temperature between 22 and 24°C resulted in a small decrease in production and SST_{aug} temperature above 26.5°C caused a sharp decrease in production. SST_{aug} higher than 26.5°C was reached in 21% of the cases in our study area, especially towards the continental coasts and the Dodecanese Islands, while regions towards the North Aegean and the Ionian Seas, which have been characterized as particularly vulnerable to MHWs (Androulidakis & Krestenitis, 2022), showed SST_{aug} values as high as 28.5°C. Our results agree with previous studies that showed a reduction in *P. oceanica* production with increasing temperatures (Pansini *et al.*, 2021; Stipcich *et al.*, 2022a), as well as in other seagrass species, for example *Cymodocea serrulata*, *Zostera muelleri* and *Halodule uninervis* (Collier *et al.*, 2017). In particular, the deterioration of *P. oceanica* growth performance was reported at $> 27^\circ\text{C}$ (Guerrero-Meseguer *et al.*, 2017), whereas the limit for *P. oceanica* shoot survival was determined at 28°C

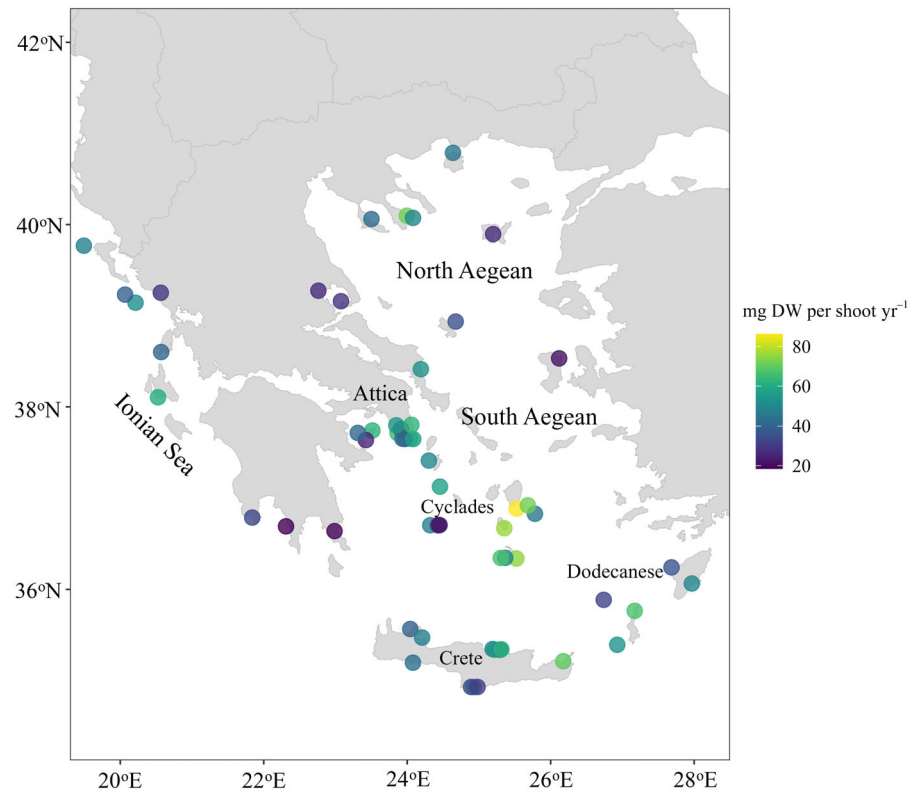


Fig. 3 Geographical distribution of mean (i.e. for the whole reconstructed period) *Posidonia oceanica* production (mg DW per shoot yr⁻¹) per site. Points have been jittered to improve visualization.

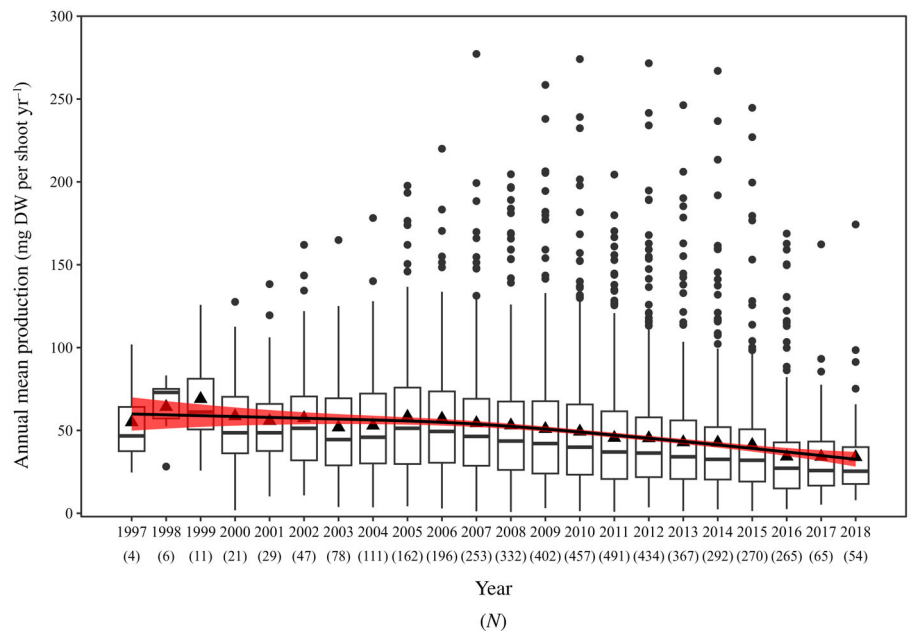


Fig. 4 Box plots of the annual mean (i.e. across all sites) *Posidonia oceanica* production (mg DW per shoot yr⁻¹) per year. The black lines represent the medians, the boxes encompass the 25 and 75% quantiles, and the black circles show data points beyond the whiskers. The black triangles present the mean values. The black line represents the temporal trend of production based on generalized additive model (GAM) and the red-shaded areas the confidence intervals. The number of measurements in each year (*N*) is given in parenthesis.

from experimental and empirical estimates (Marbà *et al.*, 2022). Nevertheless, these estimates derive from the Western Mediterranean and the results obtained in our study are not necessarily comparable due to intraspecific variation in the thermal limits depending on local adaptation, plasticity and the thermal origin of the plants (Bennett *et al.*, 2022b; Marbà *et al.*, 2022). Indeed, the Eastern Mediterranean populations are living closer to the

warmer edge of their distribution (29°C; Chefaoui *et al.*, 2017) and are historically subjected to higher temperatures than the western meadows (Templado, 2014), and thereby they likely display higher thermal resilience. Therefore, extreme climatic events (MHWs) close to the identified thresholds, that could be devastating for Western Mediterranean meadows (Díaz-Almela *et al.*, 2009; Marbà & Duarte, 2010), encompass temperatures

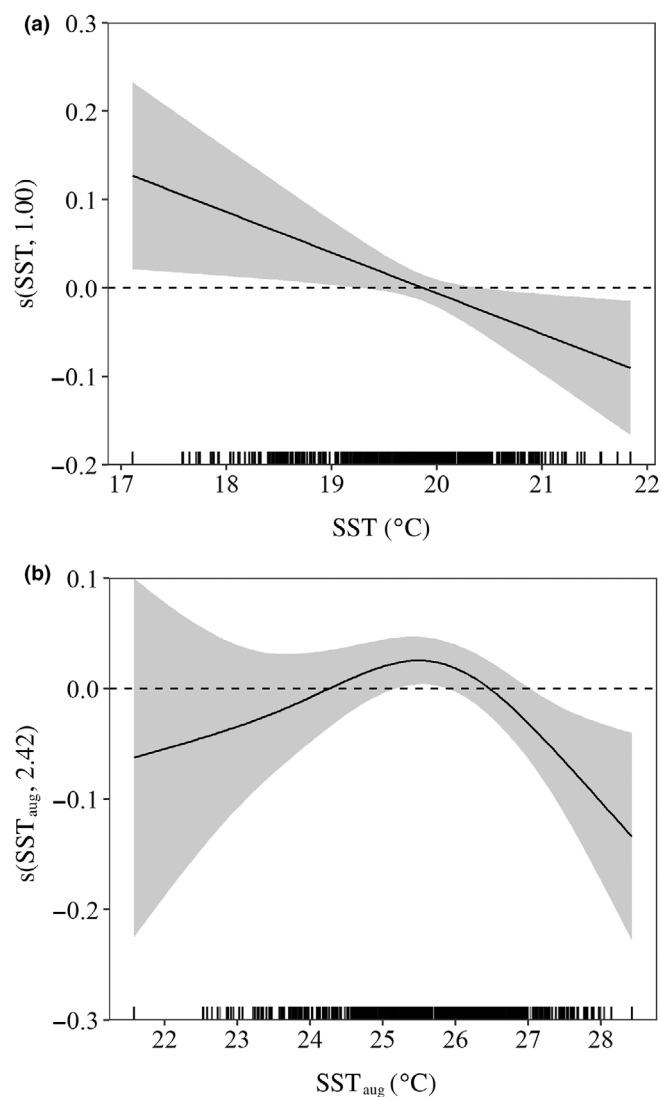


Fig. 5 Partial effect of (a) annual sea surface temperature (SST) and (b) maximum sea surface temperature (SST_{aug}) on *Posidonia oceanica* production based on generalized additive mixed model (GAMM). The shaded areas indicate the upper and lower 95% confidence intervals and dashed horizontal line on zero delimits positive (above zero) or negative (below zero) effect on production. Values on y-axis represent the partial residuals of the smoother product.

within the already realized thermal distribution in the Eastern Mediterranean, according to the present study. Nonetheless, our dataset encompassing longer, and larger scale variability showed that populations living close to the warm edge of their distribution are indeed impacted by the increase in annual SST and SST_{aug} . This hypothesis is further supported by a previous study showing a negative relationship between *P. oceanica* production and the number and duration of MHWs per year, and a decrease in phenological traits with increasing summer temperature across a longitudinal gradient (from Italy to Greece and Cyprus; Stipich *et al.*, 2022a), suggesting that eastern populations can be also affected by the fast warming at this part of the basin.

High temperature reduces seagrass photosynthetic rates due to an alteration of the photosynthetic apparatus, mostly the heat-

stress-sensitive PSII (Marín-Guirao *et al.*, 2016). The resulting increase in respiration in relation to photosynthesis can lead to a negative carbon balance, impeding growth and production in different seagrass species (York *et al.*, 2013; Collier & Waycott, 2014) including *P. oceanica* (Olsen *et al.*, 2012; Hendriks *et al.*, 2017; Pansini *et al.*, 2021). Apart from the direct physiological stress that high temperatures pose to the meadows, the increase in temperature can indirectly affect seagrass meadow by altering other factors that are crucial for their well-functioning, including salinity (Ruiz *et al.*, 2009; Borghini *et al.*, 2014), nutrient availability (Mvungi & Pillay, 2019), anaerobic mineralization (García *et al.*, 2012) and herbivore pressure (Buñuel *et al.*, 2021). Warming can also alter the relative distribution of the seagrass species inhabiting the Mediterranean, including the spread of species more adapted to warm temperatures (i.e. *Cymodocea nodosa* and *Halophila stipulacea*) at the expense of *P. oceanica*. Previous studies suggested that *C. nodosa* tends to occupy areas where *P. oceanica* has already regressed (Boudouresque *et al.*, 2009), owing to its higher thermal tolerance ($> 34^{\circ}\text{C}$; Savva *et al.*, 2018) and thereby probability to expand (Chefaoui *et al.*, 2018). Similarly, the tropical seagrass *H. stipulacea* is expanding in the region facilitated by warming (Wesselmann *et al.*, 2021) and possibly faster than originally thought (Thibaut *et al.*, 2022). Although the species has not yet shown generalized signs of competition with *P. oceanica* (Winters *et al.*, 2020), the expansion of *H. stipulacea* at the expense of *C. nodosa* has been reported in Tunisia (Sghaier *et al.*, 2014) and the Aegean Sea (Conte *et al.*, 2023). Therefore, there is an imminent threat of further expansion and possible replacement of *P. oceanica* meadows of the Mediterranean Sea with other seagrass species that do not necessarily provide ecosystem services of similar magnitude (Campagne *et al.*, 2015; Mtwana Nordlund *et al.*, 2016).

Despite the increase in Chl a during the study period, it did not contribute to the observed decline of production, neither did SPM and Secchi depth, suggesting that the water quality at the study sites was not aggravating for seagrass. The concentration of Chl a ranged generally at low values across our study sites and even the maximum value recorded at Thasos located at North Aegean (0.68 mg m^{-3}) was well below the $> 2.21 \text{ mg m}^{-3}$ threshold for eutrophic conditions (Simboura *et al.*, 2005) that could impact seagrass performance (Connell *et al.*, 2017; Heuvel *et al.*, 2019; Pazzaglia *et al.*, 2020; Viana *et al.*, 2020). Even the mean production of the meadows of Saronikos Gulf ($49.0 \text{ mg DW per shoot yr}^{-1}$), a region impacted by industrial and urban sewage (Tsiamis *et al.*, 2013) ranged close to the grand mean of our study. Similarly, the low SPM range across our sites, with higher values seldom measured and only near riverine outputs (e.g. 1.10 g m^{-3} at Parga located at the Ionian Sea), suggests that turbid conditions, which affect seagrass performance (Ruiz & Romero, 2003) and have even exacerbated the effect of warming elsewhere (Krause-Jensen *et al.*, 2020), were not recorded across our sampling sites. In addition, the high mean Secchi depth, despite the high range of values estimated across our study area, suggests sufficient water transparency and hence light availability at our sites. Indeed, *P. oceanica* in Greece reaches depths as low as 43 m while the mean lower depth limit is 30 m (Gerakaris *et al.*, 2021) as the ultraoligotrophic crystal clear waters allow higher light penetration. Yet, in lagoons and enclosed gulfs of the Greek Seas (e.g.

Amvrakikos Gulf), Chla and SPM can reach values as high as 6.5 and 10 g m⁻³, respectively, and Secchi depth as low as 4 m (Fig. 1), but the specific environmental regime and geomorphology at those areas do not represent suitable habitat for *P. oceanica* (Panayotidis *et al.*, 2022) and as a result, the species is not present there (Fig. 1). Therefore, the environmental stressors that affect water quality and contribute to *P. oceanica* degradation on local scales (e.g. nutrient discharges, Apostolaki *et al.*, 2009) do not constitute cumulative pressures to the effect of warming on *P. oceanica* meadows of the Greek Seas when assessed at larger spatiotemporal scales.

It appears that the factor that has changed significantly along the Greek Seas, and especially during the last decade, is the sea temperature (Androulidakis & Krestenitis, 2022), which according to our study compromised seagrass performance. Nevertheless, other biotic and abiotic factors acting at local scales not considered in this study should also be held responsible for the observed pattern in production. For example, water circulation or coastal geomorphology varies at small spatial scales and can drive differences in the availability of particles and nutrients (Gerakaris *et al.*, 2021). Intrinsic factors such as genetic background could also play a significant role in shaping seagrass production, and its response and resilience to warming. Available data from *Z. marina* suggest that seagrass vulnerability to thermal stress may depend on genetic diversity (Ehlers *et al.*, 2008; DuBois *et al.*, 2021) and could vary within the geographical distribution of the species (Jueterbock *et al.*, 2016). Our knowledge of the molecular capacity of *P. oceanica* to adapt to heat stress is limited (Marín-Guirao *et al.*, 2016; Ruiz *et al.*, 2018; Traboni *et al.*, 2018) and derives from Western Mediterranean meadows (Marín-Guirao *et al.*, 2016; Traboni *et al.*, 2018). Early data show that there is a strong genetic separation between Western and Eastern Mediterranean *P. oceanica* meadows (Procaccini *et al.*, 2002), with some private alleles found only in the eastern part (Chefaoui *et al.*, 2017), suggesting that Eastern Mediterranean meadows hold unique diversity which might be relevant for their thermal response. Further information regarding the resilience and adaptive capacity of Eastern Mediterranean meadows is thereof needed.

It is important to note here that mean production in most of the sites situated in the Cyclades Islands exceeded the grand mean of the study. This could be explained by their location away from intense industrial or urban development (Giakoumi *et al.*, 2011), the cyclonic gyre current formed at the Cyclades plateau (Olson *et al.*, 2007) and the prevailing strong north-west Etesian winds (Anagnostopoulou *et al.*, 2014) that keep the mean annual SST (19.6 ± 0.6°C) and SST_{aug} (25.5 ± 0.6°C) relatively cold which based on our study are within the optimal range for seagrass production (17 to 20°C for SST and 25 to 26°C for SST_{aug}). These results unveil the relevance of the meadows extending in this region as hot spots for conservation and render their protection imperative.

Our study underlies the necessity for management measures to confront the threat rapid warming poses to *P. oceanica* production in the Eastern Mediterranean. The in-depth knowledge of the response of Eastern Mediterranean ecosystems to global change is of vital importance to ensure well-established management and conservation plans, especially during the current

consensus on ocean restoration. The use of warning indicators, such as the trend in production presented here, can draw the attention of management authorities to act before the regression becomes irreversible. The information on seagrass functional traits (e.g. production) in combination with future projections of seagrass performance under different climate scenarios and prioritization of conservation actions based on specific seagrass traits (e.g. heat resilient genotypes) could be effective tools towards the sustainable management of the meadows (Serrano *et al.*, 2021). Management efforts should include local-scale planning accounting for the dynamic nature of the meadows and be multidisciplinary, bringing together the scientific community with local authorities and stakeholders and focusing primarily on prevention before mitigation (Unsworth *et al.*, 2019).

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Competing interests







None declared.

Author contributions

ETA and VL-M designed the study. VG, ETA and OS collected the samples. VL-M and PTE performed the laboratory work.

VL-M analysed the data and wrote the first draft. MT, VG, OS, PTE and ETA revised the manuscript. ETA acquired the funding and supervised the study. All authors approved the submitted manuscript.

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Data availability

Data generated during this study are included in the Supporting Information files (Table S2).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Map of 60 *Posidonia oceanica* sampling sites across the Greek Seas.

Table S1 Forward GAMM model selection process.

Table S2 Location of *Posidonia oceanica* sampling sites, mean values of environmental variables and mean range and mean values of seagrass variables for the reconstructed period at each site.

Table S3 Linear regression outputs of daily Chl_a and monthly suspended particulate matter (SPM) and Secchi depth measurements against the reconstructed period (1997–2018).

Table S4 Statistical details of selected GAMM models.

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