Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records

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Abstract

Posidonia oceanica, a seagrass endemic to the Mediterranean forms extended and extremely persistent meadows. It is a clonal plant with an apparently irregular pattern of flowering events. An extensive bibliographic review allowed the reconstruction of past flowering events of this species around the Mediterranean, with a high degree of confidence for the last 30 years. The data series on annual flowering prevalence (FP, flowering records per total records) and flowering intensity (FI, fraction of flowering shoots) produced have been compared with four series on Sea Surface annual Temperature maxima (SST_{max}) obtained for the NW Mediterranean (averaged from the local data series of l'Estartit and Villefranche: 1957–2005) and for the Eastern, Western basin and the whole Mediterranean sea (extracted from NCEP Reynolds interpolated SST maps: 1982–2005). Significant warming trends are detected in the Mediterranean SST_{max} series, at a rate of (mean + SE) $0.04 \pm 0.01\,°C\,yr^{-1}$ ($R^2 = 0.24$, $P < 0.01$, $N = 24$ years), in the Eastern basin series ($0.06 \pm 0.01\,°C\,yr^{-1}$, $R^2 = 0.43$, $P < 0.001$, $N = 24$ years) and in the long SST_{max} series of the NW Mediterranean ($0.02 \pm 0.01\,C\,yr^{-1}$, $R^2 = 0.12$, $P < 0.02$, $N = 49$ years). The magnitudes of the SST_{max} anomalies around the absolute warming trend do not increase with time in any SST_{max} series. Peaks of FP and FI in the Mediterranean seem to occur each 9–11 years, and coincide with peaks of annual SST_{max}. Annual FP and FI increase with the residuals of annual SST_{max} warming trend in all Mediterranean basins (FP_{MED}: $R^2 = 0.27$, $P < 0.01$, $N = 23$; FP_{NW}: $R^2 = 0.34$, $P < 0.01$, $N = 31$; FP_E: $R^2 = 0.20$; $P < 0.10$, $N = 23$). An outstanding event of *P. oceanica* flowering across the Mediterranean has been registered in Autumn 2003; 1 month after the highest annual SST_{max} recorded in the series. The hypothesis of flowering induction by thermal stress as the possible cause of this relationship is discussed, as well as the potential use of *P. oceanica* flowering record as early indicator of biological change induced by global sea warming in Mediterranean marine ecosystems.

Keywords: angiosperms, biological footprints, climate change, flowering, life history, Mediterranean, *Posidonia oceanica*, sea warming, seagrass, sea-surface temperature

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Introduction

As part of the observed secular global warming (Pollack *et al.*, 1998), a likely anthropogenic global ocean warming has been detected over the last decades (Barnett *et al.*, 2001). Increased seawater temperature has also been observed in Mediterranean deep ($0.004\,°C\,yr^{-1}$ in Bethoux *et al.*, 1990) and surface (Metaxas *et al.*, 1991; $0.009\,°C\,yr^{-1}$ between 1977 and 1990 in Bethoux & Gentili, 1996; Marbà & Duarte, 1997: $0.004\,°C\,yr^{-1}$ be-

tween 1975 and 1994; Xoplaki, 2002) waters over the last few decades. Global warming affects a range of biological processes (Peñuelas *et al.*, 2002; Parmesan & Yohe, 2003), which by integrating variability often provide clearer signals of climate trends than meteorological records (typically noisy) do.

Plant flowering is often affected by climatic change, both in terms of timing (Post, 2003; Schwartz *et al.*, 2006) and intensity (e.g. Roussopoulos *et al.*, 1998; Iglesias *et al.*, 2003). Thus, climate change may affect plant reproductive phenology (Schwartz, 1999), which could be one of the mechanisms involved on changes of plant population distribution and abundance in the short

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(Carey *et al.*, 2002) and long (Hoek, 2001) term. Although there is abundant evidence for changes in plant flowering in response to climate change, most have been observed on land species, the existence of similar patterns in marine flowering plants has not been clearly observed. There is, however, evidence of biological responses to warming in the Mediterranean Sea, such as an increasing presence of subtropical species in the NW basin (Francour *et al.*, 1994; Astraldi *et al.*, 1995; Grau & Riera, 2001) or mass mortalities of sessile invertebrates in the same basin following anomalously high seawater temperature (Romano *et al.*, 2000).

Time series of changes in Mediterranean marine communities are even fewer than temperature records (cf. Duarte *et al.*, 1992), but some species are able to record temperature variability through thermal-induced changes in their structure or composition (Kennedy *et al.*, 2001; Silenzi *et al.*, 2005). In this context, the analysis of biological trends in long-lived species, which are able to integrate decadal climatic changes in their structures and functions, is a possible alternative (Duarte *et al.*, 1999).

Posidonia oceanica is the dominant seagrass in the Mediterranean, where it is endemic (den Hartog, 1970). This submerged plant forms extensive meadows, which are believed to occupy between 2.5 and $5 \times 10^{10} \, \text{m}^2$, extending from 0.3 to 45 m depth (Bethoux & Copin-Monteagut, 1986; Pasqualini *et al.*, 1998) and play a key role in coastal ecosystems (Hemminga & Duarte, 2000). *P. oceanica* forms extraordinarily persistent meadows (several millennia, Mateo *et al.*, 1997), and the individual shoots of this clonal plant can live more than 30 years (Marbà *et al.*, 1996b). The presence of regular growth marks along the rhizomes of the plant allows the determination of their age and the reconstruction of their growth and reproductive dynamics (Pergent & Pergent-Martini, 1990; Duarte *et al.*, 1994) For example, a general reduction in vertical rhizome growth of this plant over the last two decades has been detected in the Spanish Mediterranean coast, coinciding with regional sea level rise, warming and a reduction of water transparency (Marbà & Duarte, 1997). Reconstruction techniques also provided evidence of a parallel widespread demographic decline in the Spanish meadows (Marbà *et al.*, 1996b), consistent with similar reports, derived from long-term meadow surveys, for other Mediterranean areas (e.g. Zavodnik & Jaklin, 1990)

As an angiosperm, *P. oceanica* produces flowers, although flowering of *P. oceanica* is considered a rare event (Hemminga & Duarte, 2000). The inflorescences leave a distinct scar in the rhizome, at the insertion point of their stalk, therefore allowing the detection, and age determination, of past flowering events. Flowering of this species is a sparse and apparently unpre-

dictable phenomenon. There is some indication that, as in some land angiosperms (e.g. Roussopoulos *et al.*, 1998; Iglesias *et al.*, 2003) *P. oceanica* flowering could be triggered by high temperature, because widespread and intense flowering events have been associated with specially high summer seawater temperatures (e.g. Giraud, 1977; Mazzella *et al.*, 1983; Boyer *et al.*, 1996), and because a significant amount of flowering frequency (FF) variability occurs at the regional scale (Diaz-Almela *et al.*, 2006). The link between *P. oceanica* flowering and seawater temperature has not been formally established because not every time that a warm episode has occurred, *P. oceanica* flowers have been detected (Mayot *et al.*, 2005).

Here, we examined possible relationships between temperature change and *P. oceanica* flowering on the basis of a large data set, derived from two centuries of published reports of *P. oceanica* flowering along the Mediterranean basin and seawater temperature series. The aim was to explore large-scale patterns of interannual variability in the occurrence and intensity of this phenomenon, and to test the hypothesized relationship between flowering, seawater temperature and global warming.

Materials and methods

We searched the published international and national literatures concerning reports of *P. oceanica* flowering. A total of 82 references were detected, of which 59 articles were obtained. The articles not recovered correspond to ancient works (XVIII and XIX centuries) or modern, cited in the obtained papers for their flowering records. Most revised articles (49) reported observations of meadow flowering along the Western Mediterranean and only 16 focused on meadow flowerings along the Eastern basin (Fig. 1). A total of 48 papers reported
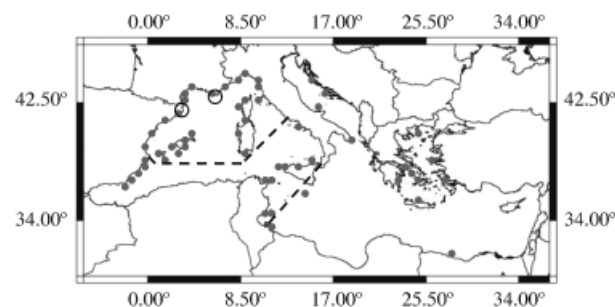

Fig. 1 Abridged scheme of the distribution of localities with flowering citations (full circles) and with the data series on seawater temperatures used in this work (open circles). The curve delineates localities included in the NW Mediterranean group. The straight line over the Sicily Strait marks the division of localities in Western and Eastern Mediterranean groups.

direct observations while 12 studies revealed past flowering events using reconstructive techniques, which are based on flowering marks. The complete database obtained, as well as the source references are given in Appendix S1.

Positive flowering citations (i.e. reports of flowering events) derived both from direct observations and reconstruction studies, while most negative records derived from reconstruction, as direct observation reports are usually produced in response to the particular observation of a flowering event, and are, thus, biased. The minimum flowering intensity (FI, fraction of flowering shoots) detection threshold to retain a negative citation from reconstructive techniques as reliable has been arbitrarily fixed at 5%, requiring, therefore, a minimum of 20 shoots for each year analysed to consider a negative report as reliable.

In order to avoid artificial duplications, *in situ* records were considered to belong to different localities when the distance among them was equal to or greater than 1 km. Delocalized citations (free material stranded on the beach) were taken into account only if they were observed at least 60 km away from any other contemporaneous record. When several flowering records were available for the same locality (usually stations at different depths), a composite record of annual FI was calculated by averaging FI across stations (in the case of direct observation reports) or compounding the shoots sampled in the different depths (with reconstruction data). This allowed estimating a unique annual flowering record per site.

Meadow FF (number of flowering years per total number of years reported in a given meadow) was only estimated for meadows where reconstructed or systematic direct records where available during 5 years or more.

The annual flowering prevalence (FP, flowering records per total records) was calculated for years when observations were available for a minimum of 10 localities (thus since 1975).

Annual average FI has been estimated from the average of positive FI reports across the Mediterranean for a given year. Meadow FI data in the literature consisted on percentages of flowering shoots or inflorescences densities. When records consisted on inflorescence densities, FI values were estimated dividing them by mean shoot densities (when provided in the article). Data in the articles where usually presented as average plus SE or ranges. In the latter case, the average between the extremes of the range was calculated and retained as an individual record of FI. The reports of FI used were obtained from direct observation records as well as reconstructed estimates, but for the latter, only those based on a minimum of 50 shoots in a given flowering year were retained for the analysis.

Local time series of annual Surface seawater temperature maxima (SST_{max}) were available from two localities around the Western Mediterranean, which were combined to yield a general trend over the last 40 years. The longest time series available was obtained at Villefranche-Sur-Mer Bay (South East France), spanning from 1957 to 2005 (discontinued between 1980 and 1983 and with a gap in 1994; http://www.obs-vlfr.fr/Rade/index.htm). Further information on the properties of this data series can be obtained from Etienne *et al.* (1991) and Prieur (2002). Annual maxima were extracted from the data, collected from 1 m depth at weekly intervals. Another seawater temperature data set was available from a station located 2 miles off L'Estartit (North-East Spain), spanning from 1968 to 2005 (http://www.gencat.net/servmet/marcs/marcos_observacio/marcs_temp.htm). The characteristics (seasonality, warming trends, depth variability) of this time series are reported elsewhere (i.e. Pascual *et al.*, 1995; Salat & Pascual, 2002). We extracted the annual maximum temperature averaged between 0.5 and 5 m estimates obtained at weekly intervals.

The standardized (mean = 0 and SD = 1) temperature series for L'Estartit was scaled to the standardized Villefranche series by bringing it to the same mean and standard deviation of the period of the reference set (Villefranche-sur-Mer) corresponding to the period of the shortest series (Estartit). Both data sets were then averaged to derive a composite, standardized seawater temperature series, representative of temperature changes in the NW Mediterranean.

Shorter but more global time series (1982–2005) of annual SST_{max} were obtained from the NCEP Reynolds Optimally Interpolated Sea Surface Temperature data sets (Reynolds *et al.*, 2002). The interpolated SST maps are produced using *in situ* (from ship and buoys) and corrected satellite (NOAA-AVHRR) data. SST analyzed fields have an accuracy of 0.5 °C and are available on weekly and monthly 1° latitude/longitude spatial grid at http://podaac.jpl.nasa.gov/products/product119.html. A detailed description of the Optimal interpolation analysis can be found in Reynolds & Smith (1994) and in Reynolds *et al.* (2002). We have extracted the analyzed SST data for the Mediterranean area (2.5°W–34.5°E and 30.5–45.5°N, 231 grid points), from which we produced three separate weekly SST series: (i) a series for the Western Mediterranean basin (2.5°W–15°E, 30.5–45.5°N, 101 grid points), (ii) a series for the Eastern Mediterranean basin (15–34.5°E, 30.5–45.5°N, 130 grid points), excluding data from the Black Sea and (iii) a series for the whole Mediterranean basin. In all cases, land areas have been masked and series of annual maxima

(SST_{max}) were extracted. Mean annual temperature minima (SST_{min}) were also extracted from the Reynolds series in the Mediterranean basins.

The existence of long-term monotonous trends in SST_{max} series was explored by fitting least-squares linear regression equations to each time series with the linear regression procedure of SPSS™ 11. The degree of correlation between the SST_{max} series from the different Mediterranean basin levels was subsequently explored. Finally the relationships between flowering parameters and the temperature data series (SST_{max} values and also residuals from SST_{max} vs. time regressions) at the different basin levels were also explored through regression analysis with the general linear models-Univariate procedure of SPSS™ 11. Variables were log-transformed when necessary to comply with the requirements of the analysis.

Results

The basin SST_{max} series (1982–2005) extracted from Reynolds data showed warming trends for the Eastern Mediterranean at a rate of (mean + SE) $0.06 \pm 0.01\,°C\,yr^{-1}$ ($R^2 = 0.43$, $P = 0.0003$, $N = 24$ years, Fig. 2) and for the whole Mediterranean basin in $0.04 \pm 0.01\,°C\,yr^{-1}$ ($R^2 = 0.24$, $P = 0.009$, $N = 24$ years, Fig. 2), but not for the Western Mediterranean (Fig. 2, $R^2 = 0.01$, $P = 0.27$, $N = 24$). However, the longer annual SST_{max} series of l'Estartit (1968–2005) and Villefranche (1957–2005), both located in the NW Mediterranean, showed significant warming trends at rates of $0.06 \pm 0.02\,°C\,yr^{-1}$ ($R^2 = 0.24$, $P < 0.001$, $N = 38$ years) and $0.02 \pm 0.01\,°C\,yr^{-1}$ ($R^2 = 0.12$, $P < 0.02$, $N = 44$ years), respectively (Fig. 3). The NW Mediterranean average SST_{max} series, obtained by aggregation of the two local series also showed a warming trend of $0.03 \pm 0.01\,°C\,yr^{-1}$ ($R^2 = 0.17$, $P < 0.002$, $N = 49$ years, Fig. 3). The NW Mediterranean SST_{max} data were positively correlated with Western Mediterranean ($R^2 = 0.72$, $P < 2 \times 10^{-8}$, $N = 24$) and Mediterranean basins SST_{max} series ($R^2 = 0.48$, $P = 10^{-4}$, $N = 24$) extracted from Reynolds data, but were very weakly correlated with the SST_{max} values extracted for the Eastern Mediterranean basin ($R^2 = 0.12$, $P < 0.06$, $N = 24$). The magnitude of the residuals of SST_{max} values around the warming trend, as described by the fitted least square linear regression equations, did not increase significantly with time in any of the Mediterranean series. SST_{min} series did not increase with time in any of the basin series between 1982 and 2005.

The data set compiled included 951 independent reports of meadow flowering, 430 being positive (i.e. indicative of flowering meadows) and 521 negative, for a total of 308 localities around the Mediterranean (see Appendix S1). Meadows studied in the literature
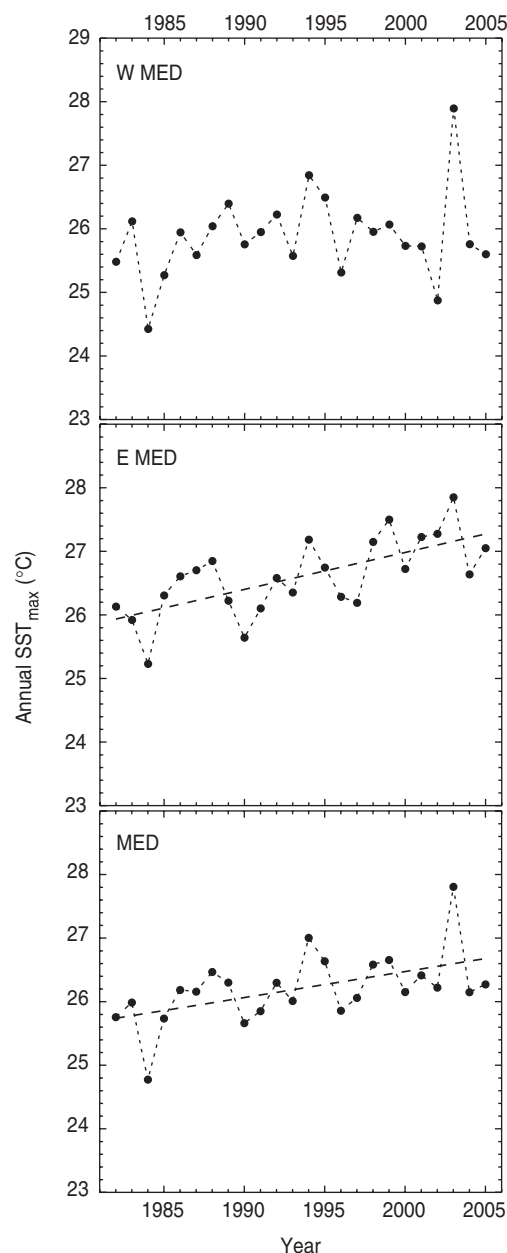

Fig. 2 Surface seawater temperature maxima (SST_{max}) (°C) series extracted from Optimally Interpolated Reynolds data for the Western, Eastern and the whole Mediterranean basin. The dashed lines represent the increase of SST_{max} with time observed with the regression analysis (Mediterranean: 0.04 $(\pm 0.01) \cdot t$ (years), $R^2 = 24$, $P = 0.009$; Eastern Mediterranean: 0.06 $(\pm 0.01) \cdot t$ (years) -89.21 (± 26.81), $R^2 = 0.43$, $P < 0.001$).

covered the distribution range of the species but most flowering reports were concentrated in the European Western Mediterranean coasts, while records along the Eastern basin (42 records in 27 meadows) and along the African coasts (34 records in 15 meadows) are much
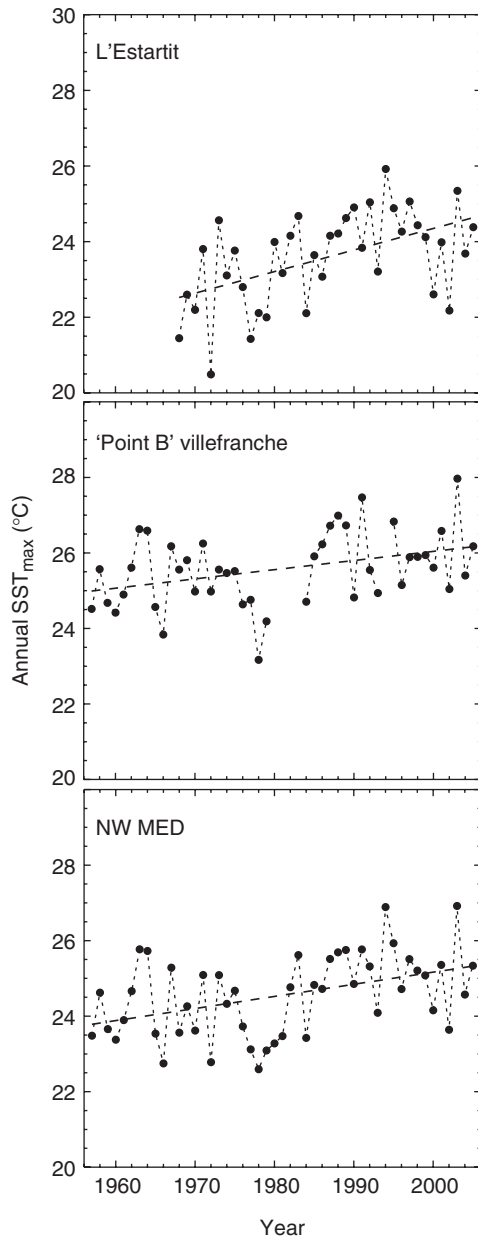
more scarce. Available flowering records extend from 1733 to 2004, but most are concentrated on the second half of the 20th century, as a result of increasing
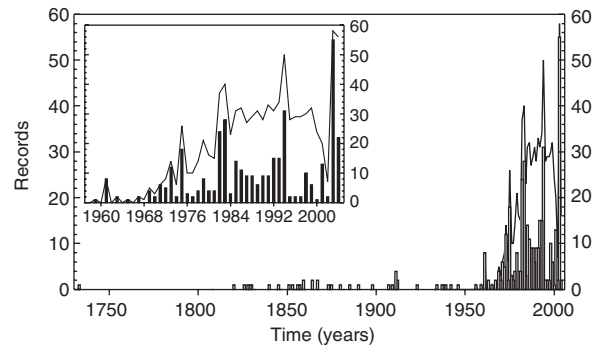

Fig. 4 Evolution of annual flowering records (bars) and observation effort (line represents total records) based on the available literature database (see Appendix S1).

observational effort (Fig. 4). Multi-annual records available for 58 meadows across the Mediterranean provided evidence of substantial variability in flowering frequency among sites (Fig. 5a), ranging from 23 meadows where flowering has never been detected along the observational period to six meadows where flowering occurred more than half of the years examined. The annual FP showed a distribution skewed towards low values, but its deviation from normal distribution was not significant (Saphiro–Wilks: $P > 0.05$, $N = 32$): each year on average 37% of the meadows observed produced flowers, ranging between 4% and 90% (Fig. 5b). The FI varied greatly, ranging from 0.001 to 0.54 inflorescences per shoot in flowering meadows (Fig. 5c) and the distribution of FI significantly deviated from normal distribution (Saphiro–Wilks: $P < 0.001$, $N = 138$).

The time series of FP showed peaks of synchronous widespread flowering in the NW Mediterranean in years 1973, 1975, 1983, 1994 and 2003, coinciding with SST_{max} peaks in the aggregated time series from this area (Fig. 6, NW MED). Peaks of maximum FP and of SST_{max} were observed in the same years, between 1982 and 2004, in the Western an in the entire Mediterranean basin series. Indeed, examination of *P. oceanica* FP time series filtered for long-term (20-year moving average) and interannual variability (4-year moving average), clearly showed a cyclical behaviour with decadal intervals between periods of maximum and minimum FP at NW, W and whole Mediterranean basin levels (Fig. 6, only shown NW Mediterranean filtered FP series). There was a significant positive correlation between NW Mediterranean FP values and NW Mediterranean SST_{max} ($R^2 = 0.23$; $P = 0.003$, $N = 31$). The strength of the correlation increased when comparing FP with the residuals of SST_{max} vs. time (i.e. temperature anomalies; $R^2 = 0.34$, $P = 0.0003$, $N = 31$; Fig. 7 upper graph), and was very high for FP data grouped by 1 °C temperature anomaly bins ($R^2 = 0.89$, $P < 0.04$, $N = 4$). FP across the
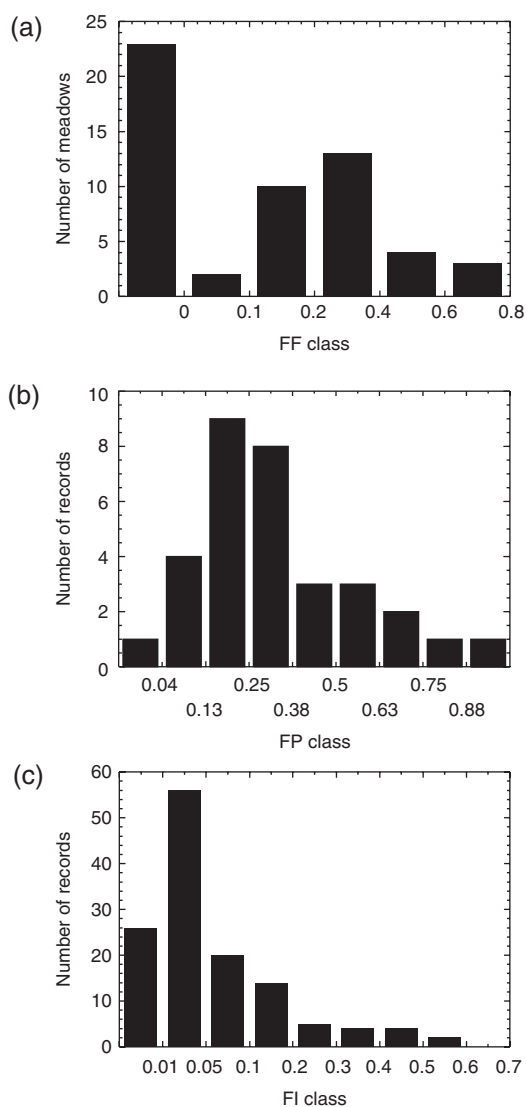
Fig. 5 (a) Histogram of the number of meadows within each flowering frequency class (flowering events per year). (b) Frequency distribution of annual flowering prevalence (FP, flowering records per record) and (c) Frequency distribution of the flowering intensity (inflorescences per shoot) records.

Fig. 6 Evolution of annual flowering prevalence (bars, FP: flowering records per total records) since 1973 until 2004 in the NW Mediterranean, upper graph: the dashed line represents the annual mean NW Mediterranean sea surface temperature maxima (°C) for the same period. NW Mediterranean FP time series filtered for long-term (20 years moving average) and interannual variability (4 years moving average), showing a decadal cyclic behaviour, lower graph.

entire Mediterranean basin also increases with detrended SST_{max} anomalies in the Mediterranean basin (ungrouped data: $R^2 = 0.27$, $P < 0.01$, $N = 24$; grouped by 1 °C bins: $R^2 = 0.86$, $P < 0.05$, $N = 4$). Western Mediterranean FP estimates were also positively correlated with mean SST_{max} annual values in this basin (1982–2004), both ungrouped ($R^2 = 0.20$, $P < 0.02$, $N = 24$) or grouped by 1 °C bins ($R^2 = 0.87$, $P < 0.05$, $N = 4$). In the Eastern Mediterranean, FP was correlated only with SST_{max} anomalies ($R^2 = 0.20$, $P < 0.10$, $N = 24$). FP estimates in the Western and Eastern basins were positively correlated ($R^2 = 0.54$, $P < 0.007$, $N = 11$). Nevertheless, FP estimates in the Eastern basin are based in a low
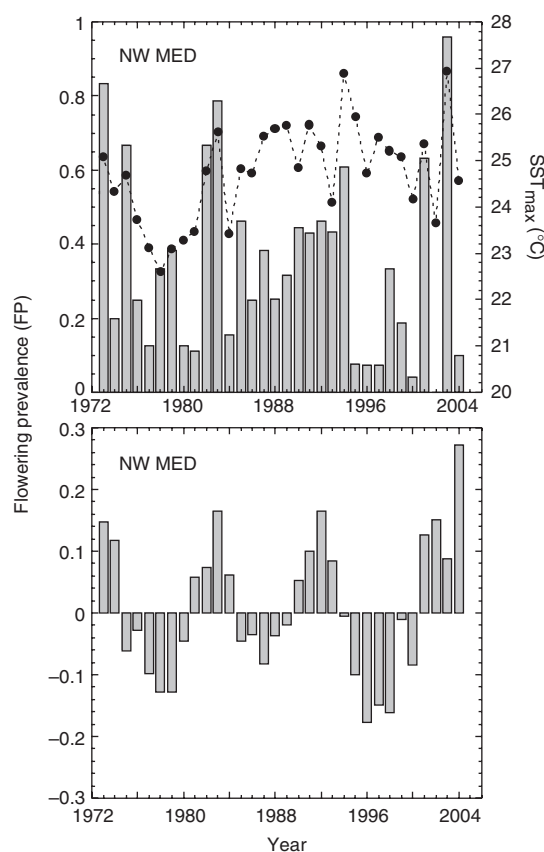
number of records (2–5 year^{-1}). None of the FP series showed significant monotonous trends with time and were, accordingly, independent of SST_{max} values predicted from mean warming trends ($P > 0.05$).

The annual FI, as the average fraction of reproductive shoots within flowering meadows varied greatly with time (Fig. 8). A sharp increase in FI was observed in the warmest years, such as 1975, 1994 and especially in 2003. The annual FI significantly increased with SST_{max} in the Mediterranean basin ($R^2 = 0.26$, $P = 0.02$ for log-transformed FI, $N = 18$), and the correlation was greater with detrended SST_{max} anomalies ($R^2 = 0.30$, $P = 0.01$, $N = 18$, for log-transformed FI; Fig. 7 lower graph). Nevertheless, such correlations are dependent on the extreme values of year 2003. No correlation of SST_{min} with FP or FI was found in any of the Mediterranean basins analysed.
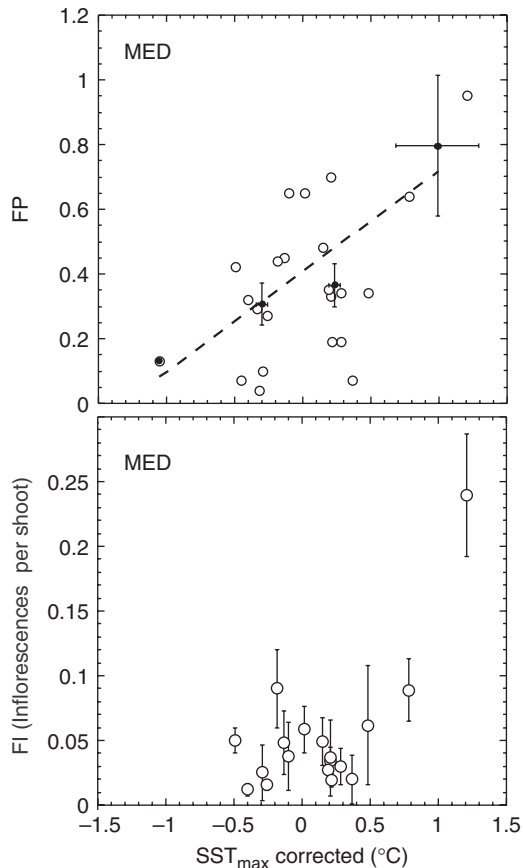
Fig. 7 (Upper graph) Flowering prevalence (FP, annual flowering records per total records) and surface seawater temperature maxima (SST$_{max}$) (°C) residuals of warming trend in the whole Mediterranean basin. White dots represent ungrouped data and black points correspond to means of data grouped by 0.5 °C intervals. Horizontal and vertical bars indicate dispersion (SE) within bin groups. The dashed line represents linear regression from the grouped data [$y = 0.35 (\pm 0.08) \times (°C) -0.43 (\pm 0.07)$, $R^2 = 0.86$; $P = 0.046$]. (Lower graph) mean flowering intensity (FI, inflorescences per shoot) across the Mediterranean in relation to SST$_{max}$ (°C) in the whole Mediterraean basin. Empty circles represent data ungrouped and vertical bars represent FI SE.

Discussion

The results presented portray flowering of the seagrass *P. oceanica* as an irregular and sporadic phenomenon, consistent with previous reports (Giraud, 1977; Pergent *et al.*, 1989). The extensive records compiled here indicate that any one meadow flowers, on average, every 5 years, which suggests that sexual reproduction may be more relevant in the life history of this long-lived clonal species than previously thought. Moreover, closer examination of the time trends in flowering occurrence, further suggests the existence of near-decadal cycles in the prevalence of flowering of
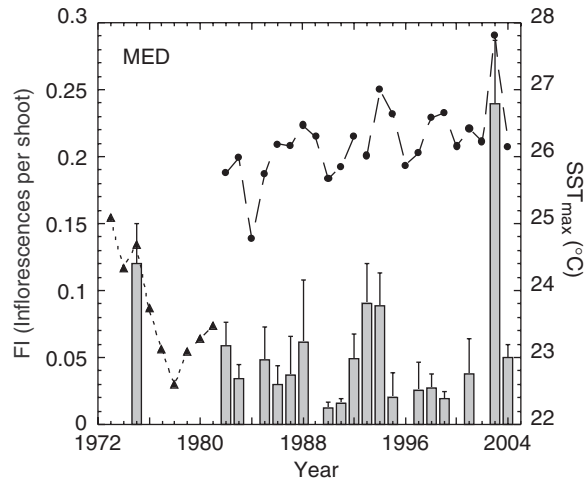

Fig. 8 Evolution of flowering intensity (FI: inflorescences per shoot) in the Mediterranean basin between 1975 and 2004. The circles linked with a dashed line represent the Mediterranean surface seawater temperature maxima (SST$_{max}$) (°C) values between 1982 and 2004. The triangles linked with a dashed line represent NW Mediterranean SST$_{max}$ series between 1973 and 1981. Bar lines represent SE.

P. oceanica meadows, which may indicate the existence of cyclic changes in their environment (consistent with near-decadal SST cycles in the Mediterranean, Duarte *et al.*, 1999; Xoplaki, 2002) and/or physiology which could be reflected on the life history of this species.

Flowering events involve, on average (± SE) 8 ± 1% of the shoots at any one meadow. Mean FI across the whole Mediterranean basin is, therefore, somewhat lower than mean FI previously estimated along the Western European coasts (11 ± 2%; Diaz-Almela *et al.*, 2006), but still near the 10% proportion of flowering shoots typically observed in flowering seagrass meadows (Duarte *et al.*, 1997).

In 2003 the fraction of flowering meadows in the Mediterranean (FP = 0.95) far exceeded the average values for the species and was the greatest ever reported. The same occurred with the average fraction of flowering shoots within flowering meadows [24 ± 5 (SE)%], even though FI varied significantly among regions (Diaz-Almela *et al.*, 2006). Those high FP and mean FI values indicate that an exceptional widespread flowering was observed in the Mediterranean. Most of 2003 citations correspond to the Western basin, but meadow flowering has also been observed in several parts of the Ionian Sea (M. Salomidi, personal communication), and in the Southern part of the Aegean Sea (C. O. Invers, personal communication). Year 2003 was characterized by an extended heat wave throughout Europe (Luterbacher *et al.*, 2004) that generated anomalously high sea surface temperature maxima: 1.60 °C

above the mean SST_{max} and 1.21 °C above the detrended anomalies mean, registered in the Mediterranean between 1982 and 2005. In the Western Mediterranean SST_{max} in 2003 reached 2 °C above the mean (1982–2005), while in the NW Mediterranean area it was 2.37 °C above the mean SST_{max} and 1.66 °C above the anomalies mean between 1957 and 2005.

The results demonstrated a significant, positive relationship between the prevalence and intensity of flowering of *P. oceanica* meadows (thus the flowering probability for any one shoot) and the annual maximum sea-surface temperature, applicable across the entire Mediterranean, as well as the individual basins. This provides evidence for an effect of summer maximal seawater temperatures on flowering in *P. oceanica* meadows, as hypothesized by Buia & Mazzella (1991), who found a delay of 1 month in the flowering timing of deep *P. oceanica* meadows, coinciding with a parallel delay of the maximum seawater temperature in deep meadows (during break of the thermocline).

Gobert *et al.* (2001) challenged the hypothesis of flowering induction by high summer temperature, based on retrospective analysis of leaf growth, because they found longer old leaves in reproductive shoots and estimated them to have appeared 7 months before anthesis, which usually takes place in October. Their estimation assumed a constant leaf plastochrone interval, which is incorrect as the leaf appearance rate increases in summer (Marbà *et al.*, 1996a). On the other hand, the appearance of longer old leaves in reproductive shoots does not necessarily imply that flowering induction takes place at the time the longer leaves are formed. This could also be observed if shoots that have produced less leaves in the previous months, which significantly bear longer leaves (Marbà *et al.*, 1996b) would flower preferentially. Indeed, an hypothetical flowering induction before summer is compatible with a temperature signal as trigger for inflorescence development.

While being a significant driver of flowering, summer maximal seawater temperatures account for only a modest fraction of the variance in the prevalence ($R^2 = 0.27$) and intensity ($R^2 = 0.30$) of flowering of *P. oceanica* in the Mediterranean, although stronger patterns are obtained when flowering parameters are grouped by 1 °C SST bins. Local (Xoplaki *et al.*, 2003; Abboud-Abi Saab *et al.*, 2004) and depth (Salat & Pascual, 2002) variability in thermal regime, could account, at least partially, for the large spatial variability in flowering occurrence and intensity at any mean regional sea surface temperature. The reported correlations of meadow flowering frequency with latitude and longitude (Diaz-Almela *et al.*, 2006) and the reduction of flowering frequency, intensity, as well as later flower-

ing, with depth (Buia & Mazzella, 1991; Diaz-Almela *et al.*, 2006) reinforce this idea. But other factors may affect flowering occurrence and intensity, such as local resource availability (Gobert *et al.*, 2005), or meadow age structure (Balestri & Vallerini, 2003; Diaz-Almela *et al.*, 2006). Genetic diversity has been shown in other clonal aquatic species to influence flowering (Dorken & Eckert, 2001).

A relationship between temperature changes and altered flowering patterns is well documented for land species (e.g. Peñuelas *et al.*, 2002; Iglesias *et al.*, 2003). Episodes of massive flowering have been linked to ENSO (Intachat *et al.*, 2001) and increased plant sexual reproduction has been attributed to sustained decadal warming trends, leading to enhanced expansion of plant populations (Carey *et al.*, 2002). Within aquatic plants, synchronous widespread flowerings have been linked to seawater temperature in some Australian and Philippine Seagrasses (Inglis & Lincoln Smith, 1998; Rollón *et al.*, 2003).

Our results confirmed previous reports of warming trends in the Mediterranean Sea, at a mean ($\pm$ SE) rate of 0.04 ± 0.01 °C yr^{-1}. The warming seems faster in the Eastern basin and slower in the Northwestern basin. Summer SST_{max} seem to increase faster than do mean annual seawater temperatures previously reported in shallow (Metaxas *et al.*, 1991; Bethoux & Gentili, 1996; Xoplaki, 2002) and deep waters (Bethoux *et al.*, 1990) over similar time scales.

Temperature affects seagrass at multiple levels, from physiological to life history (Short & Neckles, 1999), often in opposite directions, thereby precluding predictions on the effects of global warming and temperature anomalies on seagrass meadows (Duarte 2002; Duarte *et al.*, in press). Within seagrasses, there is some evidence that high seawater temperatures could constitute a source of stress for the plants either directly (physiological disruption) or through external mechanisms, such as increasing anoxia in the sediment (Greve *et al.*, 2003).

The observed increase in Mediterranean seawater temperatures coincides with widespread decline of *P. oceanica* meadows in the area, affecting even meadows with no evident anthropogenic impacts (Marbà *et al.*, 1996b). Indeed, this decline seems to have been accelerated during the last years (Marbà *et al.*, 2005), when record high temperatures have been reached. Moreover, during summer 2001, increased shoot mortalities were observed, coinciding with a local maximum temperature peak of 28.01 °C in the Bay of Magalluf (Mallorca, Spain) followed by a flowering event that fall. High mortalities were registered at the same meadow two years later, from autumn 2003 to summer 2004, following an exceptional flowering event,

after a local summer peak temperature of 29.3 °C, in August 2003 (E. Diaz-Almela, unpublished data). In the Gulf of Lion, Mayot et al. (2005) observed a decline of rhizome growth in deep meadows of P. oceanica, during the year subsequent to a warm-water episode on those coasts (1999), but no flowering was detected that fall.

Although the mechanisms responsible for an increased flowering subsequent to warming events, increased induction or increased development, remain unknown, the shoot decline associated with high temperature suggests that flowering in this clonal species could represent a response to heat stress. Similarly, different kinds of stress have been demonstrated to induce or enhance flowering in terrestrial species (e.g. Ofir & Kigel, 2003) as a mechanism of escape.

We further decomposed the temperature response of P. oceanica flowering between a response to the monotonous warming trend and that to temperature anomalies superimposed on the monotonous trend. The absence of a temporal increasing trend in FP and the stronger correlation of FP with the annual residuals of the warming trend indicate that flowering may be more responsive to seawater temperature anomalies than to the warming trend. However, these two effects may compound as the absolute SST reached in warm years is increasing over time, as a similar anomaly occurs over a shifting baseline. If flowering in P. oceanica was a stress response to high temperature, it could be expected that the absolute warming trend added to positive thermal anomalies could induce increased widespread and intense meadow flowering of this temperate species, and thus, less intense thermal anomalies would be needed to produce widespread flowerings.

The more intensive and extensive flowering event ever reported was observed in Autumn 2003, coinciding with the highest summer temperature maxima registered over the last 40 years in the available SST series and in air temperature over the last five centuries in Europe (Luterbacher et al., 2004), although the thermal anomaly observed that year was not the greatest registered in the long NW Mediterranean series (1994: +1.92, 1963: +1.80). Further systematic monitoring of P. oceanica meadow flowering is needed to confirm whether the shifting baseline SST_{max}, with seawater warming, enhances the flowering response of P. oceanica to temperature anomalies, as suggested by the extreme 2003 flowering event.

The IPCC panel predicts an increment in the frequency of extreme temperature events and a temperature increase in the Mediterranean for the period 2021–2050, with respect to the period 1961–1990, of 1–4 °C (multi-model maps of change of annual mean temperature on scenarios IPCC-DDC IS92a and SRES A2 and B2; Cubasch et al., 2001). Our results indicate that in this scenario, P. oceanica flowering may become a more frequent event than it was in the past. Thus, climate change in the form of sea warming or more frequent warm episodes could affect both the stability of the seagrass meadows (Marbà & Duarte, 1997) and, through the effects on flowering reported here, also their potential recolonization.

The long lived P. oceanica shoots are able to register environmental changes of different nature, as heavy metal or radioisotopes loads (e.g. Calmet et al., 1988; Warnau et al., 1995), interannual variability of rainfalls, sea level and temperature, that influence vertical rhizome growth (Marbà & Duarte, 1997; Mayot et al., 2005). Given the relationship of P. oceanica flowering with high sea surface temperatures, reconstruction of past flowering events may potentially serve to reconstruct local to regional SST summer maxima. Such reconstruction could go further in the past than it has been done until now as P. oceanica meadows form reefs of highly recalcitrant rhizome material accumulating in situ over millennia (Mateo et al., 1997), potentially offering opportunities to investigate P. oceanica flowering across the centennial time scale.

P. oceanica meadows appear to amplify the temperature footprint of global warming, as a difference of 1–2 °C seems to induce widespread flowering throughout the Mediterranean coasts, such as demonstrated for the events in 1973–1975, 1982–1983, 1992–1994, 2001 and, particularly, 2003. Moreover, the prevalence and intensity of flowering increases with the amplitude of the anomaly, providing evidence of global sea climate change at a much longer scale than that possibly encompassed by the sparse or short seawater temperature time series in the Mediterranean. Hence, systematic records of P. oceanica flowering may provide a footprint of climate change in the Mediterranean Sea, as well as evidence of the effects of global warming and or of temperature anomalies on the life history and ecosystems therein. Whereas P. oceanica flowering is difficult to observe, compared to that of terrestrial plants, the growing effort to monitor these fragile ecosystems is enhancing the empirical basis to assess flowering events and, therefore, also providing an alert to the consequences of the climate change on Mediterranean coastal ecosystems.

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Supplementary Material

The authors have provided the following supplementary material, which is available alongside the article at http://www.blackwell-synergy.com

Appendix S1. Database of observations.