

Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality

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Abstract

Rapid warming of the Mediterranean Sea threatens marine biodiversity, particularly key ecosystems already stressed by other impacts such as *Posidonia oceanica* meadows. A 6-year monitoring of seawater temperature and annual *P. oceanica* shoot demography at Cabrera Archipelago National Park (Balearic Islands, Western Mediterranean) allowed us to determine if warming influenced shoot mortality and recruitment rates of seagrasses growing in relative pristine environments. The average annual maximum temperature for 2002–2006 was 1 °C above temperatures recorded in 1988–1999 (26.6 °C), two heat waves impacted the region (with seawater warming up to 28.83 °C in 2003 and to 28.54 °C in 2006) and the cumulative temperature anomaly, above the 1988–1999 mean annual maximum temperature, during the growing season (i.e. degree-days) ranged between 0 °C in 2002 and 70 °C in 2003. Median annual *P. oceanica* shoot mortality rates varied from 0.067 year⁻¹ in 2002 to 0.123 year⁻¹ in 2003, and exceeded recruitment rates in all stations and years except in shallow stations for year 2004. Interannual fluctuations in shoot recruitment were independent of seawater warming ($P > 0.05$). *P. oceanica* meadows experienced a decline throughout the study period at an average rate of -0.050 ± 0.020 year⁻¹. Interannual variability in *P. oceanica* shoot mortality was coupled ($R^2 > 0.40$) to seawater warming variability and increasing water depth: shoot mortality rates increased by 0.022 year⁻¹ (i.e. an additional 2% year⁻¹) for each additional degree of annual maximum temperature and by 0.001 year⁻¹ (i.e. 0.1% year⁻¹) for each accumulated degree water temperature remained above 26.6 °C during the growing season. These results demonstrate that *P. oceanica* meadows are highly vulnerable to warming, which can induce steep declines in shoot abundance as well indicating that climate change poses a significant threat to this important habitat.

Keywords: angiosperms, degree-day, demography, marine, mortality, net population growth, recruitment, temperature

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Introduction

Global warming is emerging as a threat to ecosystems worldwide, with a major loss of biodiversity predicted as warming progresses during the 21st Century (IPCC, 2007). Whereas there is ample documentation of the impacts of climate change on terrestrial biodiversity, allowing the working group II of the IPCC report to review more than 28 501 evidences of these impacts in their 2007 report, the information available for marine and freshwater biodiversity is comparably meager, as reflected in the 85 evidences noted by the IPCC (Richardson & Poloczanska, 2008). The marine climate

change impacts literature mostly deals with coral reefs (IPCC, 2007), which are under threat due to stresses associated with climate change and CO₂ increase (e.g. Carpenter *et al.*, 2008; De'ath *et al.*, 2009). Beyond coral reefs however, the literature does not adequately reflect the potential vulnerability of many, if not all, marine habitats to climate change (Duarte *et al.*, 2008a).

Marine ecosystems that are already stressed may be particularly vulnerable to the impacts of climate change (e.g. Scavia *et al.*, 2002). Seagrass ecosystems rank among the marine habitats currently experiencing the most rapid recession, with global declines rates estimated at 2–5% year⁻¹ (Duarte, 2002; Duarte *et al.*, 2008a; Orth *et al.*, 2006; Waycott *et al.*, 2009). This decline is attributable to a number of cumulative impacts primarily involving eutrophication of the coastal ocean,

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mechanical impacts and submarine erosion (Orth *et al.*, 2006). There is also growing evidence that seagrass meadows are vulnerable to climate change (e.g. Duarte *et al.*, 2008b; Short & Neckles, 1998), particularly through the impacts of elevated seawater temperature on shoot survival (Duarte, 2002), as supported by reports of stress responses following heat waves such as increased shoot population mortality rates (Díaz-Almela *et al.*, 2009; Oviatt, 2004; Reusch *et al.*, 2005) and mass flowering events (Díaz-Almela *et al.*, 2007). Increasingly, climate change is emerging as a force accelerating the loss rate of already stressed seagrass meadows (Waycott *et al.*, 2009).

Current conceptual frameworks on the response of marine ecosystems to multiple stresses assume that these interact in a synergistic manner (e.g. Jackson, 2008), implying that local stresses, such as excess nutrient inputs, weaken the resistance of marine ecosystems to climate change (e.g. Duarte, 2002; Hansen *et al.*, 2003; Knowlton & Jackson, 2008; Scavia *et al.*, 2002). As a corollary, pristine and undisturbed ecosystems may be expected to be more resistant to the stress associated with warming. However, this is a relatively untested proposition, particularly for seagrass habitats. Recent assessments of the demographic status of the seagrass *Posidonia oceanica* in the 1970s and the 1990s in the Spanish Mediterranean showed a trend towards a general decline, including protected, relatively pristine areas (Marbà *et al.*, 1996, 2005). These studies, however, were not based on long term monitoring data on seagrass demography, thereby preventing examination of the temporal trends of decline and the analysis of the possible role of the relationship between seagrass decline and seawater temperature. However, the Mediterranean Sea has been warming for some decades (Coma *et al.*, 2009), suggesting that the decline reported in the past could be possibly associated with seawater warming. Since these studies, the rate of seawater warming in the Mediterranean has clearly increased, including, in particular, 2 years of intense warming in 2003 and 2006. Indeed, the Mediterranean Sea is particularly vulnerable to warming and shows rates of seawater warming that exceed threefold those of the global ocean (IPCC, 2007; Vargas-Yáñez *et al.*, 2007). Hence, there is a need to test if seawater warming is associated with increased seagrass loss only in meadows already impacted by other stresses or if warming may be associated with seagrass loss in the absence of significant local stresses.

P. oceanica meadows, endemic to the Mediterranean Sea, are the dominant ecosystem on sandy sea beds, covering a total basin extension of 50 000 km² (Bethoux & Copin-Montégut, 1986). Like all seagrass species, *P. oceanica* is a clonal plant and spreads mostly vegetatively through clonal growth. *P. oceanica* clones spread

very slowly (horizontal rhizome elongation rate 1–6 cm yr⁻¹, Marbà & Duarte, 1998) and produce only small amounts of sexual propagules in an average year (Díaz-Almela *et al.*, 2007). *P. oceanica* is an extremely long-living plant, with shoots living for several decades (e.g. Marbà *et al.*, 2005) and meadows persisting for several millennia (Mateo *et al.*, 1997). Because of the slow growth and limited production of sexual recruits of *P. oceanica*, the meadows of this species require centuries to millennia to develop (Duarte, 1995; Kendrick *et al.*, 2005), and therefore, to recover from decline, rendering these ecosystems highly vulnerable to impacts resulting in plant losses.

Here, we provide evidence of a close relationship between seawater warming and seagrass shoot mortality and net seagrass loss in the marine protected area and relatively pristine Cabrera National Park (Balearic Islands, Spain) over the period 2002–2007. We do so by using annual data on *P. oceanica* shoot demography, shoot abundance, annual maximum seawater temperature and the cumulative temperature anomaly (relative to the average maximum annual temperature recorded in surface waters of Palma Bay between years 1988 and 1999) during the growing season.

Materials and methods

Study area

The study was conducted in two bays (Santa Maria Bay and Es Port Bay) and one cove (Es Castell, close to Es Port Bay) of Cabrera Island, the largest island of the Cabrera Archipelago National Park (39°9'N; 2°56'E). Cabrera Archipelago is located in the Algerian subbasin of the Western Mediterranean, which receives fresh surface water from the Atlantic (López-Jurado *et al.*, 2008). Surface waters of the Cabrera archipelago, as the rest of the Mediterranean, are characterized by high water column stability and high temperature during summer, resulting in a strong stratification of the water column (e.g. Coma *et al.*, 2009). The temperature regime observed at Cabrera Archipelago follows the same interannual temperature patterns as other seagrass meadows in this region (Díaz-Almela *et al.*, 2009). Cabrera Archipelago was declared a national park in 1991, and, since then, conservation policies to protect both land and marine ecosystems have been in place. Human pressure at Cabrera Archipelago is very low, as no permanent residents inhabit the islands. Access by visitors is prohibited in Santa María Bay and restricted in Es Castell Cove, whereas Es Port Bay receives up to 380 visitors per day in summer (Marbà *et al.*, 2002). *P. oceanica* meadows extend along the coastal carbonate-rich sediments of Cabrera Archipelago between 0.5 and

46 m depth, the deepest limit yet reported for this species (Marbà *et al.*, 2002), reflecting the clear (light attenuation coefficient 0.063 m^{-1} , Ballesteros & Zabala, 1993) and pristine conditions of seawater in the park. The largest meadows are located at Santa Maria Bay, followed by those at Es Port Bay.

Data acquisition

Seawater temperature was recorded continuously since October 2001 with a 32 K calibrated, submersible Stow-Away TidbiT[®] (Onset Computer Corporation, Bourne, MA, USA) (temperature range from -5 to $+37$ °C, precision: ± 0.2 °C, resolution: 0.16 °C) deployed in Es Port Bay at 17 m depth, the average water depth of the *P. oceanica* stations studied. This lies above the summer thermocline (which is located between 30 and 40 m depth, López-Jurado *et al.*, 2008; Vives, 1993). The data logger recorded temperature every 2 h. The logger was retrieved at least once a year and replaced with an empty logger. The data loggers were calibrated with a high precision thermometer (from Dotsmann Electronic model P650-P670, Dostmann, Wertheim-Reicholzheim, Germany) in the laboratory before deployment and after retrieval to test logger function and precision. Calibration exercises demonstrated no drift in the temperatures recorded by the data logger. Maximum annual seawater temperature was the highest temperature recorded during a chronologic year. Degree-days (in °C) were calculated as the accumulated anomaly between May 1 and September 30, the period when *P. oceanica* biomass attains its maximum development (e.g. Cebrián *et al.*, 1997), of average daily seawater temperature above 26.6 °C. This is the average maximum annual temperature recorded in surface waters of Palma Bay (Algerian sub-basin, Balearic Islands) between years 1988 and 1999 (Table 1).

P. oceanica shoot demography was monitored at nine stations (three at Santa María Bay, five at Es Castell Cove, and one at Es Port Bay). The stations at Santa María Bay and Es Castell Cove were distributed between 7 and 17 m water depth and 5 and 25 m water depth respectively, and that at Es Port Bay was located at 17 m water depth. At each station, SCUBA divers installed three permanent plots ranging between 0.09 and 0.25 m^2 depending on shoot density, over 3 months from November 2001. Plot perimeters were delimited by a rope connecting four metal corner bars. All shoots within the plots were tagged by putting plastic cable ties around their vertical rhizomes (Marbà *et al.*, 2005). The plots were visited every 293–811 days (median frequency 474 days) until 2007. During each visit, the number of surviving shoots (i.e. alive shoots with plastic cable ties) and that of new shoots (i.e. shoots

Table 1 Monthly average seawater temperature (0–7 m water depth) for the warmest summer month in the area of Palma Bay (Mallorca, Balearic Islands, Western Mediterranean)

Year	Maximum temperature (°C)
1988*	26.1
1989*	26.4
1990*	26.4
1991*	26.6
1994†	27.0
1995†	27.0
1996†	26.3
1997†	26.0
1998†	27.4
1999†	27.0
Average period 1988–1999	26.6

The sources of the values are provided.

*Jansà *et al.* (1994).

†Fernández de Puelles *et al.* (2003).

produced after the last visit; young shoots without cable tie) were counted. New shoots were then marked with a plastic cable tie using a plastic cable tie of a different color each year. Repeated shoot census allowed estimation of shoot density and annual rates of shoot mortality, recruitment and net population growth. The shoot mortality rate (M ; in year) was calculated as,

$$M = \frac{(\ln(NT_{i-1}/NS_i))365}{t_i - t_{i-1}},$$

where NT_{i-1} is the number of alive shoots during the previous census (t_{i-1} , days) at each plot and NS_i the number of marked shoots surviving at t_i (days). The shoot recruitment rate (R ; in yr^{-1}) was estimated as,

$$R = \frac{(\ln(NT_i/NS_i))365}{t_i - t_{i-1}},$$

where NT_i was the number of living shoots at t_i at each plot, comprising both surviving and recruited shoots. The net shoot population growth rate (μ ; yr^{-1}) was estimated as

$$\mu = \frac{(\ln(NT_i/NT_{i-1}))365}{t_i - t_{i-1}}.$$

Statistical analyses

The relationships between maximum annual temperature (and degree-days) during year_{*i*}, water depth and the interaction between both covariate variables on variability of *P. oceanica* annual demographic parameters quantified between October 1 of year_{*i*} and

September 30 of year_{*i*+1} were examined using multiple least squares regression analyses.

Results

The maximum seawater temperature in Cabrera Island exceeded the mean maximum temperature (MMT) of 26.6 °C (1988–1999, Fernández de Puelles *et al.*, 2003; Jansá *et al.*, 1994) in all but one year in the study period between 2002 and 2006 (Fig. 1). Indeed, the average annual maximum temperature over the study period (mean ± SE = 27.62 ± 0.55) was 1 °C above the earlier value. Year 2002, the first year of the study, was the only year with an annual maximum temperature below 27 °C. The maximum temperature reached 28.83 °C in 2003, when a heat wave impacted Europe. A secondary maximum of seawater temperature was recorded in 2006, with 28.54 °C. The number of days with water temperature above the MMT of 26.6 °C (1988–1999, Table 1) ranged from 0 in 2002, the coolest year in the study, to a maximum of 58 in 2006. The average number of days when the MMT was exceeded for each year in the study period was 29 ± 11.7 days. The degree-days over the 1988–1999 MMT of 26.6 °C accumulated between May 1 and September 30 each year ranged between 0 °C, in year 2002, and 70 °C, in year 2003 (Fig. 1), with an average of 28.7 ± 16.3 °C per year during the study period.

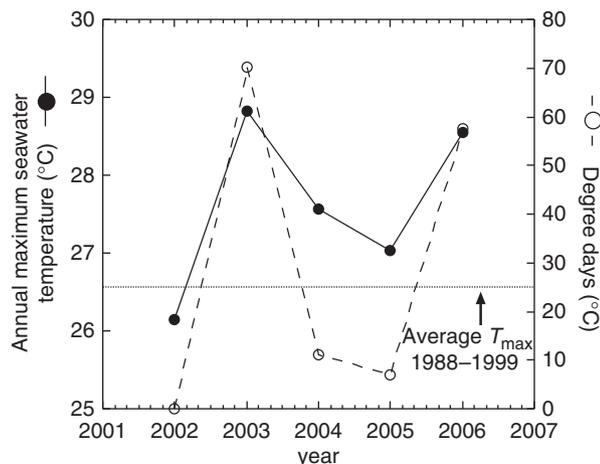


Fig. 1 Annual maximum seawater temperature (°C, continuous line and black circles) and degree-days (°C, dashed line and white circles) recorded at 17 m depth in the *Posidonia oceanica* meadow of Es Port Bay (Cabrera Archipelago National Park, Balearic Islands, Western Mediterranean). Dotted horizontal line indicates the average annual maximum temperature at 0–7 m depth in Palma Bay (Balearic Islands) recorded during the period 1988–1999 (Table 1).

All stations investigated exhibited a net decrease in shoot density between 2002 and 2007 (Fig. 2). Shoot density decline was sustained for the entire study period at stations located deeper than 10 m water depth (Fig. 2). Conversely, shallow (between 5 and 10 m water depth) stations showed the largest losses of shoot density after the summer of 2003, the warmest during the study period. After summer 2004, shoot density in shallower than 10 m stations recovered up to similar, or even higher, values as those observed prior summer 2003 (Fig. 2), but declined again after the warm 2006 summer (Fig. 2). Examination of trajectories of shoot density with annual maximum seawater temperature revealed that shoot density losses occurring after a warming event were able to recover within 2 years in shallow stations, whereas in deeper stations shoot loss continued, despite decreasing annual maximum seawater temperature.

Median shoot mortality rates across stations ranged from 0.067 year⁻¹ in 2002, the coolest year in the series, to a maximum of 0.123 year⁻¹ in 2003, the warmest year in the series (Fig. 3a). Shoot mortality was on average (± SE) 0.102 ± 0.015 year⁻¹ for the study period. Seagrass shoot mortality rates exceeded recruitment rates in all stations and years except in shallow stations for 1 year, 2004, when exceptionally high recruitment followed the catastrophic mortalities in 2003 (Fig. 3). Shoot recruitment rates (Fig. 3b) averaged 0.033 ± 0.028 year⁻¹ for the 2002–2007 period, being twofold lower than average shoot mortality rate. As a consequence, the meadows experienced a decline throughout the study period, despite the positive net shoot population growth for 1 year (2004) in stations located above 10 m depth, with a net shoot population rate of change averaging -0.050 ± 0.020 year⁻¹.

Variability in shoot mortality was significantly ($R^2 = 0.40$; $P < 0.0005$; $N = 49$) coupled with variability in maximum annual seawater temperature and water depth (Table 2). Shoot mortality significantly ($P < 0.05$) decreased with increasing station water depth (Table 2) and increased by 0.022 ± 0.008 year⁻¹ (i.e. an additional 2.5% year⁻¹) for each additional degree of warming (Table 2, Fig. 4a). Similarly, variability in shoot mortality rate significantly ($R^2 = 0.44$; $P < 0.0001$; $N = 49$) coupled differences in water depth and the accumulated degree-day anomaly (°C) over the MMT of 26.6 °C (1988–1999) during the growing season (Table 2). Therefore, shoot mortality rates increased by 0.001 ± 0.0002 year⁻¹ (i.e. 0.1%) for each accumulated degree-day that water temperature remained above 26.6 °C during the plant-growing season (Table 2, Fig. 4b). On the contrary, shoot recruitment rate significantly ($R^2 = 0.25$; $P < 0.05$; $N = 49$) decreased with increasing water depth, but it was independent of maximum annual temperature or

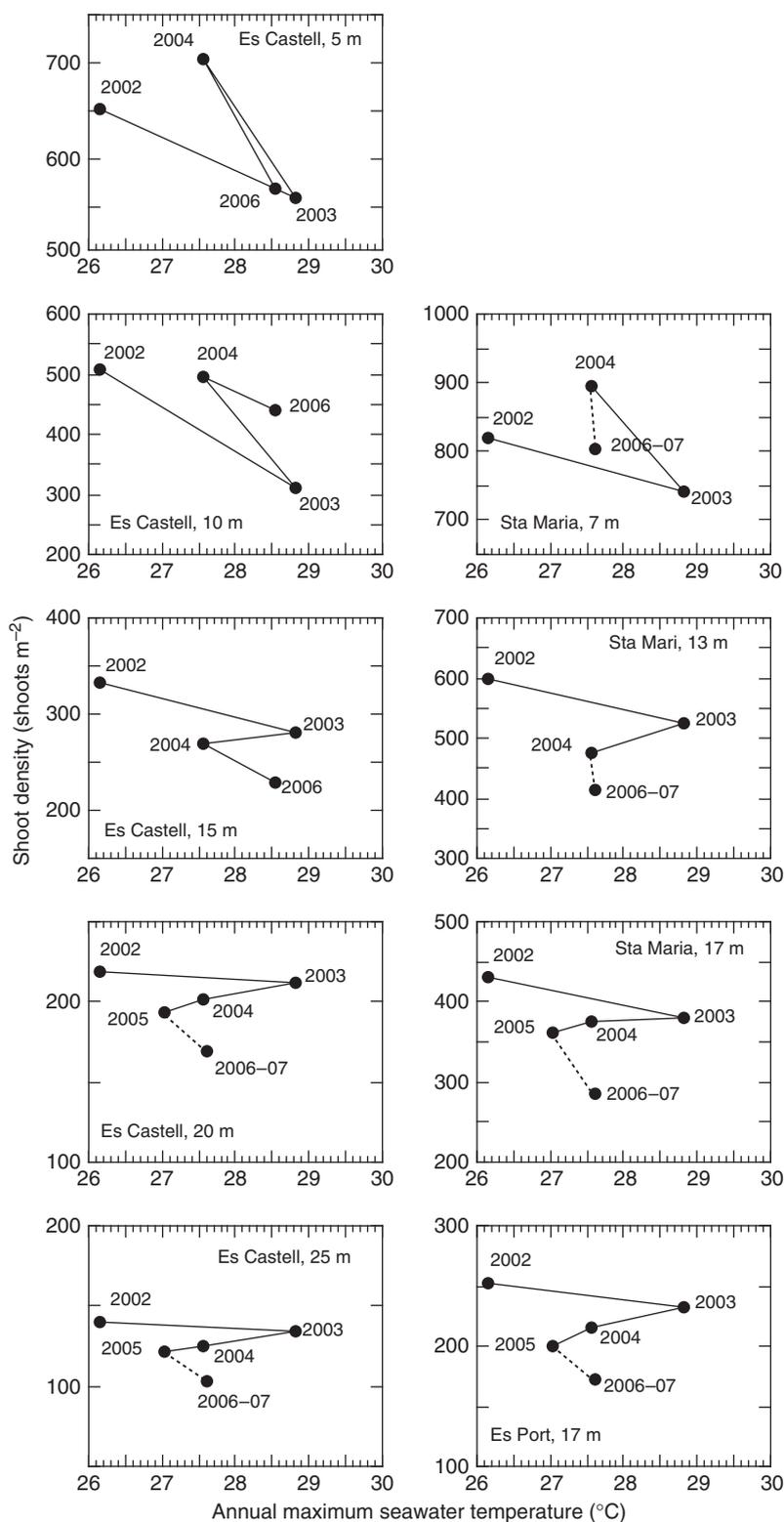


Fig. 2 Trajectories of shoot density of *Posidonia oceanica* along variability in annual maximum seawater temperature at 9 stations of the Cabrera Archipelago National Park (Balearic Islands, Western Mediterranean) between years 2002 and 2007. Shoot density was measured at three permanent plots per station between October 1 of year_{*t*} and September 30 of year_{*t*+1}. Year_{*t*} is indicated near each shoot density value.

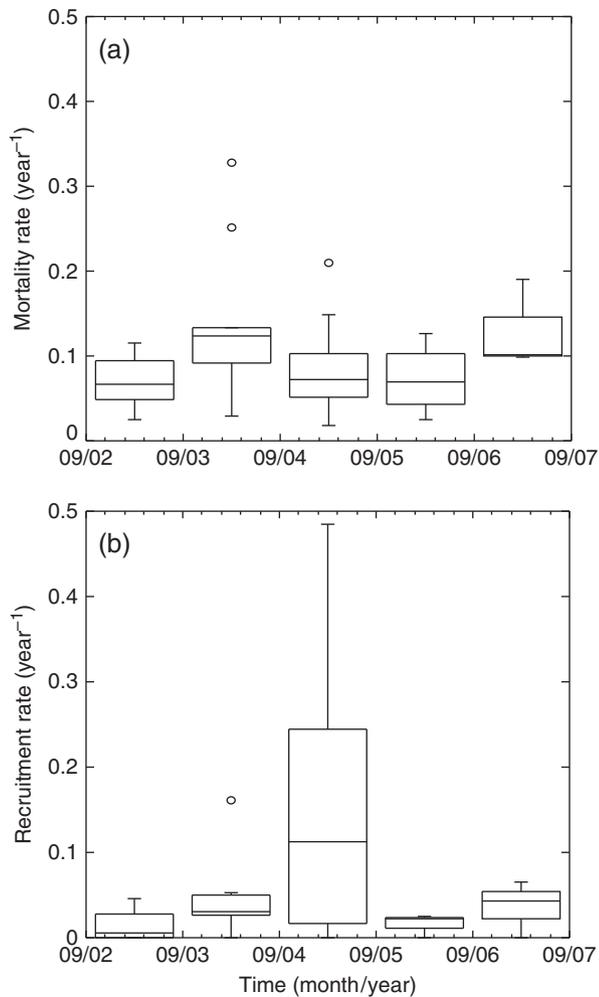


Fig. 3 Box plots of (a) annual shoot recruitment (year^{-1}) and (b) mortality (year^{-1}) rates of *Posidonia oceanica* at nine stations of the Cabrera Archipelago National Park (Balearic Islands, Western Mediterranean) between year 2002 and 2007.

the accumulated degree-day anomaly ($P > 0.05$, Table 2). As a result of the change in shoot recruitment and mortality rates with water depth, and the enhanced shoot mortality rates with seawater warming, net shoot population growth rates significantly ($R^2 = 0.25$; $P < 0.05$; $N = 49$) decreased with increasing accumulated degree-day anomaly ($^{\circ}\text{C}$) over the MMT of 26.6°C (1988–1999) during the growing season and with increasing depth (Table 2).

Discussion

The results presented show a clear relationship between increasing seagrass shoot mortality rates and increased warming (Table 2, Fig. 4), as well as enhanced net seagrass shoot losses with increased warming (Table

2, Fig. 2), for the nearly pristine meadows of the Cabrera Island National Park. The average decline rates at Cabrera Island meadows during the study period exceeded by about fivefold the net population rate of change that the same meadows experienced during the 1990s when the meadows were in steady-state ($-0.01 \pm 0.02 \text{ year}^{-1}$, Marbà *et al.*, 2002). Hence, there is evidence of a considerable increase in mortality and decline rates in the 2002–2007 period, when two heat waves were reported in this area, one in 2003, when seawater temperature reached the maximum values yet observed, and a second in 2006, when maximum seawater temperature reached to 0.3°C below the 2003 maximum. Because the close coupling of seagrass mortality to maximum temperature reached and degree-days, and that of net population change and degree-days, seawater warming appears to affect seagrass populations by (1) exceeding a threshold temperature above which plant mortality increases and (2) extending the duration of anomalously high temperatures during the growing season.

One of the meadows in Cabrera Island, located at 17 m in the Es Port Bay of Cabrera Island is impacted by organic inputs from visitors (Marbà *et al.*, 2002), but the remaining eight meadows included in this study are not subject to any local stresses, growing over carbonate sand in highly transparent oligotrophic waters. The relationship between maximum annual temperature and seagrass mortality in the pristine meadows at Cabrera Island provides evidence that warming alone has the potential to cause abrupt seagrass mortality. The heat waves recorded in 2003 and 2006 lead to the mortality of 13% of the *P. oceanica* shoot population the subsequent year, so that only 60% of the shoots present at the onset of the six-year study survived throughout the study period.

Recruitment was insufficient to compensate for the warming-enhanced mortality experienced by the entire meadow during the study period, even though recruitment was enhanced in year 2004–2005 (Fig. 2), following the 2003 warming event, particularly in shallow meadows. The high recruitment in year 2004–2005 mostly resulted from enhanced clonal growth. Despite sexual recruits were observed in the studied meadows in year 2004, as occurred across the entire Western Mediterranean in 2004 (Díaz-Almela *et al.*, 2007, 2009), their contribution to total shoot recruitment was negligible (i.e. $2 \pm 1\%$, data not shown). The average recruitment rate remained well below the mortality rate during the study, leading to a negative rate of population change averaging -0.05 year^{-1} , or a net loss of $5\% \text{ year}^{-1}$ during the study period. *P. oceanica* meadows could be decimated within a couple of decades if warming events in the future occur with the same

Table 2 Multiple least regression equations fitted between annual *Posidonia oceanica* demographic parameters (variable Y) and maximum annual seawater temperature or degree-days water depth, and the interaction between both covariate terms

Variable Y	Term	Parameter estimate (SE)	P parameter estimate	R ² model	P model
Mortality rate (year ⁻¹)	Intercept		ns	0.40	<0.0005
	T _{max} (°C)	0.022 (0.008)	<0.05		
	Depth (m)	-0.003 (0.001)	<0.05		
	T _{max} × depth	-0.004 (0.001)	<0.01		
Mortality rate (year ⁻¹)	Intercept	0.118 (0.022)	<0.0001	0.44	<0.0001
	Degree-days (°C)	0.001 (0.0002)	<0.01		
	Depth (m)	-0.003 (0.001)	<0.05		
	Degree-days × depth	-0.0002 (0.000)	<0.01		
Recruitment rate (year ⁻¹)	Intercept		ns	0.25	<0.05
	T _{max} (°C)		ns		
	Depth (m)	-0.008 (0.002)	<0.005		
	T _{max} × depth		ns		
Recruitment rate (year ⁻¹)	Intercept	0.194 (0.041)	<0.0001	0.28	<0.01
	Degree-days (°C)		ns		
	Depth (m)	-0.008 (0.000)	<0.0001		
	Degree-days × depth		ns		
Net population growth rate (year ⁻¹)	Intercept		ns	0.13	ns
	T _{max} (°C)		ns		
	Depth (m)		ns		
	T _{max} × depth		ns		
Net population growth rate (year ⁻¹)	Intercept		ns	0.25	<0.05
	Degree-days (°C)	-0.001 (0.001)	<0.05		
	Depth (m)	-0.006 (0.003)	<0.05		
	Degree-days × depth		ns		

The parameter estimates, SE and significance of parameter estimates and the coefficient of determination and significance of the models fitted are provided.

frequency as observed during the first decade of 21 century. Warming rates in the Mediterranean, which currently average 0.04 °C year⁻¹ (Díaz-Almela *et al.*, 2007), double those in the global ocean (Vargas-Yáñez *et al.*, 2007) and the occurrence of extreme temperature events has increased over the past 50 years (Coma *et al.*, 2009).

The decline rates observed in this study for *P. oceanica* meadows after heat waves are within the range reported for most *P. oceanica* meadows in unprotected areas of the Spanish Mediterranean for the late 20 Century (Marbà *et al.*, 1996). Hence, if the time window in between two consecutive heat waves does not suffice for shoot population recovery, the impact of seawater warming on *P. oceanica* meadows is within the range of that caused by human activities operating at local scale in the Spanish Mediterranean.

Warming is expected to continue in the next decades, leading to further increases in maximum summer seawater temperatures, an increased frequency of heat waves and an increase in the number of days with water temperatures exceeding the mean maximum value recorded during previous decades. The strong,

linear relationship between warming extent (i.e. maximum temperature) and duration (i.e. days above the previous MMT) predicts that seagrass mortality is likely to increase further in the future, at an additional 0.03 year⁻¹ mortality per degree of annual maximum warming and 0.001 year⁻¹ mortality per additional degree-day with seawater temperature above 26.6 °C. Extrapolating these figures into the future suggests that a four degree warming along the 21 Century would raise mortality rates by 0.12 year⁻¹ over the current 0.09 year⁻¹ mortality rate, leading to a loss of 20% of shoots per year. This is well beyond the plant's capacity to compensate for losses, except occasionally for shallow meadows (<10 m water depth), suggesting an uncertain future for *P. oceanica* meadows under climate warming. This projection, however, assumes gradual seawater warming in the Mediterranean along the 21 Century, whereas the recent experience shows that the impacts are driven by heat waves more so than gradual changes in the mean annual temperature. These heat waves are likely to increase in frequency and magnitude in the Mediterranean, driving the long-term trends in mean annual seawater temperature. Hence, a warm-

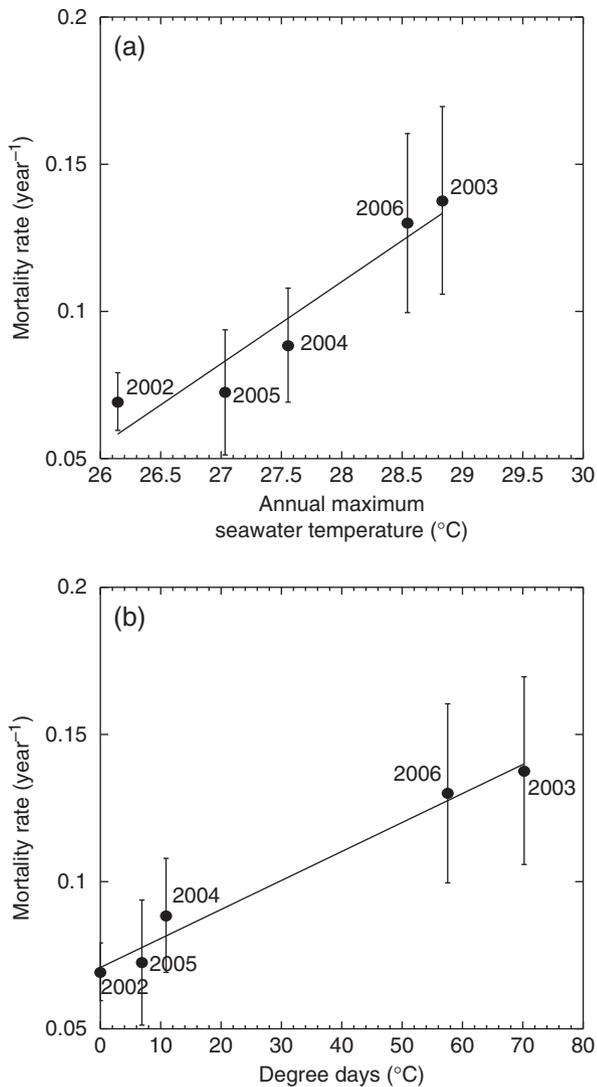


Fig. 4 The relationship between *Posidonia oceanica* annual shoot mortality rate and (a) annual maximum seawater temperature and (b) accumulated degree-day anomaly over the 1988–1999 average maximum temperature. The lines represented the fitted regression equations mortality (year⁻¹) = $-0.674 (\pm 0.137) + 0.028 (\pm 0.005) T_{\max} (\text{°C})$, $R^2 = 0.91$, $P < 0.05$, $N = 5$; mortality (year⁻¹) = $0.071 (\pm 0.003) + 0.001 (\pm 0.0001)$ degree-days (°C), $R^2 = 0.98$, $P < 0.005$, $N = 5$. Bars show the standard error of average values. The years of temperature records are shown in the graphs. See ‘Materials and methods’ for accumulated degree-day anomaly calculation.

ing of 4 °C over the 21 century will likely involve temperature extremes well above the expected 4 °C anomaly, and thus losses in *P. oceanica* abundance could be even larger than expected from a 4 °C warming. The occurrence of heat waves, rather than a gradual, smooth elevation of the temperature also reduces the opportunities for adaptive changes.

A positive relationship between plant mortality rates and temperature has been recently postulated (Marbà *et al.*, 2007) on the basis of the metabolic theory of ecology (Brown *et al.*, 2004) and the effect of temperature on life history traits (Brown *et al.*, 2004; Savage *et al.*, 2004). However, direct evidence for such a relationship, already demonstrated for some animals (Brown *et al.*, 2004), is available only for few species of microalgae (Agustí & Duarte, 2000; Marbà *et al.*, 2007), macroalgae (Gerard & DuBois, 1988; Steen & Scrosati, 2004) and land and marine angiosperms (Kallenbach *et al.*, 1996; Massa *et al.*, 2009; Musil *et al.*, 2005; Nejrup & Pedersen, 2008; Pavlik & Enberg, 2001). The steep increase in *P. oceanica* shoot mortality rates with increasing water temperature possibly results from multiple impacts including the direct impacts of temperature on seagrass physiological processes and indirect effects resulting from responses in other associated components of the ecosystem, such as the metabolism of benthic microbes. Seagrasses, and *P. oceanica* in particular (Calleja *et al.*, 2007), are extremely vulnerable to sulfide production, a product of anaerobic microbial metabolism in seagrass sediments (Duarte *et al.*, 2005). As microbial metabolism (e.g. Vázquez-Domínguez *et al.*, 2007) and sediment anoxia, because enhanced sediment oxygen consumption (e.g. Cowan *et al.*, 1996) and lower oxygen solubility, both increase with warming, increased water temperature is likely to be conducive to enhanced stress derived from increased anoxia and the presence of sulfides in the rhizosphere. Indeed, sulphate reduction has been shown to increase with increasing temperature (Koch *et al.*, 2007; Westrich & Berner, 1988). This also suggests that warming might trigger even larger shoot losses than those reported here in *P. oceanica* meadows already impacted by other stresses, such as excessive organic matter and nutrient inputs.

P. oceanica is a key ecosystem in the Mediterranean, with a high conservation value (Hemminga & Duarte, 2000). *P. oceanica* ranks among the slowest growing plant species in the Biosphere, leading to very slow vegetative recruitment of this clonal species, and very sparse sexual reproduction (Hemminga & Duarte, 2000). Because of this slow growth, *P. oceanica* meadows require very long time spans (centuries to millennia, Duarte, 1995; Kendrick *et al.*, 2005) to develop, and very long time spans are involved in their recovery from mortality events. This renders *P. oceanica* meadows extremely vulnerable to impacts, including those derived from climate change.

Whereas other seagrass species occur in the Mediterranean, they unlikely fully replace *P. oceanica* in structure or function. For instance, *P. oceanica* harbors a number of endangered species, such as the large fan

mussel *Pinna nobilis* that are restricted to this habitat and do not occur in meadows of other seagrass species (Richardson *et al.*, 1999). Moreover, *P. oceanica* meadows have a high capacity to sequester carbon in the sediments (e.g. Gacia *et al.*, 2002), which exceeds that of other Mediterranean seagrass species. Further, where lost *P. oceanica* meadows are being replaced, they are largely being replaced by exotic, invasive species of tropical and subtropical origin, notably the macroalgae *Caulerpa racemosa*, considered among the most damaging exotic species in the Mediterranean (Streftaris & Zenetos, 2006). Hence, the decline of *P. oceanica* meadows involved a reduction in natural carbon sink capacity.

In summary, Mediterranean seawater warming is triggering *P. oceanica* shoot mortality and enhancing the thinning of the meadows in relative pristine areas. Steep *P. oceanica* shoot mortality, however, occurs when seawater exceeds 28 °C associated with the occurrence of heat waves in the Mediterranean, which were observed twice in this 6-year study (2002–2007). Whereas the shallow margins of the meadow were able to recover their shoot abundance one year after the heat wave event, net shoot losses persisted for the following years in deeper areas. Hence, our results demonstrate that climate change poses a significant threat to seagrasses, which are important habitats already impacted by proximate stresses in many coastal areas (Waycott *et al.*, 2009). Management strategies to conserve these habitats should, therefore, depend on mitigating climate change, through global-scale action, and engage in actions to remove other stresses, thereby enhancing the resistance and resilience of the plants to warming, as an adaptive strategy to cope with climate change.

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