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RESEARCH ARTICLE

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Patterns of seagrass (*Posidonia oceanica*) flowering in the Western Mediterranean

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Abstract The intensive reconstructive sampling (1957–2004, 39 localities), a systematic direct observation (1992–2004, 1 locality) and particular direct observations (66 localities) of *Posidonia oceanica* meadows were analysed together with temporal series of flowering available in the literature (19 localities). This allowed the examination of temporal and spatial variability in annual flowering prevalence (FP, the fraction of meadows flowering in a given year) and of annual meadow flowering intensity (FI, number of inflorescences per shoot) for the period 1979–2004 across the Western Mediterranean, as well as spatial variability of flowering frequency (FF, the fraction of years that a given meadow has flowered) and shoot flowering probability (Pf, fraction of flowering stalks appeared per annual segment). Each year, on an average 17% of the investigated meadows flowered, ranging from 3 to 86% of meadows among the years. The highest annual FP and FI values were obtained in 2003 (FP = 0.86 and mean FI = 0.23 ± 0.03 inflorescences shoot^{-1}). A secondary peak of FP and mean FI occurred 9 years earlier, in 1994 (FP = 0.44 and mean FI = 0.08 ± 0.02). Both peaks of flowering occurred after hot summers. Flowering synchrony in particular years across the Western Mediterranean and clines of increased meadow flowering frequency towards the North and East, suggests the existence of large-scale environmental mechanisms controlling the floral induction. On the other hand, meadow FF and Pf were highly heterogeneous among and within the meadows, indicating that local factors also may play a significant role in flowering induction. When flowering, the Western Mediterranean meadows showed an average 0.11 ± 0.02 inflorescences shoot^{-1}, but FI greatly varied among and along the series (from 0.002 to 0.54 inflorescences shoot^{-1}) and decreased significantly with depth but was independent of meadow shoot density and meadow latitude or longitude. The shoot flowering probability was quite low (0.007 ± 0.002 inflorescences shoot^{-1} year^{-1}) and exponentially increased with shoot age.

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Introduction

Seagrasses are clonal plants for which sexual reproduction is believed to play a modest role, compared to clonal reproduction (Hemminga and Duarte 2000). This is the case for *Posidonia oceanica* (L.) Delile (e.g. Marbà et al. 1996a), the dominant seagrass in the Mediterranean (occupying between 2.5 and 5×10^{10} m^2, Bethoux and Copin-Monteagut 1986; Pasqualini et al. 1998), where it is endemic (den Hartog 1970). This statement has been supported by the observation of low genetic diversity in most *P. oceanica* meadows (Procaccini and Mazzella 1996; Procaccini et al. 1998, 2000), and, specially, by the paucity of flowering observations (Giraud 1977; Pergent et al. 1989). Nevertheless, reports of *P. oceanica* flowering have greatly increased in the past two decades, parallel to the observational effort (e.g. Thelin and Boudouresque 1985; Buia and Mazzella 1991; Balestri 2004), and reports of seedling recruitment have also become more frequent (Gambi et al. 1996; Buia and Peirano 1988; Balestri et al. 1998). Moreover, high clonal diversity has been reported in many meadows, as

more powerful molecular markers have been discovered (Alberto et al. 2003; Jover et al. 2003; Arnaud-Haond et al. 2005). These recent developments suggest that sexual reproduction may play a more important role, at least in the long-term population dynamics of the species, than it is believed so far.

Flowering is a first bottleneck on the sexual reproduction of *P. oceanica*. Flowering is an irregular phenomenon both spatially and temporally, but the potential patterns of this variability, which may suggest factors that influence the flowering, remain largely unexplored. Pergent et al. (1989) suggested, on the basis of reconstructive analyses of *P. oceanica* flowering, that meadows may flower about once in a decade, but more recent studies have reported meadow flowerings in consecutive years (Buia and Mazzella 1991; Semroud 1993; Balestri and Cinelli 2003). Patchiness in flowering intensity is often high, even at small spatial scales of a few metres (Gambi et al. 1984; Balestri 2004), as also reported for other species of the same genus (Inglis and Smith 1998; Campey et al. 2002). Furthermore, some reports indicate that flowering occurrence and intensity may vary with depth (Gambi et al. 1984; Semroud 1993).

The multiple observations of intensive and widespread flowering events especially after warm summers (Jahandiez 1914 in Giraud 1977; Mazzella et al. 1983; Pergent et al. 1989; Stoppelli and Peirano 1996; Balestri and Vallerini 2003) have provided evidence that flowering could be inducted by high seawater temperature. This evidence, as well as some observations of the consecutive flowerings in Southern meadows, led to the speculations that *P. oceanica* would flower only after warm summers in their northern range of distribution, while the meadows in the southern distributional limit of the species would flower almost annually (Molinier and Picard 1953). The hypothesis of the floral induction by temperature has been recently challenged on the basis that it seems to occur 7 months before anthesis and could be limited by resource availability instead (Gobert et al. 2001, 2005), and because of the high variability in flowering occurrence observed in neighbouring meadows, which probably experience comparable temperature regimes (Semroud 1993; Balestri 2004).

Despite the accumulation of flowering reports in the Mediterranean (e.g. Thelin and Boudouresque 1985; Panayotidis and Liapi 1990) and systematic studies over time (Pergent et al. 1989; Buia and Mazzella 1991; Bussotti and Guidetti 1996; Balestri and Vallerini 2003; Balestri 2004), the broad-scale spatial and temporal patterns of *P. oceanica* flowering which could help to define the factors influencing flowering occurrence and intensity, remain poorly understood because the information is fragmented.

In the present study, we aim at identifying temporal and regional patterns in *P. oceanica* flowering occurrence and intensity in the Western Mediterranean. To evaluate this purpose we used reconstructions of meadow flowering and systematic inter-annual observations in 40 meadows, as well as particular observations in 66 additional localities, most of them distributed along the Spanish and Italian Mediterranean coasts. The analysis of flowering geographic variability has been amended with published reports also derived from reconstructive or systematic surveys for 19 more localities along the Western Mediterranean. Finally, the power of a possible dependence of flowering on meadow latitude, longitude, depth, shoot age and shoot density has been tested using regression analysis.

Materials and methods

Flowering temporal series

A total of 47 flowering temporal series have been obtained both from reconstructive techniques and systematic direct observations in 40 *P. oceanica* meadows (Table 1, Fig. 1).

In Spain, we sampled a total of 36 meadows from the Balearic Islands ($N = 19$, Table 1) and the Iberian coasts ($N = 17$, Table 1) by SCUBA diving. Between 66 and 501 vertical shoots attached to 15 to 200 horizontal rhizome pieces (allowing the calculation of shoot age at flowering) were haphazardly harvested in the inner part of each meadow, in areas of around 50 m^2 in July 1992, October 2000, and May 2001. In all the meadows, shoot density was measured within 3–20 quadrats of (0.25 m^2) haphazardly deployed in the meadows. In Santa María and Es Castel meadows from Cabrera Island (Balearic Islands), sampling has been repeated in several stations following a depth gradient (four stations at 7, 13, 18 and 28 m and five stations at 5, 10, 15, 20 and 25 m, respectively). In some of these stations sampling has been repeated in September 2004 (69 shoots per station), in order to complete the series until that year.

In Northern Italy, 150 shoots from three meadows (Table 1) have been harvested in a hierarchical sampling design (see Balestri 2004), in which the station level had an area of 50 m^2. Additionally, one meadow (Antignano) in the Ligurian Sea (North-Western Italy) has been examined systematically over 13 years, obtaining a temporal series from direct observations (Table 1). The complete data set of temporal series obtained (inflorescences per shoots examined per year) is available in Appendix (Tables 4, 5, 6, 7, 8, 9).

Reconstructive techniques

Past flowerings of a *P. oceanica* shoot can be detected because of the base of inflorescences stalks that remain attached to the shoots decades after flowering (Pergent and Pergent-Martini 1990). Annual cycles of rhizome vertical growth, which are detected by measuring the leaf sheaths thickness (Pergent and Pergent-Martini 1990, method used in Italian samples) or the rhizome internodal lengths (Duarte et al. 1994, method used in Spanish samples), allowed the past flowerings to be da-

Table 1 Localities where the data series relative to the flowering of *Posidonia oceanica* have been collected. All records, with the exception of those marked in italics, come from reconstructive analyses

	Latitude (N)	Longitude (E)	Depth (m)	Series	Flowering years
Iberian Peninsula					
Jonquet	42°29.70′	2°58.99′	< 10	1977–1991	87, 88, 90
Port Lligat	42°27.30′	2°58.36′	< 10	1986–1991	90, 91
St. J. D'Alfama	40°59.10′	0°44.01′	< 10	1983–1991	
Torre de la Sal	40°8.13′	0°10.72′	9.3	1994–2000	
Campomanes	38°37.54′	0°0.568′	5.3	1992–2000	
El Arenal	38°38.37′	0°3.06′	6	1993–2000	
La Fosa	38°38.59′	0° 4.56′	3	1988–2000	
La Azohía	37°32.16′	−1°18.12′	< 10	1986–1991	
Bolnuevo	37°31.62′	−1°8.46′	< 10	1986–1991	
Calnegre	37°30.96′	−1°25.56′	< 10	1983–1991	
Cabo Cope	37°26.34′	−1°28.38′	< 10	1984–1991	
Villaricos	37°16.26′	−1°44.34′	7	1988–1991	
Aguamarga	36°55.92′	−1°56.76′	< 10	1984–1991	
Rodalquilar	36°48.42′	−2°0.14′	< 10	1985–1991	
Aguadulce	36°47.52′	−2°34.86′	< 10	1982–1991	76, 88, 90
Roquetas	36°44.58′	−2°37.80′	< 10	1986–1991	
P. Encinas	36°40.02′	−2°44.58′	< 10	1989–1991	
Balearic Islands					
S. María 7 m	39°9.00′	2°56.96′	7	1990–2004	78, 84, 87, 91, 92, 94, *01*, 03
S. María 13 m	39°9.07′	2°56.92′	13	1977–2001	*01*
S. María 18 m	39°9.156′	2°56.891′	18	1988–2003	91, 94, 03
S. María 26 m	39°9.23′	2°56.92′	26.3	1995–2004	
Es Castel 5 m	39°9.16′	2°55.83′	4.5	1995–2000	*01*, 03
Es Castel 10 m	39°9.16′	2°55.83′	10	1983–2000	77, 83–87, 91–94, *01, 03*
Es Castel 15 m	39°9.16′	2°55.80′	15	1988–2000	*03*
Es Castel 20 m	39°9.177′	2°55.766′	20	1976–2000	91, *03*
Es Castel 25 m	39°9.177′	2°55.766′	25	1988–2000	
Sa Paret	39°8.81′	2°55.86′	17	1982–2003	94, 03
C. St. Jordi	39°18.664′	2°59.960′	4	1982–2000	
Banyalbufar 1	39°40.651′	2°29.342′	26.4	1991–2001	87, 98, 99
Banyalbufar 2	39°39.692′	2°27.995′	25.4	1986–2001	90, 98, 99, 00
Illetas-Calviá	39°32.104′	2°35.562′	9	1993–2000	
Magalluf	39°30.25′	2°32.59′	6.5	1990–2004	94, 98, 99, *01, 03*
Pollença	39°53.792′	3°05.523′	4.1	1991–2001	94, 98
P. Colom	39°25.052′	3°16.183′	6.4	1996–2000	
C. Enderrocat	39°27.029′	2°44.569′	6.6	1993–2000	
C. De s'Oli	38°43.49′	1°24.16′	8.4	1986–2000	*01, 03*
Es Pujols	38°43.740′	1°27.272′	4	1994–2000	*03*
Ses Illetes	38°45.365′	1°25.828′	9	1994–2000	*03*
S'espalmador	38°46.43′	1°25.27′	4	1992–2000	93, 98
C. Torreta	38°43.454′	1°25.179′	7.6	1992–2000	98
I. des Porcs	38°47.924′	1°25.222′	5.5	1993–2000	98
Sa Talaia 1	39°05.980′	1°33.781′	27.1	1992–2001	
Sa Talaia 2	39°06.121′	1°34.598′	24	1995–2001	96, 99
Italy					
Rosignano	43°24	10°58	9.5	1985–1999	89, 92, 93, 94, 95, 96, 97
Cecina	43°19	10°31	9.5	1988–1999	90, 91, 93, 94, 95, 97
Calafuria	43°28′	10°20	9.5	1989–1999	
Antignano	43°28	10°19	2.5	1992–2004	*92, 93, 94, 03*

ted. Both techniques have been shown to release equivalent results (Guidetti 2000).

Particular flowering observations

In the Ligurian Sea (NW Italy) nine meadows were checked over 1–3 years for the presence/absence of inflorescences between 1992 and 1994, allowing quantitative estimates of flowering intensity (FI, number of inflorescences per shoot). Quantitative measures of flowering intensity have been performed at 2–4 m depth, by counting the number of shoots and inflorescences within ten quadrats (0.25 m^2) randomly placed in an area of 100×100 m^2.

In the Balearic Islands and Spanish mainland, all the meadows visited between autumn 2001 and autumn 2004 have been surveyed for the presence/absence of inflorescences, obtaining qualitative records of flowering/no flowering during these years from an additional of 51 meadows. In some meadows of the Balearic islands, FI estimations have been obtained by direct count

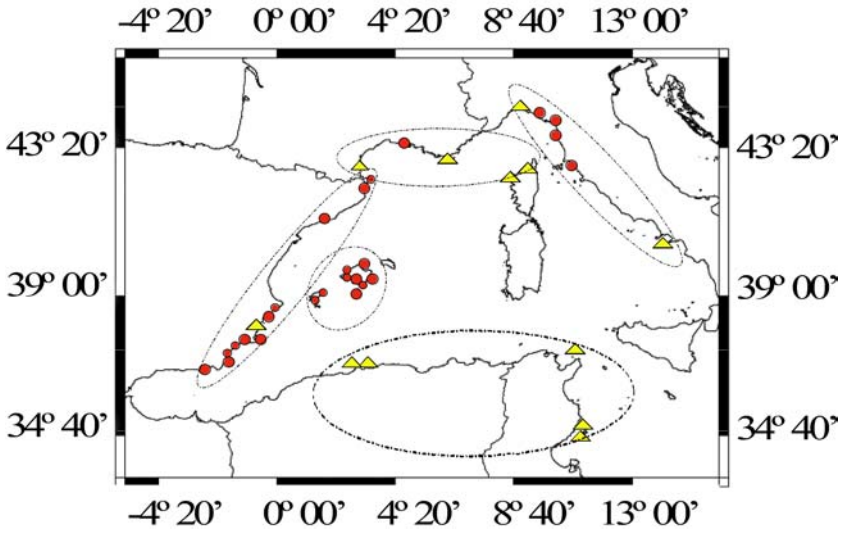

Fig. 1 Distribution of the *Posidonia oceanica* meadows sampled (*dark circles*) and obtained from the literature (*triangles*) for flowering data, along the Western Mediterranean. *Broken lines* identify the groups formed for the analysis of variability of flowering among regions

of shoots and inflorescences within 7–20 quadrats (0.25 m^2) randomly deployed along 40–60 m transect, at a uniform depth, parallel to the coastline. Additionally, an extensive measurement of FI has been performed in Magalluf Bay (Mallorca, Balearic Islands), at 7 m depth, where inflorescences and shoot densities (i.e. inflorescences or shoots per m^2) have been measured in 66 quadrats (0.25 m^2) randomly established in an area of 40×80 m^2. Direct observations in five meadows of the Balearic Islands, for which reconstructive series have been carried out (Magalluf, in Mallorca island, Es Port Bay, Es Castel and Sta. Maria bay, in Cabrera island), allowed the extension of these time series (Table 1).

In the meadows from Murcia (8), the shoot coverage (i.e. percentage of area covered by alive rhizomes) and the inflorescences density were measured along four depth transects of 50×1 m^2, using 12 randomly placed quadrats (0.16 m^2), while shoot density was measured haphazardly within 6 quadrats (0.04 m^2) in areas of the meadows with 100% coverage. shoot density in each quadrat was estimated as the product of the fractional cover and the average shoot density within dense (100% cover) areas of the meadow. Flowering intensity was then calculated for each quadrat.

Additional qualitative flowering records have been obtained for six meadows from Spanish (5) and French (1) Mediterranean coasts through personal communications from other authors. The resulting flowering (and non-flowering) citations, sources and estimates of flowering intensity from particular observations are shown in Appendix (Table 10), available as electronic supplementary material.

Data analysis

The minimum number of shoots examined from reconstructive analysis to retain a positive or negative flowering citation as reliable for any 1 year, has been arbitrarily set at 20 shoots, equivalent to a detection limit of 0.05 inflorescences $shoot^{-1}$.

The annual flowering prevalence (FP, the fraction of meadows flowering at any 1 year) for the Western

Table 2 Published time series of *Posidonia oceanica* flowering in the Western Mediterranean, indicating the type of data extracted for the geographic analysis

Reference	Localities	Series	Type	Data	Code
Bussotti and Guidetti (1996)	Noli (NW Italy)	1985–1994	Reconstructive	FF, FI, Pf	II
Buia and Mazzella (1991)	La Nave, San Pancrazio, Lacco Ameno[a] (Ischia, SW Italy)	1979–1985	Direct observation	FF, FI	III
Sánchez-Lizaso and Ruiz-Fernández (1993)	Tabarca Island, Aguilas (E Spain)	1977–1989	Reconstructive	FF, FI, Pf	IV
Pergent et al. (1989)Pergent and Pergent-Martini (1988)	Kerkenah Islands (four localities, Tunisia), Baie d'Elbu, Galeria (Corsica Island, France), Banyuls-Sur-Mer (two localities) and Port Cross (France)	1970–1985	Reconstructive	FF, FI, Pf	V
Boudouresque et al. (1986)	Zembra Islands (Tunisia)	1982–1985	Reconstructive	FF, Pf	VI
Semroud (1993)	La Marsa, Tamenfoust (Algeria)	1984–1988	Reconstructive	FF, Pf	VII
Stoppelli and Peirano (1996)	Monterosso	1992–1994	Direct observation	FI	VIII

FF Flowering frequency; *FI* flowering intensity; *Pf* shoot flowering probability
[a]The FF estimate from this locality (0.82) has been considered outstanding and has not been included in the analysis

Mediterranean was estimated both from time series and scattered flowering (and non-flowering) records.

Meadow flowering frequency (FF) was estimated as the fraction of years that a particular meadow has flowered, for meadows in which direct or reconstructive records were available for at least 4 consecutive years. When several series of flowering occurrence were available for the same locality (different stations or depths within less than 1 km distance), a unique FF local value was obtained for global analysis by averaging the FF estimates from the different stations. This strategy was selected in order to minimize the possible effects of the increase in sampling area in these localities with respect to localities with a unique sampling station. Only when shoots sampled within each station were not sufficient to yield long-enough series (minimum 20 shoots year^{-1}, minimum 4 years), a unique series of flowering occurrence was obtained by compounding the shoots sampled in the different stations, and a local FF value was calculated from it.

Meadow flowering intensity for each year was estimated from direct and reconstructive data as the fraction of shoots presenting inflorescences or stalks within a particular year. Meadow FI from reconstructive data was estimated only for years where a minimum of 50 shoots could be examined. Mean annual FI was estimated as the average of positive FI records obtained from different meadows within the same year. Mean local FI was calculated as the average of all positive annual FI recorded within a meadow. For localities with several stations, a mean local FI value was obtained for the global analyses by averaging positive annual flowering intensity estimates obtained from all stations, unless there were not enough shoots available for FI estimation from reconstructive data. In those cases, meadow FI was estimated by compounding shoots from different stations in a unique series.

The shoot flowering probability, Pf, defined as the probability that any one shoot will flower in any 1 year (Gallegos et al. 1992) was estimated in each meadow from reconstructive data, as the fraction of stalks appeared per the total number of shoot annual segments examined in each locality.

The shoot flowering probability for shoots of a particular age was estimated from Spanish reconstructive data as the fraction of flowering shoots in each age class per the total number of shoots that reached or surpassed this age class. We performed correlation and regression analyses between shoot flowering probability and shoot age.

In order to fill the geographic gaps in the analysis of geographic variability in flowering frequency and intensity, additional reconstructive and direct observation data series (19 localities) of flowering in the Western Mediterranean were obtained from published reports (see Table 2, Fig. 1). The detection thresholds for FI and FF calculations as well as integrative rules (several stations in one locality) defined for original data from this study have been equally applied to bibliographic data.

Latitude and longitude of each meadow (from this study or from bibliography) have been recorded in situ, using GPS technology, recorded from literature or indirectly estimated from an Atlas.

The variability in flowering intensity among regions and years was estimated for the 1989–1999 decade (represented in 26 data series), using the (χ^2) replicated goodness of fit test (GENMOD proc. of SAS v. 6.12, SAS Institute Inc.), as the data did not fulfil the assumption of normality of residuals necessary to perform analysis of variance. Region (Western Italy, Balearic Islands and Eastern Iberian coasts, Fig. 1) was included as a fixed factor, year as a within-subject (i.e. repeated measures) fixed factor and locality as a random factor (subject). We used a binomial distribution and logit link function (0: non-flowering shoot, 1: flowering shoot).

The same analysis was applied to test the homogeneity of annual FI between decades 1981–1989 and 1990–1999 in nine meadows where flowering time series extended over both decades. Decade was included as a within-subject (i.e. repeated measures) fixed factor and locality as a random factor (subject). We used a binomial distribution and logit link function (0: non-flowering shoot, 1: flowering shoot). Years were considered as replicates within decades. This analysis was performed to test the existence of decadal differences and to decide if FF, Pf and average FI from different series, which overlapped but did not cover exactly the same years, could be compared directly or if the spatial variability in those variables should be performed only on estimates from the same period. As no significant difference was found between decades in the nine longest time series, we compared FF, shoot flowering probability and average flowering intensity (of flowering years) estimated from the whole data series.

Spatial variability of FF, Pf and average FI was analysed among and within the regions (Western Italy, Balearic Islands, Eastern Iberian coasts, France and Maghreb), using Kruskal-Wallis non-parametric test. Variability of these parameters among and within regions was estimated using the maximum likelihood method (Variance components procedure in Generalized Linear Models of STATISTICA 6.0^{TM}). The relationship of meadow FF, Pf, mean FI (of positive FI annual values) and FI in 2003 (when flowering was prevalent in the regions studied) with meadow latitude and longitude was examined using correlation and regression analyses. FF, Pf and mean FI of series (not grouped in localities) were directly used to explore possible relationships with depth and shoot density, also through correlation and regression analyses.

Results

Temporal variability

The shoots collected and direct observations allowed us to obtain 150 new records of flowerings and 367 of

non-flowering, spanning from 1977 to 2004, along the Western Mediterranean (Table 1 and Appendix tables).

The time series of annual FI showed synchronous flowering in distant meadows across the Western Mediterranean in years 1992–1994 and in 2003 (Table 1), when the highest FI values were recorded. FI in the decade 1989–1999 showed large and significant variability among years ($P < 0.001$) and regions ($P < 0.001$).

Flowering was most prevalent in 1982, 1994, 2001 and 2003 (Fig. 2a). The annual inter-meadow average FI also showed high temporal variability, with maxima in 1993 and 2003 (Fig. 2b, Table 3). FI and FP were not significantly correlated after removing the outstanding values of year 2003 ($P = 0.125$; Fig. 2c). No significant monotonous trends in FP or mean annual FI were detected over time, although both FP and mean FI were maximal in the year 2003. Moreover, annual FI did not differ significantly ($P = 0.34$) between the decades of 1980–1989 and 1990–1999 in the nine temporal series encompassing the entire period.

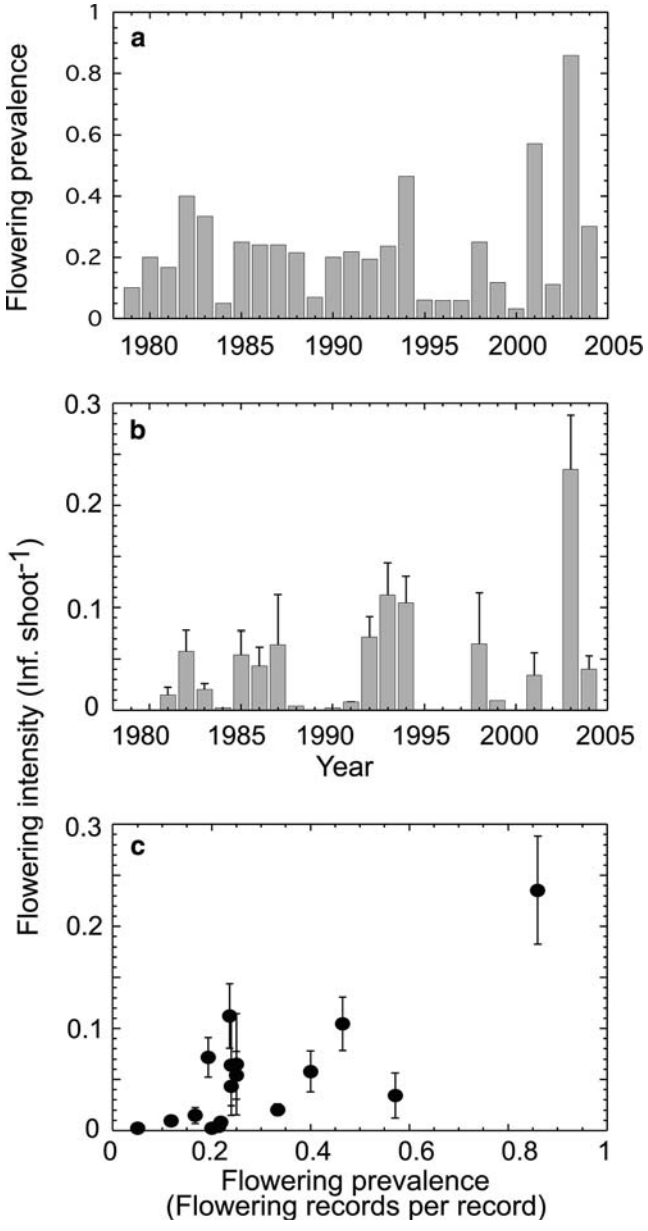

Fig. 2 Time series of **a** *Posidonia oceanica* flowering prevalence (FP annual fraction of flowering meadows per total meadows studied) and **b** the average annual flowering intensity (FI number of inflorescences per shoot) in the Western Mediterranean. **c** Flowering intensity with respect to flowering prevalence. Correlation ($R^2 = 0.56$; $P < 0.001$) is only significant with the values of 2003 (without 2003: $R^2 = 0.1$; $P = 0.13$)

Meadow flowering frequency

The FF in the 54 meadows, where such data were available (40 from this work plus 14 out of the 19 localities from literature), showed significant heterogeneity among regions (39.2% of the variance), although most of the variability was due to the differences between localities within the regions (60.8% of the variance). No flowering was detected in almost half of the meadows, while flowering frequency was distributed normally in the rest (Fig. 3a).

The mean global FF was estimated at 0.17 ± 0.02 (SE, Table 3), and FF differed significantly ($P < 0.01$) among regions (Italy, Balearic Islands, Eastern Iberia, France and Maghreb). FF significantly and positively correlated with latitude ($R^2 = 0.17$; $P < 0.002$; Fig. 4a) across the Western Mediterranean. The strength of the correlation increased when the meadows were grouped by bins of 3° latitude ($R^2 = 0.78$; $P > 0.06$). Meadow FF also increased significantly towards the East, both when examining individual meadows ($R^2 = 0.35$; $P < 2{\cdot}10^{-6}$; Fig. 4b) and meadows grouped by bins of 3° longitude ($R^2 = 0.84$; $P < 0.007$). FF along the Spanish coast was significantly higher in the Balearic meadows than in the meadows along the Eastern Iberian Coasts (Kruskal-Wallis test; $P < 0.03$, Table 3).

Within two meadows in the Cabrera Island, Sta. María and Es Castel, for which several sampling stations were available at increasing depths, all the variability in flowering frequency was significantly correlated with depth ($P < 0.04$) and was independent of shoot density (Fig. 5). But no significant correlations were found between FF and depth or FF and shoot density when adding the rest of series of the Western Mediterranean ($P > 0.5$), suggesting that the correlation with depth observed may help to explain FF variability within meadows, but not across the region.

Flowering intensity

When meadows flowered, the mean FI in the Western Mediterranean (only European coasts) was 0.11 ± 0.02 inflorescence shoot^{-1}. Nevertheless, FI differed greatly among the regions for a given year. In the Balearic Islands, flowering in 2003 was outstanding (on an average 0.37 ± 0.12 inflorescence shoot^{-1}), and more

Table 3 Average (±SE) meadow flowering frequency (FF, flowering years per year), flowering intensity (inflorescences Shoot^{-1}, calculated from meadows FI means), maximum and minimum of annual FI means, and average shoot flowering probability (Pf, inflorescence. shoot^{-1} year^{-1}) of *Posidonia oceanica* in different regions of the Western Mediterranean

Region	Time span	Range (°N; °E)	FF ± (SE) $n_{meadows}$	FI ± (SE) $n_{meadows}$	Annual FI minimum (year)	Annual FI maximum (year)	Pf $n_{meadows}$	Source
Italy	1985–2003	40.70/44.39 8.34/ 13.94	0.43 ± 0.08 (n_m = 7)	0.08 ± 0.02 (n_m = 9)	0.002 (1984)	0.271 (2003)	0.0180 ± 0.082 (n_m = 4)	I–III, VIII
France (with Corsica)	1970–1984	42.43/43.01 3.93/8.67	0.24 ± 0.09 (n_m = 5)	0.04 ± 0.01 (n_m = 3)	0.015 ± 0.005 (1982)	0.101 ± 0.099 (1985)	0.0133 ± 0.0058 (n_m = 5)	V, VII
Balearic Islands	1972–2004	38.72/39.90 1.40/3.28	0.14 ± 0.03 (n_m = 19)	0.06 ± 0.02 (n_m = 7)	0.002 (1997)	0.340 ± 0.041 (2003)	0.0035 ± 0.0011 (n_m = 19)	I
East Iberian Peninsula	1975–2004	36.41 42.49 −2.74/2.98	0.08 ± 0.03 (n_m = 19)	0.03 ± 0.02 (n_m = 5)	0.01 ± 0.01 (1988)	0.13 ± 0.13 (1989)	0.0031 ± 0.0017 (n_m = 19)	I, IV
Maghreb	1978–1988	34.83/37.13 3.26/11.25	0.20 ± 0.10 (n_m = 5)	–	–	–	0.0143 ± 0.0121 (n_m = 6)	V–VII
Western Mediterranean	1972–2004	34.83/44.39 −2.74/13.94	0.17 ± 0.02 (n_m = 54)	0.11 ± 0.02 (n_m = 48)	0.003 ± 0.001 (1984)	0.222 ± 0.043 (2003)	0.0066 ± 0.0017 (n_m = 53)	I–VIII

Data source code I = this work, II–VIII = references listed in Table 2. Time span column indicates the maximum time span encompassed by the time series in each region (minimum of 20 shoots). Number of meadows from which each mean is calculated is indicated within parenthesis (n_m)

than 20 times higher (Kruskal-Wallis: $P < 0.001$) than in the coasts of Murcia in the same year (0.02 ± 0.01 inflorescence Shoot^{-1}), while the only FI value available for Italy in 2003 (Antignano: 0.27 ± 0.06 inflorescence Shoot^{-1}) was comparable to those observed in the Balearic Islands. In autumn 2003, 64.3% of the heterogeneity in FI was associated with differences between the Balearic Islands and the Eastern Iberian coasts, while differences among meadows within a region and patchiness within a meadow accounted for 18.2 and 17.4% of the variability in FI, respectively.

Flowering intensity in 1994 was on an average six times higher in Italian meadows (0.107 ± 0.027 inflorescence shoot^{-1}) than in Spanish meadows (0.018 ± 0.002 inflorescence shoot^{-1}). An intensive flowering event was observed in 2004 in the meadows of Murcia, where 20 out of 35 meadows visited had flowered (FI = 0.05 ± 0.01 inflorescence shoot^{-1}, J. M. Ruiz, unpublished data) while in the Balearic Islands only two single inflorescences, in two meadows out of 15 surveyed, were found. Despite those annual differences among regions, all the heterogeneity in mean local FI occurred among localities and no significant differences among the regions were found (Table 3; $P = 0.17$). The variability in mean local FI did not depend on latitude or longitude ($P > 0.05$, $N = 24$).

Flowering intensity in 2003 decreased slightly with depth in Murcia ($R^2 = 0.08$; $P < 0.05$; Fig. 6b) and in the Balearic Islands ($R^2 = 0.21$; $P < 0.05$; Fig. 6c). FI in 2003 in Murcia was also significantly but weakly correlated with meadow shoot density ($R^2 = 0.1$; $P < 0.03$). But this correlation could be spurious, derived from the negative correlation of shoot density with depth ($R^2 = 0.14$; $P < 0.04$). Moreover, FI in 2003 was independent of shoot density in the Balearic Islands (where shoot density also decreased with depth: $R^2 = 0.46$; $P < 0.008$). In Magalluf, FI was found to be independent of shoot density ($P > 0.05$) in an intensive survey at constant depth (7 m) in autumn 2003.

The variability in the averages of FI series was also negatively correlated with meadow depth ($R^2 = 0.14$; $P < 0.04$, Fig. 6a).

Flowering probability and shoot age

Only 2.4% of the shoots examined had flowered at least once. The flowering probability per shoot and per year (Pf) was quite low (0.007 ± 0.002 (SE) inflorescence shoot^{-1} year^{-1}, Table 3), ranging between 0 and 0.068 across the Western Mediterranean, with an exponentially decreasing frequency distribution (Fig. 3b). Pf showed significant heterogeneity among regions (14%, $P < 0.001$, 5 regions, Table 3), although most heterogeneity occurred among localities within regions (86%). Pf was not correlated with latitude, but increased towards the East (0.18; $P < 0.001$). There was also a very slight, although significant negative correlation between Pf and depth across sites and stations ($P < 0.001$).

Within the Spanish samples, the distribution of shoots that reached or surpassed a certain age decreased exponentially with shoot age (Fig. 7a). The frequency distribution of shoot ages at flowering also seemed to decrease with age, although there was a peak at the 9 years-age class (Fig. 7b). Despite of this decrease and of this particular peak, the shoot flowering probability increased exponentially with shoot age (Fig. 7c), as described by the fitted regression Eq. 1 ($R^2 = 0.78$; $P < 10^{-6}$):

$$\ln(\text{Pfa}) = 1.36 \cdot \ln(a) - 8.94 \quad (1)$$

where *"a"* represents the shoot age, expressed in years and "Pfa" represents the shoot flowering probability at age *"a"*.

Discussion

The described results support the notion of a high inter-annual flowering variability in *P. oceanica* meadows along the Western Mediterranean (Giraud 1977; Pergent et al. 1989; Balestri 2004). In years with high flowering prevalence (e.g. 2003), inflorescences can be found, on an average in four out of the five meadows visited in this basin, while in other years only 3% of meadows would bear inflorescences. Years with widespread flowering along the Western Mediterranean, as observed in 1994 and 2003, coincide with peaks of meadow flowering intensity. In particular, the flowering prevalence and flowering intensities registered in 2003 are the highest ever reported in the Mediterranean ($FP_{2003} = 0.86$, $FI_{2003} = 0.45 \pm 0.04$ (SE) inflorescences shoot^{-1} in Magalluf Bay, Mallorca). The values observed were twice as high as those in the year with the second highest annual mean FI, observed in 1993, and four times above the global mean FI (0.11 ± 0.02 inflorescences shoot^{-1}) of flowering meadows. This outstanding flowering occurred following the hottest summer registered in Europe over the past 500 years (Luterbacher et al. 2004). This year extensive flowering was also detected in some meadows of the Eastern Mediterranean, along the Ionian Sea (M. Salomidi, personal communication) and in the Cretan coast (O. Invers, personal communication). As reported by several authors (Stoppelli and Peirano 1996; Balestri and Vallerini 2003), the high flowering prevalence of 1993 and 1994 also coincided with summer temperatures above the normal values. The observations of simultaneous flowering events across and within the regions indicate that large-scale factors (e.g. seawater temperature, Giraud 1977; Boyer et al. 1996) could play an important role in the induction of *P. oceanica* flowering. Synchronous widespread flowerings have been linked to seawater temperature variability in some Australian (Inglis and Smith 1998) and Philippine seagrasses (Rollón et al.

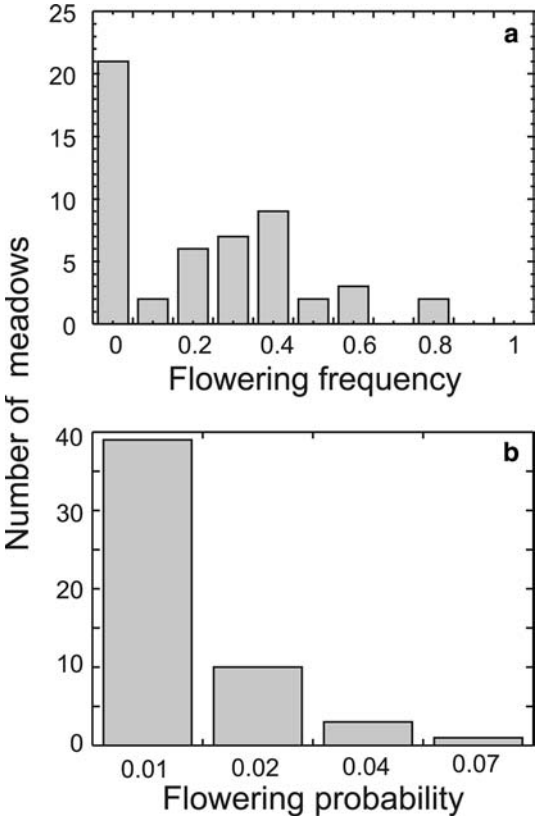

Fig. 3 Frequency distribution of *Posidonia oceanica* **a** flowering frequency (*FF* flowering years per year) and **b** flowering probability (Pf inflorescences shoot^{-1} year^{-1}) in the W Mediterranean. Classes are defined by their upper limits

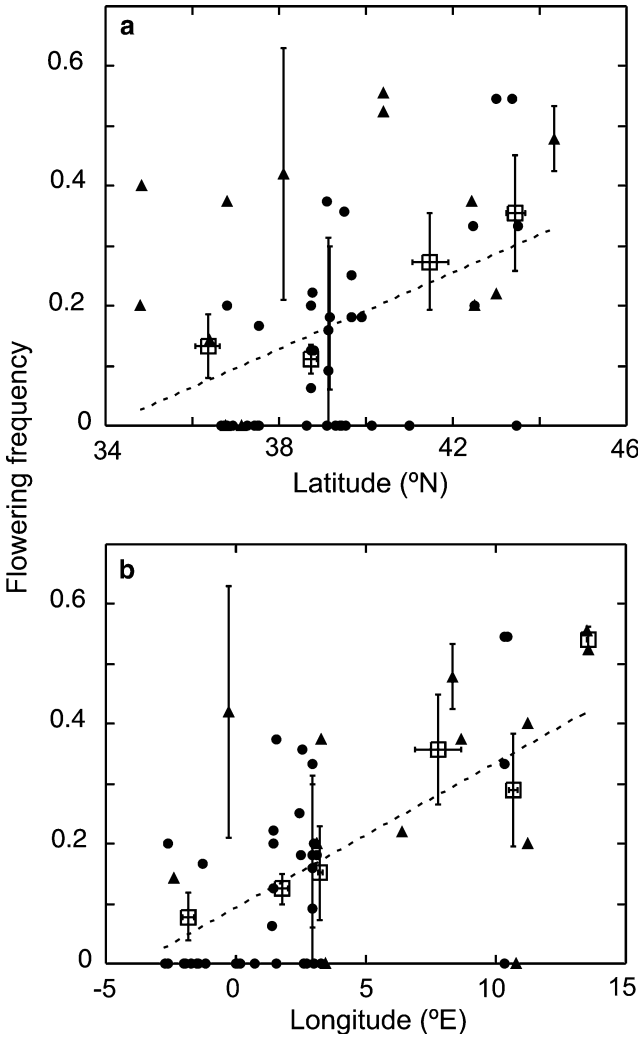

Fig. 4 The relationship between *Posidonia oceanica* flowering frequency and: **a** latitude (°N; $R^2 = 0.17$; $P < 0.002$; for average data grouped by 3° latitude bins: $FF = 0.03 \pm 0.01(SE) \times Lat$ (°N) – $1.16 \pm (0.40SE)$; $R^2 = 0.78$; $P > 0.06$). **b** Longitude (°E; $R^2 = 0.35$; $P < 2{\cdot}10^{-6}$; by 3° longitude bins: $FF = 0.03 \pm (0.01E) \times Long$ (°E) + $0.09 \pm (0.04E)$; $R^2 = 0.84$; $P < 0.007$). *Solid circles* represent local values from this study, *solid triangles* data obtained from literature. *Open squares* correspond to average values of data grouped by 3° bins and *horizontal* and *vertical bars* on the binned data indicate standard errors for the geographic position and FF, respectively. The *dashed line* represents the fitted regression line for the data ungrouped

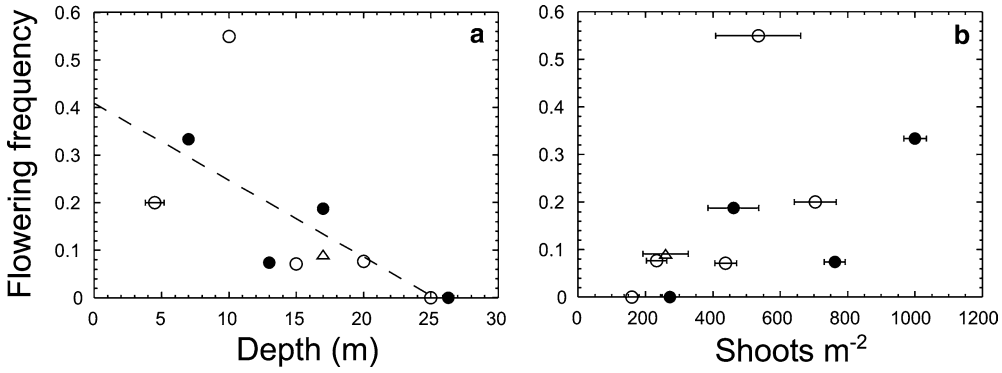

Fig. 5 Relationships between **a** FF (flowering years per year recorded) and depth (m) in the stations of Cabrera (FF = −0.017 (±0.007) × depth (m) + 0.418 (±0.111); $R^2 = 0.37$; $P < 0.04$): *solid circles* correspond to stations in Sta. Maria Bay, *open circles* stations from Es Castel, situated at the Mouth of Es Port Bay, the *open triangle* corresponds to the station of Sa Paret, in the centre of Es Port Bay. *Horizontal bars* correspond to the depth range of stations, the *dashed line* corresponds to the fitted linear regression; **b** FF and shoot density ($R^2 = 0.13$; $P = 0.133$). *Horizontal bars* correspond to standard errors of shoot density

2003). In addition to years of consistent, abundant flowering throughout the Western Mediterranean, there were years of relatively high flowering prevalence in particular regions, such as in autumn 1993 in the Ligurian Sea (Italy), 2001 in the Balearic islands (Spain), or 2004 in the coast of Murcia (Spain).

More evidence of large-scale control of flowering is the presence of significant regional differences in the meadow FF and shoot flowering probability, as well as FI in particular years. Similarly, Inglis and Smith (1998) reported that the highest variability in flowering intensity of *Posidonia australis* occurred both at the intra-meadow scale of tens of metres and at the regional scale (hundreds of kilometres).

The regional variability in the meadow FF and flowering probability appears to follow a geographic pattern, as meadows located towards the northeast of the Western Mediterranean basin seem to flower more frequently. Meadow FF apparently increases towards the north, while shoot flowering probability is not correlated with latitude. Such results are not consistent with earlier reports of more frequent *P. oceanica* flowering in the Southern Mediterranean coast (Molinier and Picard 1953; Semroud 1993), at least in the Western Mediterranean. These authors hypothesized that warmer South Mediterranean waters could be a better environment for *P. oceanica* meadow development and flowering. The results of the present study suggest that the hypothetical link between *P. oceanica* flowering and temperature may involve temperature variations as triggers of flowering, rather than absolute values. The latitudinal cline of the flowering season, slightly delayed towards the north as reported by Sandmeier et al. (1999), reinforce this idea. The reported delay in flowering by 1 month in the deep meadows compared to shallow ones, parallel to a delay in maximum temperature (Buia and Mazzella 1991) also supports the notion of temperature changes as triggers of flowering.

The significant increase in meadow FF and Pf towards the eastern range of the Western Mediterranean basin coincides with a greater genetic diversity of *P. oceanica* meadows as observed in the Central Mediterranean (Procaccini et al. 2000; Arnaud-Haond et al, submitted). The level of genetic diversity among aquatic species has been linked to the importance of sexual reproduction in their life histories (Barret et al. 1993; Eckert and Barrett 1993). Sexual reproduction is expected and has been shown (Gavino et al. 2000) to increase genetic diversity of populations. It could be the case for *P. oceanica* meadows if higher FF implies higher sexual reproduction. Conversely, low genetic diversity can potentially reduce flower production and seed set in clonal aquatic plants (Dorken and Eckert 2001). Both possibilities are not mutually exclusive.

Nevertheless, latitude and longitude are not linked to the meadow FI and only account for a modest fraction of the variance in FF and probability. Most of the variability of FF and Pf and all of the variability in mean local FI occur among localities within the regions. Thus, local factors like nutrient availability (Gobert et al. 2001) should also play an important role in flower induction and abundance. The local factors explored in this study (shoot density and depth) do not appear to influence meadow FF. Yet, the fraction of inflorescences per shoot seems to decrease with depth, but is independent of shoot density at a given depth. Hence, the lack of relationship between FI and shoot density previously reported for two Italian meadows by Balestri (2004) appears to be a general pattern in the Western Mediterranean.

Light availability and mean and maximum water temperature decline with depth, inducing important adaptations of *P. oceanica* meadows (Pirc 1984). The reduced *P. oceanica* FI and Pf with depth suggest a role for these variables, similar to their demonstrated role in flowering induction in many terrestrial species (e.g. Heide 1994; Roussopoulos et al. 1998). If a seasonal change in water temperature is the signal inducing *P. oceanica* inflorescences development, as suggested by Buia and Mazzella (1991), then the lower temperature amplitude

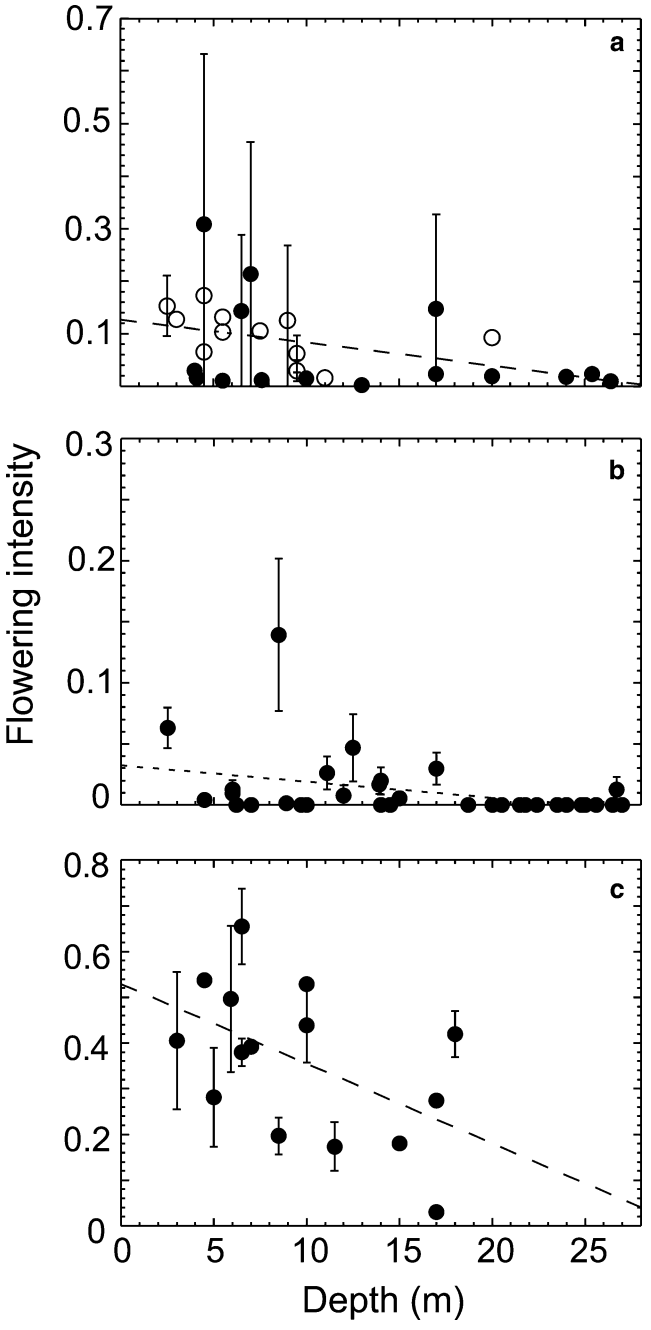

Fig. 6 Relationships between depth (m) and **a** the average FI (mean series FI, inflorescences per shoot, excluding no flowering years; (FI = −0.004 (±0.002) × Depth (m) + 0.127 (±0.024); $R^2 = 0.14$; $P < 0.04$), **b** the FI in 2003 in meadows from Murcia (Spain); (FI = −0.0011 (±0.0005) × Depth (m) + 0.028 (±0.009); $R^2 = 0.08$; $P \leq 0.05$), **c** The FI in 2003 in meadows in the Balearic Islands (Spain); (FI = −0.018 (±0.008) × Depth (m) + 0.53 (±0.09); $R^2 = 0.21$; $P \leq 0.05$). *Dashed lines* represent the fitted linear regressions

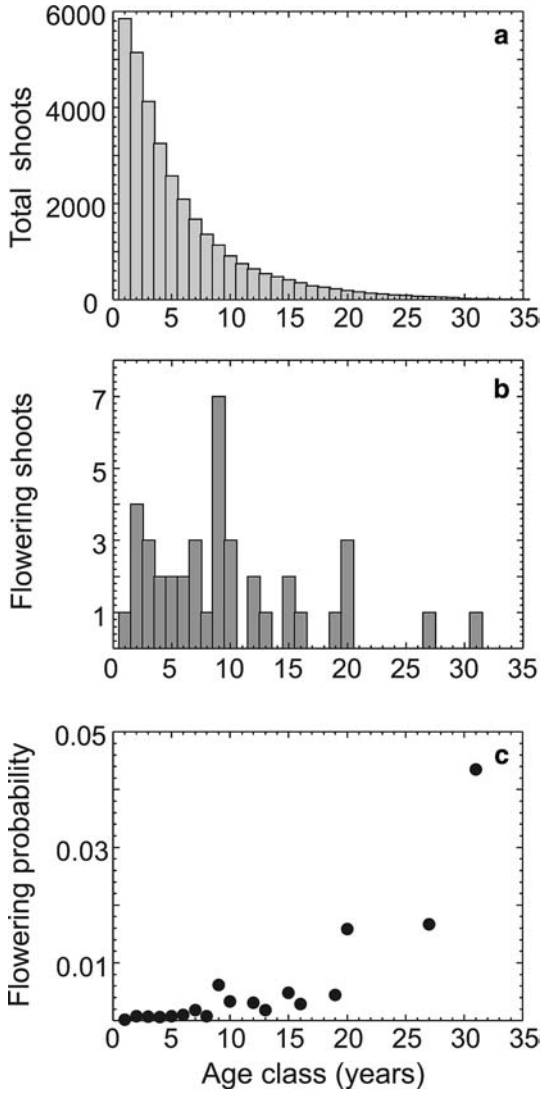

Fig. 7 **a** Frequency distribution of shoots that reached or surpassed a certain age (in years), **b** Frequency distribution of shoot flowering ages. **c** The relationship between the flowering probability (*Pf*) of *Posidonia oceanica* shoots and shoot age

in deep meadows would represent a weaker trigger of flowering, which could be reflected on a reduced FI.

The shoot flowering probability was extremely low, and the fraction of shoots examined that flowered at least once during their lives (less than 2.4%) was lower than in most seagrasses for which it has been reported, as *Thalassia testudinum* (14%; Gallegos et al. 1992, *T. hemprichii* (17%), *Cymodocea rotundata* (5.6%) and *Enhalus acoroides* (97.7%) (Duarte et al. 1997), despite the long shoot lifespan of this species, which can reach 50 years, as reported by Marbà et al. (1996b).

We observed the shoot flowering probability to increase exponentially with shoot age. This observation is in contrast with the reported pattern of flowering probability reaching a maximum at 6-year-old shoots in two Ligurian *P. oceanica* meadows (Balestri and Vallerini 2003). The latter observation may be anomalous, as the shoots sampled in that work were relatively young (maximum 16 years), compared to the lifespan of *P. oceanica* shoots in most meadows (Marbà et al. 1996b). In addition, the frequency distribution of shoots that reached or surpassed a certain

age was constant in age classes 1–6 years old, instead of exponentially declining, as observed in most meadows (Duarte et al. 1994).

An increase in the shoot flowering probability with an increasing shoot age has been reported for other seagrass species (Gallegos 1992; Vantussenbroek 1994; Duarte et al. 1997). As in many terrestrial plants, the increase in flowering probability with plant age or size may be related to the need of a certain amount of reserves accumulated, in order to provide or compensate for reproductive costs.

In summary, the results presented here provide an evidence of clear temporal and regional patterns in flowering of *P. oceanica* meadows in the Western Mediterranean. FF and flowering probability of the meadows showed a tendency to increase towards the eastern and/or northern regions of the Western Mediterranean. Extensive flowering events were relatively synchronous across the regions, with the most intense flowering event yet reported occurring in 2003, the warmest year in the past centuries across Europe. There was a high variance in the FI and frequency within and among meadows, with a tendency towards a reduced FI with depth and patchiness possibly related to the age structure of the meadow, as the probability to flower increased exponentially with increasing shoot age. The patterns in *P. oceanica* flowering, reported here suggest that temperature changes or other large-scale factors co-varying with latitude and longitude may act as important drivers, explaining a significant part of both spatial and temporal heterogeneity in meadow FF and shoot flowering probability in the Western Mediterranean, although the high flowering variability among localities point to local factors as exerting a strong control on flowering.

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Appendix

Table 4, Table 5, Table 6, Table 7, Table 8, Table 9, Table 10

Table 4 Flowering temporal series from Italy

Ligurian Sea	Rosignano	Cecina	Calafuria	Antignano
Date	07-09-99	08-09-99	07-09-99	-
Latitude °N	43°24	43°19	43°28′	43°28
Longitude °E	10°58	10°31	10°20	10°19
Depth (m)	9.5	9.5	9.5	2.5
Shoots m^{-2}	535	519	525	631
SE	20.7	11.6	12.9	25.5
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
2004				*0*
2003				*0.27 ± 0.31*
2002				*0*
2001				*0*
2000				*0*
1999	0/150	0/150	0/150	*0*
1998	0/150	0/150	0/150	*0*
1997	9/150	2/150	0/150	*0*
1996	2/150	0/150	0/148	*0*
1995	5/150	1/150	0/139	*0*
1994	38/150	2/150	0/104	*0.198*
1993	4/149	18/150	0/79	*0.079*
1992	4/144	0/120	0/66	*0.063*
1991	0/144	1/96	0/54	
1990	0/134	1/74	0/41	
1989	2/116	0/40	0/27	
1988	0/81	0/24	0/13	
1987	0/81	0/11	0/9	
1986	0/55	0/5	0/3	
1985	0/22	0/1	0/1	
1984	0/10		0/1	
1983	0/4			

Records obtained from direct observations are in italics*X* Inflorescence stalks; *Y* shoots examined within this year

Table 5 Flowering temporal reconstructive series from Mallorca island

Mallorca	C. St. Jordi	Banyalbufar 1	Banyalbufar 2	Illetas-Calviá	Magalluf	Pollença	P. Colom	C. Enderrocat
Date	28-06-01	03-02-02	05-02-02	06-08-01	05-10-00	10-10-01	05-07-01	10-07-01
Latitude °N	39°18.664′	39°40.651′	39°39.692′	39°32.104′	39°30.25′	39°53.792′	39°25.052′	39°27.029′
Longitude °E	2°59.960′	2°29.342′	2°27.995′	2°35.562′	2°32.59′	3°05.523′	3°16.183′	2°44.569′
Depth (m)	4	26.4	25.4	9	7	4.1	6	7
Shoots m^{-2}	980	397.9	364.6	363	562.67	783.7	414.67	535
SE	87	102.4	81.8	114	54.76	111.3	80.74	11
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
2004					*0*			
2003					*0.66*			
2002					*0*			
2001		0/147	0/209		*0.01*	0/162		
2000	0/243	0/140	1/200	0/161	0/112	0/155	0/99	0/253
1999	0/200	1/121	6/190	0/139	2/100	0/130	0/75	0/193
1998	0/159	1/89	5/150	0/102	1/95	1/102	0/56	0/153
1997	0/136	0/68	0/101	0/69	0/94	0/85	0/37	0/108
1996	0/123	0/59	0/80	0/53	0/86	0/69	0/23	0/84
1995	0/109	0/50	0/65	0/42	0/77	0/58	0/15	0/63
1994	0/93	0/43	0/56	0/29	1/68	1/47	0/11	0/38
1993	0/86	0/34	0/53	0/22	0/61	0/40	0/8	0/24
1992	0/80	0/26	0/45	0/16	0/54	0/30	0/8	0/18
1991	0/79	0/21	0/38	0/7	0/40	0/21	0/7	0/13
1990	0/72	0/15	2/35	0/2	0/29	0/12	0/6	0/7
1989	0/62	0/9	0/33	0/2	0/19	0/8	0/6	0/5
1988	0/53	0/5	0/30		0/16	0/3	0/4	0/4
1987	0/47	1/5	0/24		0/8		0/4	0/4
1986	0/40	0/5	0/20		0/6		0/3	0/3
1985	0/31	0/4	0/16		0/3		0/3	0/2
1984	0/25	0/4	0/15		0/3		0/3	0/1
1983	0/23	0/2	0/10		0/3		0/3	0/1
1982	0/20		0/9		0/3		0/3	0/1
1981	0/17		0/7		0/2		0/1	0/1
1980	0/15		0/4		0/1		0/1	0/1
1979	0/10		0/4					
1978	0/8							
1977	0/7							
1976	0/7							
1975	0/6							
1974	0/5							
1973	0/5							
1972	0/5							
1971	0/5							
1970	0/5							
1969	0/3							
1968	0/2							
1967	0/2							
1966	0/2							
1965	0/1							
1964	0/1							
1963								
1962								
1961								
1960								
1959								
1958								
1957								

Records obtained from direct observations are in italics
X Inflorescence stalks; *Y* shoots examined within this year

Table 6 Flowering temporal reconstructive series from Cabrera Island

Cabrera	Es Port	S. María 1	S. María 2	S. María 3	S. María 4	Es Castel 1	Es Castel 2	Es Castel 3	Es Castel 4	Es Castel 5
Date	20-11-00	07-02-01	17-10-00	05-02-01	07-02-01	16-10-00	26-10-00	21-11-00	22-11-00	24-11-00
Latitude °N	39° 8.81′	39° 9.00′	39° 9.07′	39° 9.156′	39° 9.23′	39° 9.16′	39° 9.16′	39° 9.16′	39° 9.177′	39° 9.177′
Longitude °E	2° 55.86′	2° 56.96′	2° 56.92′	2° 56.891′	2° 56.92′	2° 55.83′	2° 55.83′	2° 55.80′	2° 55.766′	2° 55.766′
Depth (m)	17	7	13	17	26.3	4.5	10	15	20	25
Shoots m^{-2}	259.33	1000	762	461	272	704	535	438	233	159
SE	67.23	33.9	31.2	75	28	62.14	126	32	30	22
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
2004		0/69				0/67				
2003	*0.03*	27/69		14/53		36/67				
2002	*0*	0/60		0/48		0/63				
2001	*0*	*0.04*	*0.002*			*0.08*				
2000	0/102	0/83	0/88	0/108	0/71	0/102	0/100	0/155	0/104	0/119
1999	0/102	0/70	0/78	0/106	0/70	0/88	0/97	0/152	0/100	0/119
1998	0/97	0/53	0/67	0/99	0/67	0/64	0/90	0/137	0/96	0/111
1997	0/93	0/40	0/58	0/86	0/60	0/53	1/85	0/118	0/89	0/103
1996	0/80	0/28	0/52	0/62	0/56	0/39	0/80	0/90	0/81	0/95
1995	0/69	0/25	0/47	0/56	0/50	0/25	0/70	0/74	0/75	0/87
1994	1/63	1/22	0/47	1/51	0/42	0/18	1/54	0/58	0/67	0/69
1993	0/60	0/22	0/45	0/46	0/35	0/16	1/38	0/49	0/61	0/53
1992	0/56	1/22	0/42	0/40	0/26	0/15	2/36	0/41	0/59	0/44
1991	0/53	1/22	0/39	1/35	0/18	0/12	2/36	0/31	1/53	0/36
1990	0/50	0/21	0/35	0/29	0/13	0/11	0/34	0/26	0/53	0/29
1989	0/50	0/19	0/33	0/24	0/10	0/11	0/32	0/23	0/52	0/26
1988	0/50	0/18	0/33	0/20	0/8	0/9	0/31	0/20	0/51	0/23
1987	0/48	1/18	0/33	0/14	0/8	0/9	1/28	0/18	0/50	0/17
1986	0/39	0/16	0/32	0/9	0/6	0/8	1/28	0/14	0/48	0/13
1985	0/37	0/16	0/31	0/5	0/4	0/8	1/23	0/11	0/46	0/9
1984	0/31	1/14	0/26	0/5		0/7	1/21	0/7	0/45	0/6
1983	0/23	0/14	0/25	0/5		0/6	1/20	0/4	0/41	0/5
1982	0/20	0/14	0/24	0/5		0/5	0/17	0/3	0/39	0/4
1981	0/19	0/13	0/24	0/3		0/4	0/13	0/3	0/33	0/4

Table 6 (Contd.)

Cabrera	Es Port	S. María 1	S. María 2	S. María 3	S. María 4	Es Castel 1	Es Castel 2	Es Castel 3	Es Castel 4	Es Castel 5
Date	20-11-00	07-02-01	17-10-00	05-02-01	07-02-01	16-10-00	26-10-00	21-11-00	22-11-00	24-11-00
Latitude °N	39° 8.81′	39° 9.00′	39° 9.07′	39° 9.156′	39° 9.23′	39° 9.16′	39° 9.16′	39° 9.16′	39° 9.177′	39° 9.177′
Longitude °E	2° 55.86′	2° 56.96′	2° 56.92′	2° 56.891′	2° 56.92′	2° 55.83′	2° 55.83′	2° 55.80′	2° 55.766′	2° 55.766′
Depth (m)	17	7	13	17	26.3	4.5	10	15	20	25
Shoots m^{-2}	259.33	1000	762	461	272	704	535	438	233	159
SE	67.23	33.9	31.2	75	28	62.14	126	32	30	22
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
1980	0/17	0/13	0/24	0/2		0/4	0/11	0/2	0/28	0/3
1979	0/17	0/11	0/23	0/2		0/3	0/8	0/2	0/26	0/3
1978	0/15	2/11	0/22	0/2		0/2	0/7	0/2	0/24	0/3
1977	0/14	0/10	0/20	0/2		0/1	1/7	0/2	0/22	0/3
1976	0/12	0/9	0/19	0/1		0/1	0/7	0/2	0/21	0/2
1975	0/12	0/8	0/15	0/1		0/1	0/5	0/2	0/19	0/2
1974	0/8	0/6	0/13				0/4	0/2	0/19	0/2
1973	0/5	0/5	0/11				0/2	0/2	0/18	0/2
1972	0/5	0/4	0/8				0/2	0/2	0/16	0/2
1971	0/4	0/2	0/8				0/2	0/2	0/13	0/2
1970	0/4	0/1	0/7				0/2	0/2	0/12	0/2
1969	0/1	0/1	0/6				0/2	0/2	0/8	0/1
1968		0/1	0/5				0/2	0/2	0/7	0/1
1967		0/1	0/4				0/2	0/2	0/6	0/1
1966		0/1	0/2				0/2	0/1	0/6	
1965							0/2		0/4	
1964							0/2		0/4	
1963							0/2		0/3	
1962							0/2		0/2	
1961							0/2			
1960							0/1			
1959							0/1			
1958							0/1			
1957							0/1			

X Inflorescence stalks; *Y* shoots examined within this year

Table 7 Flowering temporal reconstructive series from Ibiza and Formentera islands (Pitiusas)

Pitiusas	C. De s'Oli	C. Torreta	S'espalmador	Es Pujols	Illetes-Form	I. des Porcs	Sa Talaia I	Sa Talaia 2
Date	15-1-2001	16-1-2001	17-1-2001	24-4-2001	26-4-2001	26-4-2001	16-2-2002	17-2-2002
Latitude °N	38°43.49′	38°43.454′	38°46.43′	38°43.740′	38°45.365′	38°47.924′	39°05.980′	39°06.121′
Longitude °E	1°24.16′	1°25.179′	1°25.27′	1°27.272′	1°25.828′	1°25.222′	1°33.781′	1°34.598′
Depth (m)	8	8	4	4	6	6	27.1	24
Shoots m^{-2}	402.66	527.31	660.41	745.83	666.67	864.6	447.9	397.9
SE	1.63	97.55	102.2	24.03	14.58	99.4	22.2	27.0
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
2004								
2003	+	+		+	+			
2002								
2001							0/78	0/61
2000	0/110	0/102	0/83	0/200	0/226	0/262	0/78	0/60
1999	0/104	0/94	0/79	0/166	0/188	0/233	0/77	1/56
1998	0/73	1/85	2/67	0/116	0/114	2/194	0/63	0/42
1997	0/57	0/67	0/62	0/82	0/81	0/158	0/44	0/35
1996	0/43	0/56	0/58	0/47	0/57	0/128	0/38	1/26
1995	0/35	0/46	0/53	0/29	0/40	0/97	0/35	0/20
1994	0/34	0/35	0/39	0/22	0/22	0/67	0/31	2/17
1993	0/32	0/27	1/32	0/18	0/13	0/36	0/29	0/17
1992	0/31	0/24	0/21	0/10	0/10	0/17	0/21	0/17
1991	0/31	0/17	0/7	0/9	0/8	0/12	0/14	0/12
1990	0/30	0/12	0/4	0/9	0/4	0/5	0/8	0/8
1989	0/30	0/8	0/4	1/6	0/3	0/3	0/5	0/5
1988	0/25	0/5	0/2	0/5	0/2	0/1	0/2	0/5
1987	0/22	0/5	0/2	0/5		0/1	0/1	0/5
1986	0/21	0/5	0/2	0/5		0/1		0/3
1985	0/16	0/5		0/4				0/2
1984	0/9	0/4		0/4				
1983	0/8	0/4		0/3				
1982	0/5	0/4		0/2				
1981	0/4	0/2		0/2				
1980	0/2	0/1		0/2				
1979				0/2				
1978				0/2				
1977				0/2				

+ Qualitative records obtained by direct observation; *X* inflorescence stalks; *Y* shoots examined within this year

Table 8 Flowering temporal reconstructive series from North-East Iberian peninsula (Spain)

North-East Spain	Jonquet	Port Lligat	St. J. D'Alfama	Torre de la Sal	Campomanes	El Arenal	La Fosa
Date	26-02-92	01-06-92	25-06-92	20-07-01	18-07-01	06-09-01	17-07-01
Latitude °N	42° 29,70′	42° 27,30′	40° 59,10′	40 ° 8.13′	38 °37.54′	38 ° 38.37′	38 ° 38.59′
Longitude °E	2° 58,99′	2° 58,36′	0° 44,01′	0° 10.72′	0° 0.568′	0° 3.06′	0° 4.56′
Depth (m)	shallow	shallow	shallow	9.25	5.3	6	3
Shoots m^{-1}	529	627	977	350	426.67	430.67	1551.21
SE	17	88	63	42.7	25.44	23.13	454.06
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
2000				0/114	0/196	0/161	0/113
1999				0/94	0/152	0/124	0/91
1998				0/75	0/123	0/102	0/68
1997				0/57	0/100	0/82	0/50
1996				0/41	0/79	0/74	0/41
1995				0/27	0/71	0/54	0/34
1994				0/22	0/54	0/35	0/33
1993				0/18	0/36	0/21	0/27
1992				0/13	0/29	0/11	0/25
1991	0/501	2/79	0/210	0/9	0/16	0/4	0/25
1990	1/444	2/72	0/195	0/7	0/4	0/2	0/24
1989	0/334	0/49	0/143	0/6	0/3	0/2	0/23
1988	1/249	0/37	0/97	0/6	0/2		0/22
1987	1/191	0/30	0/70	0/5	0/1		0/19
1986	0/166	0/22	0/49	0/5	0/1		0/17
1985	0/138	0/12	0/36	0/5	0/1		0/16
1984	0/111	0/7	0/26	0/4	0/1		0/15
1983	0/87	0/5	0/18	0/4	0/1		0/15
1982	0/62	0/4	0/12	0/4			0/14
1981	0/53	0/4	0/9	0/2			0/13
1980	0/37	0/2	0/7	0/2			0/11
1979	0/28		0/7				0/11
1978	0/27		0/7				0/9
1977	0/23		0/4				0/5
1976	0/19		0/4				0/4
1975	0/17		0/4				0/2
1974	0/17		0/3				
1973	0/14		0/2				
1972	0/12		0/1				
1971	0/11						
1970	0/11						
1969	0/9						
1968	0/8						
1967	0/5						
1966	0/3						
1965	0/3						
1964	0/3						
1963	0/3						
1962	0/1						
1961							
1960							

X Inflorescence stalks; *Y* shoots examined within this year

Table 9 Flowering temporal reconstructive series from South-East Iberian peninsula (Spain)

South-East Spain	La Azohía	Bolnuevo	Calnegre	Cabo Cope	Villaricos	Aguamarga	Rodalquilar	Aguadulce	Roquetas	Punta Encinas
Date	12-07-92	12-07-92	02-07-92	03-07-92	06-07-92	06-07-92	08-07-92	10-07-92	05-07-92	12-07-92
Latitude °N	37° 32,16′	37° 31,62′	37° 30,96′	37° 26,34′	37° 16,26′	36° 55,92′	36° 48,42′	36° 47,52′	36° 44,58′	36° 40,02′
Longitude °E	−1° 18,12′	−1° 8,46′	−1° 25,56′	−1° 28,38′	−1° 44,34′	−1° 56.76′	−2° 0,14′	−2° 34,86′	−2° 37,80′	−2° 44,58′
Depth (m)	shallow	shallow	shallow	shallow	7	shallow	shallow	shallow	shallow	shallow
Shoots m^{-2}	619	858	652	1008	408	348	966	855	425	-
SE	75	133	37	11	47	91	122	350	59	-
Year	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)	Inflorescence $shoot^{-1}$ (X/Y)
1991	0/121	0/92	0/94	0/68	0/106	0/66	0/93	0/99	0/118	0/81
1990	0/111	0/75	0/85	0/58	0/75	0/59	0/84	1/96	0/107	0/50
1989	0/80	0/58	0/67	0/40	0/46	0/53	0/60	0/81	0/76	0/31
1988	0/52	0/43	0/52	0/32	0/26	0/51	0/49	1/66	0/54	0/17
1987	0/33	0/28	0/46	0/25	0/9	0/44	0/42	0/52	0/41	0/4
1986	0/25	0/20	0/38	0/20	0/2	0/38	0/32	0/43	0/20	0/1
1985	0/18	0/10	0/33	0/20	0/1	0/32	0/22	0/38	0/14	0/1
1984	0/11	0/5	0/28	0/20	0/1	0/24	0/14	0/33	0/12	0/1
1983	0/10	0/4	0/21	0/18	0/1	0/18	0/8	0/30	0/10	
1982	0/10	0/2	0/15	0/16		0/11	0/6	0/23	0/7	
1981	0/8	0/2	0/10	0/15		0/8	0/3	0/16	0/7	
1980	0/8	0/1	0/8	0/14		0/6	0/2	0/14	0/7	
1979	0/7	0/1	0/6	0/14		0/3	0/2	0/11	0/6	
1978	0/7	0/1	0/2	0/12		0/3	0/2	0/10	0/5	
1977	0/7	0/1	0/2	0/10		0/1	0/1	0/7	0/5	
1976	0/5		0/1	0/10		0/1	0/1	1/6	0/5	
1975	0/5		0/1	0/8		0/1	0/1	0/5	0/3	
1974	0/4		0/1	0/3		0/1		0/4	0/3	
1973	0/4		0/1	0/2		0/1		0/2	0/1	
1972	0/3		0/1	0/1		0/1		0/2		
1971	0/3		0/1			0/1		0/2		
1970	0/2		0/1							
1969	0/1									
1968	0/1									
1967	0/1									
1966	0/1									
1965	0/1									
1964	0/1									

X Inflorescence stalks; *Y* shoots examined within this year

Table 10 Particular records obtained from direct observation between 1992 and 2004

Particular Records	Latitude (°N)	Longitude (°E)	Depth (m)					
Balearic Islands				2004	2003 FI ± SE	2002	2001	
S Xoriguer(Menorca)	39.56	3.51	11		+			
Cala Fornells (Me)	40°03,510	4°08,267′	7		+			
Cala Tirant (Me)	40°03,264	4°06,168′	11		+			
Sa Nitja (Me)	40°04,565	4°05,236′	11		+			
Es Talaier (Me)	39.57	3.54	11		+			
Biniancolla (Me)	39°51,845	4°18,471	7		+			
Migjorn (Mallorca)	39° 21.451′	2° 54.095′	< 10				+	
Caló de la Reina (Ma)	39.28	2.43	5	*0*	*0.281 ± 0.108*			
Puig de Ross (Ma)			9	*0*	+			
El Arenal 1 (Ma)	39° 31.478′	2° 41.272′	27				+	
El Arenal 2 (Ma)	39° 29.563′	2° 44.225′	3				+	
Cala Nova (Ma)	39° 32.85	2° 35.995′	10		*0.185 ± 0.032*			
I del Sec (Ma)	39° 28,719′	2°32,490′	18		+			
Cala Figuera (Ma)	39°27,811	2°31,366′	15	+	*0.420 ± 0.050*			
Portals Vells (Ma)	39.29	2.31	3	*0*	*0.400 ± 0.150*			
C. d'en Monjo (Ma)	39.31	2.26	10		*0.439 ± 0.082*			
C. Marmacén (Ma)	39.32	2.23	10		*0.497 ± 0.160*			
Cala Tuent (Ma)	39.5	2.5	12	*0*	+			
La Victoria (Ma)	39.55	3.10	6	*0*	+			
Can Picafort (Ma)	39° 46.298′	3° 9.989′	10				+	
Colonia Sant Pere	39.46	3.20	4		+			
Es Caló (Ma)	39°46.367′	3°20.048′	4	*0*	+			
Cala Matzoc (Ma)	39°45,605	3°24,392	10	+	+			
Cala Lliteras (Ma)	39.43	3.27	10		*0.529 ± 0.110*			
Cala Millor 1 (Ma)	39° 36.394′	3° 24.900′					+	
Cala Millor 2 (Ma)	39° 35.662′	3° 23.257′					+	
Porto Cristo (Ma)	39.32	3.20	5	*0*	+			
Cala Murta (Ma)	39.56	3.06	5	*0*				
Cala d'Or (Ma)	39° 22.164′	3° 13.887′		*0*	*0.381 ± 0.030*			
Es Caragol (Ma)	39.16	3.02					+	
Es Burrí (Cabrera)	39.09	2.58					+	
I. Malvins N (Ibiza)			7		+			
Cap Nono (Ib)	39.02	1.18	13		+			
Cala Salada (Ib)	39.01	1.18	10		+			
Punta Galera (Ib)	39.00	1.18	13		+			
Isla Conejera (Ib)	38.59	1.13	12		+			
Cap Negret (Ib)	38.59	1.17	15		+			
I. Sta Eulalia (Ib)	38° 58,943′	1° 35,014′	15		+			
St. Antonio B. (Ib)	38.58	1.18	3		+			
I. S'Esparto (Ib)	38.57	1.11	7		+			
Cap Blanc (Ib)	38.52	1.14	13		+			
Punta Gavina (Ib)	39.17	1.19	12	*0*	+			
I. des Cargolers (Ib)	38° 49,554′	1° 24,346′	10		+			
Iberian Peninsula				2004	2003 FI ± SE	2002	2001	1998
I. Medas[c]	42.03	3.14			+			+
Cala Ferriola[c]					+			
Cabo de Palos 1	37° 38.132′	0° 41.92′	6		*0.053 ± 0.021*			
Cabo de Palos 1			24		*0 ± 0*			
Cabo de Palos 2	37°37.973′	0° 41.333′	7		*0.005 ± 0.002*			
Cabo de Palos 2			18		*0 ± 0*			
La Manga Sur 1	37° 41.675′	0° 43.845′	9		*0.012 ± 0.006*			
La Manga Sur 1			26		*0.004 ± 0.004*			
La Manga Sur 2	37° 39.508′	0° 42.478′	10		*0*			
La Manga Sur 2			20		*0*			
Isla Grosa	37° 43.575′	0° 42.57′	10		*0.011 ± 0.004*			
Isla Grosa			24		*0*			
La Manga Norte 1	37° 50.173′	0° 45.234′	10		*0.005 ± 0.005*			
La Manga Norte 1			21		*0.002 ± 0.002*			
La Manga Norte 2	37° 48.044′	0° 44.83′	9		*0.033 ± 0.018*			
La Manga Norte 2			22		*0.010 ± 0.005*			
La Azohía	37° 33.254′	−1° 0.102′	9	*0*	*0.022 ± 0.008*			
La Azohía			22	*0.043 ± 0.008*	*0 ± 0*			
Cala Higuera[a]	Almeria				+			
San José[a]	36.45	−2.05				+		
Cabo de Gata[a]	36.44	−2.09					+	

Table 10 (Contd.)

Particular Records	Latitude (°N)	Longitude (°E)	Depth (m)				
Gulf of Lyon (France)				2004	2003	1998	
Plateau des Chevres	43.22	5.45	*< 10*		+[b]	+	
Ligurian Sea (Italy)				2004	1994	1993	1992
Boccale	43°28′30″	10°19′48″	11	*0*	*0.016*		
Follonica	42°51′45″	10°45′54″	7		*0.024*	*0.226*	
Meloria	43°36′30″	10°12′54″	13		+	+	*0*
Talamone	42° 33′30″	11° 07′12″	3		*0.128*	*0*	*0*
Argentario	42°26′18″	11°06′00″	4.5		*0.066*	*0*	
Gorgona 1	43°25′42″	9°54′30″	8		*0*	*0*	*0.105*
Gorgona 2	43°26′07″	9°53′42″			*0.093*		
Capraia	43°02′45″	09°50′57″	6		*0.103*	*0*	*0*
Elba	42° 52′12″	10°24′18″	5		+	*0*	*0*

+ Qualitative flowering record; *0* no flowering
[a]Records from personal communications J. Moreno Lampreave
[b]Records from personal communications R. Graille
[c]Records from personal communications N. Muñoz Bonet

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