Marine Pollution Bulletin 206 (2024) 116721

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

How the seagrass *Posidonia oceanica* flowering will benefit from climate change

Patrizia Stipcich[a,b,c,*], Ivan Guala[c,d], Gabriella La Manna[b,c], Mariangela Moro Merella[c], Arianna Pansini[c], Riccardo Vargiu[c], Simonetta Fraschetti[a,b], Giulia Ceccherelli[b,c]

[a] *Department of Biology, University of Naples Federico II, Naples, Italy*
[b] *National Biodiversity Future Centre, Palermo, Italy*
[c] *Department of Chemical Physical Mathematical and Natural Sciences, University of Sassari, Sassari, Italy*
[d] *IMC - International Marine Centre, Oristano, Italy*

A R T I C L E I N F O

Keywords:
Anthesis
Genetic diversity
Lepidochronological analysis
Sexual reproduction
SST range
Thermal descriptors

A B S T R A C T

This study aimed at identifying the importance of the thermal framework preceding *Posidonia oceanica* flowering induction (autumn before the flowering year) and anthesis (summer of the flowering year). In 53 locations of Sardinia (Italy), 35 vertical shoots were collected in 2001, 2020 and 2023 and analyzed through lepidochronology, detecting past flowering events from 1991 to 2022. Flowering probability was positively correlated with autumn SST range and MHWs, stressing the importance of the temperature in the year preceding the flowering. Summer SST mean and Marine Cold Spell duration (the latter emerged as a novel outcome) also positively influenced flowering. A negative association was highlighted with the summer SST range. As the occurrence of MHWs will increase, and the SST range will also increase in the autumn and decrease in the summer, *P. oceanica* might benefit through a higher flowering frequency, leading to a greater resilience to disturbances due to higher genetic variation.

Extended periods anomalously warm or cold, known as Marine Heat Waves (MHWs) and Marine Cold Spells (MCSs), have increased in the Mediterranean Sea over recent years, exhibiting a discernible warming trend over the last decades (Ciappa, 2022). This pattern is marked by an increase in mean Sea Surface Temperature (SST) of 0.04 °C/yr and an expansion in the autumn SST range, juxtaposed with a reduction in the summer SST range (Pastor et al., 2020). Temperature anomalies can seriously affect habitat-forming species, such as seagrasses, inducing also mass mortalities (Garrabou et al., 2022). Concurrently, these changes can stimulate species adaptations *e.g.* physiological variation, changes in pattern of sexual reproduction, herbivore resistance or morphological changes (Duarte et al., 2018). The endemic seagrass *Posidonia oceanica* (L.) Delile is not an exception. Understanding how temperature anomalies affect reproduction patterns of the most important habitat-forming species of the Mediterranean Sea is of critical importance.

Posidonia oceanica forms extended meadows that are distributed along most of the coasts of the Mediterranean basin (Telesca et al., 2015) and they are recognized as priority natural habitats (Habitat Directive 92/43/EEC) for the key services they provide, such as nursery area, coastal protection from the erosion, carbon sink, nutrient recycling (Terrados and Borum, 2004). *Posidonia oceanica* reproduces both vegetatively and sexually, the latter used for dispersal and colonization of new coastal habitats and to increase genetic diversity of the meadows (Orsini et al., 2001).

Posidonia oceanica flowering has commonly been considered a sporadic event, but in the last decades it occurred more frequently, even though triggers remain largely unknown. Warming is believed to be an important driver for the sexual reproduction (Diaz-Almela et al., 2007; Stipcich et al., 2024), since past flowering events detected across the whole Mediterranean basin through a reconstruction technique coincided with the warmest years of the last decades (Diaz-Almela et al., 2007; Montefalcone et al., 2013; Sghaier et al., 2013). Overall, these observations have fueled a debate which remains unsolved as to whether *P. oceanica* flowering should be considered an evolutionary strategy to maximize survival under adverse settings (Marín-Guirao et al., 2019) or an adaptation to tropical/subtropical conditions evolved after the Tethys eastern closure in the Miocene (Martínez-Abraín et al., 2022).

* Corresponding author at: Department of Biology, University of Naples Federico II, Naples, Italy.
E-mail address: patrizia.stipcich@unina.it (P. Stipcich).

https://doi.org/10.1016/j.marpolbul.2024.116721
Received 4 June 2024; Received in revised form 11 July 2024; Accepted 12 July 2024
Available online 17 July 2024

Flowering in *P. oceanica* is induced seven months before anthesis (flower expansion process) which starts in August and lasts roughly three months (Fig. 1a; Gobert et al., 2001), but until now, only warm temperature anomalies occurring in the flowering year have been considered.

This correlative study aims to identify the thermal framework including both MHWs and MCSs, preceding flowering induction (the autumn before the flowering year) and anthesis (the summer of the flowering year) that may trigger flowering, thus considering a large temporal window in which anomalous temperature might affect *P. oceanica* sexual reproduction. Gaining such information is beneficial to comprehend the seagrass biology and to plan the collection of seeds for active restoration interventions, considering the level of degradation of the seagrass in several areas of the Mediterranean Sea.

In Sardinia (Italy) the East and West coast are characterized by different thermal regime, due to the Mediterranean water circulation (Olita et al., 2013), and along these coasts 31 and 22 locations were chosen, respectively. In each location, 35 vertical shoots were collected in 2001, 2020 and 2023. Past flowering events were identified through lepidochronological analysis, with the identification of flower stalk remnants between the leaf sheaths (Fig. 1b, Pergent-Martini and Pergent, 1994). Data from the reconstruction spanned from 1991 to 2022 (10,166 observations), with only years with a minimum of 20 available shoots being considered in data analysis.

The thermal descriptors considered were the SST mean and range (°C) and the number and the mean duration (days) of MHWs and MCSs, calculated for both the autumn and summer of each reconstructed year. Two generalized linear mixed models were applied to determine the influence of the thermal descriptors in interaction with the coast (factor with two levels: West and East) on the presence/absence of flowering. Since flowering can be influenced by the local environmental condition, Locality was included in the model as random term (Zuur et al., 2009).

Flowering was positively associated with the autumn SST range (especially in the West coast) and autumn MHW duration (especially in the East coast) (Fig. 1c), stressing for the first time the importance of the thermal regime preceding flower induction in *P. oceanica* ontogeny. The flowering variability between coasts might depend on plant adaptation to selective pressures from contrasting thermal environments or local factors (Planes et al., 2011; Stipcich et al., 2022, 2024). The summer thermal regime also influenced the probability of flowering, which was positively associated to the SST mean and MCS duration, but negatively related to the SST range (Fig. 1d): while the positive correlation with the SST mean is a confirmatory result, the association with the duration of past MCS is a novel outcome. MCSs drive predictable community changes in the subtropical communities, with consequent impact in biodiversity (Boucek et al., 2016; Masanja et al., 2023). However, even

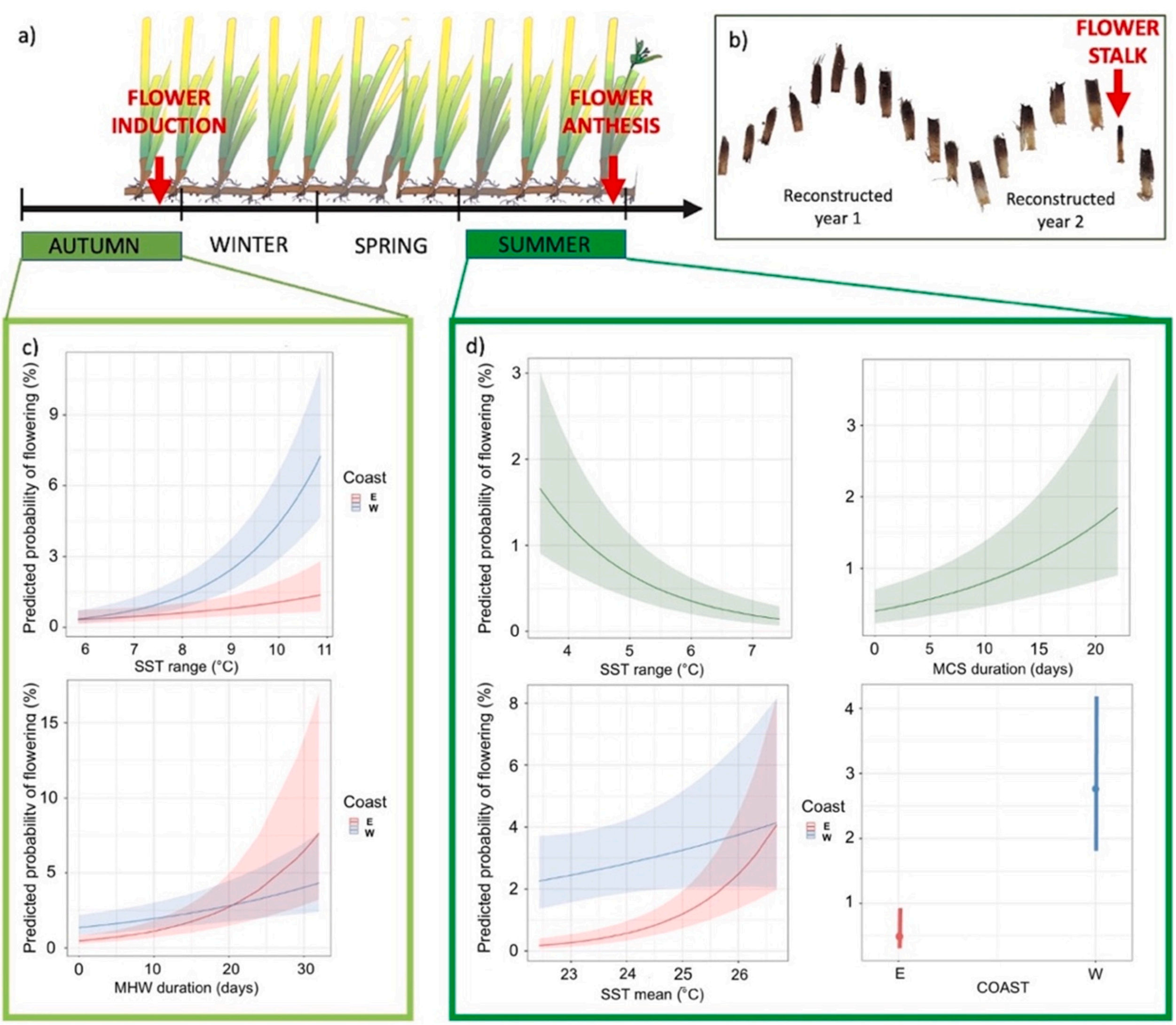

Fig. 1. a) Seasonal timeline of *P. oceanica* life cycle. b) *P. oceanica* leaf sheaths corresponding to reconstructed years. Effects of the significant explanatory (c) autumn and (d) summer thermal descriptors on the predicted probability of flowering. The shaded areas indicate 95 % confidence interval.

though MCSs have been following an opposite trend to the MHWs (Yao et al., 2022), how they affect seagrasses has been neglected and information is needed to disentangle the complexity of the effects of climate anomalies.

Overall, *P. oceanica* flowering is influenced by both warm and cold anomalous temperatures, with effects already in the year before the flowers appear. Since, according to future predictions, the occurrence of MHWs will increase, and the SST range will increase in the autumn and decrease in the summer (Darmaraki et al., 2019; Pastor et al., 2020; Soto-Navarro et al., 2020), *P. oceanica* will likely increase flowering frequency as response to climate changes. Such response will lead to a higher genetic variation of meadows with a consequent greater resilience to disturbances (Jahnke et al., 2015), and a greater quantity of seeds whose use (through collection of floating or beached fruits) in restoration efforts has been encouraged (Terrados et al., 2013). *Posidonia oceanica* sexual reproduction is considered a significant investment of energy for the plant (Balestri and Cinelli, 2003), and recruitment also involves critical phases, therefore understanding the ideal conditions to ensure seed development (Alagna et al., 2020; Escandell-Westcott et al., 2023) is needed to increase success in sexual reproduction and for *P. oceanica* to benefit from increasing flowering events. Our findings suggest the importance to frame research about *P. oceanica* reproduction in the climate change scenario. The identification of the thermal descriptors associated to flowering may assist seagrass ecologists to predict future reproductive events of *P. oceanica*, to model future changes in species distribution and to plan effective management strategies by enhancing the likelihood of restoration success.

CRediT authorship contribution statement

Patrizia Stipcich: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Ivan Guala:** Investigation, Funding acquisition, Conceptualization. **Gabriella La Manna:** Writing – original draft, Formal analysis. **Mariangela Moro Merella:** Investigation. **Arianna Pansini:** Investigation. **Riccardo Vargiu:** Investigation. **Simonetta Fraschetti:** Writing – original draft, Supervision. **Giulia Ceccherelli:** Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgment

Data prior to 2001 were collected within the project “Mappatura delle praterie di *Posidonia oceanica* lungo le coste della Sardegna e delle piccole isole circostanti” funded by the Italian Ministry of the Environment. We thank Dr. Maria Cristina Buia (Stazione Zoologica di Napoli) for providing some data. We acknowledge the European Union’s Horizon Europe Research and Innovation Programme ACTNOW, grant agreement N. 101060072. We also acknowledge the project “National Biodiversity Future Center - NBFC”, project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research.

References

Alagna, A., Zenone, A., Badalamenti, F., 2020. The perfect microsite: how to maximize *Posidonia oceanica* seedling settlement success for restoration purposes using ecological knowledge. Mar. Environ. Res. 161, 104846.

Balestri, E., Cinelli, F., 2003. Sexual reproductive success in *Posidonia oceanica*. Aquat. Bot. 75 (1), 21–32.

Boucek, R.E., Gaiser, E.E., Liu, H., Rehage, J.S., 2016. A review of subtropical community resistance and resilience to extreme cold spells. Ecosphere 7 (10), e01455.

Ciappa, A.C., 2022. Effects of Marine Heatwaves (MHW) and Cold Spells (MCS) on the surface warming of the Mediterranean Sea from 1989 to 2018. Prog. Oceanogr. 205, 102828.

Darmaraki, S., Somot, S., Sevault, F., Nabat, P., Cabos Narvaez, W.D., Cavicchia, L., Sein, D.V., 2019. Future evolution of marine heatwaves in the Mediterranean Sea. Climate Dynam. 53, 1371–1392.

Diaz-Almela, E., Marbà, N., Duarte, C.M., 2007. Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. Glob. Chang. Biol. 13 (1), 224–235.

Duarte, B., Martins, I., Rosa, R., Matos, A.R., Roleda, M.Y., Reusch, T.B., Jueterbock, A., 2018. Climate change impacts on seagrass meadows and macroalgal forests: an integrative perspective on acclimation and adaptation potential. Front. Mar. Sci. 5, 190.

Escandell-Westcott, A., Riera, R., Hernández-Muñoz, N., 2023. *Posidonia oceanica* restoration review: factors affecting seedlings. J. Sea Res. 102337.

Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Harmelin, J.G., 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. Glob. Chang. Biol. 28 (19), 5708–5725.

Gobert, S., Defawe, O., Lepoint, G., Demoulin, V., Bouquegneau, J.M., 2001. Anthesis effects on *Posidonia oceanica* (L.) Delile phenology in the Bay of Calvi (Corsica, Mediterranean Sea). Hydrobiologia 455, 121–125.

Jahnke, M., Olsen, J.L., Procaccini, G., 2015. A meta-analysis reveals a positive correlation between genetic diversity metrics and environmental status in the long-lived seagrass *Posidonia oceanica*. Mol. Ecol. 24 (10), 2336–2348.

Marín-Guirao, L., Entrambasaguas, L., Ruiz, J.M., Procaccini, G., 2019. Heat-stress induced flowering can be a potential adaptive response to ocean warming for the iconic seagrass *Posidonia oceanica*. Mol. Ecol. 28 (10), 2486–2501.

Martínez-Abraín, A., Castejón-Silvo, I., Roiloa, S., 2022. Foreseeing the future of *Posidonia oceanica* meadows by accounting for the past evolution of the Mediterranean Sea. ICES J. Mar. Sci. 79 (10), 2597–2599.

Masanja, F., Xu, Y., Yang, K., Mkuye, R., Deng, Y., Zhao, L., 2023. Surviving the cold: a review of the effects of cold spells on bivalves and mitigation measures. Front. Mar. Sci. 10, 1158649.

Montefalcone, M., Giovannetti, E., Morri, C., Peirano, A., Bianchi, C.N., 2013. Flowering of the seagrass Posidonia oceanica in NW Mediterranean: is there a link with solar activity? Mediterr. Mar. Sci. 416–423.

Olita, A., Ribotti, A., Fazioli, L., Perilli, A., Sorgente, R., 2013. Surface circulation and upwelling in the Sardinia Sea: a numerical study. Cont. Shelf Res. 71, 95–108.

Orsini, L., Acunto, S., Piazzi, L., Procaccini, G., 2001. Sexual reproduction and recruitment in *Posidonia oceanica* (L.) Delile, a genetic diversity study. In: Mediterranean Ecosystems: Structures and Processes. Springer Milan, Milano, pp. 385–389.

Pastor, F., Valiente, J.A., Khodayar, S., 2020. A warming Mediterranean: 38 years of increasing sea surface temperature. Remote Sens. (Basel) 12 (17), 2687.

Pergent-Martini, C., Pergent, G., 1994. Lepidochronological analysis in the mediterranean seagrass *Posidonia oceanica* state-of-the-art and future-developments. Oceanol. Acta 17 (6), 673–681.

Planes, S., Raventós, N., Ferrari, B., Alcoverro, T., 2011. Fish herbivory leads to shifts in seagrass *Posidonia oceanica* investments in sexual reproduction. Mar. Ecol. Prog. Ser. 431, 205–213.

Sghaier, Y.R., Zakhama-Sraieb, R.Y.M., Charfi-Cheikhrouha, F., 2013. Patterns of shallow seagrass (*Posidonia oceanica*) growth and flowering along the Tunisian coast. Aquatic Botany 104, 185–192.

Soto-Navarro, J., Jordá, G., Amores, Á., Cabos, W., Somot, S., Sevault, F., Sein, D., 2020. Evolution of Mediterranean Sea water properties under climate change scenarios in the Med-CORDEX ensemble. Climate Dynam. 54, 2135–2165.

Stipcich, P., Marín-Guirao, L., Pansini, A., Pinna, F., Procaccini, G., Pusceddu, A., Ceccherelli, G., 2022. Effects of current and future summer marine heat waves on *Posidonia oceanica*: plant origin matters? Front. Clim. 4, 844831.

Stipcich, P., La Manna, G., Ceccherelli, G., 2024. Warming-induced flowering and fruiting in the seagrass *Posidonia oceanica* and uncertainties due to context-dependent features. Mar. Biol. 171 (3), 67.

Telesca, L., Belluscio, A., Criscoli, A., Ardizzone, G., Apostolaki, E.T., Fraschetti, S., Salomidi, M., 2015. Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. Sci. Rep. 5 (1), 12505.

Terrados, J., Borum, J., 2004. Why are seagrasses important? Goods and services provided by seagrass meadows. European seagrasses: an introduction to monitoring and management 8–10.

Terrados, J., Marin, A., Celdran, D., 2013. Use of *Posidonia oceanica* seedlings from beach-cast fruits for seagrass planting. Bot. Mar. 56 (2), 185–195.

Yao, Y., Wang, C., Fu, Y., 2022. Global marine heatwaves and cold-spells in present climate to future projections. Earth’s Future 10 (11), e2022EF002787.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., Zuur, A.F., Smith, G.M., 2009. GLMM and GAMM. In: Mixed Effects Models and Extensions in Ecology With R, pp. 323–341.