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Mass flowering of the seagrass *Posidonia oceanica* after 2022 record-breaking marine heatwaves, a Pan-Mediterranean study

Running title: Seagrass flowering after marine heatwaves

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Abstract

Following the unprecedented marine heatwaves of summer 2022, extensive flowering of the endemic seagrass *Posidonia oceanica* was witnessed across the western Mediterranean. To unravel the causes of this event, we conducted a pan-Mediterranean analysis across 442 sites spanning all Mediterranean ecoregions, with 76% exhibiting flowering. Flowering differed regionally, with both highest flowering prevalence (over 90%) and flowering intensity (up to 0.75) recorded in the Liguro-Provençal and Balearic Seas. We demonstrate that regions experiencing large summer sea surface temperature anomaly with high marine heatwave cumulative intensity displayed the highest flowering intensity. The probability of flowering was very likely when marine heatwave cumulative intensity exceeded ~120°Cdays. These findings suggest that marine heatwaves trigger flowering in *P. oceanica* and, given the high energetic cost of sexual reproduction, continued ocean warming may shift energy allocation toward flowering. This shift could profoundly affect the species' reproductive strategies, posing major challenges and uncertainties for its long-term evolution.

Keywords: climate change, sea warming, global warming, extreme events, solar activity, sexual reproduction

1 Introduction

Ongoing ocean warming and marine heatwaves (MHWs) are dramatically impacting coastal foundation species, including kelp forests, seagrasses, corals, and many invertebrates [1, 2]. MHWs are becoming increasingly frequent and severe globally [3]. Summer 2022 saw record-high MHWs in the Mediterranean Sea [4, 5], resulting in mass mortality events of many sessile benthic organisms [6, 7]. The mean Sea Surface Temperature (SST) anomaly ranged between 1.3 and 2.6°C above the long-term average (1982-2011) [4], reaching up to 4.6°C in some areas of the western Mediterranean, which are record-breaking thermal conditions obtained over the past four decades [8] (Supplementary Figure 1).

Seagrasses' primary strategy for meadow maintenance, growth, and recovery to disturbance is through vegetative horizontal clonal growth [9, 10] and sexual reproduction, with frequencies and intensities that can vary significantly within and among species, leading to infrequent but massive and synchronized reproductive efforts [11]. Flowering in *Posidonia oceanica*, a foundational species endemic to the Mediterranean, has been rarely documented over the past century [12]. Nevertheless, sexual reproduction is crucial for introducing new genetic material necessary for evolutionary processes. Still, flowering is energetically costly [13], with *P. oceanica* needing to store starch and nutrients in its rhizomes over two to three years before undergoing flowering [14]. Flowering is sometimes massive and synchronized, which may be stimulated by elevated Summer SST [15], and could also reflect a reproduction strategy of producing a large quantity of fruits to saturate predators [16]. A greater investment in sexual reproduction may shift energy from other vital processes such as shoot growth, clonal propagation [13]; potentially disrupting the balance of the meadow and compromising its long-term ecosystem functioning and resilience. Since flowering patterns of marine and terrestrial plants are highly sensitive to environmental factors, particularly temperature [17, 18], it is critical to understand how extreme thermal events impact these coastal foundation species, which play a paramount role in biodiversity, climate regulation, and the provision of essential ecosystem services, as is the case for *P. oceanica* in the Mediterranean Sea [19].

Here, we provide a pan-Mediterranean quantification of flowering records on *P. oceanica* following the record-breaking summer of 2022 across 442 sites (Supplementary Figure 2). We assessed the spatial distribution of flowering, characterized summer thermal conditions using high-resolution satellite-derived SST data, and examined potential links with both biotic (e.g., meadow structure) and abiotic (e.g., depth, management level, temperature) factors. Additionally, we compared flowering intensity (proportion of shoots bearing an inflorescence) between the 2022 event and the Mass Flowering Event (MFE) that followed the intense 2003 MHW in the western Mediterranean [12]. Understanding shifts in reproductive strategies offers key insights into plant resilience and evolution in the face of climate change, at a time when accelerated change in the Mediterranean basin is particularly critical.

2 Results

Flowering data were obtained from all nine Mediterranean ecoregions (Supplementary Data 1): 159 records from the Liguro-Provençal ecoregion, 134 records from the Balearic Sea, 60 records from the Aegean Sea and 30 from the Alboran Sea. The other ecoregions were represented by fewer records: 27 from the Tyrrhenian Sea, 26 from the Adriatic Sea, 16 from the Ionian Sea, 7 from the Levantine Sea and 4 from the Tunisian Plateau (Supplementary Table 1).

2.1 Thermal regimes and warming trends in the Mediterranean

The Mediterranean Sea exhibits strong seasonality with an annual SST amplitude > 10°C, also undergoing wide east-west and north-south gradients, as summarized by the climatological data for the different ecoregions (Supplementary Figure 1A). The year 2022 was the warmest for the Mediterranean since the beginning of satellite SST records in 1982 (mean = 20.81°C), 0.91°C above the 1982-2021 average (Supplementary Figure 1B). The highest anomalies were detected in the western Mediterranean, particularly during the meteorological summer (June, July and August, hereafter JJA) with mean SST Anomalies (SSTA) 2.42°C above the 40-year average (Supplementary Figure 1B).

Significant correlations were detected between MHW, SST and SSTA descriptors (Spearman test: $p < 0.001$; Figure 1). MHW cumulative intensity (MHW-icum) was positively related to summer SST in June-July-August (JJA) and positively related to SSTA-JJA (Spearman test: $p < 0.001$; Figure 1), while SSTA-JJA was negatively related to SST-JJA (Spearman test: $R = -0.856$; $p < 0.001$), highlighting that the highest anomalies occurred in colder regions (e.g., Liguro-Provençal).

2.2 Flowering prevalence and intensity

Following the summer of 2022, flowering occurred in 333 out of the 442 sites monitored, corresponding to a Flowering Prevalence (FP: number of records reporting flowering in relation to the total number of records) of 76%. The highest FP values were observed in the Liguro-Provençal region and the Balearic Sea. Intermediate FPs were observed in the Alboran and

Tyrrhenian Seas. The Aegean and Ionian Seas were characterised by low FPs, while no flowering was recorded within the Adriatic Sea (Table 1, Figure 2).

The overall mean Flowering Intensity (FI; proportion of shoots bearing inflorescence in relation to the total number of shoots) was 0.15 ± 0.16 across the whole Mediterranean basin, ranging between 0 (e.g., Adriatic Sea) and 0.75 (Giglio Island, Tuscany, Liguro-Provençal ecoregion). Strong differences in FI were observed between ecoregions ($p < 0.001$; Figure 2, Supplementary Table 2), particularly between western and eastern ecoregions (pairwise test, $p < 0.05$). A higher mean FI was observed in the Tunisian Plateau with 0.60 ± 0.19 (n = 4 records), followed by the Balearic Sea, the Liguro-Provençal ecoregion, and the Tyrrhenian Sea. The mean FI was low in the Alboran Sea and very low in the Aegean and Ionian Seas (Figures 2 and 3; Table 1).

There was no significant influence of meadow structure category ($p = 0.062$), depth ($p = 0.056$), nor Management level ($p = 0.111$) on FI across ecoregions (i.e., Alboran Sea, Balearic Sea, Liguro-Provençal and Tyrrhenian Sea). Shoot density and FI did not exhibit any significant correlation across western ecoregions (Alboran Sea, Balearic Sea, Liguro-Provençal and Tyrrhenian Sea; Spearman test: $R = -0.03$, $p = 0.649$).

2.3 Relationships between marine heatwave descriptors and the mass flowering event

MHW-icum and marine heatwave duration (MHW-dur) were significantly correlated with FI ($R = 0.523$ and $R = 0.449$, respectively; $p < 0.001$) (Figure 1). The extent of the 2022 MFE exhibited strong spatial overlap with the exceptional MHWs, which occurred at subregional scales during summer, covering most of the western Mediterranean, the Alboran Sea, and the Tunisian Plateau (Figure 2, Figure 3). Analysis of local thermal conditions for the flowering records (n = 442) indicates that flowering (n = 333) occurred preferentially under the warmest conditions (Figure 4), with a probability of flowering higher than 50% when MHW-icum exceeds 120°Cdays (Supplementary Figure 3).

The analysis of FI quantitative data above zero (n = 193) highlighted contrasted patterns depending on thermal conditions. Most of the records exhibiting moderate to large FI level (3, 4 or 5 FI level; n = 126, mean = 0.29 ± 0.16) were associated with elevated MHW-icum (mean = 246 ± 72 °Cdays). In contrast, large scatter of thermal exposure (mean = 180 ± 72 °Cdays) was found for small and isolated flowering (1 or 2 FI levels; n = 82, mean = 0.05 ± 0.16). When flowering was absent (FI = 0; n = 110), thermal exposure was found lower (mean = 128 ± 75 °Cdays).

To explore spatial variation in *P. oceanica* FI across the Mediterranean, we modelled continuous FI values as a function of mean summer SST (SST-JJA) and cumulative marine heatwave intensity (MHW-icum), while accounting for inherent baseline temperature differences among the different Mediterranean ecoregions (Figure 5A). Our results reveal a positive relationship between thermal anomalies and flowering: both SST-JJA and MHW-icum were positively associated with FI across the dataset, with variations across regions. The highest MHW-icum values were recorded over the Tyrrhenian Sea, corresponding to some of the most intense flowering events observed. Similarly, the Balearic Sea and the Tunisian Plateau experienced both high MHW-icum and SST-JJA values, which also coincided with substantial flowering. These findings suggest that the most extreme flowering events may arise from the combined influence of high SST-JJA and elevated MHW-icum. Region-specific modelling further showed that all intercepts were negative (Figure 5B), indicating that baseline flowering was generally unlikely in the absence of strong thermal forcing, particularly in western regions. In contrast, the slope estimates for both SST-JJA and MHW-icum were predominantly positive (Figures 5C and 5D), reinforcing the role of thermal anomalies in driving flowering. The regional slopes in Figures 5B–D reflect variation in the strength of the flowering response to MHW-icum across ecoregions. For SST-JJA and the intercept, 75% credible intervals did not cross zero, making these coefficients interpretable. Credible intervals for MHW-icum were wider and often including zero, reflecting greater uncertainty and contrasting trends among regions. Positive regional slope values indicate that flowering in that region responds more strongly to thermal anomalies than the entire Mediterranean.

2.4 Comparison with the 2003 Mass Flowering Event (western Mediterranean) and other historical records

To further contextualize our findings, we compared our results with the historical MFE of *P. oceanica* reported for the western Mediterranean in 2003 [12] completed by additional historical records available from 1982-2001 [12] and 2009-2021 [20]. Analysis of SSTA-JJA in the western Mediterranean from 1982 to 2022 (Figure 6A) revealed that both 2003 and 2022 were characterized by anomalously high summer SST, exceeding the historical range of the 1982–2021 time series. Summers 2022 and 2003 ranked as the warmest and 2nd warmest, respectively, since 1982 (26.10°C and 25.84°C, respectively). Median SSTA-JJA values during these two years reached 2.53°C [Q25: 1.96°C, Q75: 2.80°C] and 2.12°C [Q25: 1.72°C, Q75: 2.55°C] for 2022 and 2003 respectively (Figure 6A). Consistent with our earlier analysis, high-intensity flowering in 2003 was associated with MHW-icum values above 150 °Cdays [182 ± 9 °Cdays] (Figure 6B), closely aligning with the probability identified in our 2022 dataset (Figure 6C). However, it is worth noting that the sparse historical records from 1982-2021 (excluding 2003) are associated with low MHW-icum (Fig 6B; mean = 26 ± 40 °Cdays), confirming the exceptional nature of 2003 and 2022 MFEs and MHWs (Fig 6A).

3 Discussion

Our study highlights an exceptional basin-wide flowering of *P. oceanica* in the aftermath of the 2022 MHWs, eclipsing the benchmark 2003 heatwave [21] and its associated MFE in the north-western Mediterranean [22]. Based on the currently available historical records [12, 20], the 2022 event appears to be one of the most intense flowering events ever documented for this species. Despite strong differences among ecoregions, flowering after summer 2022 was observed in 76% of the study sites, with 90 to 100% occurrences for western Mediterranean regions. Flowering intensity (FI) reached 0.15 across the Mediterranean, with the highest values in the Tunisian Plateau and the western basin (up to 0.73 and 0.75 respectively), far higher than previous maximum FIs recorded in 2003 (i.e., 0.54 in the Balearic Islands; see [12]). Eastern regions such as the Aegean and Ionian Seas underwent lower FI (up to 0.01 to 0.04 respectively). We also showcase that the probability of flowering was very likely when MHW-icum exceeded ~120°Cdays, raising questions about *P. oceanica*'s reproductive strategies and patterns in the face of global change.

While *P. oceanica* can flower yearly, flowering is usually sparse and localized [23], but large-scale flowering events have been observed throughout the past decades across the Mediterranean. However, the event observed in 2022 is unprecedented in terms of both intensity and scale. For instance, meadows that flowered intensively between 1957 and 2004 exhibited an average FI of 0.11 ± 0.02, with a maximum of 0.54 [12]. In our study, FIs surpassed this value in numerous locations, exceeding 0.60 in Tunisia, Sardinia, Tuscany and Provence, highlighting the magnitude of the 2022 MFE. Furthermore, unprecedented FI values (up to 0.06) were recorded in 2022 in the westernmost part of *P. oceanica*'s distribution range (i.e., Southern Spain).

In the context of warming oceans, temperature appears to be a key driver of *P. oceanica* flowering [12, 18, 24, 25, 26, 27]. Although the exact physiological mechanisms and triggers remain unresolved, the strong link between MHW-icum and flowering intensity supports the hypothesis that prolonged elevated temperature are necessary to trigger *P. oceanica* MFE. When the MHW-icum exceeded 150°Cdays or more, FI was high (i.e., > 0.1) and regionally widespread (> 60% of records). In contrast, low FI values, such as those observed in previous works (e.g., [12, 20]), coincided with low MHW-icum (e.g., up to 75°Cdays for 2010 in the Greek Seas; [20]). The importance of temperature for flowering is well-documented in terrestrial plants, which is also influenced by photoperiod, light quality, and other factors [28]. Besides ocean warming, SST increases are also linked to solar activity cycles [29], which also impact various biological processes. Indeed, peaks in *P. oceanica* flowering every 9-11 years correlate with solar cycles [12, 30] and, in fact, the 2022 flowering event, occurring 10 years after the sunspot peak of 2012, was predicted based on this pattern [30] (Supplementary Figure 4). However, recent solar cycles (e.g., of 2022-2024) were weaker (150-160 sunspots per month) than the solar cycles peaking in 2000-2002 (> 200 sunspots per month; Supplementary Figure 4), after which the 2003 MFE occurred [12]. Such a decrease in solar intensity, combined with increasing flowering events, suggests that rising temperatures driven by climate change are likely playing a key role in influencing mass flowering. Elevated temperatures can affect plant metabolism and, consequently, influence the ability of *P. oceanica* to accumulate reserves [31, 32]. In fact, observations of mass beach-cast *P. oceanica* fruits and seeds have been reported for the Warm Roman Period (i.e., from ca 250 BCE to 400 CE; [33]) in southeast Spain, and central and southern Italy. Unfortunately, quantitative information is lacking for the Little Ice Age (ca. 1300-1850 CE) which underwent particularly cold thermal conditions [34] and only some flowering records are available for that age (e.g., Provence, Tyrrhenian Sea, Adriatic Sea, Sardinia, Algeria, southeast Spain; see [12]), which in turn might underline the strong relationship between high thermal conditions and MFE.

Flowering is metabolically costly, and *P. oceanica* plants accumulate reserves (starch) about two years prior to flowering [13, 30]. These temporal dynamics may help explain the low flowering observed in 2022 in the Tyrrhenian Sea and the Aegean Sea, where high fruit and seed beaching (in the Tyrrhenian Sea; [35]) and widespread flowering (in Greek waters; [20]) occurred in 2021. However, it is worth noting that mass flowering still follows an endogenous rhythm of the plant, which is not directly induced but regulated by environmental factors including solar activity [36]. Continuous warming, as seen in other biological systems, could disrupt synchrony and endogenous rhythm [37]. Given that temperature drives reserve accumulation and flowering events are becoming more intense (see [12, 27]; present work), *P. oceanica* flowering patterns may no longer strictly follow solar cycles.

Interestingly, no flowering was observed after summer of 2022 in the Adriatic Sea, the last flowering being observed in 2011 [38], although recent very localised flowering and fruit production was observed in early winter 2024 in Biševo Island (Croatia, Jelena Kurtović pers. obs.). However, following summer 2024 MHW, an unprecedented MFE has occurred along the Italian coast of the Adriatic Sea and in Montenegro ([27]; Vesna Mačić pers. obs.). The drivers of such flowering patterns remain to be understood, but genetic composition and structure of seagrass populations are also likely influencing flowering patterns at different spatial scales. High genetic relatedness and heterozygosity have been linked to greater inflorescence abundance in *P. oceanica* [39]. Two main genetic groups exist in the western and eastern basins, probably resulting from past glaciation events that limited gene flow [40]. These groups exhibited distinct flowering patterns in 2022, with genetic differences within regions such as the Tyrrhenian Sea [41], the Aegean and the Levantine Seas [42, 43] and the Adriatic Sea [44]. Additionally, *P. oceanica* cuttings and seedlings obtained from 13 different localities across the Mediterranean were planted at Port-Cros National Park (Provence, France) in the frame of a transplant experiment in 1987 [45]. In 2022, all transplanted patches flowered, but FI varied significantly by origin with 0.01 for cuttings from Malta (Ionian Sea) and 0.79 for those from Mallorca (Balearic Sea) (Heike Molenaar pers. obs.), highlighting the key role of genetics in influencing flowering patterns.

MFEs do not always lead to significant fruiting the following spring [46, 47]. After the 2022 MFE, beach-cast fruits and seeds were seen in southern France**,** but abortion (i.e., interrupted development of inflorescences and fruits) occurred at several sites [24, 48]. Furthermore, successful recruitment of seedlings is very low [49, 50] and young seedlings and plantlets have a lower tolerance threshold to warming than adult plants [51, 52]. Therefore, many seedlings may not survive frequent MHWs, potentially preventing the benefits of mass flowering.

The increased flowering observed in the last years could suggest that the species is now encountering better thermal conditions and that sexual reproduction will positively bolster population genetic variability and resilience. Nevertheless, the assumption that *P. oceanica* is benefiting from seawater warming remains a speculation. The complete picture should be considered, including the metabolic investment and carbon balances in the face of more frequent sexual events, and the possible drawback on the resilience of flowering clones. Indeed, MHWs can cause widespread mortality of *P. oceanica* meadows [53, 54] and mass flowering after warming has been interpreted as a stress-triggered strategy to compensate for mortality by promoting recruitment, dispersal, and greater genetic diversity to support adaptation under warming conditions [55, 56]. A better understanding of shifts in reproductive strategies is critical not only for uncovering plant resilience and adaptive potential but also for conservation efforts as the Mediterranean undergoes accelerated ecological transformation.

Author contributions

PA: writing, conception, data curation /analysis, figures/tables editing, data provider, review; NB: writing, conception, data curation /analysis, figures/tables editing, review; SA: writing, conception, data curation /analysis, figures/tables editing, data provider, review; CFB: writing, conception, data provider, review; FT: writing, data provider, review; NT: writing, data provider, review; JC: data curation/analysis, figures/tables editing, review; BB: figures/tables editing, data provider; CGE: data provider, review; BA: data provider, review; TA: data provider, review; EA: data provider, review; FB: data provider, review; JB: data provider, review; AB: data provider, review; MC: data provider, review; ECa: data provider, review; GC: data provider, review; TE: data provider, review; YFT: data provider, review; VG: data provider, review; SG: data provider, review; DGr: data provider, review; DK: data provider, review; VM: data provider, review; JMCr: data provider, review; CMM: data provider, review; HM: data provider, review; DM: data provider, review; JLSL: data provider, review; TS: data curation/analysis, data provider; JT: data provider, review; GTJ: data provider; DV: data provider, review; AZe: data provider, review; BAO: data provider; VB: data provider; ABD: data provider; WB: data provider; JBS: data provider; JBE: data provider; CNB: writing, review; IC: data provider; ECe: data provider; ECha: data provider; AChe: data provider; ECh: data provider; AChi: data provider; GCo: data provider; JMCo: data provider; ICv: data provider; GDA: data provider; MD: data provider; FD: data provider; MFC: data provider; BF: data provider; RG: data provider; DGui: data provider; JEGN: data provider; AG: data provider; VH: data provider; NH: data provider; AIM: data provider; ZJ: data provider; SJ: data provider; OK: data provider; PK: data provider; JKM: data provider; AL: data provider; VL: data provider; IM: data provider; GMa: data provider; NM: data provider; MM: data provider; NMi: data provider; AM: data provider; BM: review; CMo: review; PCNM: data provider; AO: data provider; APa; data provider, review; CPM: review; APe: data provider; LP: data provider; GPr: data provider, review; JMRe: data provider; SRo: data provider; JR: data provider; JMRu: data provider; NSB: data provider; MSF: data provider; ASc: data provider; FS: data provider; PS: data provider, review; AZu: data provider; MMo: writing, data provider, review.

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4 Online Methods

4.1 Assessment of the 2022 Mass Flowering Event across the Mediterranean

4.1.1 Spatial extension of the study

A comprehensive database covering the entire Mediterranean basin was established to document the flowering occurrences following summer 2022 marine heatwaves (MHWs). More than a hundred people from 10 countries and 47 teams (Non-Governmental Organisations, universities, research laboratories, marine protected areas (MPAs)) were involved. A total of 463 records were collected from the sea surface to 25 m depth, between latitudes ranging from 33.19°N to 44.91°N and longitudes ranging from 5.12°E to 33.66°E. A meadow structure category was assigned to each site when the information was available in order to test its influence on flowering patterns, specifically: (i) naturally fragmented (e.g., meadow cover under 80%, see [58]), (ii) fragmented by anthropogenic pressures (e.g., anchoring, other mechanical degradation, low water quality), and (iii) continuous (over 80% of meadow cover). Records were collected from areas under different levels of management: (i) areas without regulation, (ii) MPAs, most of them Natura 2000 sites (EU Habitat Directive, 92/43/CEE) without significant management measures; (iii) intermediate level of protection, involving conservation measures and regulation of most of the human activities (e.g., small-scale fishing, anchoring – Multi-Use-Management) and (iv) No-Entry Zones (i.e., fully protected areas). Compiled data included qualitative, semi-quantitative and quantitative estimates of flowering obtained between September 2022 and July 2023, spanning the entire sequence from inflorescence formation to fruit dispersal.

Sampling sites were classified according to the Marine Ecoregions of the World [59]: 1: Alboran Sea; 2: Western Mediterranean; 3: Adriatic Sea; 4: Ionian Sea; 5: Tunisian Plateau and Gulf of Sidra (hereafter 'Tunisian Plateau'); 6: Aegean Sea; 7: Levantine Sea. For the purpose of this work, and given the extensive sampling effort in the western Mediterranean (zone 2), this ecoregion was divided into three sub-regions: 2.1 Balearic Sea, 2.2 Liguro-Provençal and 2.3 Tyrrhenian Sea (adapted from [60]; Supplementary Figure 5).

4.1.2 Types of flowering data

Qualitative records (n = 41). When flowering or fruiting was observed for a given site, at least the date and the geographical coordinates were recorded. Null occurrence records, corresponding to the absence of flowering in a site, were also noted.

Semi-quantitative records (n = 186). The magnitude of flowering was assessed using the following categories: (I) Isolated flowering, (II) Small flowering, (III) Moderate flowering, (IV) Large flowering, (V) Exceptional flowering (See Supplementary Table 3; [61]). Available *in situ* photographs were also used to estimate flowering density categories, when available. The record was also considered as semi-quantitative if less than three replicates from quantitative records were available for a given site (n = 18 sites).

Quantitative records (n = 236). The number of living shoots and the number of inflorescences were counted within a quadrat randomly replicated at least three times in the meadow. The number and size of quadrats differed according to the data provider, but were always of standardized size (e.g., 20 cm x 20 cm, 25 cm x 25 cm, 25 cm x 30 cm, 40 cm x 40 cm), enabling a density estimation per m². Lepidochronological analysis data (i.e., rhizome analysis for annual growth rate and sheet production allowing the identification of floral stalks and an estimation of the flowering intensity

(FI); see [62]) were also considered (Supplementary Figure 6). Sampling was conducted at different depths, ranging from 0 to 25 m, and three depth categories were considered following [48]: shallow (< 7.5 m), intermediate (between 7.5 and 12.5 m), and deep (> 12.5 m).

During data collection, 21 sites were not considered in the analysis as they corresponded to observations of beach-stranded inflorescences or fruits (n = 14; e.g., Sicily, Liguria, Corsica) or were based on reports lacking specific field observations (n = 7; e.g., Sicily, Montenegro). (Supp. Mat. 1).

4.1.3 Flowering prevalence and flowering intensity descriptors

Flowering Prevalence (FP) was estimated as the number of records reporting flowering in relation to the total number of records obtained throughout the study [12]. FP was calculated for each ecoregion that contained at least 10 records, as well as for the whole Mediterranean basin. Flowering Intensity (FI; see [21, 22]) was estimated as the proportion of shoots bearing inflorescence in relation to the total number of shoots within the quadrats. To relate flowering density to total shoot density, a classification based on FI (hereafter FI level) was used (Supplementary Table 3). As Giraud's classification [61] and FI level are strongly correlated (Spearman test: R = 0.965, p-value < 0.001), FI level, more representative of actual flowering at each site, was used to display the results.

4.2 Thermal conditions and MHWs metrics

4.2.1 Temperature data set

In order to obtain accurate information throughout an extensive geographical area, SST time series over the Mediterranean Sea at 0.05° resolution grid were obtained from the Copernicus Marine Environment Monitoring Service (CMEMS, https://doi.org/10.48670/moi-00173https://doi.org/10.48670/moi-00173; [63, 64]). The data consists of daily (night-time), optimally interpolated (level 4), satellite-based estimates of the foundation SST from January 1st 1982 to the end of 2022, reprocessed with increased stability and consistency for climate applications. Importantly, this dataset exhibited high agreement with near-shore *in situ* time series around the Mediterranean Sea and was found relevant for trends and extreme events analysis in the coastal zone [65].

4.2.2 Temperature data analysis

Individual SST analyses were conducted per pixel at 0.05° grid resolution. Following Hobday et al. [66], a MHW is defined as a prolonged (at least five consecutive days) and discrete warming event, when the local temperature exceeds the seasonally varying threshold defined on the basis of 30 years of climatology data. MHW metrics were computed using the Zaho & Marin [67] package for Matlab, with climatological mean and 90th percentile calculated over the 1982-2011 period. Seasonal MHW statistics were calculated by considering all MHW days (number of days when SST exceeds the 90th percentile threshold) during meteorological summer (from 1st June to the end of August each year – hereafter JJA). These three months correspond to the warm period that precedes the sexual reproductive phase. Summer MHW total duration (MHW-dur, in days) and cumulative intensity (MHW-icum, in °Cday) were defined as the total of all MHW days and the sum of all MHW daily intensities (i.e., anomaly relative to the climatological mean), respectively.

Additional SST descriptors were calculated to assess their correlation with the flowering dataset: (i) maximum SST (SST_{max}), (ii) mean SST (SST_{mean}) and (iii) mean SST Anomaly (SSTA) with respect to the 1982-2021 average. SST_{mean} and SSTA were calculated considering two different time windows (yearly and for the summer season).

4.2.3 Comparison with 2003 flowering event and other available historical records

The dataset from Díaz-Almela et al. [12] on flowering records reported after the 2003 MHWs, was completed with authors' records, and was imported in numerical format and graphically analysed. The validated dataset consists of quantitative FI data for 24 sites for which nearest satellite SST time series were extracted and considered for MHW analysis. The dataset validated with original authors consists of 24 records (sites) for 2003 (available in Supplementary Data 1). In addition, historical records from 1982-2001 (from [12]; n = 101) and from 2009-2021 (from [27]; n = 42) were also considered for MHW analysis (Supplementary Data 1).

4.3 Statistical analysis

First, to test the effects of biotic and abiotic factors (ecoregions, depth, management level and meadow structure) on FI, PERMANOVAs [68] were conducted with 9999 permutations, completed by a pairwise test. Spearman tests were conducted to test the correlation between FI and biotic and abiotic factors.

Then, to evaluate the probability of flowering occurrence in *P. oceanica* during the 2022 event, we first applied a Bayesian modelling framework using a binomial distribution (Eq. 1). The response variable was coded as binary (1 = flowering observed, 0 = no flowering), and the single predictor variable included was the MHW cumulative intensity (MHW-icum) (Eq.2):

$$\text{Flowering} \sim \text{Bernoulli}(\mu_{\text{Flowering}}) \qquad \text{(Eq. 1)}$$

$$\mu_{\text{Flowering}} = \text{logit}^{-1}(\beta_0 + \beta_1 \times \text{MHW-icum}) \qquad \text{(Eq. 2)}$$

$$\beta_0 \sim \text{Student-t}(3, 0, 10);\ \beta_1 \sim \text{Student-t}(3, 0, 2.5) \qquad \text{(Eq. 3)}$$

Here, β_0 is the intercept and β_1 is the coefficient for MHW-icum. Both parameters were assigned Student-t priors, specified by three values: degrees of freedom (3), location (mean, 0), and scale (spread; 10 for β_0, 2.5 for β_1). These weakly informative priors allow the data to primarily drive the inference while limiting extreme values. We chose a Bayesian approach to fully propagate uncertainty in parameter estimates and to accommodate the hierarchical structure of the data. The model was implemented using the brms package [69] with four Markov chains of 4 000 iterations each (1 000 warm-up steps). Convergence was assessed via R-hat values (<1.01) [70] and trace plots. We set adapt_delta = 0.99 and max_treedepth = 15 to ensure efficient and reliable sampling.

We further applied a second Bayesian approach to track flowering intensity continuously. Because FI is bounded between 0 and 1, values were logit-transformed, and a normal likelihood was applied on the transformed scale (Eq. 4–7).

$$\text{FI} \sim \text{Normal}(\mu_{\text{FI}}) \qquad \text{(Eq. 4)}$$

$$\mu_{\text{FI}} = \beta_0 + \beta_1 \times \text{MHW-icum} + \beta_2 \times \text{SST-JJA} + \zeta_{\text{Ecoregion}} \qquad \text{(Eq. 5)}$$

$$\zeta_{\text{Ecoregion}} = (\Omega Z)\delta_s \qquad \text{(Eq. 6)}$$

$\mathrm{diag}(Z) = \sigma_\zeta$ (Eq. 7)

$\beta_0 \sim \text{Student-t}(3, 0, 10)$; $\beta_1, \beta_2, \delta_s \sim \text{Student-t}(3, 0, 2.5)$; $\sigma, \sigma_\zeta \sim \Gamma(0.01, 0.01)$; $\Omega \sim \mathrm{LKJ}(1)$
(Eq. 8)

The model includes MHW-icum, SST-JJA and a vector of n = 9 levels of ecoregions observed. These vectors construct a hierarchical matrix ζ with n rows and two columns, representing ecoregion-level additive deviationns from β_0. In this model, Ω is the Cholesky factor of the correlation matrix among hierarchical effects, Z is a diagonal matrix with a vector of among-ecoregion standard deviations (σ_ζ), and δ_s is an s-by-two matrix of standardized hierarchical effects. We ran the model with four chains, each with 4 000 draws and a warm-up period of 1 000 steps, retaining 12 000 posterior draws for analysis. Models (1), and (4) displayed R^2 of 0.32 and 0.68 respectively. All statistical analyses were conducted using R v. 4.4.3 [71].

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Data availability statement

The full dataset is available in figshare (10.6084/m9.figshare.32140954) and as an excel file: supplementary_data_1_dataset_2022-2021-1982_flowering_Posidonia_final.xlsx

Competing interests

The authors declare no competing interests.

Figures' captions

Figure 1: Correlation matrix (Spearman test) between Flowering Intensity (FI, proportion of shoots with inflorescences), latitude (Lat, decimal degree), longitude (Long, decimal degree), Marine heatwave cumulative intensity (MHW-icum, °Cday), MHW duration (MHW-d, day), Sea Surface Temperature in June July and August (SST-JJA, °C), maximum SST (SST-max, °C), SST Anomaly (SSTA-JJA, °C), SSTA-max (°C). Lower panels show scatterplots with Loess smoothing (in black) and 95% confidence intervals (light gray), upper panels show Spearman correlation coefficients, and diagonal panels display variable distributions. *: $p < 0.05$; ** $p < 0.01$; ***: $p < 0.001$.

Figure 2: A) Number of records per Flowering Intensity (FI) level (0: No flowering; 1: Isolated flowering; 2: Small flowering; 3: Moderate flowering; 4: Large flowering; 5: Exceptional flowering; see Supplementary Table 3 for definitions), and B) Marine heatwave cumulative intensity (MHW-icum, in °Cdays, grey columns) and Flowering Prevalence (%; FP, green dots, no data for Tunisian Plateau and Levantine Sea) per ecoregion.

Figure 3: Location of 2022 flowering records within the Mediterranean basin. Flowering Intensity (FI, proportion of shoots bearing an inflorescence per total number of shoots. FI levels: 0: No flowering; 1: Isolated flowering; 2: Small flowering; 3: Moderate flowering; 4: Large flowering; 5 Exceptional flowering (see Supplementary Data 1 for more details). Flowering occurrence (in grey) corresponds to presence data of flowering. The black lines indicate areas without *P. oceanica* living meadows (Telesca et al., 2015; Tutar et al., 2022). MHW-icum (°Cday) is displayed across the Mediterranean basin for the period between 1st June and 31st August 2022. Photographs (from left to right): Provence, France (©Bruno Belloni); Corsica, France (©Tristan Estaque); Balearic Islands, Spain (©Jonathan Delgado); Ionian Sea, Greece (©Daniele Ventura). Leaves are approximately 0.8 to 1 cm wide.

Figure 4: Relative distribution of the marine heatwave cumulative intensities (MHW-icum; ºCday) associated with the probability of *Posidonia oceanica* flowering occurrence (i.e., observation of a flowering event).

Figure 5: Relationships between flowering intensity (FI), summer sea surface temperature (SST-JJA), and cumulative marine heatwave cumulative intensity (MHW-icum) across nine Mediterranean ecoregions. A) Three-dimensional scatterplot illustrating the relationships among FI, SST-JJA, and MHW-icum. Each point represents a site, scaled by FI magnitude and connected

to its corresponding regional centroid. No FI observations are filled in white. (B–D) Standardized random-effect deviations from the hierarchical Bayesian model of logit-transformed FI as a function of SST-JJA and MHW-icum (see Online Methods section 4.3, equation 8). These values represent how much each ecoregion departs from the global intercept or global slopes, expressed in standard deviation units: B) deviation from the global intercept, C) deviation from the global SST-JJA effect, D) deviation from the global MHW-icum effect. Colours denote regions: Alboran Sea (red), Balearic Sea (orange), Liguro-Provençal Basin (yellow), Tyrrhenian Sea (green), Adriatic Sea (light green), Ionian Sea (light blue), Tunisian Plateau (dark blue), Aegean Sea (light purple), and Levantine Sea (dark purple).

Figure 6: A) Summer daily sea surface temperature anomaly (SSTA in °C, referenced to the period 1982-2021) and marine heatwave cumulative intensities (MHW-icum in °Cday) from 1982 to 2022 in the western Mediterranean; Flowering Intensity (FI) in relation to MHW-icum for: B) 2003 in dark green and 1982-2001 and 2009-2021 in light green (from Diaz-Almela et al. 2007 and Garcia-Escudero et al., 2024) and for C) 2022 (present work). The mean ± standard deviation values are shown in black.

Table

Table 1: Synthesis of the quantitative data records per Mediterranean ecoregion (FI: flowering intensity; FP: flowering prevalence; SD: standard deviation).

Ecoregions	n	mean FI	SD FI	Min FI	Max FI	FP
1-Alboran Sea	30	0.08	0.11	0	0.37	63%
2.1-Balearic Sea	133	0.21	0.14	0	0.48	93%
2.2-Liguro-Provençal (NW Med)	156	0.19	0.15	0.01	0.75	100%
2.3-Tyrrhenian Sea	20	0.14	0.19	0	0.61	63%
3-Adriatic Sea	25	0	0	0	0	0%
4-Ionian Sea	14	0.01	0.02	0	0.04	25%
5-Tunisian Plateau	4	0.60	0.19	0.32	0.73	-
6-Aegean Sea	59	0.02	0.05	0	0.33	30%
7-Levantine Sea	1	0.05	-	0.05	0.05	-
Total	442	0.15	0.16	0	0.75	76%

Editorial summary:
Marine heatwaves trigger mass flowering in the seagrass Posidonia oceanica, according to a pan-Mediterranean analysis spanning all Mediterranean ecoregions following extreme marine heatwaves in 2022.file is available.

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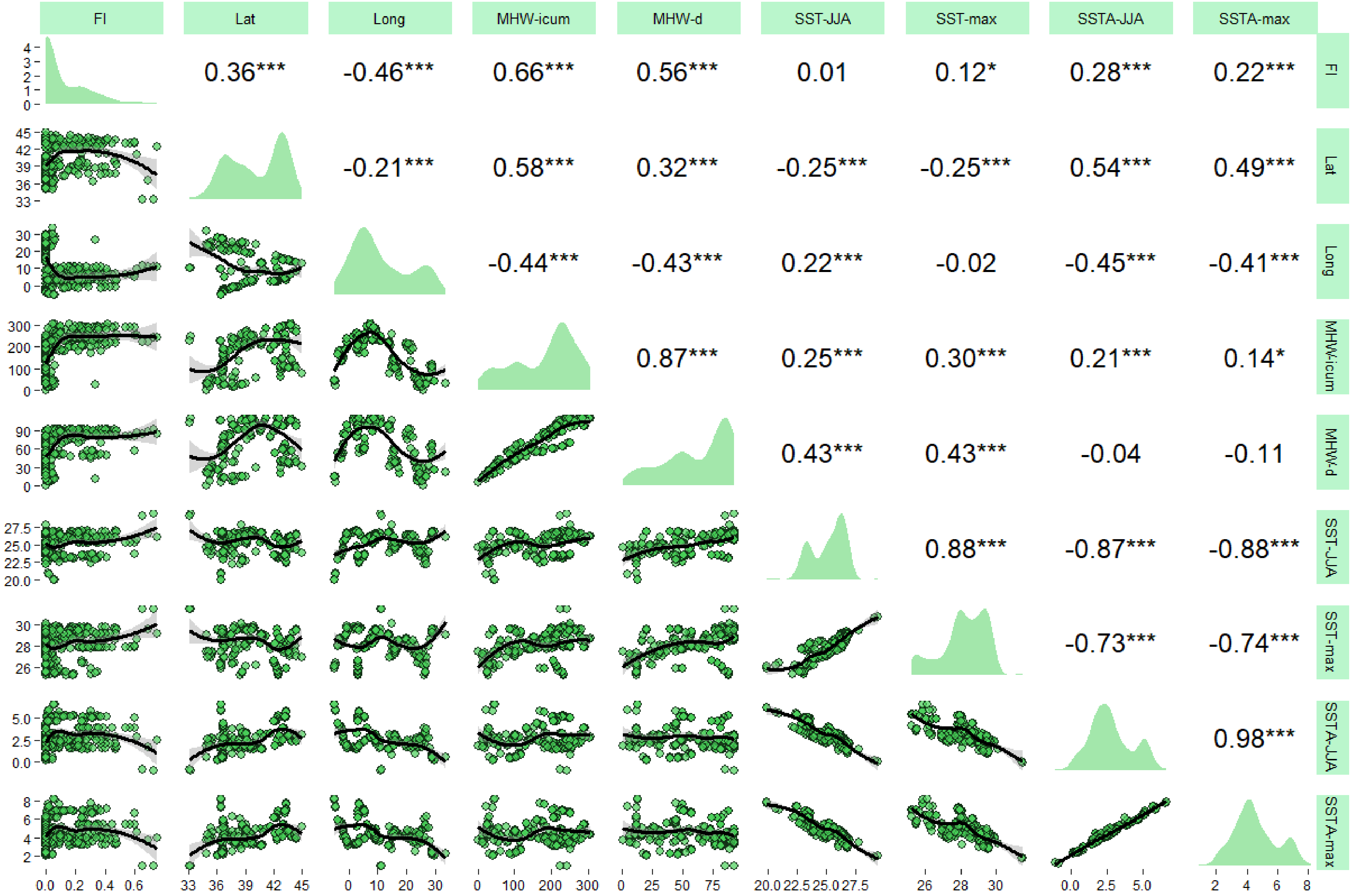
FI
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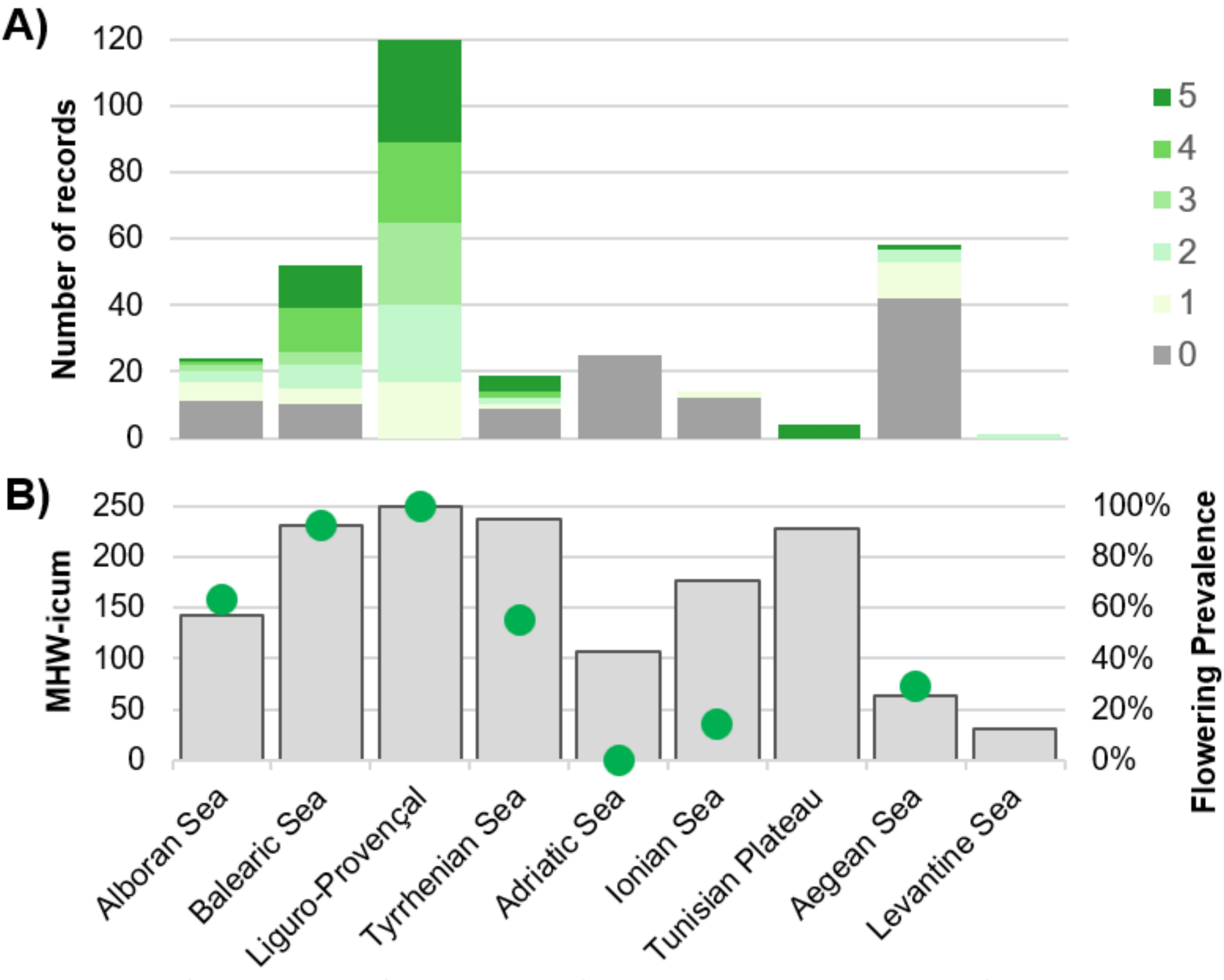
A)
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B)
MHW-icum
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150
200
250
Flowering Prevalence
0%
20%
40%
60%
80%
100%
Alboran Sea
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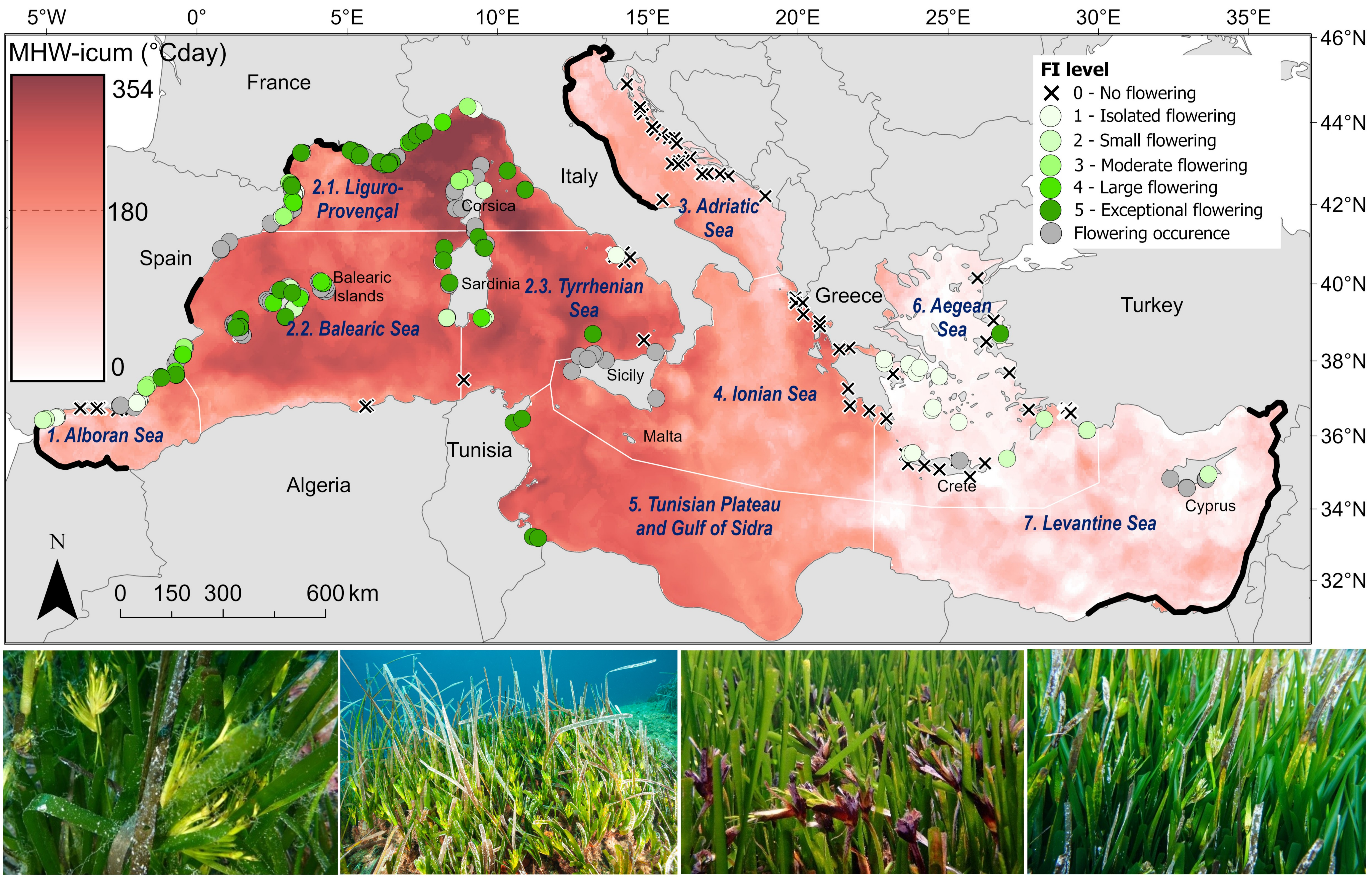
Liguro-Provençal
Tyrrhenian Sea
Adriatic Sea
Ionian Sea
Tunisian Plateau
Aegean Sea
Levantine Sea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38°N
36°N
34°N
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MHW-icum (°Cday)
354
180
0
FI level
✕ 0 - No flowering
1 - Isolated flowering
2 - Small flowering
3 - Moderate flowering
4 - Large flowering
5 - Exceptional flowering
Flowering occurence
France
Spain
Italy
Greece
Turkey
Tunisia
Algeria
Corsica
Sardinia
Balearic Islands
Sicily
Malta
Crete
Cyprus
1. Alboran Sea
2.1. Liguro-Provençal
2.2. Balearic Sea
2.3. Tyrrhenian Sea
3. Adriatic Sea
4. Ionian Sea
5. Tunisian Plateau and Gulf of Sidra
6. Aegean Sea
7. Levantine Sea
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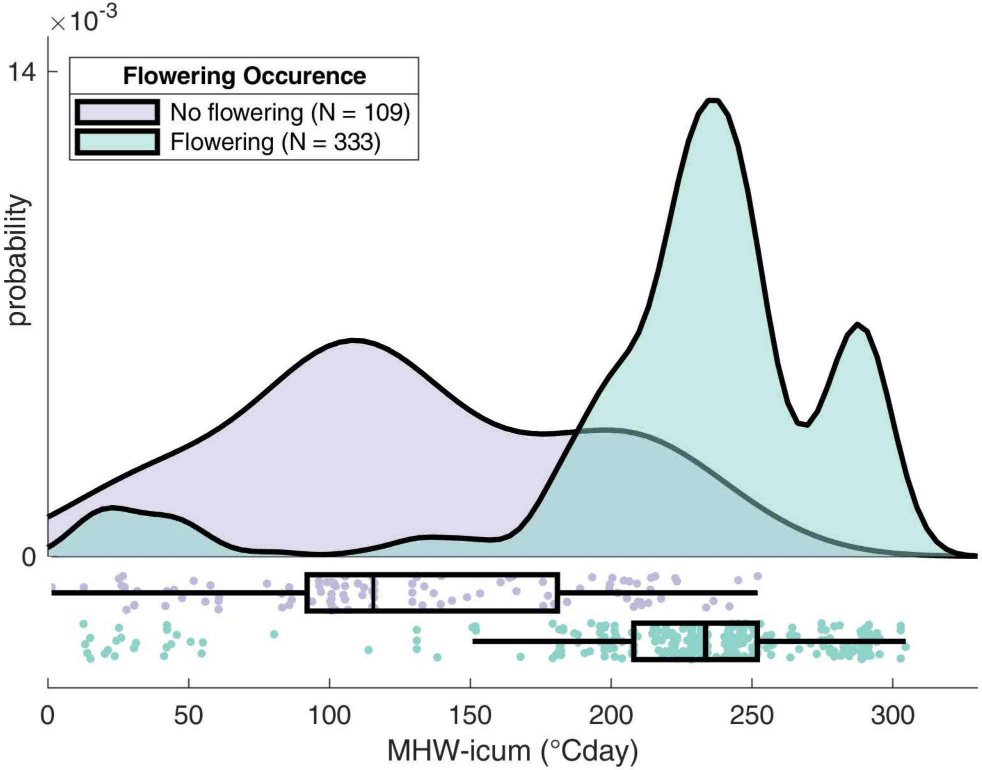
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probability
Flowering Occurence
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Flowering (N = 333)
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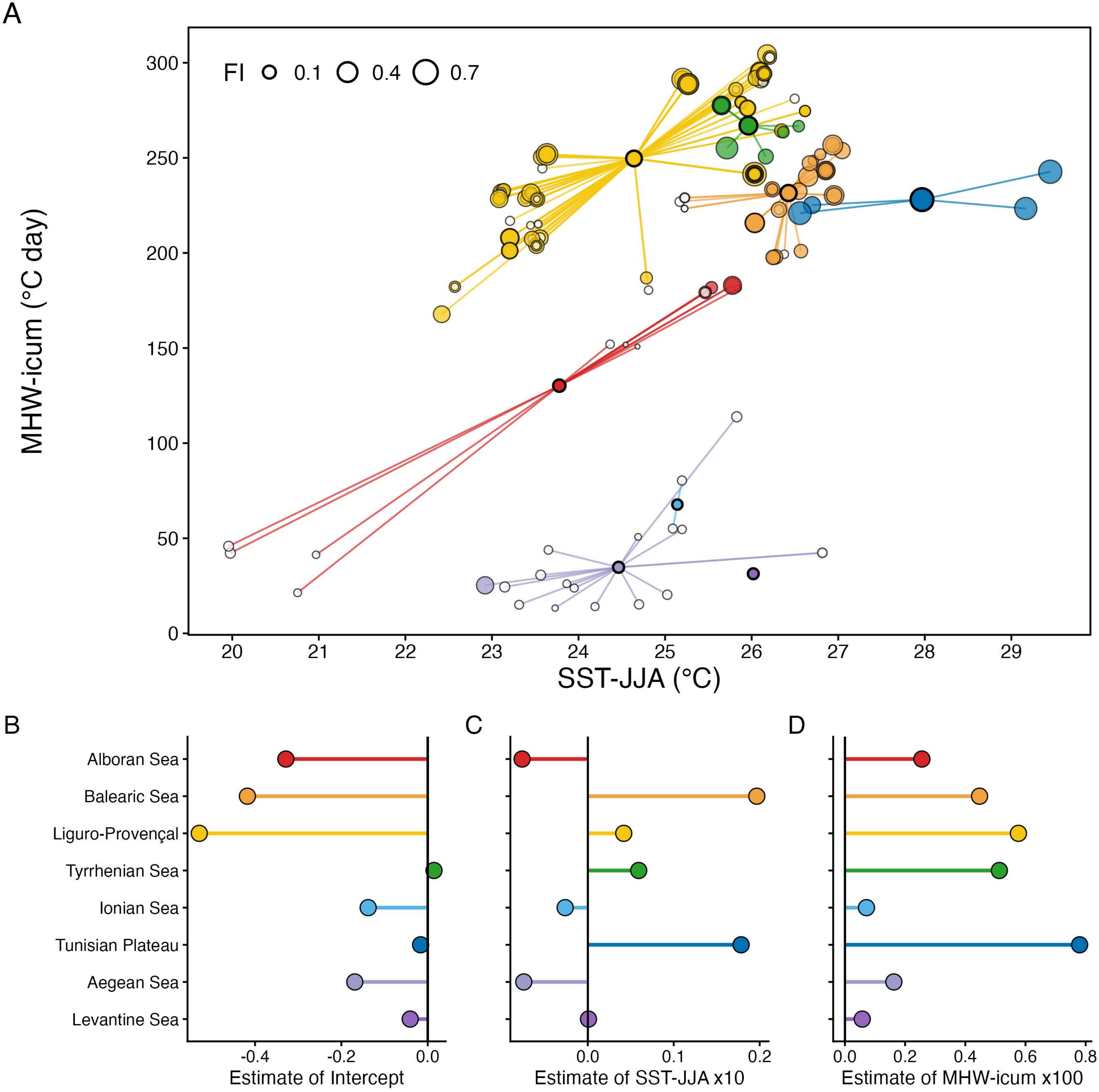
MHW-icum (°Cday)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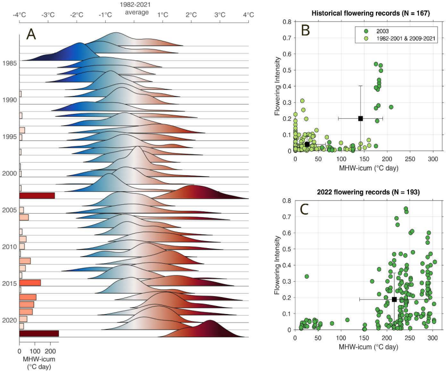
Alboran Sea
Balearic Sea
Liguro-Provençal
Tyrrhenian Sea
Ionian Sea
Tunisian Plateau
Aegean Sea
Levantine Sea
-0.4
-0.2
0.0
Estimate of Intercept
0.0
0.1
0.2
Estimate of SST-JJA x10
0.0
0.2
0.4
0.6
0.8
Estimate of MHW-icum x100


1982-2021
average
-4°C
-3°C
-2°C
-1°C
1°C
2°C
3°C
4°C
A
1985
1990
1995
2000
2005
2010
2015
2020
0
100
200
MHW-icum
(°C day)
Historical flowering records (N = 167)
B
2003
1982-2001 & 2009-2021
Flowering Intensity
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
300
MHW-icum (°C day)
2022 flowering records (N = 193)
C
Flowering Intensity
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
300
MHW-icum (°C day)