



# Warming-induced flowering and fruiting in the seagrass *Posidonia oceanica* and uncertainties due to context-dependent features

Patrizia Stipcich<sup>1</sup> · Gabriella La Manna<sup>1,2</sup> · Giulia Ceccherelli<sup>1</sup>

Received: 10 October 2023 / Accepted: 3 January 2024 / Published online: 5 February 2024  
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## Abstract

This study explores the impacts of global warming on the reproductive efforts of *Posidonia oceanica*, a key seagrass species endemic to the Mediterranean Sea. By analyzing data from five areas in Sardinia in February 2023, we have investigated the relationship between thermal descriptors and *P. oceanica* flowering and fruiting variables. In fact, whether climate change has been affected the distribution of seagrasses by changing their reproductive efforts is still controversial and our findings contribute to this ongoing debate, highlighting a noticeable increase in reproductive events potentially affected by rising temperature. Overall, mean summer sea surface temperature (SST) was positively associated to inflorescence density, presence of living fruits and fruit size; living fruits and fruit size were also influenced positively by the maximum SST within 3 months before sampling (November–February). Both flowering and fruiting were negatively affected by the maximum SST within 1 month before inflorescence observation and mean winter SST, respectively, suggesting that *P. oceanica* reproductive effort depends on the duration and the temporal context in which the anomaly occurs. However, the high variability between meadows of the same area highlights the need of future studies to focus on the uncertainties related to local factors.

**Keywords** Adaptive strategy · Climate change · Mediterranean Sea · Sexual reproduction · Thermal descriptor

## Introduction

The increase in sea surface temperature (SST) and the occurrence of extreme climatic events (ECE) due to climate change are affecting several marine ecosystems at multiple levels (Brierley and Kingsford 2009; Hoegh-Guldberg and Bruno 2010; Poloczanska et al. 2013). In semi-enclosed basins, temperature is rising even faster than in open oceans and, in Mediterranean Sea, for example, SST has increased in the last decades at an average ( $\pm$  SD) rate of  $0.03 \pm 0.008$  °C yr<sup>-1</sup> for the western basin and  $0.05 \pm 0.009$  °C yr<sup>-1</sup> for the eastern basin (Nykjaer 2009; Pastor et al. 2019).

Among the most important marine systems, seagrasses, flowering marine plants that form meadows in temperate and tropical waters (Short et al. 2007), are severely threatened by increasing SST and ECEs (Tang and Hadibarata 2022). Seagrasses provide globally valuable socio-economic goods and services (Fonseca and Koehl 2006; Larkum et al. 2006), but they are generally suffering a global decline mainly due to anthropogenic local (*e.g.* coastal modification and water quality decrease) and global pressures such as ocean warming (Orth et al. 2006; Jordà et al. 2012). To overcome the continuous environmental changes, seagrasses have developed several adaptive strategies such as distribution shifts, changes in pattern of sexual reproduction or morphological changes that allow the provision of goods and services to be maintained (Short and Neckles 1999; Hogarth 2015; Hastings et al. 2020; Stipcich et al. 2022a). In this regard, several investigations have focused on *Posidonia oceanica* (L.) Delile, an endemic seagrass to the Mediterranean Sea, which forms extensive meadows in the whole basin (Telesca et al. 2015). Past mortalities of *P. oceanica* meadows have been associated to sudden increase of SST (Marbà and Duarte 2010; Chefaoui et al. 2018). However, how climate change is affecting the performance of this seagrass remains far to

Responsible Editor: M Roleda.

✉ Patrizia Stipcich  
patriziastipcich@libero.it

<sup>1</sup> Department of Chemical Physical Mathematical and Natural Sciences, University of Sassari, Via Piandanna 4, 07100 Sassari, Italy

<sup>2</sup> MareTerra Onlus – Environmental Research and Conservation, Alghero, Italy

be understood since recent field studies support a good resilience of *P. oceanica* to high temperature and marine heat waves in relation to local adaptations (Bennett et al. 2022; Stipcich et al. 2022b, 2023). Nevertheless, further investigations are needed to define its performance in a future climate scenario, and one of the aspects to be studied regards the change that its reproductive potential might undergo under new conditions.

*P. oceanica* can reproduce both vegetatively and sexually depending on external environmental conditions and internal signals (Buia and Mazzella 1991; Hempel et al. 2000; Paulo et al. 2019), although the frequency and intensity of sexual reproduction can be highly variable both in time and space (Balestri and Vallerini 2003) and it has commonly been described as a very infrequent event (Diaz-Almela et al. 2006; 2007), as supported by molecular estimates of the proportion of sexually derived recruitment (Arnaud-Haond et al. 2005, 2007). The reproductive season starts with flowering events in autumn in shallow areas (generally a month later in deeper meadows), when *P. oceanica* produces hermaphroditic flowers (Buia and Mazzella 1991; Calvo et al. 2010) organized in inflorescences (Remizowa et al. 2012). Fruiting occurs roughly during the subsequent 4 months and when fruits are mature (in early spring) and released, they float and drift away from parental meadows, travelling very long distances (Buia and Mazzella 1991; Balestri et al. 2006; Micheli et al. 2010). Flowering and fruits production have been considered irregular and sporadic phenomena (Pergent et al. 1989; Balestri 2004), initially reported at a frequency of 8–10 years (Balestri and Cinelli 2003; Balestri 2004). However, in the last 2 decades *P. oceanica* flowering seems to occur more frequently, likely due to global warming (Diaz-Almela et al. 2007). Even though flowering events have been increasingly studied (Piazzi et al. 2000; Balestri and Cinelli 2003; Balestri 2004; Diaz-Almela et al. 2006; Montefalcone et al. 2013), what exactly affects this phenomenon remains poorly understood. Combinations of genetic (heterozygosity) and ecological factors seem to cause the heterogeneity in flowering patterns within the same region (Jahnke et al. 2015). Local factors, such as shoot age (Diaz-Almela et al. 2006), nutrient availability (Gobert et al. 2001, 2005) and presence of herbivores (Planes et al. 2011), have been found to influence *P. oceanica* flowering (while shoot density was found irrelevant, Balestri 2004; Diaz-Almela et al. 2007) providing some evidence to explain the flowering variability among locations within the same region (Montefalcone et al. 2013). However, large scale patterns have also been investigated and the hypothesis that the low latitude could promote flowering and fruiting (Semroud 1993) has recently given way to the theory that it is the high temperature their real trigger (Diaz-Almela et al. 2006), although this debate remains open. Results based on past flowering events detected through a reconstruction technique applied to the plant rhizomes, highlighted a positive relationship between the prevalence and

intensity of flowering of *P. oceanica* meadows and the annual maximum SST, applicable across the entire Mediterranean (Diaz-Almela et al. 2007): flowering was most prevalent in 1982, 1994, 1998, 2001, and 2003 coinciding either with summer temperature anomalously high, or with the occurrence of long and intense summer marine heat waves (MHWs) (Calvo et al. 2006; Diaz-Almela et al. 2007; Marbà and Duarte 2010; Montefalcone et al. 2013; Sghaier et al. 2013). Further evidence has also suggested that intense solar activity raises the SST, indicating high sunspot number as one the main triggers of massive *P. oceanica* flowering events (Montefalcone et al. 2013). The complexity of this topic is also corroborated by other evidence that suggest *P. oceanica* flowering to be induced 7 months before the anthesis (time or process of expansion of a flower), supporting the importance of the mean temperature before the summer period rather than the summer period itself (Gobert et al. 2001), and other that focused on the association between flowering events and temperature increase, involving temperature variations more than absolute values (Diaz-Almela et al. 2007). Furthermore, in a mesocosm experiment *P. oceanica* flowering was caused only after 2 weeks of a simulated MHW in early summer plants (Marín-Guirao et al. 2019), a response considered as the result of an evolutionary strategy to maximize the survival under adverse conditions (Kazan and Lyons 2016). Therefore, evaluating if temperature descriptors can be useful predictors of the timing and the success of flowering and the fruiting events in *P. oceanica* has become a crucial topic to answer specific questions about the biology of the species in the climate change scenario and to address a more effective fruit collections for restoration efforts especially in case of massive events (Balestri and Lardicci 2008; Paling et al. 2009; Pansini et al. 2022; Escandell-Westcott et al. 2023).

A massive *P. oceanica* flowering event has been observed in late autumn 2022 in several regions of the western Mediterranean Sea. Meadows located in several areas of Sardinia (Northwestern Basin) have been surveyed in October 2022 and during winter 2023 to explore the association of several SST descriptors with meadow flowering and fruiting. The aim of this correlative study was to evaluate the thermal influence on flowering (density of inflorescences) and fruiting (probability of living or dead fruits, and fruit size) of *P. oceanica*, by identifying the SST descriptors (among mean and range seasonal SST, mean and max SST of 3 months, 2 months or 1 month before sampling day) that may mostly contribute to changes in sexual reproduction.

## Materials and methods

### Study area and data collection

In Sardinia five areas in different coastal sectors were chosen and, within each area, three locations were considered: North-East (NE: Capo Ceraso, Isola di Patron Fiaso, Sos Aranzos), North (N: Palau A, Palau B, Palau C), North-West (NW: Porto Conte, Cala del Fortino, Punta Negra), South-East (SE: Serpentara, Isola dei Cavoli, Scoglio de Piscadeddus) and South-West (SW: Carloforte A, Carloforte B, Carloforte C) (Fig. 1). Due to seawater circulation around the island (Olita et al. 2013; Pinardi et al. 2015), Sardinia coastal sectors have different thermal regimes, with the largest difference in SST between areas in summer (Fig. S1), that influence the meadow structure of *P. oceanica* (Pansini et al. 2021; Stipcich et al. 2022a).

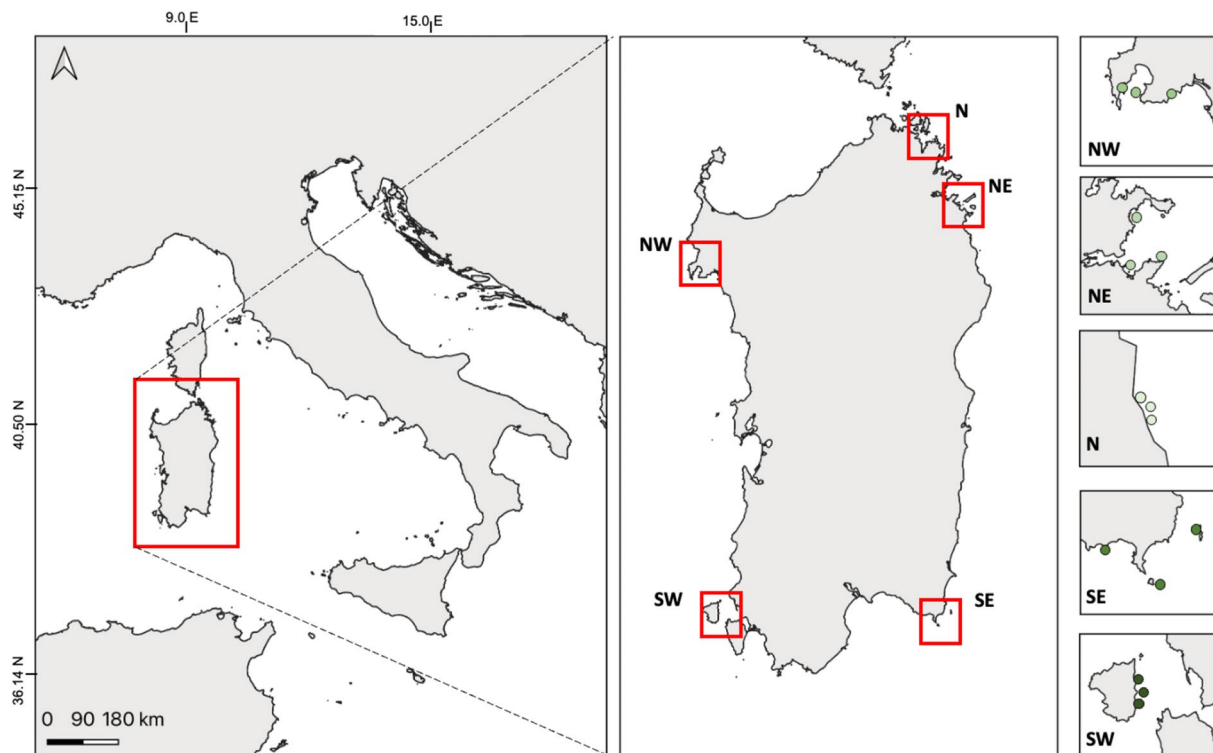
In each area, flowering first observation was recorded at the end of October 2022. Then, a *P. oceanica* meadow at 5 m of depth was sampled in each location during the first 2 weeks of February 2023, before the fruits were completely mature and released. Shoot and inflorescence density were estimated by counting the number of shoots and inflorescences in 40 × 40 cm quadrats randomly placed within the meadows ( $n=6$ ). The inflorescence density was

later expressed as the number of inflorescences over the number of shoots per m<sup>2</sup>. Fruiting variables were estimated using 15 infructescences collected in each location. In the laboratory, the total number of fruits in each infructescence was counted, the presence of living (green) and dead (brownish but still attached to the stipe) fruits was noted. Total number of fruits and total number of alive fruits were calculated in each area considering 15 infructescences. Also, the size of each fruit was measured (length in cm).

### Thermal descriptors

To characterize the thermal environment of each location, daily Multi-Scale Ultra-high Resolution SST from the beginning of Summer 2022 (June 21) to the last day of sampling in 2023 (February 14) were acquired from the website <https://coastwatch.pfeg.noaa.gov/erddap/griddap>.

A total of twelve thermal descriptors were considered (Table 1 and Fig. S2) to estimate their association with the flowering and fruiting of *P. oceanica*. Mean seasonal SST and seasonal SST range referred to three different seasons (summer, autumn and winter only until the sampling day) were calculated; mean SST of 2 months and 1 month were measured considering the relative 2 months and 1 month



**Fig. 1** Study area. Contextualization of Sardinia and the five areas: NW =North-West; NE=North-East; N=North; SE=South-East; SW =South-West. In each area, green dots indicate the three locations

**Table 1** Thermal descriptors

Tag	Thermal descriptor
sst_win	Mean SST from December 21 to the sampling day in February
sst_aut	Mean SST from September 21 to December 20 (autumn)
sst_sum	Mean SST from June 21 to September 20 (summer)
range_win	Difference between maximum and minimum winter SST
range_aut	Difference between maximum and minimum autumn SST
range_sum	Difference between maximum and minimum summer SST
max_3months	Maximum SST in 3 months before fruit sampling/inflorescence observation
max_2months	Maximum SST in 2 months before fruit sampling/inflorescence observation
max_1month	Maximum SST in the month before the fruit sampling/inflorescence observation
sst_2months	Mean SST of 2 months before fruit sampling/inflorescence observation
sst_1month	Mean SST of the month before fruit sampling/inflorescence observation
sst_2weeks	Mean SST of 2 weeks before inflorescence observation

Thermal descriptors whose influence on flowering and fruiting of *P. oceanica* was tested

previous to either the first flowering observation (end of October 2022 for the inflorescence density) or to the specific sampling day of each area (beginning of February 2023 for fruiting variables); the same procedure was applied to measure maximum SST in the 3 months, 2 months and 1 month before the sampling day (end of October 2022 for flowering and beginning of February 2023 for fruiting). To understand the association between thermal descriptors and flowering and fruiting variables, all the thermal descriptors were used with all the variables with two exceptions: (i) sst\_2weeks was related only to inflorescence density, according to the results found by Marín-Guirao et al. (2019); (ii) sst\_win and sst\_aut were only related to the fruiting variables (presence of living and dead fruits and to fruit size), since inflorescences were already produced in autumn.

## Data analyses

Spatial variability of *P. oceanica* shoot density, flowering and fruiting were estimated by permutational analyses of variance (PERMANOVA; Anderson 2014) for each variable using a similarity matrix based on the Euclidean distance of untransformed data. The design consisted of one factor (Area) with five levels (NW, NE, N, SE, and SW) for the total number of fruits and number of living fruits per locality, while for shoot density, inflorescence density and fruit size the two factors Area (five levels) and Locality (three levels, nested in Area) were considered. The factors were all treated as random.

Furthermore, Generalized Linear Models (GLMs) were used to test the influence of the thermal descriptors on the response variables: inflorescence density, presence of living fruits, presence of dead fruits, and fruit size. Before running the analyses, collinearity between predictors was

assessed visually and tested with generalized variance inflation factors (GVIF, calculated using the “car” package; Fox and Weisberg 2019). Consequently, to estimate the influence of the thermal descriptors on the inflorescence density, a GLM (with beta distribution) was run using sst\_sum, sst\_1month and max\_1month as predictors. To investigate the factors associated with the presence of dead and living fruits two binomial GLMs were run using sst\_win, sst\_sum and max\_3months as predictors, while for fruit size a GLM (with gamma distribution) was run using sst\_win, sst\_sum and max\_3months as predictors.

The GLMs were fitted in R (R Foundation for Statistical Computing, Vienna, Austria) using the “mass” package (Venables and Ripley 2002). The Akaike Information Criterion with second-order correction for small sample size (AICc; Burnham and Anderson 2002) was used for model ranking. A graphical model validation was applied to check patterns in the residuals (Fig. S3–6).

## Results

### Spatial variability

Although the meadows sampled were all at the same depth and far from anthropogenic sources of disturbance, large spatial variability at the scale of area and locality were found in terms of shoot density (Table 2, Fig. 2a). The inflorescence density (from 0.01 and 0.47) differed between localities (Table 2, Fig. 2c), while fruit size (from 0.4 to 2.7 cm) depended on the area (Table 2, Fig. 2d). No spatial variability was found for the total number of fruits per infructescence and the number of living fruits which did not differ between areas (Table 2, Fig. 2b).

**Table 2** PERMANOVA results

PERMANOVAs	Area	Locality
	<i>Pseudo-F</i> <sub>4,75</sub>	<i>Pseudo-F</i> <sub>10,35</sub>
Shoot density	4.78*	2.61*
Inflorescence density	2.15	9.54*
	<i>Pseudo-F</i> <sub>4,438</sub>	<i>Pseudo-F</i> <sub>10,438</sub>
Fruit size	11.29*	0.83
	<i>Pseudo-F</i> <sub>4,14</sub>	
Total <i>n.</i> of fruits	3.05	
<i>n.</i> of living fruits	2.88	

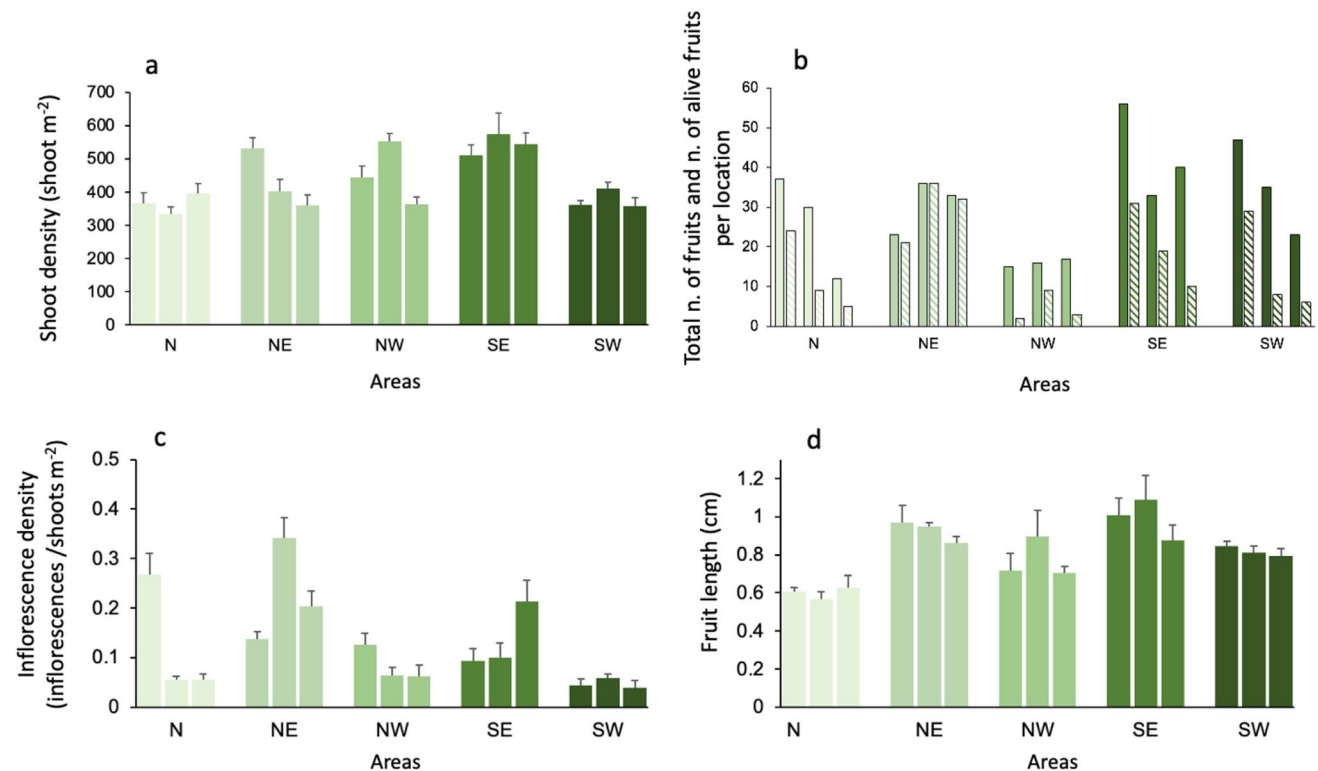
Differences of shoot density, inflorescence density and fruit size were tested between areas and localities and of the total number of fruits and total number of living fruits over 15 infructescences in areas.

\*Corresponds to significant values ( $P < 0.05$ )

### Influence of the thermal descriptors on *P. oceanica* flowering and fruiting

Distinct collinearities among thermal descriptors were identified for each dataset, encompassing inflorescence density, living and dead fruits, and fruit size (Table 3).

Significantly, multiple associations emerged between thermal descriptors and plant variables (Fig. 3). Inflorescence density exhibited connections with *sst\_sum*, alongside *range\_sum* and *max\_3months* due to collinearities, as well as *sst\_1month* (and consequently with *max\_1month*, *max\_2months*, *sst\_2months*, and *sst\_2weeks*): specifically, higher mean summer SST and mean SST of the month before sampling were related to higher and lower flowering, respectively (Table 4a and Fig. 4a). Furthermore, the presence of living and dead fruits was related to *sst\_win* (alongside *sst\_aut*, *sst\_2months* and *sst\_1month*), *sst\_sum* (and *range\_sum*; *range\_aut*; *sst\_2months*) and *max\_3months* (and *max\_2months* due to collinearities) (Table 4b–c); particularly, the probability of finding living fruits increased with higher mean summer SST and maximum SST in 3 months before sampling and lower mean winter SST (Fig. 4b) and, conversely, the probability of finding dead fruits decreased with higher mean summer SST and maximum SST in 3 months before sampling, and lower mean winter SST (Fig. 4c). Finally, fruit size was positively related to both the mean summer SST and the maximum SST in 3 months before sampling (therefore, to *range\_sum*, *range\_aut*, *sst\_2months*; *max\_2months*) (Table 4d, Fig. 4d).



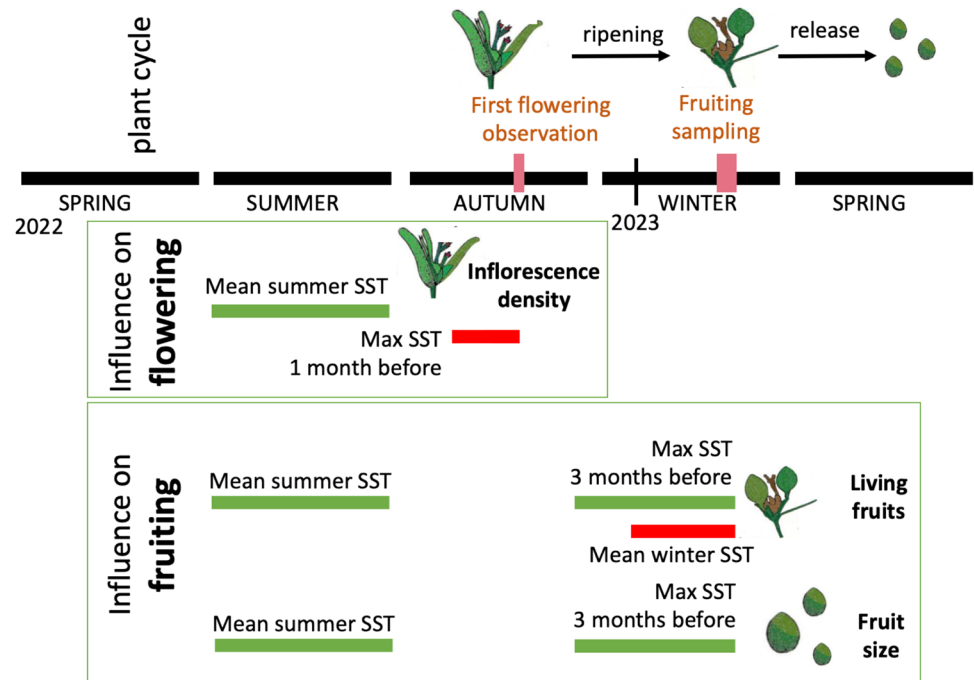
**Fig. 2** *P. oceanica*: (a) shoot density per  $m^2$  (mean+SE), (b) total number of fruits and number of living fruits in 15 infructescences in each area and each location (solid color bars represent the total number of fruits, striped bars represent the number of living fruits), (c) inflorescence density (mean+SE) expressed as flower density/

shoot density per  $m^2$ , (d) fruit size (length in cm) at the five areas (mean+SE). N=North; NE=North-East; NW=North-West; SE=South-East; SW=South-West), each area is represented by three locations

**Table 3** Collinearity between thermal descriptors used in the GLMs

Dataset	Thermal descriptor	Correlated descriptors			
Inflorescence density	sst_sum	range_sum	max_3months		
	max_1month	sst_1month	sst_2months	sst_2weeks	max_2months
Living and dead fruits	sst_win	sst_aut	sst_2months	sst_1month	
	sst_sum	range_sum	range_aut	sst_2months	
	max_3months	max_2months	max_1month		
Fruit size	sst_sum	range_sum	range_aut	sst_2months	
	max_3months	max_2months			
	sst_win	sst_aut	sst_2months	sst_1month	

**Fig. 3** Schematic representation of the results. Upper, the timing of *P. oceanica* life cycle is described, and the time of the first flowering observation and fruiting sampling are indicated in light red. Lower, the significant associations between the thermal descriptors selected and the plant variables (specified beside) are described; the green and red bars indicate positive and negative relationships, respectively. The length and position of each colored bar corresponds to the period (see the black timeline on the top of the figure)



## Discussion

The sexual reproduction of *P. oceanica* exhibits considerable variability both spatially and temporally (Balestri and Cinelli 2003). Despite lingering uncertainties regarding local factors influencing flowering, recent associations indicate an increase in flowering events linked to rising temperatures (Diaz-Almela et al. 2007). This study aims to identify the primary thermal descriptors that significantly impact sexual reproduction.

Overall, results highlighted that the mean summer temperature was positively associated to all the flowering and fruiting variables considered, and living fruits and fruit size were also positively affected by the maximum SST within November–February. However, inflorescence density was negatively affected by the maximum SST between end of September and end of October (1 month before the first inflorescence observation) and living fruits by the

mean winter SST (calculated from December 21 to the sampling day in February), suggesting that the impact of the high temperature on sexual reproduction might change depending on the duration and temporal context.

Particularly, the mean summer SST (ranging from 26.07 to 27.22 °C) affected positively both inflorescence density, presence of living fruits, and fruit size, also decreasing the probability of finding dead fruits. This result is in accordance with previous studies which suggested that the maximum annual SST (occurring during summer) affects the flowering events (Balestri 2004; Diaz-Almela et al. 2007). However, since the mean summer SST was correlated with summer SST range, it was not possible to derive whether flowering is more affected by the summer SST variations or mean values, but evidence suggests the importance of both thermal conditions. According to the sea water climatologies and past SST data of the five areas, summer 2022 was one of the warmest in the last decades and a MHW lasting the whole summer period (92 days) occurred in

**Table 4** GLM results

	Estimate	Std. Error	z value	P
<b>(a) Inflorescence density</b>				
Intercept	-8.8884	5.7123	-1.556	0.12
sst_sum	1.0151	0.2535	4.004	<0.0001
max_1month	-0.8739	0.1811	-4.825	<0.0001
<b>(b) Living fruits</b>				
Intercept	-54.9602	12.8829	-4.266	<0.0001
sst_win	-5.7071	0.6894	-8.279	<0.0001
sst_sum	3.5652	0.4630	7.700	<0.0001
max_3month	2.2651	0.4290	5.281	<0.0001
<b>(c) Dead fruits</b>				
Intercept	60.9748	12.9036	4.725	<0.0001
sst_win	5.5765	0.7513	7.423	<0.0001
sst_sum	-3.2674	0.4826	-6.771	<0.0001
max_3month	-2.8449	0.4457	-6.384	<0.0001
<b>(d) Fruit size</b>				
Intercept	-13.5892	2.6742	-5.082	<0.0001
sst_sum	0.3614	0.0638	5.666	<0.0001
max_3month	0.1812	0.0716	2.531	0.0117

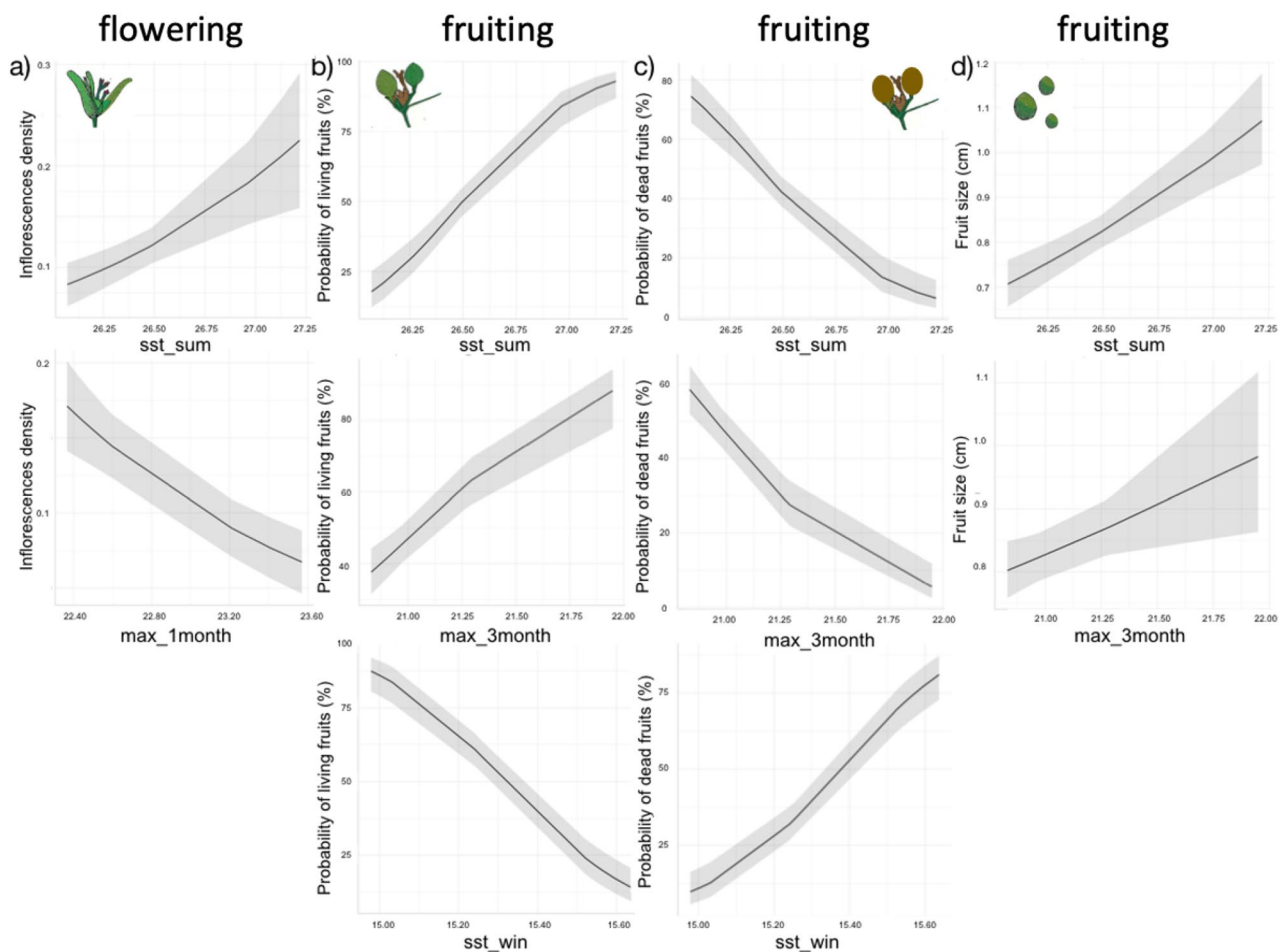
The models were run on (a) inflorescence density, (b) presence of living fruits, (c) presence of dead fruits, (d) fruit size

all the areas considered in this study (Fig. 5). Recently, the resilience of *P. oceanica* to high temperature has been interpreted as the expression of an adaptation due to the tropical/subtropical conditions in which it evolved (the former Tethys Sea, the tropical ancestor of the Mediterranean Sea, Aires et al. 2011) and, accordingly, flowering would be the plant response to already experienced conditions (Martínez-Abraín et al. 2022). However, this hypothesis seems controversial, since there is molecular evidence that suggest flowering as a response to a stress (Marín-Guirao et al. 2019), as highlighted in terrestrial plants for different kinds of stressor, temperature increase included (Post 2003; Menzel et al. 2006; Jansson and Davies 2008; Takeno 2012). The stress-induced flowering is considered an adaptive strategy, especially in species with long-distance seed dispersal, to colonize new areas with more favorable conditions, and to increase the level of genetic connectivity among populations enhancing fitness and thus the resilience against different stressors (Kendrick et al. 2017; Ruiz et al. 2018; Marín-Guirao et al. 2019).

The evidence gained in this study indicates that mean summer sea surface temperature (SST) is not the only influential thermal descriptor for flowering. The descriptor 'two weeks SST before flowering' also plays a significant role, having a correlation with the maximum temperature in the month preceding flowering. Our results affirm the critical importance of the temperature immediately preceding anthesis. While flower induction appears to initiate months

in advance (Gobert et al. 2001), we postulate the existence of a temperature threshold that may trigger inflorescence development. This descriptor (sst\_2weeks) was selected because, in a mesocosm experiment, *P. oceanica* flowering in cold adapted shoots was induced only after a 2-week simulated MHW (4 °C higher than control SST, Marín-Guirao et al. 2019) and not inhibited like in our study. This apparent inconsistency could be explained by both temperature intensity and the plant biorhythm that might have affected the results. In fact, the temperature used in the two studies varied considerably (27 °C in Marín-Guirao et al. 2019, and 22.19 °C in this study), suggesting that the determinant stimulus to activate the sexual reproduction of the plant might depend on the temperature value (as if there was a temperature threshold over which flowering occurs). However, also the timing of warming (June in Marín-Guirao et al. 2019, and the last 2 weeks of October in this study) were different, stimulating the plant at different stages, since anthesis lasts roughly 3 months and the flowering is induced 7 months before anthesis (Gobert et al. 2001). A further explanation for the inconsistency between the two experiments could also be due to the prolonged MHWs occurred in all the study areas from May to October 2022 with very few lag days of interruption (Fig. S7). The high temperature condition might have induced flowering which might have been subsequently inhibited by the anomalous extension of the MHW, which likely induced a change in balancing energy investment through seasons for the high energetic cost required for sexual reproduction (Pirc 1985; Balestri and Cinelli 2003; Calvo et al. 2006). This interpretation would also be supported by the negative influence of the maximum SST of the month before on the first inflorescence observation (i.e. October 2022, ranging from 22.37 to 23.57 °C), as the higher was the maximum SST in the previous month, the lower was the inflorescence density.

Fruit size was positively affected not only by the mean summer SST, but also by the maximum SST of 3 (and 2) months before fruit sampling (November–December–January), likely indicating that high temperature during the whole period could either induce the production of larger fruits or accelerate fruit maturation. Accordingly, the maximum SST of 3 months before (20.83–21.95 °C) also affected the presence of living and dead fruits, positively and negatively, respectively, while the mean winter SST (from December 21 until the sampling day in February) (14.97–15.63 °C) had an opposite association type with the same fruiting variables, indicating that the temperature plays an important role in the whole period of fruit development. Fruit production represents a significant investment of energy for *P. oceanica* (Balestri and Cinelli 2003) and while a high temperature from the beginning of the summer to the end of November can induce a major development of fruits in terms of length and viability, temperature below a certain value might prompt an



**Fig. 4** Effect of the significant explanatory thermal descriptors of the model on (a) inflorescence density, (b) presence of living fruits, (c) presence of dead fruits, (d) fruit size as predicted by the GLMs. The

y-axis represents the partial effect of each variable as predicted by the model; the shaded area indicates 95% confidence interval

opposite result inducing fruit abortion, with the consequent loss of a good part of the investment. Fruit abortion alone has been estimated to be responsible for the loss of ca. 87% of the reproductive material (Balestri and Cinelli 2003), but very little information about post-fertilization factors driving to fruit mortality are known: the results of this study highlight the important contribution of the SST (both maximum and average) from autumn until February (last month considered in this study), previously neglected.

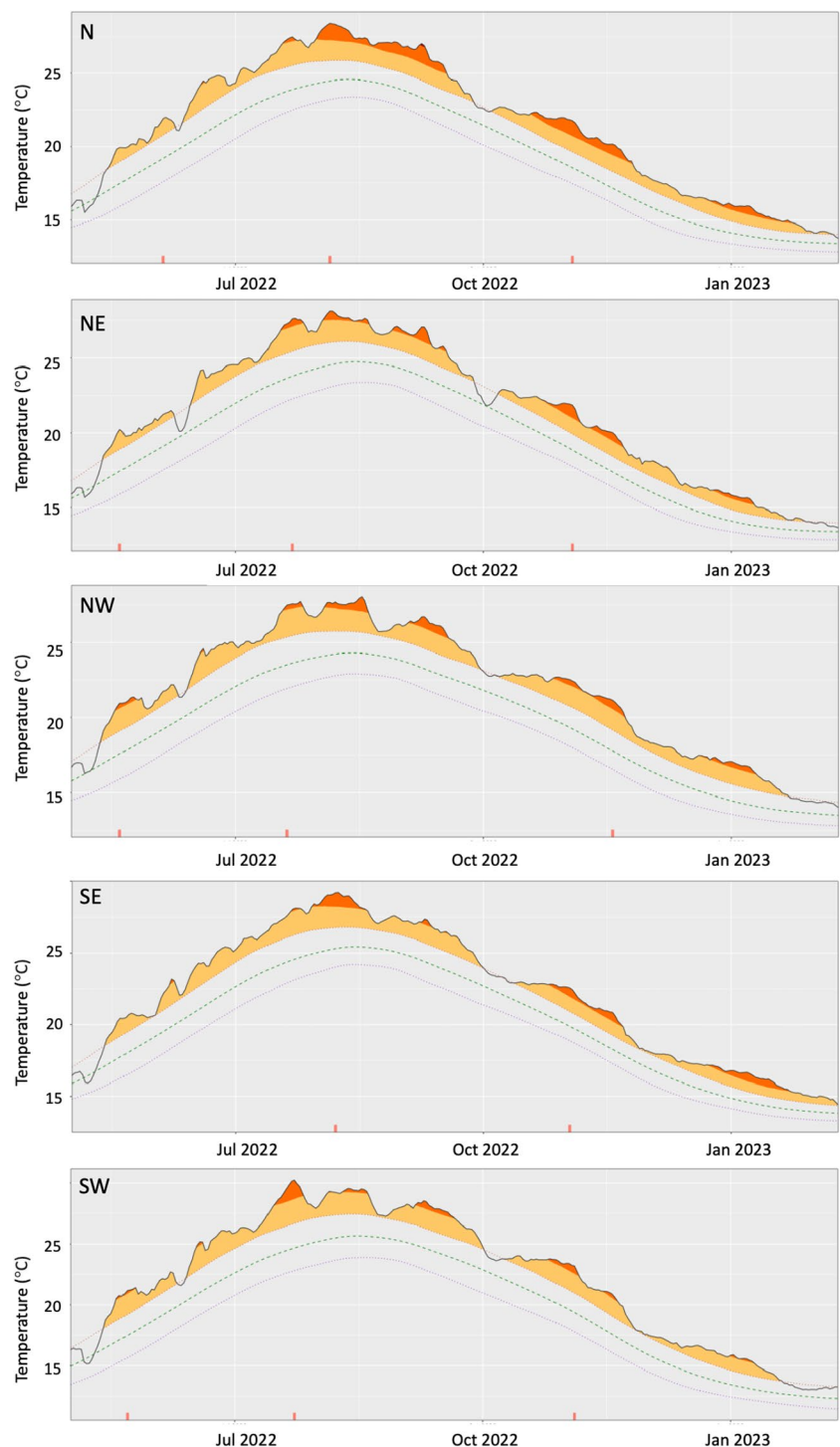
Overall, our results strongly support the hypothesis that sea surface temperature (SST) significantly influences the development of inflorescences and fruits in *P. oceanica*. Importantly, our findings emphasize that the effects, whether positive or negative, are contingent upon the duration, intensity, and temporal context of the temperature anomaly. High summer temperature seems to induce flowering and fruiting in *P. oceanica*, producing a higher number of inflorescences with larger and more viable fruits, increasing the investment of energy in the reproduction. Nevertheless, high

temperature conditions close to the sampling days (October for flowering and from December for fruiting) seem to inhibit the reproductive effort: however, without molecular analysis, it is not possible to determine whether flowering inhibition is due to the duration of the high temperature or because temperature intensity from December to February is not enough to induce a stress-response such as the sexual reproduction, even though values are higher than those of the climatology (30 years of SST data). However, even though an overall positive relation was found between high SST and flowering events, it is relevant to note that certainly not only positive effects are coming from high SST: in fact, the induction of the sexual reproduction following a period of high temperature has been considered an adaptive strategy due to stressful conditions (Marín-Guirao et al. 2019) and fruit formation represents a significant investment of energy for *P. oceanica* (Balestri and Cinelli 2003).

In conclusion, although previous studies have already found a correlation between high temperature and



**Fig. 5** Marine heat waves occurred from May 2022 to February 2023 in the five areas: N=North; NE=North-East; NW=North-West; SE=South-East; SW=South-West. The violet dotted line represents the climatology; the green dotted line the threshold (90th percentile); the red dotted line the beginning of the category I of a MHW; the black line represents the SST. The area filled in yellow represents a moderate MHW and the orange a strong MHW



flowering events (Diaz-Almela et al. 2006; Montefalcone et al. 2013; Marín-Guirao et al. 2019), the novelty of the present study was the identification of several temperature descriptors for a successful of *P. oceanica* flowering and fruiting by considering a period that goes from the plant anthesis until the maturation of fruits. To the best of our knowledge, this was the first time that different thermal descriptors were associated to phenological variables

related to the reproductive events in plants. Defining the best thermal descriptors associated to the success of the sexual reproduction of the seagrass *P. oceanica* will help identifying in advance the ‘good’ years of fruit production, assisting restoration projects that rely on seedlings rather than plant cuttings. In fact, since flowering events have been increasing in the last decades and seeds represent an easy material to collect without affecting the meadow, the

use of seeds and seedlings of *P. oceanica* has been encouraged in restoration operas (Terrados et al. 2013).

Nevertheless, it is worth highlighting that data used for this study were taken during a long period of anomalously high SST and it remains unknown what would have been the results if temperature conditions were below the sea water climatology threshold. Therefore, we support the need to implement this work by correlating data taken for wider geographical areas and for several years, possibly by relying on dataset built through reconstruction techniques (lepidochronological analysis), for which the effectiveness of the thermal descriptors here highlighted should be tested.

However, considering also the variability found in Sardinia between locations of the same area in terms of both flowering and fruiting traits, we suggest that the combination of local conditions have a large influence on the reproductive potential of *P. oceanica*. In fact, temperature conditions can only partially explain the flowering and fruiting variability suggesting the importance of local factors, such as changes in environmental conditions (e.g. nutrient availability, Gobert et al. 2001, 2005), shoot age (Diaz-Almela et al. 2006), presence of herbivores (Planes et al 2011), and genetic variability (Jahnke et al. 2015), in determining the success of the sexual reproduction.

A strong positive relationship between flower density and heterozygosity was recently found, indicating that genetic factors play a major role in driving flowering synchronicity within and between mass-flowering patches (Jahnke et al. 2015). Nevertheless, our results corroborate that flowering is triggered by seawater warm temperature, thus providing evidence to formulate the hypothesis that heterozygosity would also be positively associated with the local sea water climatology, regardless the cause-effect mechanisms. Therefore, future studies are absolutely needed to focus on the uncertainties related to the local factors that might affect the reproductive strategy of a meadow to fully understand the future success of the sexual reproduction of *P. oceanica* in a climate change scenario.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04388-4>.

**Acknowledgements** Authors would like to thank Federico Pinna and Arianna Pansini for the help provided during the field work.

**Author contributions** P Stipcich: Conceptualization, Methodology, Investigation, Writing—original draft, review & editing; G La Manna: Formal analysis, Writing—review & editing; G Ceccherelli: Conceptualization, Methodology, Writing—original draft, review & editing.

**Funding** Open access funding provided by Università degli Studi di Sassari within the CRUI-CARE Agreement. This study was funded by the project Marine habitats restoration in a climate change-impaired Mediterranean Sea (MAHRES), funded by the Italian Ministry of Research under the PRIN 2017 Program (Project N. 2017MHHWBN; CUP: 74119001320001). GC and GLM acknowledge the support of

NBFC to University of Sassari, funded by the Italian Ministry of University and Research, PNRR, Missione 4, Componente 2, “Dalla ricerca all’impresa”, Investimento 1.4 Project CN00000033.

**Data Availability** The data that support the findings of this study are available on request from the corresponding author (PS).

## Declarations

**Conflict of interest** Author PS declares that she has no conflict of interest. Author GC declares that she has no conflict of interest. Author GLM declares that she has no conflict of interest.

**Ethical approval** This article does not contain any studies with animals performed by any of the authors.

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